Habitat Assessment of the Rare and At-Risk Species Umtanum Desert Buckwheat (*Eriogonum codium*) for Increased Successes with Assisted Migration

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Abstract

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"Edaphic islands" are comprised of unique or challenging soil habitats and host 15-20% of global floral taxa including numerous rare and endangered species. These communities in general, and small populations of edaphic endemic species in particular, are at increasing risk from climate change related stress, threats from invasion by generalist non-native species, and exposure to novel anthropogenic disturbances, including altered fire intervals. The rare and endangered Umtanum Desert Buckwheat (*Eriogonum codium*) is a slow growing, long-lived perennial plant highly restricted to a 1.9 acre discontinuous band in the shrub-steppe of Hanford Reach Nuclear Facility (Department of Defense). Little is known about the habitat characteristics of its single population or whether its extremely limited distribution is due to the presence of unique soil properties at this location. Previous work has theorized *E. codium* may require

specific edaphic conditions and/or low inter-species competition. The single population is in decline and outplanting efforts undertaken at nearby locations with similar site and soil conditions have largely failed. Assisted migration could enable otherwise impossible translocations of this species outside its native site, greatly reducing its risk of decline, genetic loss, and extinction. In 2020, the Washington Natural Heritage Program (WNHP) developed a habitat suitability model for *E. codium* which identified 115 acres of likely habitat, and seedlings were planted at five sites across two locations in 2020 and 2021. The intent of this study is to inform management strategies for the assisted migration of *E. codium* and determine the effects of outplanting locations and site selection on outplanted seedling success. To do so, this study characterizes *E. codium*'s current habitat and compares these habitat characteristics to past, current, and potential future assisted migration locations at two different spatial scales.

In Chapter 1, site, soil, and vegetation habitat characteristics were measured at the single location where *E. codium* occurs (Native Site). Differences in *E. codium* site occupancy, abundance, and between the five remaining subpopulations and sampling transects was used to characterize *E. codium*'s associated habitat type and responses to a range of biotic and abiotic habitat variables. Inter-species competition was found to be an important factor shaping *E. codium* habitat. Site and soil characteristics, such as heat load, rock and bareground cover, and the abundance of fine and very fine gravel grades, were found to interact and form spatially heterogenous microhabitats and vegetation community dynamics directly impacting *E. codium's* growth and survival. Cluster analysis of vegetation functional group composition identified six distinct vegetation habitat types delineating three perennial graminoid community types, each associated with either high, medium, or low abundance of *E. codium*. Site, soil and vegetation characteristics were compared between these "optimal" *E. codium* habitat groups to elucidate *E.*

codium's ability to occupy a range of microhabitat conditions. These results are explored as a means to theorize on *E. codium*'s evolutionary ecology and the role of microhabitat differences on its current confinement to the edge of Umtanum Ridge.

In Chapter 2, site, soil and vegetation habitat characteristics were measured at past, present, and potential assisted migration locations, and compared to characteristics at the Native Site. Badger Mountain is considered a highly suitable past assisted migration location where seedlings were outplanted in 2020. Snow Mountain is considered a moderately suitable assisted migration location where seedlings were outplanted at three sites in 2020 and 2021, with additional trails ongoing at the time of this study. Gingko Petrified Forest State Park is considered a highly suitable assisted migration location, although no seedlings have been outplanted there to date. Site-level habitat characteristics at Gingko State Park and Snow Mountain were compared to those at the Native Site to evaluate the accuracy of the WNHP habitat model at the spatial scale utilized by managers when selecting assisted migration sites. Gingko State Park shared more habitat similarities with the Native Site than Snow Mountain did, consistent with the output from the WNHP habitat suitability model. However, similarity to the Native Site was quite different between the three Snow Mountain sites which was not reflected in the model. These results suggest that the habitat model may not be useful at selecting assisted migration sites at spatial scales finer than landscape level, or distinguishing highly suitable and moderately suitable habitats when they co-occur within a given location. Overlaps between the range of values at the Native Site and at assisted migration sites indicate the existence of potentially suitable microhabitats at fine spatial scales. Targeting these microhabitats for seedling establishment may be important for assisted migration. To assess this, differences in site, soil and vegetation characteristics around outplanted seedlings (transect-scale) were related to seedling

survival rates and to habitat characteristics at the Native Site (high, medium, and low optimal habitat groups from Chapter 1). Overall seedling survival was very low, possibly due to differences in soil characteristics from the Native Site, and/or increased inter-species competition with forbs, annual graminoids, and especially other woody shrubs including more widely adapted *Eriogonum* species. However, heterogeneity in microhabitat niches at very fine spatial scales may have allowed for very limited seedling establishment (14% at Badger Mountain, 3% at Snow Mountain) and should continue to be the focus of future studies.

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Introduction

Ecological and Edaphic Islands

Islands are known to house unique ecologies in contrast to mainland ecosystems, with processes of isolation and limited opportunities for genetic exchange making them model system for studying fundamental questions about the evolution of species and the

development of biogeography (Graham et al 2017). Since the first formal postulations on the evolution of island ecology in the 1880s and later in 1960's, parallels have been made between the evolutionary dynamics of island biogeography and "mainland islands" of climatically or edaphically distinct and often challenging habitats (Kruckerberg 1991). Many of the effects of topographic discontinuity on plant distributions and patterns of edaphic driven isolation are congruent with island biogeography theories concerning isolation and the resulting evolutionary processes that arise in the face of limited continuity between "island" environments and their surrounding substrates.

Ecological islands" are unique habitats formed by dynamic interactions between landscape features and local climate, typically surrounded by large tracts of more common, widespread, and ecology distinct habitat areas (Kruckerberg 1991). Ecological islands can be the result of changes in altitude, topography, and/or geology that foster discontinuously distributed differences in geomorphology and substrate conditions. Unique edaphic[1] conditions, such as variations in parent material and ensuing soil physical and chemical properties, result in distinct and isolated environments known as "edaphic islands" where high rates of genetic drift, adaptive specialization, isolation, and speciation occur.

Substrates found to commonly host "edaphic islands" include unique parent materials such as serpentine[2], dolomite, sandstone, gypsum, marble, granite or limestone out-croppings, alkaline-saline sites, metalliferous soils high in zinc, copper, lead, cobalt, or aluminum, hot springs, volcanic substrates (pumice, tephra), silicate-rich materials, phosphate deficient soils and toxic anthropogenic impacts such mining tailings (Macnair and Gardner 1998). Subsequent

[1] Of, produced by, or influenced by the soil.
[2] Basic (Mg;Ca ratio that is substantially greater than 1), free draining soils which are typically nutrient poor and have a high heavy metal content (particularly nickel, chromium, and cobalt).

associated floral communities are usually distinct from those occurring on adjacent "normal" substrates, and often display radical differences in taxa and high rates of narrow endemism (Kruckerberg 1991). As in island biogeography theory, species richness is correlated with the size of the outcrop and its spatial configuration with, and isolation from, similar outcrops and distances from source biota. Species richness on ecological islands result from an equilibrium between immigration and extinction and these dynamics are greatly determined by the number of species in the surrounding source pool and its proximity to the "island" environment.

Specialization and Speciation of "Edaphic Endemics"

One of the main attributes of "edaphic islands" that distinguish them from oceanic islands is that the ocean is largely void of vascular plant recruits while surrounding soil environments, often more nutrient rich and less extreme than edaphic islands, are full of potential source species for edaphic specialization. This results in mixed communities of "edaphic endemics[3]" restricted and thus unique to the topographic or edaphic islands and other species taxonomically identical to the surrounding biota. In Western North American herbaceous perennials like Common yarrow (*Achillea millefolium*), perennial graminoids such as Sandburg's bluegrass (*Poa secunda*), and woody taxa like Sagebrush (*Artemisia tridentata*) occur both on and off "island" habitats, usually with little to no taxonomic recognition beyond differentiation into ecotypes based on their respective habitats. The close proximity of diverse floral communities and species makes dispersal between them much easier than on oceanic islands. Consequently, species growing in "edaphic islands" are likely to be taxonomically related to the surrounding flora including species within common genera. This requires genetic accommodation to the unique edaphic environment by the founder colonists of a species, which is often not the case on oceanic

[3] Native and restricted to a certain place.

islands. Furthermore, the continuing close presence of common and often edaphically indifferent taxa fuels competition with edaphic endemics that may not occur on oceanic islands, with only the most incredibly isolated and stressful edaphic habitats diminishing the strength of inter-species competition as a primary evolutionary factor.

As "edaphic endemic" species are only found on soils with particular edaphic features, they can provide insights into what evolutionary dynamics have resulted in the floristic boundaries separating "edaphic islands" from more hospitable soils adjacent. The rise of edaphic relationships in plants is intrinsically linked to evolutionary relationships between adaptation and processes of plant speciation (Macnair and Gardner 1998). Certain lineages of plants have a higher proportion of species limited by substrate preference, indicating various substrates have directly influenced the evolution and formation of lineages limited by edaphic conditions (Grady 2012). Studies of serpentine endemic species in California found a disproportionate number of endemics (greater than 4% of species) belonged to four genera: *Streptanthus* (Brassicaceae), *Eriogonum* (Polygonaceae), *Hesperolinon* (Linaceae), and *Arcostaphylos* (Ericaceae) (Safford et al 2005, Gardy 2012). Furthermore, edaphic endemism often evolves independently many times in diverse taxa such as *Calochortus* (Calochortaceae) and *Eriogonum*, which have evolved associations with unique and extreme edaphic island habitats numerous times independently across multiple lineages and disjunct isolated outcroppings across Western North America (Anacker et al 2011, Grady 2012). Repeated shifts towards specialization are common during the evolution of edaphic endemics, followed by lower rates of diversification once tolerance fully evolves.

The world-wide mosaic of soil types and substrates that occur, sometimes at incredibly fine spatial scales, is a primary factor driving the distribution and diversification of unique plant

communities (Kruckeberg 1969, Hulshof 2020). Communities composed of species adapted to challenging and unproductive soils are particularly evident at locations where anthropogenic or geological processes have created soils low in nutrients, with low water-holding capacities, extreme pH, or with levels of heavy metals that may be toxic to plant growth (Rajakaruna 2004, Rajakaruna 2018). Adaption to challenging conditions combined with evidence of low genetic migration between outcrops creates locally adapted species with high proportions of rarity and endemism (Kruckeberg 1991). Understanding why certain species have come to occupy these harsh environments, what adaptations allow them to survive, and what the effects of those adaptations are on their distributions remain critical questions for the fields of plant evolution, biogeography and plant conservation.

Defining Habitat for Rare Plants

In general, understanding both a species range distribution and its specific habitat/ niche requirements are essential components in the development of management strategies for its conservation (Crain et al 2015, Mendoza-Maya et al 2022). In particular, identifying a species' specific niche requirements and localized habitat needs are foundational to shaping a broader understanding of its geographical range, and ultimately determining the commonness, endemism and/or rarity of the species (Griggs 1940, Gaston 1997, Margules and Pressey 2000, Peterson 2006a, Fiedler et al 2007, Crain et al 2015). Adequate and accurate information on a species' distributions and habitat requirements is especially important for rare species, in which active management and sometimes intervention is necessary to sustain existing populations and avoid extinction vortices in the face of stochastic events, changing environmental conditions and anthropogenic habitat degradation (Wiser et al 1998). For species, such as *E. codium*, that have limited known distributions and are facing imminent extinction where they currently occur,

accurate information on habitat and niche requirements are essential for the successful facilitation of a species' range expansion to additional locations.

A species' niche is defined by the intersections of physical, biotic, and dispersal conditions that limit the habitats in which a species is able to persists (Peterson 1999, Peterson 2006a). Information on a species "abiotic niche", or "the physical and biotic conditions necessary for a species' survival and reproduction", defines its "fundamental ecological niche" (Hutchinson 1957, MacArthur 1972, Peterson 1999, Peterson 2006a). This is then compared to the species' "biotic niche", or "the biotic conditions necessary for a species' survival and reproduction", to determine the "realized ecological niche" of the species. Information on a species realized ecological niche can then be combined with information on a species past and current dispersal capabilities to further determine its niche distribution i.e. the spatial areas in which a species' realized ecological niche exists and can be colonized by that species (Peterson 2006a). Areas where both abiotic and biotic requirements are fulfilled but are not currently accessible to the species through natural dispersion represents areas where the species could survive if introduced, or the "potential distribution" of the species. This approach to exploring "why species occur where they are, and do not occur where they currently are not" requires considering both the nature of a specie ecological needs and barriers that can interrupt or reduce its distribution (Grinnell 1917, Grinnell 1924, Peterson 2006a, Peterson 2006b). Understanding barriers to dispersal is particularly important as most species, regardless of if they are common or rare, will likely be unable to inhabit all areas that meet their realized ecological niche requirements. Physiological dispersal limitations combined with increasing habitat fragmentation and the isolation of formerly contagious populations and habitats at landscape scales, indicate barriers to dispersal that restrict species to a subset of areas are increasingly important factors to

consider when defining a species habitat niche and modeling potential future habitat (Peterson et al 1999, Peterson 2003, Peterson 2005, Peterson 2006a).

The approach to defining a species' habitat and niche requirements through the assessment of its range distribution has numerous applications in the conservation of native species in general and rare species in particular. This approach can help elucidate the ecological requirements and basic life history of the species, and can act as a key first step in determining basic ecological factors relevant to a species' geographic distribution (Hirzel et al 2002, Peterson 2005, Peterson 2006a). Similarly, this approach can aid in better understanding how dispersal barriers shape a species' biogeography, including helping to identify important geographic phenomena or other spatially delineated environmental factors limiting a species' potential distribution (Peterson et al 2005). Finally, this approach has been utilized to both predict the location of unknown populations of a species, and identify suitable sites for translocation and reintroduction (i.e. assisted migration).

One potential issue with this approach to defining both a species' realized ecological niche and its potential distribution is that a species' niche is defined by the habitat and vegetation associations where it currently grows. However, current species distributions may not entirely encompass a species' full range of tolerance to abiotic and biotic conditions or even account for past changes in that species' distribution, especially when changes occur in response to non-environmental impacts such as anthropogenic habitat degradation (Araújo and Pearson 2005, Soberón and Peterson 2005). This is especially limiting for species such as *E. codium* that are known to occur in a limited number of areas or only at a single location, have extremely limited distributions within the areas where it grows, and/or for which no information on its historical distribution is available.

The Role of Vegetation Associations in Defining Rare Species Habitat

The established practice of including biotic factors in determining a species' realized ecological niche recognizes the important influence ecological relationships have on rare plant species' population sizes and distributions (Hutchinson 1957, MacArthur 1972, Peterson 2006a). Numerous physiological and ecological factors impact rare species habitat specificities, local population sizes, and restricted geographic ranges including negative and positive interactions with other species (Rabinowitz et al 1981, Walck et al 1999, Lloyd et al 2002, Levine et al 2010, Smart et al 2015). Smart et al 2015 proposes an approach to defining a rare species' habitat based on identifying "indicator" associates that most frequently grow with the rare plant. These associated indicator species can be used to infer the suitability of habitat conditions for the rarer species. One advantage to this approach is it is easily repeated and lists of indicator species can be updated as the known range of the rare species is expanded, either through the discovery of previously unknown populations or the establishment of additional populations via assisted migration. Identifying associated indicator species and vegetation community types is a useful management tool that can assist with the identification at assisted migration locations of potentially suitable vegetation patches for rare species introduction.

Identifying and describing rare species' vegetation associations highlight important spatial patterns shaping habitat suitability, while providing an ecological reference for mangers to target when assessing potential habitats for assisted migration. The indicator species approach proposed by Smart et al 2015 seeks to identify indicator species on a continuum, with the best indicators species being those that always grow in association with a rare species, but are not common or widespread outside of this association. In contrast, species that always grow in association with the rare species but are also common and widespread where the rare species

does not occur are not deemed to be good "discriminators" of suitable habitat conditions for the rare species. Ideally, this results in a list of indicator species that vary in the strength of their of association with the rare species. As both the distributions of rare plant populations and their associated indicator species are constrained by spatially variable environmental conditions and resource gradients, insights can then be drawn between the number, identities, and association strength of indicator species and environmental gradients potentially impacting rare species populations (Guisan and Zimmermann 2000). Establishing a range of vegetation conditions associated with a rare species can help managers identify key environmental conditions impacting vegetation patterns and rare species' biogeography.

Distribution and Population Dynamics of Umtanum Desert Buckwheat

This project seeks to provide habitat information to aid in the development of strategies for the management and assisted migration of a rare endemic species in the face of climate change and increasing fire risk. Umtanum Desert Buckwheat (*Eriogonum codium*) is a slow growing, long-lived (>100 years), low woody perennial plant which grows as a mat-forming "sub-shrub" (Dunwiddie et al. 2001, USFWS 2019) (Fig 1A). The species range is highly restricted to a 25-to-150 meter-wide discontinuous band (total population area 1.9 acres) atop the eastern end of Umtanum Ridge in the semi-arid shrub-steppe of Washington state's Columbia

Plateau (Fig 1B). Because *E. codium's* singular population is in decline, it has been state listed as endangered and was federally listed as threatened under the Endangered Species Act in 2013 (USFWS 2013a).



Figure 1 Photo of Umtanum Desert Buckwheat (*Eriogonum codium*) and the area of Umtanum Ridge where the single population occurs
E. codium is a low growing (cespitose), long lived (>100 years) perennial sub-shrub (A) with a single known population growing along the edge of Umtanum Ridge in the Hanford Nuclear Facility, Benton Co., WA (B). Image is taken from the most eastern subpopulation in this study looking west. Photos taken by M. D. Kahn-Abrams

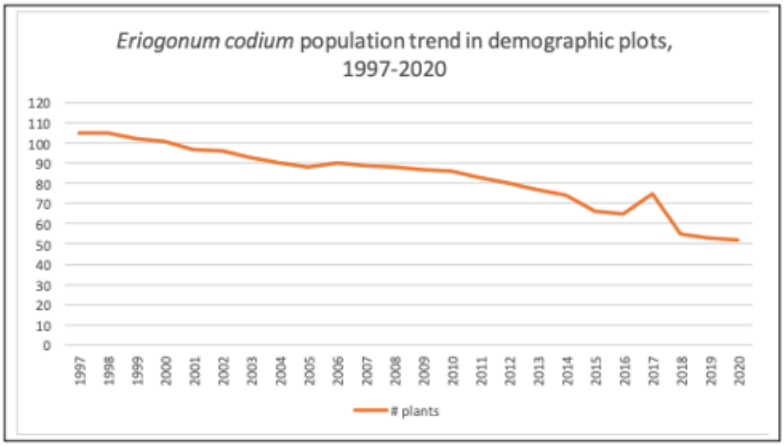
The single population of *E. codium* is threatened by its highly restricted range and low abundance, low recruitment, and low geographic, ecological, and niche diversity. Despite high flower and seed production, an estimated 5,228 plants in 1997 decreased significantly to 2,354 plants by 2023 (45% decline) (Jesse Miller, personal communication). *E. codium* has extremely low recruitment, with a Population Viability Analysis (PVA) reporting an annual population

growth rate of 0.9935 indicating mortalities exceed recruitment (Caplow et al 2007). Nine years of monitoring found only five seedlings that survived beyond germination and only a single seedling recorded in 1999 that was tracked to flowering (Beck and Caplow 2006). A study tracking the survival of 64 seedlings from germination in the spring of 2022 found 100% seedling mortality by September 2022 even with supplemental watering (Howell et al 2024). This species' ability to adapt to change appears to be low, and changes to habitat quality resulting from stochastic events and shifts in global climate pose severe threats to *E. codium's* continued existence. A 2007 population viability analysis based on 10 years of data determined a 72% chance of a 50% decline within the next 100 years not taking into account stochastic events such as wildfires (Caplow et al 2007).

Threats to Umtanum Desert Buckwheat's Population

E. codium occupancy of a narrow and confined habitat range makes it vulnerable to stochastic events such as wildfire which is one of its primary threats (USFWS 2019). Two wildfire events in 1996 and 2017 have destroyed a significant portion of the population while changing the surrounding native habitat by opening charred soils to annual invasive species (Shank 2019). The wildfire in 1996 killed an estimated 10-20% of the entire population, while the fire in 2017 burned 63% of the population. Adult individuals are negatively affected by fire, with high mortality for both completely burned and partially burned individuals. *E. codium* appears to be extremely sensitive to exposure of both heat and smoke, with even singed but not visibly charred plants dying within a year after fire while significant decreases in seed production and seedling germination were observed a year after the fire (USFWS 2010, Shank 2019). With a

population decline of 36% between the last wildfire in 2017 and 2023, this species is predicted to be extinct within 14 years (Jesse Miller, personal communication).



Population Estimates		Change Population Size
1997	**5,228**	
2011	5,169	-59 (2%)
2019	3,016	-2,153 (42%)
2023	**2,354**	-662 (22%)

WNHP Polygon	Subpopulation Number	# Plants 2019	# Plants 2023	Change in Subpopulation Size
16298	I	2239	1756	-483 (22%)
16300	III	120	92	-28 (24%)
16299	V	657	506	-151 (23%)

Figure 2 Population decline of Umtanum Desert Buckwheat (*Eriogonum codium*)
Figure (top) shows steady population decline of *E. codium* populations since monitoring began in 1997 until 2020. Increases in population estimates in 2005-2006 and 2016-2017 correspond with the discovery of additional plants in previously unknown subpopulations at the single native site. Sharp population decline 2017-2018 shows the impacts of a wildfire event in 2017 that burned 63% of the population (Figure from Fertig 2021). Table (bottom) shows change in population estimates from 1997-2023 (Data and figure from Jesse Miller, WNHP personnel).

Regional models of climate change in the Columba Basin predict increased summer and winter temperatures and decreased precipitation and winter snowfall between now and 2040 (Littell et al 2009). Increasingly rapid rates of global change pose a substantial threat to the continued survival of *E. codium* as stress from decreased rainfall and increased temperatures may exceed this species' range of tolerance beyond survivable limits (Corlett 2020). Small populations of rare species are at especially high potential risk of extinction due to the combination of weakened environmental tolerance, invasion of generalist non-native species, exposure to novel anthropogenic threats and reduced fire intervals. Physiological stress and habitat loss resulting from current increases in average temperatures and reduced average rainfall are likely already causal in the current decline of the species, while hotter and drier conditions

produce a less stable environment and increase the frequency and intensity of larger fires. Due to its extremely limited distribution (< 2 acres), another single catastrophic event could cause the extinction of the species from the wild.



Figure 3 Decline of Umtanum Desert Buckwheat (*E. codium*)
Deceased reproductive adult plant in 2023. Presence of previous season flowers on dead plant indicate individual died shortly after flowering the previous year. Presence of invasive annual graminoid Cheatgrass (*Bromus tectorum*) is visible encroaching into *E. codium* habitat in the top left of the photo. Photo taken by M. D. Kahn-Abrams

Recovery of Umtanum Desert Buckwheat

To date, the United States Fish and Wildlife Service (USFWS) has designated critical habitat for the species (USFWS 2013b), produced a recovery plan (USFWS 2022), and prepared a species biological report (USFWS 2021a) and recovery implementation strategy (USFWS 2021b). Management for this species recovery has prioritized both attempting to address habitat

changes at the single native site, and build redundancy by augmenting the existing population through the establishment of new populations at other locations. Priority I and II recovery actions (Table 1) focus on better understanding this species ecology with aims to identify what



Figure 4 Changes to *E. codium* Population and Surrounding Habitat Pre and Post 2017 Wildfire Event
Photos taken at largest and most abundant area of *E. codium* population facing south towards the Columbia River. Photo taken before wildfire event in 2017 (left) shows higher abundance (total cover) of *E. codium* and intact native vegetation communities including presence of shrubs on hillslope west of population. (Photo courtesy of WA-DNR). Photo taken six years after wildfire event in 2023 (right) shows decline of *E. codium* population and loss of native vegetation community including presence of shrubs on hillslope west of population. (Photo taken by M. D. Kahn-Abrams)

characterizes the "optimal" habitat for this species where it currently grows, what constitutes suitable habitat for successful assisted migration, and how to best model potential suitable habitat given the extremely low distribution of the species and high levels of habitat heterogeneity across the Columbia Plateau bioregion.

Project Goals

The purpose of this study is to address priority 1 and 2 recovery actions outlined by U.S. Fish and Wildlife as necessary for the successful conservation of Umtanum Desert Buckwheat (*E. codium*). This work primarily concentrates on recovery action 2.6.1, investigating *E. codium*'s ecology and 1.2.4, determining the most effective methodology to establish individuals in the field, while also providing insights into recovery actions 1.3.3, ground truth model of suitable habitat and 1.4.1, determine best augmentation and reintroduction methods in suitable habitat (Table 1). To address these recovery actions, this study aims to explore what habitat variables constitute *E. codium*'s "fundamental" and "realized" ecological niches, and to what extent these niches are being accurately identified by the WNHP potential suitable habitat model and successfully targeted during assisted migration attempts.

Chapter 1 seeks to address priority action 2.6.1 through the exploration of habitat characteristics within the single native population, and their implications for understanding *E. codium*'s evolutionary ecology, rarity, and current confinement to the edge of Umtanum Ridge (Table 1). Utilizing the non-destructive field assessment of site, soil, and vegetation characteristics, this chapter aims to identify key habitat variables, and their variation within the single existing population, to consider what evolutionary drivers have come to shape *E. codium*'s current habitat requirements. The first part in this chapter assesses the importance of habitat variables on *E. codium* occupancy by describing differences between where *E. codium* is present and absent, and relationships between habitat characteristics and patterns in *E. codium* abundance where it is present. The second part in this chapter explores differences within and between *E. codium*'s five subpopulations to investigate the evolutionary drivers of *E. codium*'s

current distribution. The third part of this chapter evaluates similarities in niche variation across the five subpopulations to define "optimal" and "less-optimal" *E. codium* habitat types.

Chapter 2 seeks to address priority action 1.2.4 through the comparison of similarities and differences in habitat characteristics between *E. codium*'s single native population and assisted migration locations. The first part of this chapter seeks to address priority action 1.3.3 to ground truth the WNHP potential suitable habitat model through the comparison of habitat characteristics measured at the single native population with those present at sites identified by the model as suitable habitat for assisted migration. A "highly suitable" site at Gingko Petrified Forest State Park where assisted migration attempts have not yet occurred is compared to three "moderately suitable" sites at Snow Mountain where assisted migration attempts were ongoing at the time of this study, providing insight into the ability of the model to accuracy identify habitat suitability at the scale associated with the selection of assisted migration sites within a target location. The second part of this chapter seeks to address priority action 1.4.1 by assessing relationships between seedlings survival outcomes at assisted migration sites and habitat suitability at the fine spatial scales influencing seedling mortality. Microhabitat characteristics at outplanting transects where year old seedlings were planted at Badger and Snow Mountains from 2020-2021 are compared to "optimal" habitat groups associated with high, medium and low *E. codium* abundance. These findings aim to support managers in better targeting *E. codium'*s realized ecological niche within the fine scale variation and heterogenous landscapes found within sites selected for assisted migration.

Ultimately, this study is an exploration of *E. codium*'s habitat requirements, the evolutionary drivers that have resulted in this species current habitat associations, and how the outcomes of ongoing experimental assisted migration attempts test these evolutionary theories.

By linking *E. codium*'s niche ecology with current efforts to expand this species' range, this study aims to provide important insights that can support the development of more effective methodologies for successful establishment of additional populations.

Table 1 Relationship of USFWS Recovery Actions for *E. codium* to Project Goals and Thesis Sections
List of priority I and II actions outlined by the US Fish and Wildlife Service for the recovery if *E. codium* addressed in the study (USFWS 2021b). Top table indicates priority 1 and 2 recovery actions stipulated by USFWS and indicates which project goals address each recovery action. This study aims to investigate this species known habitat (priority 2) to support effective methods of site selection for assisted migration (priority 1). Bottom table describes the project goals and indicates in which thesis section each project goal is addressed.

Recovery Actions	Priority	Description	Project Goal
1.2.4	1	Determine the most effective methodology to establish viable individuals in the field	1,2,3,4
1.3.3	1	Ground truth model of suitable habitat for introduced efforts	1,2,3
1.4.1	1	Determine the best augmentation and reintroduction methods in suitable habitat	2,4
2.6.1	2	Investigate the species ecology	1,4

Project Goal	Description	Thesis Section
1	Determine habitat characteristics of the native site	**Chapter 1**: Habitat Assessment of the Single Native Population
2	Determine habitat differences and similarities between the native site and assisted migration sites	**Chapter 2**: Assessment of Habitat Differences Between the Native Population and Assisted Migration Locations
3	Ground truth habitat model and explore what spatial scales variation occurs	**Chapter 2 Part I**: Site Differences Between the Native and Assisted Migration Sites
4	Monitor 2020 & 2021 outplanted seedling survival and identify habitat characteristics related to seedling success	**Chapter 2 Part II**: Differences Between "Optimal" *E. codium* Vegetation Habitat Groups and Outplanting Transects

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Chapter 1

Habitat Assessment of the Single Native Population of Umtanum Desert Buckwheat (*Eriogonum codium*)

Introduction

Columbia Plateau and Yakima Fold Belt Bioregion

Arid ecosystems or "drylands" are characterized by limited water availability due to interactions between processes of low precipitation and evapotranspiration[4] (Steven 2017). Water limitations within these systems result in landscapes limited in biological activity and low levels of organic carbon. Resulting vegetation is diverse, with mixed shrub and grasslands commonly covering large areas of the soils surface (Steven 2017). As precipitation and temperatures can fluctuate erratically in these systems, ecosystems are usually patchy mosaics of vegetation varying by edaphic characteristics and uneven terrain at a variety of scales.

The Columbia Plateau ecoregion covers an area approximately 90,059 km2 (34,772 mi^2) and is surrounded by mountains on all sides, including the Cascades to the east, the Blue Mountains to the South and the Rockies to the east (Sleeter 2012). The climate is semi-arid with annual precipitation ranging from 18-40 cm with hot and dry summers (Crawford and Schulz 2016). Precipitation primarily occurs s as snow or spring rain during winter (October – March) promoting cool-season grasses. However, growing-season drought is characteristic and high inter-annual variation occurs. Temperatures are characteristics of dry inland areas with large

[4] Evapotranspiration is a metric of water lost from a landscape through the combined effects of evaporation and transpiration (i.e. the evaporative loss of water from plants).

seasonal and diurnal variation and can range from -15° F (lowest recorded winter temperature) to 118° F (highest recorded summer temperature).

In general, a lack of precipitation and resulting lack in soil organic carbon are large drivers in the structure and function of arid vegetation (Steven 2017). Differences in soil parent material play important roles in determining differences in water and nutrient availability and determining composition and function of vegetation communities. The water holding capacity of dryland soils depends on physical characteristics such as texture, structure, and soil depth. Landscape aspects such as slope or shading alter localized soil water retention, creating restricted soil niches. These ecological niches alter the abundance and diversity of the biotic communities' arid soils can support in any given location, resulting in patchworks of biologically active areas. Rocks can provide dynamic influences on soil water retention, creating microhabitats that support different communities of vegetation. The spatial heterogeneity of moisture and nutrient resources in arid ecosystems result in "islands of fertility" where vegetation such as shrubs collect resources and act as focal points of biological diversity and soil biological processes.

The geology and topography of the Columbia Plateau has been subject to a number of major geologic processes that have built the present-day landscape (Sullivan 2000). During the long periods of intense geologic, volcanic and hydrologic development of the eastern portion of Washington state, four distinct geologic and topographic regions evolved including the sloping Columbia Plateau and extensive river basin. Within the Columbia Plateau, the Yakima Fold Belts and basin are a series of west to east running ridges of folded rock layers formed due to tectonic stress in the southwestern region of the Columbia Plateau. 17 million years ago, while successive volcanic eruptions formed deep layers of basalt over the region, immense north to south tectonic compression from the Cascade Mountains began to fold and fault the flat-lying basalt (Sullivan

2000). Lava engulfed and cooled around ponds or lakes and partially engulfed swamps and forests, resulting in fossilized rock remains of plants at sites such as Ginkgo Petrified Forest State Park. The subsequent periods of extensive lava flow and continued folding and uplifting has resulted in a series of parallel ridges between Wenatchee and Pasco including Umtanum Ridge, Snow Mountain, Badger Mountain, Saddle Mountain, Frenchman Hills, and Horse Heaven Hills (Lenfesty and Reedy 1985).

During the last advance of continental glaciers (12,000 -15,000 years ago), large volcanoes in the Cascade mountains undergoing explosive eruptions laid thick layers of aerially deposited ash across the Columbia Plateau (Lenfesty and Reedy 1985). Glaciers advancing and retreating from the Cascades washed vast quantities of mixed ash and volcanic material into the Yakima Basin, laying down sediments of basalt gravel and minor amounts of sandstone and granitic rocks. These geologic and soil development processes played important roles in determining the erosional features carved out during the great Missoula floods. Regular breaches of the Clark Fork River ice damn in Montana during this time sent huge quantities of water surging across the Columbia Plateau, cutting through accumulated sediment deposits and leaving islands of loam separated by scablands and bedrock channels.

Today this region is characterized by a complex mosaic of canyons cut into multiple layers of basalt, each layer corresponding to a separate glacial flood, and steppe buttes where islands of older rock overlaid with river loam stand above and surrounded by lava fields of bare basalt where flood waters washed away overlaying soils. High soil heterogeneity across the entire region fosters an extremely diverse array of habitats often arranged in close proximity to each other in patchworks corresponding to dynamic interactions between topography, soil properties, and moisture dynamics.

Sagebrush steppe habitat is usually characterized by open shrub cover primarily of big sagebrush (*Artemisia tridentata*) and/or stiff sagebrush (*Artemisia rigida*), interspersed with other shrubs and woody subshrub species such as *Eriogonum* spp., perennial bunchgrasses and lower layers of associated perennial forbs. Soil depth in this zone can have a dramatic range and is an important factor in determining species composition. Areas with deeper soils store larger amounts of water and are able to support larger and more diverse vegetation, including moisture loving forbs and phreatophytic[5] species. Lithosols ("rock soils") are gravelly and extremely thin soils resulting from high velocity floodwaters scouring away the topsoil and exposing patches of the underlying basalt bedrock (Brea 2011). Plant species found in this zone are generally adapted to extreme drought and can handle extreme cold in the winter. Talus slopes are areas of basalt rubble formed as the cliffs of the canyon walls erode and crumble. The accumulation of boulders, cobbles and gravel, combined with low precipitation results in the slow formation of very thin, highly porous soils. Due to the well-draining nature of these areas, moisture percolates through the rocks collecting below and resulting in communities of species possessing well developed, far reaching root systems that can navigate between talus rocks to access water below.

Transitions between these habitats often constitute unique ecotones[6] of high botanical diversity. Ecotones between lithosolic, sagebrush- bunchgrass, sagebrush-forb, and talus slope communities yield unique floristic areas of high diversity. Southern and western exposures experience the most severe wind and water erosion, so soils are generally shallow and corresponding vegetation cover is sparse and comprised of drought-resistant species. Plant cover

[5] Plant species with root systems capable of reaching deep into groundwater supplies, which helps them survive in arid and semiarid climates where soil moisture is scarce.
[6] Transition area between two biomes; where two biological communities meet and integrate.

on northern and eastern slopes is typically more abundant, as these exposures have greater soil depths, concentration of organic matter and topographic shading. Soil within these climax community are often covered with cryptogamic biocrusts comprised of mixed communities of lichens and mosses, helping to hold water, reduce erosion, provide a medium for seed germination, and improve soil fertility through fixation of gaseous nitrogen (Brea 2011). The rarity and extreme conditions of these specialized habitats creates unique niches contributing to the numbers of rare plants found across the Columbia Plateau.

Rarity and Speciation in the Genus Wild Buckwheat (Eriogonum)

Wild buckwheat (*Eriogonum*) are members of the Eriogonoideae subfamily within Polygonaceae (Buckwheat) family (Reveal 2005). *Eriogonum* is one of the largest[7] and most diverse genera in North America with roughly 250 species, and accounts for about ¾ of the species diversity of the Eriogonoideae subfamily despite being geographically limited to North and South America (Reveal 2005). The genus *Eriogonum* is primarily distributed in geologically young arid portions of the Western U.S. that have undergone rapid evolution such as the Columbia Plateau bioregion (Fig 1.1) (Grady 2012). An estimated one-third of the species are considered uncommon or rare in their distribution and a total of thirteen taxa (species or varieties) listed as either endangered, threatened, or as a candidate for listing as endangered by the US Fish and Wildlife Service. *E. codium* is part of the subgenus *Eucycla II,* a large and diverse clade of largely perennials containing both species with widespread distributions and numerous narrowly distributed endemics of conservation concern grouped into many polytomies[8] (Grady 2012). This includes numerous species with distributions limited to one

[7] Fourth largest genus after *Carex*, *Astragalus* and *Penstemon*.
[8] Polytomy is a term for an internal node of a cladogram that has more than two immediate descendants (i.e, sister taxa). In contrast, any node that has only two immediate descendants is said to be resolved.

state, with some limited to a single mountain range or even a single peak, such as *E. codium*. Patterns in haplotype[9] diversity found within multiple gene regions and numerous species including several species with rare and isolated singular populations, indicate that despite the current geographic isolation of rare species from the closest members of their respective clades, these isolated species were likely historically more widespread in their distribution (Grady 2012).

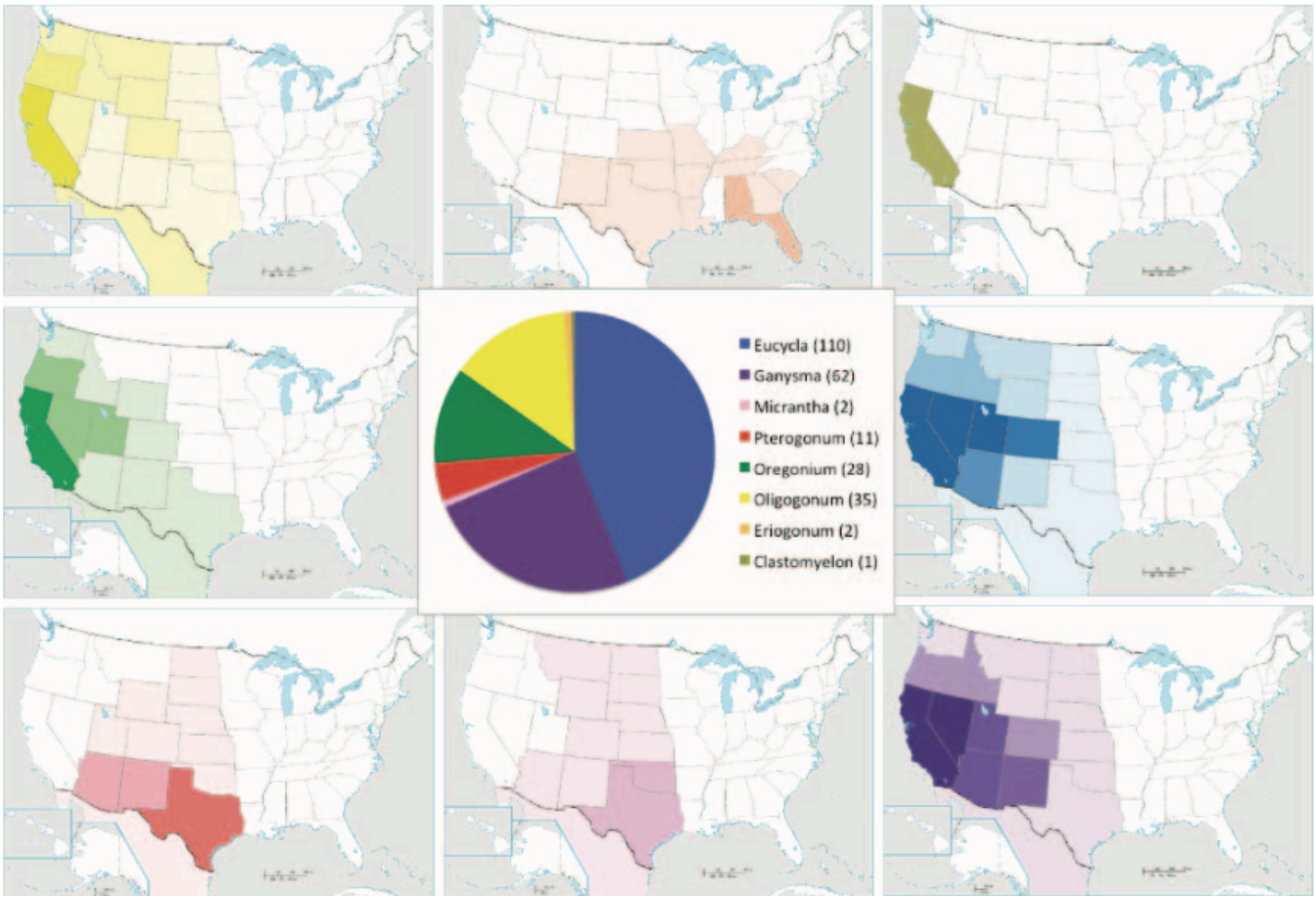


Figure 1.1 Distribution of *Eriogonum* subgenera in the United States and Mexico
Colors represent different subgenera and intensity is indicative of species diversity within each state (number of taxa). *E. codium* belongs to the subgenera *Eucycla* which has the highest species diversity in California, Nevada, Utah and Colorado. (Figure taken from Grady 2012)

[9] A haplotype is a group of alleles in an organism that are inherited together from a single parent.

In general, two evolutionary models have been proposed to explain phylogenetic patterns of soil endemism, rarity and speciation within *Eriogonum* (Grady 2012). In the "refuge model" or "generalist model", stress-tolerant generalist species or populations proliferate by growing on marginal soils or in other extreme habitat conditions to limit competition from other less stress-tolerant species (Gankin and Major 1964). In contrast, a "specialist model" describes plant species which succeed due to adaptations to unusual chemical and physical properties associated with certain soil types (Meyer 1986). Plant lineages composed of edaphic generalists are expected to show very few patterns of edaphic similarity when compared to phylogenetic trees based on evolutionary history, while lineages of the specialist model should show strong clade specific affinities with soil characteristics when mapped onto a phylogeny of edaphic endemics grouped by specialization to soil type.

Eucycla II contains numerous highly branching, separate and incomplete lineage sortings, showing evidence of both hybridization through introgression[10] and changes in ploidy level driven by concerted evolution[11]. These processes appear to result in recent and rapid species radiations and hybridization, resulting in unrecognized polyploidy in some species and of lack genetic variation in others. The refuge/generalist model is believed to be the correct model for understanding the rapid speciation, high number of soil endemics, abundance of rare species with limited distributions, and the overlapping of distributions and phylogenetic relationships between widespread and highly rare species within *Eucycla II* (Grady 2012, McClinton et al 2020, Pearman et al 2021). When the phylogeny of 23 edaphic endemic species with similar specialized soil requirements was analyzed for correlations with soil pH, phylogenetic trees

[10] Interspecific hybridization
[11]Concerted evolution is a phenomenon where repeats within a genome (paralogs) show more sequence similarity to each other than they do to their counterparts in other species (orthologs)

constructed from plastid and nuclear gene regions found species from a diversity of distinct lineages occurred on soils belonging to a single edaphic grouping. This indicates that associations with particular soil types are not due to one evolutionary lineage that has evolved to fill a particular soil niche. Instead, polyphyletic patterns of soil specificity in which shifts to similarly specialized soils seem to occur simultaneously in distinct lineages indicate a "generalist model" of speciation, accounting for the occurrence of narrowly distributed species on similar soil substrates as widespread species, and the close phylogenetic relationships between these groups.

According to this model, it is likely that both widespread and rare species of *Eriogonum* can tolerate a variety of harsh and challenging substrates, occupy these marginal sites due to the absence of competition from surrounding vegetation (Gardy 2012). In general, *Eriogonum* species have highly plastic morphological and physiological responses to specific soil and habitat conditions**,** responding with a diversity of physical forms when growing in unique environments (Czehura 1979, Chapin 1986, Gonella 1994, McClinton et al 2020). Variation in morphology has been found to be site specific, with species demonstrating highly plastic responses to specific soil associations as well changes in localized weather and climate (Sherwood et al 2017, Gucker and Shaw 2019). *Eriogonum* species' highly plastic morphological and physiological responses to environmental factors appears to be key in enabling this genus to occupy marginal soil environments untenable for majority of other plant species. This occupation of marginalized sites, which are often characterized by repeated disturbance, is employed ubiquitously by both annual and perennial species and is widespread in rare and common members, serving as a unifying characteristic underpinning the evolutionary trajectory and life history of the genus as a whole.

Patterns in Habitat Characteristics Associated with Evolutionary Models

While the evolutionary trade-offs that drive adaptation and speciation via the generalist (or "refuge") vs specialist models can only be determined through experimentation, genetic analysis, and phylogenetic reconstruction, some patterns in habitat characteristics can be indicative of each adaptive strategy (Myer 1986, Rajakaruna 2017). Each evolutionary model represents a different set of adaptive tradeoffs species can utilize in response to landscape heterogeneity and challenging environmental pressures. These adaptative tradeoffs in turn drive responses to habitat variation that can be observed in the field and drive larger patterns in species' habitat distributions.

For a generalist species seeking "refuge" in a marginal habitat to avoid inter-species competition, complex abiotic interactions that determine biotic site productivity are key variables shaping site occupation and resulting patterns in species abundance and distribution. Habitat characteristics influencing soil moisture holding capacities, overall soil fertility and adjacent species competition is more important in shaping species' biogeography and then any specific limit or excess in soil physical or chemical properties. Thus patterns in site occupancy and abundance are linked to habitat variables such as soil moisture and nutrient content, levels of organic matter and metrics of vegetation community productivity and diversity such as leaf area index (LAI), total cover and species richness. These species demonstrate high phenotypic plasticity in response to variations in soil moisture and nutrients, and can occupy a range of abiotic conditions successfully as long as habitats remains marginal enough to limit inter-species competition. Species show improved growth and productivity in response to increase moisture and nutrient availability when grown in the absence of inter-species competition, while demonstrating increased stress and decrease grown when grown in the same conditions with

other species present. This evolutionary strategy is illustrated by the response of serpentine endemics species to differences in soil and interspecies competition, in which species grew best and were most productive when grown experimentally on non- serpentine soils in the absence of competition (Proctor and Woodell 1975).

In contrast, for edaphic specialists, soil physical and/or chemical characteristics are stronger predictors of site occupancy than vegetation community dynamics. Soil specialists experience reduced growth and competitiveness when growing in "normal" soils lacking in the property that make their associated soil distinct. Clear relationships between patterns in abundance and measurable gradients in a soil physical or chemical property is observed, as a high physiological cost is associated with soils lacking in the associated soil property. This associated soil property provides a measurable advantage to the plant species that cannot obtained through increased access to soil moisture and nutrients or decreased competition. This evolutionary strategy is illustrated by work done in the late 1960s demonstrating the co-dependence of calcicole[12] endemics to their associated calcicole soils (Rorison 1960, Clymo 1962, Jeffries and Willis 1964). Species did not grow as well and were less productive when grown on soils lacking lime chalk, even in the absence of competition, indicating the calcicole soil properties conferred some type of adaptive advantage to the adapted species .

In arid environments water availability is a basic physiological constraint driving the evolution and biogeography of all species. Because the impacts of soil moisture are ubiquitous in dryland systems, generalist species restricted to marginal soil environments as a means of avoiding competition are expected to be restricted to these habitats in response to both patterns in available soil moisture and strong patterns in other abiotic characteristics contributing to low site

[12] Plant that thrives on lime rich chalk soils.

productivity and reduced coemption (Myer 1986). Similarly, for a species considered to be soil specialists, occupancy of an extreme soil environment and adaptations to a unique soil property have to be driven by some advantage of the soil substate beyond minimizing competition with other species or increasing access to soil moisture.

Previous Work Describing Umtanum Desert Buckwheat Habitat

Publicly accessible mapped soil data is currently unavailable for this area, although previous work done by US Fish and Wildlife personal utilizing Pacific Northwest National Laboratory (U.S Department of Defense) data indicated soil may be a Kiona Silt loam. This site has historically been characterized by "pebbly or pumice-like basalt" which is thought to indicate the soil habitat Umtanum Desert Buckwheat may be specially adapted to (specialist model of edaphic evolution) (Fertig 2021, Grady 2012). The known habitat for *E. codium* is described as "the rim of north-facing basalt cliffs on fine pebbly or pumice-like basalt of the Kiona Silt loam series in a sparse cushion plant-bunchgrass community bordered by sagebrush grassland" (Fertig 2021) (Fig 1.2). This species is assumed to be an edaphic endemic restricted to the unique habitat characteristics of fine pebbly/ pumice-like basalt outcroppings visually and ecologically distinct from the surrounding habitat, which is a more productive and diverse vegetation community presumably characterized by deeper, richer soils.

The historical distribution of the species is unknown, but it likely has been confined to its current location for the last 150 years, as additional populations have not been found despite extensive survey efforts (Reveal et al 1995). Prior to the Silver Dollar fire in 1996, the surrounding vegetation was dominated by native shrubs Big sagebrush (*Artemisia tridentata*), Spiny hopsage (*Grayia spinosa*), Purple sage (*Salvia dorrii*), and perennial bunch grasses Sandburgs bluegrass (*Poa secunda*) and Bluebunch wheatgrass (*Pseudoroegneria spicata*)

(Dunwiddie et al 2001). In 2019 vegetation recorded during annual surveys by the Washington Natural Heritage Program (WNHP) consists primarily of 20-25% cover of *E. codium,* cheatgrass (*Bromus tectorum*), Russian thistle (*Salsola tragus*), Sanburg's bluegrass *(P. secunda),* Ricegrass (*Achnatherum hymenoides*), Common yarrow (*Achillea millefolium*), Wooly milkvetch (*Astragalus purshii),* Bottlebrush squaretail (*Elymus elymoides*), orange globe mallow (*Sphaeralcea grossulariifolia*), hoary tansy-aster *(Dieteria canescens),* and Carey's balsamroot *(Balsamorhiza careyana)* (Fertig 2019). Little information is available about the soil environment of its natural site nor is it known whether edaphic properties or some other habitat characteristic is the reason for its confinement to a single location.



Figure 1.2 Unique Edaphic and Vegetation Characteristics of *Eriogonum codium* Habitat
E. codium population is retracted to a series of rocky outcroppings (red arrows) along the edge of Umtanum Ridge. These area are visually and ecologically distinct from the surrounding habitat (blue arrows), which is a more productive and diverse vegetation community presumably characterized by deeper, richer soils. Photos taken by M. D. Kahn-Abrams

Current Work

The aim of this habitat assessment is to obtain quantitative information about the habitat conditions of the single population of *E. codium*. Utilizing the non-destructive assessment of site, soil, and vegetation community characteristics, chapter 1 aims to identify what habitat characteristics are empirically associated with the occurrence and abundance of *E. codium* within the areas where it currently grows. Through the identification of *E. codium*'s ecological niche, this study endeavors to provide insight into the evolutionary drivers resulting in *E. codium*'s current confinement to Umtanum Ridge. Finally, an exploration of habitat characteristics across spatial scales is used to characterize the unique *E. codium* vegetation community and classify "optimal" and less-optimal" vegetation habitat characteristics.

The fundamental research questions of chapter one are:

Part 1: Assess importance of habitat variables on *E. codium* habitat occupancy.

- How do site, soil and vegetation habitat characteristics differ between areas where *E. codium* is present and where it is absent *(E. codium* occupancy)?
- Where *E. codium* is present, how do site, soil and vegetation habitat characteristics differ by *E. codium* abundance?

Part 2: Assess differences between subpopulations to explore evolutionary drivers of *E. codium*'s distribution.

- How do site, soil and vegetation habitat characteristics differ between *E. codium's* five subpopulations?
- What are the implications of the subpopulation's inter and intra habitat variation on *E. codium*'s evolutionary strategy?

Part 3: Assess similarities between subpopulations to explore what distinguished "optimal" habitat.

- What vegetation habitat characteristics distinguish "optimal" and "less-optimal" *E. codium* habitat*?*
- How do site and soil characteristics differ between "optimal" and "less-optimal" *E. codium* habitat*?*

Methods

Field Methods

Study Location

Data were collected at the Hanford Reach Nuclear Facility within the 1.9 acre area where the single *E. codium* population grows along the north facing edge of Umtanum Ridge. The population is located along the edge of the basalt cliff overlooking the Columbia River. WNHP maps of the population indicate four subpopulations stretching perpendicular along the edge of the ridge (Polygon ID#s: 16299, 16300, 16298, 29719) and three smaller patches of plants indicate by circles (Polygon ID#s: 29720, 29721, 16296) (Fig 1.3-A). For this study only the largest area of remaining plants was targeted for data collection (Fig 2). WNHP subpopulation number 16298 is "subpopulation I", 29719 is "subpopulation II", and 16300 is "subpopulation III" (Fig 1.3-B, 1.4-A). Subpopulation 16299 is no longer one continuous subpopulation and has been split into two "subpopulations" IV and V for this study. Only the western and eastern portions of subpopulation 16299 remain, and no plants were found in between the areas where transects were laid (Fig 1.3-B, 1.4-C). Subpopulations I and V are the largest subpopulations with >100 individual plants, while subpopulations II, III and IV have <100 remaining plants as of June 2023 (Fig 2, Table 1.1).

Table 1.1 Change in Size of Subpopulations I, III, IV and V 2019-2023
Population data is based on WNHP annual monitoring of subpopulations I, III and V (Jesse Miller, WNHP personnel). No annual monitoring is currently ongoing in subpopulations II and IV and no actuate population data is available. All subpopulations experienced 22-24% decline over a four-year period, indicating decline is consistent across the three largest subpopulations. Subpopulations I and V have the largest subpopulations and the only ones with >100 individuals still remaining. The rate of decline has increased the rate of decline by 10% since the 2017 wildfire.

WNHP Polygon	Subpopulation Number	# Plants 2019	# Plants 2023	Change in Subpopulation Size
16298	I	2239	1756	-483 (22%)
16300	III	120	92	-28 (24%)
16299	IV + V	657	506	-151 (23%)

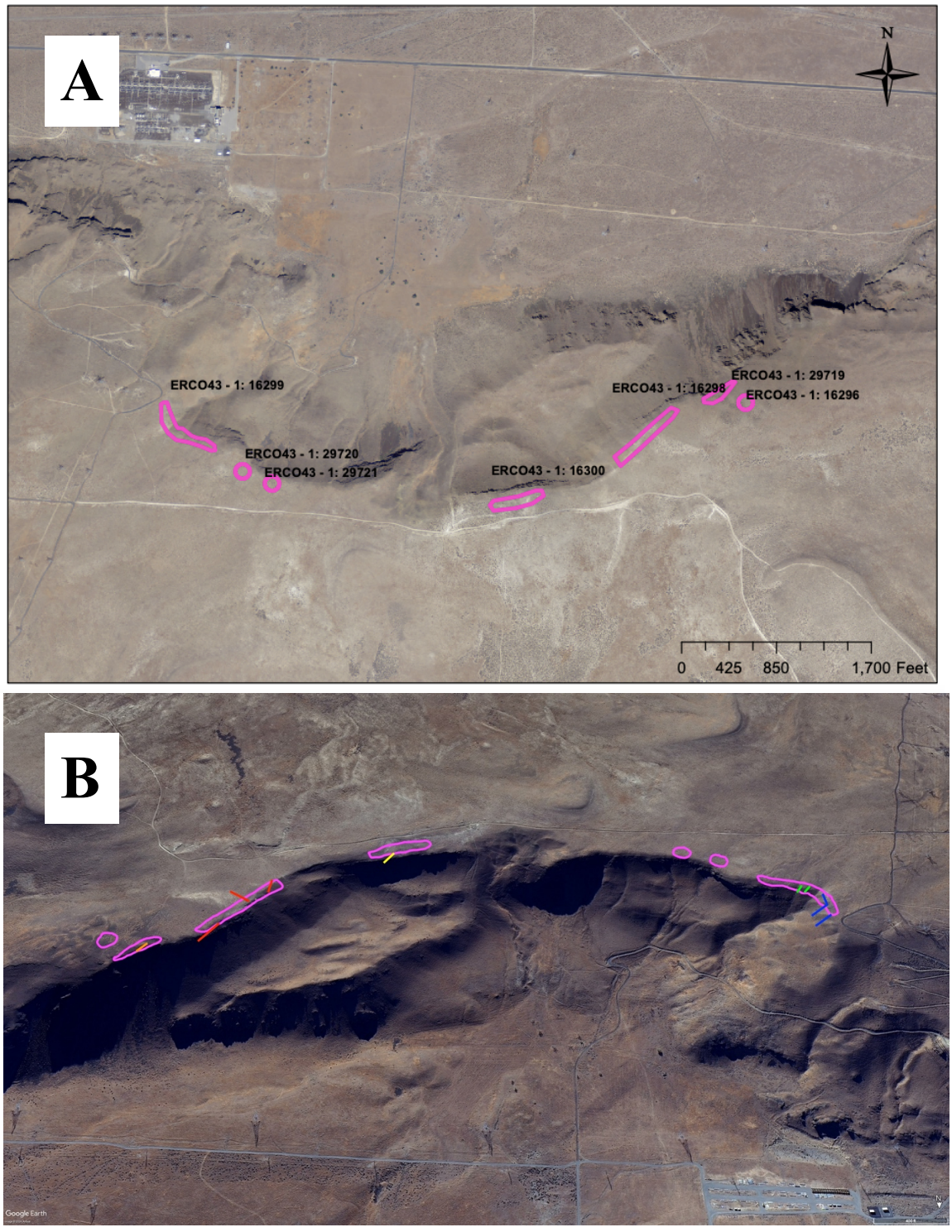


Figure 1.3 Map of Data Collection Location in Relationship to WNHP records of the *E. codium* population
Maps depict WNHP records of the single *E. codium* population on the edge of Umtanum Ridge (WA-DNR unpublished). Top map shows subpopulation polygons with WNHP ID labels looking northward from the top of the ridge towards the Columbia River (Courtesy of Rare Care Program UWBG) (A). Bottom map shows WNHP subpopulation polygons with sampling transects used in this study looking southward from the Columbia River towards the top of Umtanum Ridge (B). Different subpopulations ID used in this study are indicated by transect color: subpopulation I = red, subpopulation II = orange, subpopulation III = yellow, subpopulation IV = green, subpopulation V = blue.

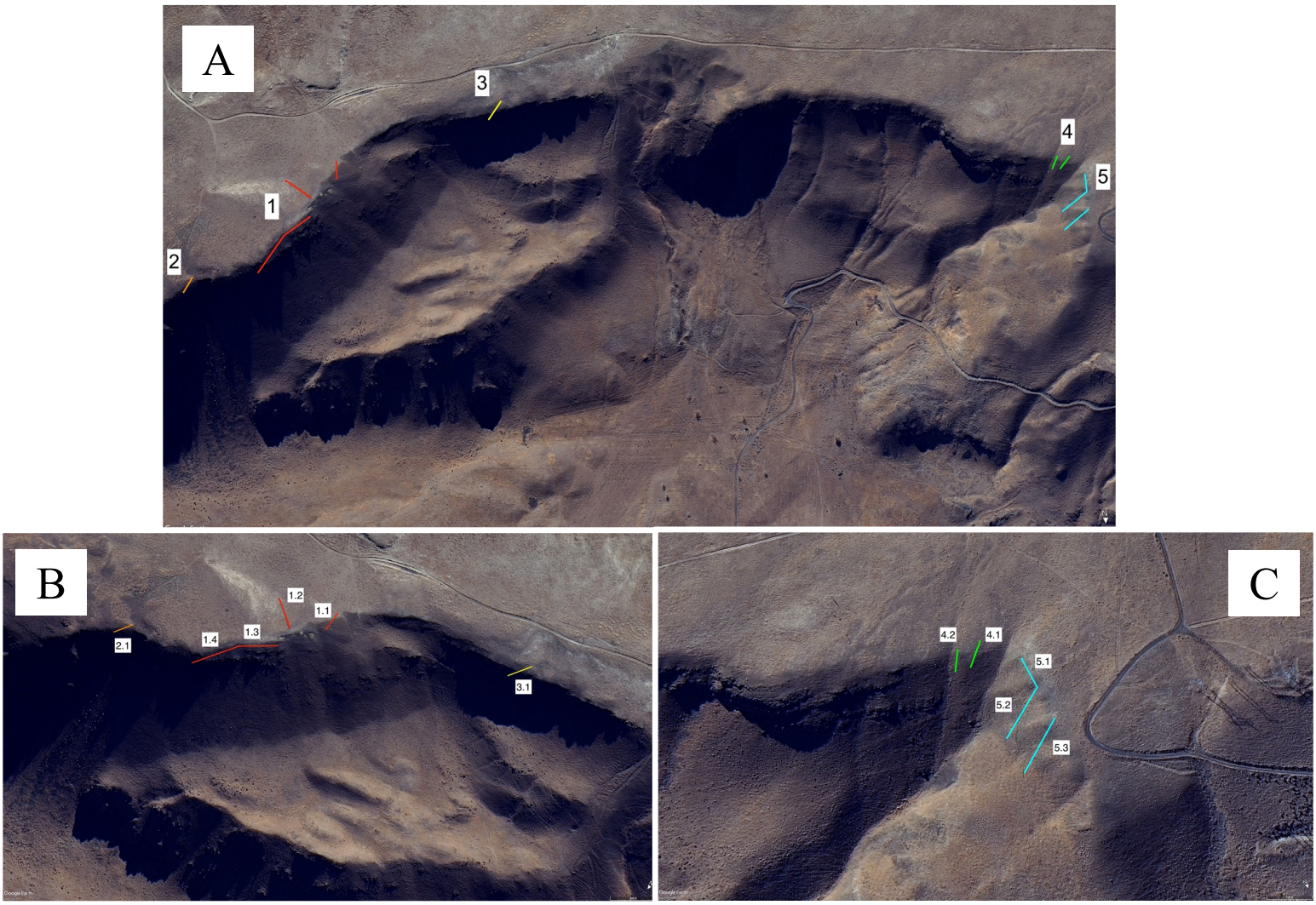


Figure 1.4 Map of *E. codium* Subpopulation and Sampling Transects
Map of *E. codium* population looking southward from the Columbia River. Subpopulations are labeled (1-5) and coded by color: subpopulation I = red, subpopulation II = orange, subpopulation III = yellow, subpopulation IV = green, subpopulation V = blue (A). Eastern side of the population includes the location of the four sampling transects in subpopulation I and their relationships to areas of subpopulations I and III sampled in this study (B). The western side of the population includes the location of the two sampling transects in subpopulation IV and three transects in subpopulation V (C).

Study Design

All data were collected between June 15-16th 2023. Eleven temporary transects between 12 and 75 meters long were established within the five subpopulations (Fig 1.4 A-C) . At subpopulations I, II and V, random sampling occurred along each transect at a consistent number of meters, capturing both plots where *E. codium* was present and absent. Transects were laid only

within the densest clusters of plants to minimize sampling in areas between clusters where plants did not occur. At subpopulation III transects were laid intentionally to maximize the number plots that contained *E. codium* plants, and plots were skipped that did not contain plants. Due to limited time and access to the sites, not all of the plants in subpopulations II and III were sampled and thus these subpopulations likely contain additional variation not captured by this study. Transects were laid either perpendicular to parallel to the slope to best follow the shape of the population and the distribution of plants. Data were collected from $1m^2$ plots oriented alternating east and west or north and south of the transect line to ensure data were not biased to either upslope or downslope of the transect in an effort to minimize any potential bias caused by elevational or ecological gradients that may exist at the site, as exploring this gradient was not the aim of this study.



Subpopulation	Transect	Length (m)	Interval (m)	No. Plots	Total
1	1.1	26	4	8	44
	1.2	50	5	10	
	1.3	55	5	11	
	1.4	75	5	15	
2	2.1	12	2	6	6
3	3.1	20	2	8	8
4	4.1	20	2	9	13
	4.2	10	1-2	4	
5	5.1	30	3	10	27
	5.2	36	3	12	
	5.3	15	3	5	

Figure 1.5 Design of Data Collection Method and Sample Size by Subpopulation and Transect
Image of $1m^2$ plot layout at various spacings along transects of various lengths (top). Table with study subpopulations, number of transects per subpopulation, transect lengths, plot intervals, numbers of plots per transect and subpopulation (bottom).

Data Collection

In each $1m^2$ plot, information on site characteristics, soil surface characteristics, soil hydrology, and vegetation community were collected.

Site Characteristics

Site characteristics included spatial location (GPS point), aspect, landform, slope position, hillslope position, slope shape, slope complexity, slope rise (cm), slope run (cm), and slope angle (degree). GPS coordinates of each plot center was recorded using the Google Maps application on an iphone 6s. Aspect was classified using cardinal directions (north (N), northeast (NE), east (E), southeast (SE), south (S), southwest (SW), west (W), northwest (NW)) using the compass app on an iphone 6s.

Slope was determined using a 120cm level. Slope rise and run was determined by measuring the height from the bottom of the slope to a point level with the top of the slope either vertically across the 1m2 plot (100 cm) or diagonally across the plot (120 cm) depending on slope direction. Slope angle was determined by laying the level across the center of the plot in the direction of the slope and recording the angle.

Landform, slope position, and hillslope position were determined through qualitative visual assessment in the field and assessment of location and site topography via Google Earth after data collection (Appendix Z). Slope shape and complexity were determined through visual qualitative assessment of the plots microtopography.

Assessments of slope rise over run, landform, hillslope, slope shape, and slope complexity were made in accordance with methods outline in the *Field Book for Describing and Sampling Soils* (Version 3.0) (Soil Survey Staff 2012) (Appendix Z).

Soil Characteristics

Due to ongoing negotiations between The Department of Defense and The Confederate Tribes and Bands of the Yakima Nation, no data collection that required disturbance or removal of soil was conducted. Soil surface characteristics that were measured included soil surface composition (SSC), soil surface rock classification (SSRFCL), soil surface rock fragment composition (SSRFC) and surface soil texture.

Soil surface composition (SSC) was assessed by estimating the cover class of each substrate (rock, bare ground, litter, moss and lichen), using Daubenmire cover classes (standard procedure, see "vegetation characteristics" for more information).

Total soil surface rock fragment classification (SSRFCL) was given a classification value based on the "Surface Fragment Class" methods in the *Field Book for Describing and Sampling Soils* (Version 3.0). Total rock fragment cover was ordinally assessed based on five classes (1 = 0.01 - <0.1%, 2 = 0.1 - <3%, 3 = 3 - <15%, 4= 15 - <50%, 5 = ≥ 50%). Although this variable was initially measured as soil characteristic to compliment SSRFC, it ultimately was considered as a site characteristic denoting the general rockiness of an area and not as a soil characteristic indicative of fine scale soil conditions.

Soil surface rock fragment composition (SSRFC) was composed of "rock and other fragment size classes for spherical-shape or cubelike fragments" (boulder = >600mm diam, stones = 250-600mm, cobble = 75-250mm diam, coarse gravel = 20-75mm diam, medium gravel = 5-20 mm diam, fine gravel = 2-5mm diam, very fine gravel = <2mm diam). Rock fragment size classes are based on methods in the *Field Book for Describing and Sampling Soils* (Version 3.0). Daubenmire cover classes were used to assess the percentage of each rock fragment component.

Soil surface texture was determined through a qualitative in-field hand texturing method (Thein 1979).

Measured soil hydrology characteristics include hydraulic conductivity based on soil water infiltration rate. Soil water infiltration rate as determined using a Mini Disk Infiltrometer (Meter) to measuring the volume (mL) of water infiltrating through the soil every 30 seconds for 330-390 seconds. Hydraulic conductivity was calculated from water infiltration rate in accordance with protocols outlines by meter utilizing R script developed by Jon Bakker (Meter 2020-2021, (Meter 2020-2021, Appendix AB). For plots where recording continuous infiltration over six minutes required stopping the run to refill the minidisk infiltrometer, multiple runs were consolidated into a single continuous six-minute run (0-360 seconds) (Appendix AA).

Vegetation Characteristics

Vegetation characteristics included vegetation composition and cover (VCSC), and Leaf Area Index (LAI).

All vascular plants rooted within the quadrat were identified or, if the plant was unknown, field photos were taken and a specimen collected from outside the plot and preserved for laboratory identification. Percentage cover class (1 = < 1%, 2= 1-5%, 3= 5-15%, 4= 15-25%, 5= 25-50%,6= 50-75%,7= >75%) was determined for foliar or aerial cover of each vascular plant species within the quadrat. Cover classes were based on classes originally proposed by Daubenmire (1959) and commonly used in vegetation sampling. This is especially useful in dryland systems as more detail is given at low cover values, because the majority of species had cover in these values.

PAR was measured within three locations in each plot using an AccuPAR LP-80 Ceptometer. Measurements were only taken in subpopulations I and V on June 15th and 16th

respectively between 10am and 3pm. Three PAR measurements were taken above the understory plant canopy and at ground level and Leaf Area Index (LAI) was calculated by the ceptometer providing values representing the density of foliage cover within the $1m^2$ plot.

Statistical Methods

Entry, review, organization, of all study data, and the correction of mini disk infiltrometer raw data, were completed using Excel (Microsoft Office). All data analysis, calculations made from raw data values, corrections and manipulations including the filling of missing values, were completed using R version 4.4.0 (R Core Team 2024).

Packages used for all analyses include “dplyr” version 1.1.4 and “tidyverse” version 2.0.0.
Packages used for data preparation included “broom” version 1.0.5, and “here” version 1.0.1.
Packages used for statistical analyses include “corrplot” version 0.92, “dendextend” version 1.17.1, “indicspecies” version 1.7.14, “labdsv” version 2.1.0, “stats” version 4.4.0, and “vegan” version 2.6.4.
Packages used for creating tables include “gt” version 0.10.1, “gtExtras” version 0.5.0, “ggdist” version 3.3.2, , “modeest” version 2.4.0 and “tibble” version 3.2.1.
Packages used for graphing data include “ggplot2” version 3.5.1, “ggdist” version 3.3.2, gghalves “version” 0.1.4, “ggpubr” version 0.6.0, “multcompView” version 0.1.10, “systemfonts” version 1.0.6, “ unpivotr” version 0.6.3, “reshape” version 0.8.9, and “wesanderson” version 0.3.7.

Data Preparation

Site Characteristics

Aspect (N, NE, E, SE, S, SW, W, NW) was recorded as a categorical factor and converted into a continuous numeric variable by replacing each factor with its associated aspect degree (0º, 45º, 90º, 135º, 180º, 225º, 270º, 315º). Aspect degree was utilized to compute heat load index. Missing continuous values were filled by taking the average value from the transect in which the plot occurred.

Heat load index was calculated using the heatload() function developed by Zeleny and Lin 2021 based on equations published by McCune and Keon 2002 and revised by McCune 2007. Equation 2 was used as recorded slope angle values are below 60º (maximum slope recorded was 30º).

Missing values were filled for slope aspect (n= 3) and slope (n=1). Missing categorical values were filled by taking the mode of the plot's transect and was filled for aspect (n=3).

Because the entire *E. codium* population and all plots assessed in this study had the same recorded landform (mountain top), categorical factors for hill slope position (summit, shoulder, backslope, footslope, toeslope) and slope position (upper third, middle third, lower third) for each plot were combined into the category "landscape position" across six levels of landform-hillslope positions:

Summit-Upper Third (SU_UT)

Summit-Lower Third (SU_LT)

Shoulder-Upper Third (SH_UT)

Shoulder-Middle Third (SH_MT)

Shoulder-Lower Third (SH_LT)

Backslope-Upper Third (BS_UT)

Soil Characteristics

For plots where recording continuous infiltration over six minutes required stopping the run to refill the minidisk infiltrometer, multiple runs were consolidated into a single continuous six-minute run (0-360 seconds) (Appendix AA).

Vegetation Characteristics

Recorded cover classes (0-7) where converted to percentage cover values by using the mid-point of each cover class (1= 0.5%, 2= 3%, 3= 10%, 4= 20%, 5 = 37.5%, 6 = 62.5%, 7 = 87.5% for VCSC, SSC and SSRFC; 0= 0%, 1= 0.05%, 2= 1.55%, 3 =9%. 4 = 32.5%, 5 = 75% for SSRFCL).

Total cover of all species in each plot (total cover) and number of total species in each plot (species richness) was calculated using VCSC data. However, as *E. codium* cover is included in the calculations of total cover for each plot, this relationship may be somewhat circular and may not constitute a truly strong or significant relationship. To better distinguish the relationship between *E. codium* and competitive total cover of other species, from the total covert of the vegetation community that *E. codium* is a part of, an adjusted total cover values (hereafter referred to as "total cover adjusted") was calculated for only the first study objective, to compare *E. codium* occurrence and abundance.

Vegetation Functional Group Cover and Composition

Data collected on vegetation composition were used to calculate the total cover of each vegetation functional group within each $1m^2$. Vegetation composition data from the Native Site were subset by only plots where *E. codium* is present (n= 72). Functional groups were created

by combining life-from and longevity information associated with each recorded species obtained from the United States Department of Agriculture Plant Species Database. Life-form refers to the plant species classification (shrub, subshrub, forb, graminoid) and longevity refers to the plant's life span (annual, perennial, and biennial). Biennial species were combined with annual species under the longevity classification "annual". Only perennial species of shrubs and subshrubs were recorded, and hereafter will be referred to only by their life-form classification "shrub" or "subshrub" as their perennial nature is assumed. In total six vegetation functional groups were used: shrub, subshrub, perennial forb, annual forb, perennial graminoid and annual graminoid.

Statistical Tests

A Euclidean distance metric was used for all data except vegetation species composition. A Euclidean distance metric was used because the data is continuous and symmetric (Bakker 2024). A Bray-Curtis distance metric was used for vegetation species composition data (VCSC) as the data is continuous and asymmetric. Distances matrices were created to analyze sets of multivariate responses of soil surface composition, soil surface rock fragment composition, and vegetation species composition data. All multivariate response data were relativized by row total before conversion to a distance matrix to better represent how the totals are distributed among compositional components.

Cluster Analysis

Hierarchical cluster analysis (stats, R Core Team 2024) was used to identify groups and classify plots based on similarities in vegetation functional group[13] composition. This approach

[13] For information on the preparation of vegetation functional group cover data from species composition data see data preparation methods in Chapter two.

utilizes an iterative agglomerative process to consolidate plots into "clusters" based on their dissimilarity (Singh et al 2011, Bakker 2024). At the start of the process each plot in the distance matrix is considered a separate cluster, and *n* sample units are then agglomerated into clusters in *n*-1 steps. At each step two plots or previously fused clusters of plots that are the most similar are fused, until one cluster contains all plots, forming a dendrogram. Hierarchical cluster analysis was chosen because it does not require explicit or implicit a priori assumptions about cluster shapes or the total number of clusters, and has been used to explore patterns linked to spatial variation (Plotkin et al 2002, Bakker 2024). Average linkage, single linkage, complete linkage, and Ward's linkage were compared, and Ward's linkage method was selected because it provided the minimum number of distinct groupings and minimized chaining (Bakker 2024).

Ward's linkage method, known as "the minimum variance method", is aimed at 'finding compact, spherical clusters' by minimizing the error sum of squares (Ward 1963, McCune et al 2000, Bakker 2024). This is achieved by continuing to minimize the sum of squared distances, while, with every agglomeration that occurs, the sum of the distance from each plot to its cluster increases from zero (i.e. when each plot is its own cluster). Optimal number of cluster analysis groups was visualized and assessed by plotting dendrogram fusion distances against the number of clusters in a scree plot (Fig K-1). Differences in *E. codium* abundance (% cover) and subpopulation and transect identity, were explored at a higher level of dissimilarity (six groups a-f) and lower level of dissimilarity (three groups 1-3).

Permutational Multivariate Analysis of Variance (PERMANOVA) and Post-Hoc Tests (Tukey Test and Pairwise ADONIS)

Permutational multivariate analysis of variance (PERMANOVA) (vegan "Community Ecology Package", Oksanen et al 2022) was used to address all analysis objectives.

PERMANOVA is a non-parametric method of multivariate analysis of variance based on pairwise distances (Anderson 2001). PERMANOVA is utilized to determine significant differences between categorical groupings of sample units and/or the range and distribution of continuous variables. Post hoc pairwise comparisons of significant differences between groups were conducted using a Tukey test (stats, R Core Team 2024) for univariate responses, and pairwise ADONIS for sets of multivariate responses (Bakker 2024). Results of Tukey tests are included in associated bar graphs and raincloud plots, while results of pairwise ADONIS is visualized with heat maps in which color is linked to statistical strength of differences between groups (p-value).

To address the first objective and explore the relationship of habitat characteristics to *E. codium* occurrence, plots were grouped based on *E. codium* occurrence i.e. "present" (n= 64) or "absent" (n= 26). Subpopulation III (n= 8) was omitted from the analysis as no data were recorded where *E. codium* was "absent". *E. codium* occurrence was run as the explanatory variable against categorical and continuous variables characterizing site characteristics (landscape position (n=90), aspect (n=90), slope shape (n=90), slope complexity (n= 90), heat load index (n=90), slope (n=90), slope angle (n=90), SSRFCL (n=90)), soil characteristics (hydraulic conductivity (n=74), SSC (n=90), SSRFC (n=90), soil texture = (n=90)) and vegetation characteristics (LAI (n=71), total cover (n=90), species richness (n=90), VCSC (n=90), and for each vegetation functional group's cover (shrub, forb, perennial graminoid, annual graminoid) (n= 90).

To address the first objective and explore the relationship of habitat characteristics to *E. codium* abundance, the data were subset to remove where *E. codium* is "absent" (n= 26). *E. codium* cover was run as the as the explanatory variable against categorical and continuous

variables characterizing site characteristics (landscape position (n=72), aspect (n=72), slope shape (n=72), slope complexity (n= 72), heat load index (n=72), slope (n=72), slope angle (n=72), SSRFCL (n=72)), soil characteristics (hydraulic conductivity (n=61), SSC (n=72), SSRFC (n=72), soil texture (n= 72)) and vegetation characteristics (LAI (n=71), total cover (n=72), species richness (n=72), and VCSC (n=72)).

To address the second objective and explore spatial relationships of site variables, data were only subset for habitat variables determined significantly different where *E. codium* is present from where it is absent (soil texture and VCSC ($p = \leq 0.05$)), otherwise the full dataset was used. PERMANOVA was used to test for differences between subpopulations (five levels: 1-5) and transects (eleven levels: 1.1-1.4, 2.1, 3,1, 4.1, 4.2, 5.1-5.3) as the explanatory variables against categorical and continuous variables characterizing site characteristics (landscape position (n=98), aspect (n=98), slope shape (n=98), slope complexity (n= 98), heat load index (n=98), slope (n=98), slope angle (n=98), SSRFCL (n=98)), soil characteristics (hydraulic conductivity (n=80), SSC (n=98), SSRFC (n=98), soil texture (n= 72)) and vegetation characteristics (total cover (n=72), species richness (n=72), VCSC (n=72), LAI (n=71)). Subpopulation and transect were analyzed together in a linear model and type I sequential sum of squares was applied to the distribution of variance explained by subpopulation and transect, to explore how much variation was explained by transect level differences only after variation related to subpopulation level difference was accounted for.

To address the third objective and explore relationships of cluster analysis groups to *E. codium* abundance (% cover) and spatial variation, PERMANOVA was used to test both six cluster groups (a-f) and three cluster groups (1-3) as the explanatory variables against *E. codium* cover, subpopulation (n= 5) and transect (n= 11) identity. The relationship between vegetation

functional groups (perennial shrub, perennial sub-shrub, perennial/annual forb, annual graminoid, perennial graminoid) and either cluster analysis groups or *E. codium* abundance, was explored by calculating the total cover of each functional group within each plot and testing each functional group as a univariate responses against cluster analysis groups or *E. codium* cover as the explanatory variable. To better understand differences in vegetation composition, cover for the most abundant species (>10% occurrence across the entire subpopulation) was tested as a response variable against subpopulation as the explanatory variable.

To better understand habitat dynamics and relationships between measured habitat variables at the native site, a subset of habitat variables was run as explanatory variables against a subset of other habitat variables as the response variables. This included:

- Soil texture was run as a response variable against subpopulation, landscape position, and the interaction between subpopulation and landscape position as the explanatory variables. Type I sequential sum of squares was applied to the distribution of variance explained by subpopulation and landscape position to explore how much variation was explained by landscape position level differences only after variation related to subpopulation level difference was accounted for.
- Soil surface rock fragment composition was run as the response variables against soil surface texture as the explanatory variable.
- Hydraulic conductivity was run as the response variable against slope shape as the explanatory variable.
- Vegetation species composition was run as the response variable against heat load index as the explanatory variable.

Data Visualization: Bar Graphs, Raincloud Plots, Scatter Plots and NMDS Ordinations

Differences between *E. codium* occurrence (present vs absent) and spatial groupings (5 subpopulations/ 11 sampling transects) in mean and variation of continuous variables were visualized with raincloud plots using raw data values. Raw values of vegetation functional group cover were calculated for *E. codium* occurrence groups and graphed using raincloud plots. Differences in categorical site and soil variables were visualized using bar graphs of raw data values. Continuous univariate responses with significant relationships to *E. codium* abundance were visualized using scatter plots. Relationships of cluster analysis groupings (six groups (a-f) and three groups (1-3)) to *E. codium* cover and subpopulation/transect identity were visualized using raincloud plots and bar graphs respectively.

Ordinations of multi-variate response matrices were created using non-metric multidimensional scaling (NMDS) (vegan "Community Ecology Package", Oksanen et al 2022). NMDS ordinations are used to visualize patterns in both groupings of plots by *E. codium* occurrence (presence vs absence), and abundance (% cover). Runs were iterative with the best solution (least stress) from each run used as the starting configuration for the next run. Maximum number of iterations was set to 300, minimum number of runs was set to 20, and maximum number of runs was set to 40 based on recommendations by McCune & Grace 2002 (Bakker 2024). Two or three dimensionalities (k= 2 or 3) were assessed in independent NMDS runs. Dimensions were evaluated based on an assessment of stress as a function of dimensionality (k=2 or 3) and Shepard plots were used to visually assess the fit of the ordination point cloud to the original dissimilarities in the distance matrix.

Data Summary Tables

Summary tables of site, soil and vegetation characteristics were created for all *E. codium* occurrence (present vs absent) and spatial groupings (5 subpopulations/ 11 sampling transects) explored in this study. For each group, mean, range (minimum/maximum), and standard deviation were calculated for continuous univariate habitat characteristics, and mode determined for categorical[14] univariate site and soil characteristics. Mean, range and standard deviation of the compositional components of soil surface composition (rock, bareground, litter biocrust) and soil surface rock fragment composition (bedrock, boulder, stone, cobble, coarse gravel, medium gravel, fine gravel, very fine gravel) were determined. To better understand spatial differences in species composition, the occurrence (total number of plots recorded) for all vegetation species growing where *E. codium* was present was calculated for the entire site, and for each subpopulation and transect. Differences between both six (a-f) and three (1-3) cluster analysis groupings in mean, range, and standard deviation of each vegetation functional group's cover were determined.

Indicator Species Analysis (ISA) and TITAN

Indicator species analysis (ISA) (indicspecies, De Cáceres and Legendre 2009, De Cáceres et al 2012) was used as a follow up test to assess which vegetation species, soil surface, and rock fragment types were associated with significant relationships with all *E. codium* occurrence (present vs absent) and spatial (5 subpopulations/ 11 sampling transects) groupings explored in this study (De Cáceres et al 2012, Bakker 2024). Classical ISA was used to distinguish differences between individual groups, while multiple groups ISA was used to assess

[14] Mode of categorical soil variable soil texture is reported in Appendix summary tables with other categorical site characteristics.

associations between groupings (Dufrêne and Legendre 1997, De Cáceres and Legendre 2009, De Cáceres et al 2010). Assessing both indicators of individual groups and indicators of multiple groups allows for a more wholistic understanding of the strength of an indictor to an associated group, as well as to what extent these associations are shared between groups. For species with significant indicator values ($p \leq 0.05$), the relative abundance (RA), relative frequency (RF), and indicator values ($IV = 100 \times (RA * RF)^2$) were calculated. While this technique was originally developed to work with vegetation composition data, it can be applied to any type of multivariate compositional data (Bakker 2024).

TITAN (TITAN2, Baker and Kahle 2013) is a permutation-based analysis used in this study to explore how compositional data changed in distribution (cover, abundance, and frequency) along gradients of continuous site variables (Baker and King 2010, 2013). By utilizing a combination of change-point analysis (univariate regression) (Qian et al 2003) and ISA (Dufrêne and Legendre 1997), TITAN has been traditionally used to detect thresholds of community taxa across an environmental gradient (Martin and Hammond et al 2016, Farwell et al 2020). However, like ISA, this technique can be applied to any type of continuous and compositional data (Bakker 2024).

Results

This research first attempts to identify and summarize *E. codium's* habitat characteristics by assessing how site, soil and vegetation characteristics relate to the presence and abundance of *E. codium*. It investigates if these characteristics differ where *E. codium* is currently present, and in areas where it is most abundant. This research also assesses to what extent *E. codium's* habitat characteristics differ spatially. Differences in site, soil and vegetation characteristics between the single native population's five subpopulations (inter- subpopulation variation) and within three of the subpopulations (I, IV, and V) (intra- subpopulation variation) are assessed. Finally, this research characterizes the vegetation habitat differences that distinguish areas of high, medium and low *E. codium* abundance.

Part I: Relationship of Site, Soil, and Vegetation Habitat Characteristics to *E. codium* Occurrence and Abundance

Site Characteristics

Most site characteristics did not vary by *E. codium* occurrence, with only mode of slope aspect differing between where *E. codium* was present (east) and absent (west) (Table B-1). PERMANOVA analysis indicated there are no significant differences in any site characteristics between where *E. codium* is present and absent (Table 1.1.1), indicating the range of measured site characteristics reflect *E. codium's* "habitat" (Fig 1.1.1, Fig 1.1.2 and Table B-1). Where *E. codium* occurs, there is a significant relationship between heat load index (HLI) and *E. codium* abundance ($p = 0.04$) (Table 1.1.1), with the highest cover (37.5%) occurring in areas where the heat load index is around 0.8 (Fig 1.1.3).

Table 1.1.1 PERMANOVA of Site Characteristics Relationship to *E. codium* Occurrence and Abundance
Significant relationships are indicated by asterisks (* = significant, ** = strongly significant, ***= very strongly significant) There is a significant relationship between heat load index (HLI) and *E. codium* abundance (p = 0.04). The lack of any other significant differences in any site characteristics between where *E. codium* is present and absent indicates the range of measured site characteristics reflect *E. codium's* general habitat requirements .

Occurance and Abundance of *E. codium*

Site Characteristics	Df	R^2	F	Pr(>F)
***E. codium* Present/Absent** (n=90)				
Heat Load	1	0.0130	1.16	0.285
Slope	1	0.0047	0.41	0.507
Slope Angle	1	0.0040	0.35	0.584
Aspect Degree	1	0.0128	1.14	0.298
Total Rock Fragment Class	1	0.0001	0.01	0.910
Landscape Position	1	0.0059	0.52	0.510
Slope Shape	1	0.0024	0.21	0.647
Slope Complexity	1	0.0039	0.35	0.618
***E. codium* Abundance** (n=72)				
Heat Load	1	0.0599	4.46	0.043 *
Slope	1	0.0225	1.61	0.216
Slope Angle	1	0.0086	0.61	0.424
Aspect Degree	1	0.0328	2.37	0.123
Total Rock Fragment Class	1	0.0136	0.97	0.325
Landscape Position	1	0.0460	3.37	0.077
Slope Shape	1	0.0031	0.22	0.647
Slope Complexity	1	0.0188	1.34	0.276

Soil Characteristics

Soil texture weakly significantly differed (p = 0.048) in relationships to *E. codium* occurrence (Table 1.1.2). Differences in soil texture were reflected in the difference in mode soil texture classification between where *E. codium* is present (sandy loam) and absent (loamy sand) (Table B-2). The significant differences determined in surface soil texture are due to the presence of a range of loam soils where *E. codium* is present and sandy clay loam soil where it is absent

(Figure 1.1.4-A). Areas where *E. codium* is present are comprised almost equally between sandy loam and loamy sand, with a small proportion of only loam soil (<5%).

ISA results identified the boulder component of surface rock fragment composition as characterizing areas where *E. codium* is absent (p = 0.03, IVij = 10.5), indicating this species does not grow well in areas where rock fragment size exceeds 60 cm (~2ft). Although soil

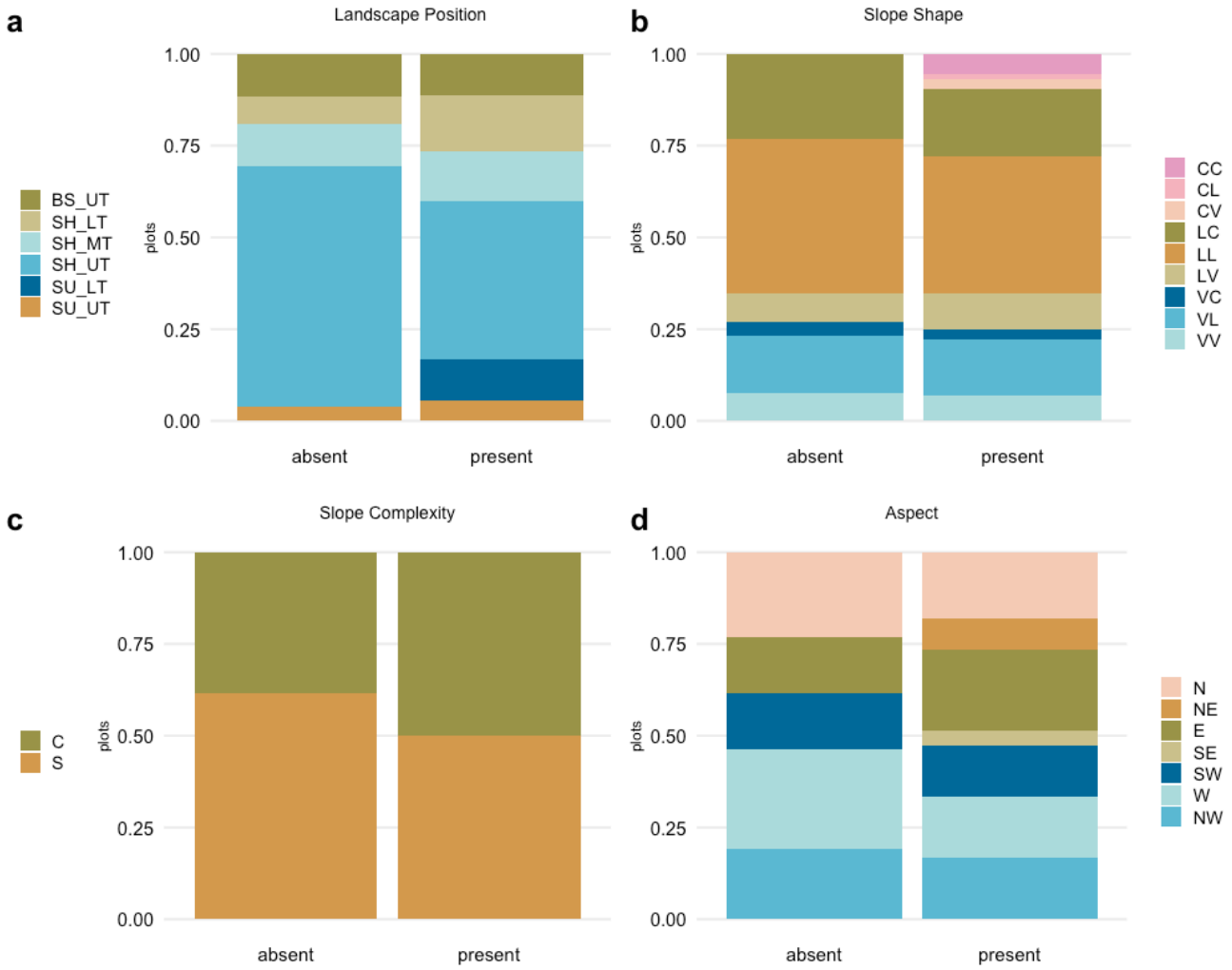


Figure 1.1.1 Bar graphs of Site Characteristics by *E. codium* Occurrence
Differences in categorical site variable between where *E. codium* is present and absent (n=90) including landscape position (A) (BS_UT = backslope- upper third, SH_LT= shoulder-lower third, SH_MT = shoulder-middle third, SH_UT= shoulder- upper third, SU_LT = summit-lower third, SU_UT = summit-lower third), slope shape (B) (CC= concave-concave, CL= concave-linear, CV = concave-convex, LC= linear-concave, LL= linear-linear, LV= linear-convex, VC= convex-concave, VL= convex-linear, VV= convex-convex, slope complexity (C) (C= complex, S= simple), and aspect (D) (N = north, NE = northeast, E= east, SE= southeast, SW= southwest, W= west, NW= northwest). Range of categorical habitat variables characterizes *E. codium* habitat. No significant differences were determined in any categorical site variables (p = >0.05).

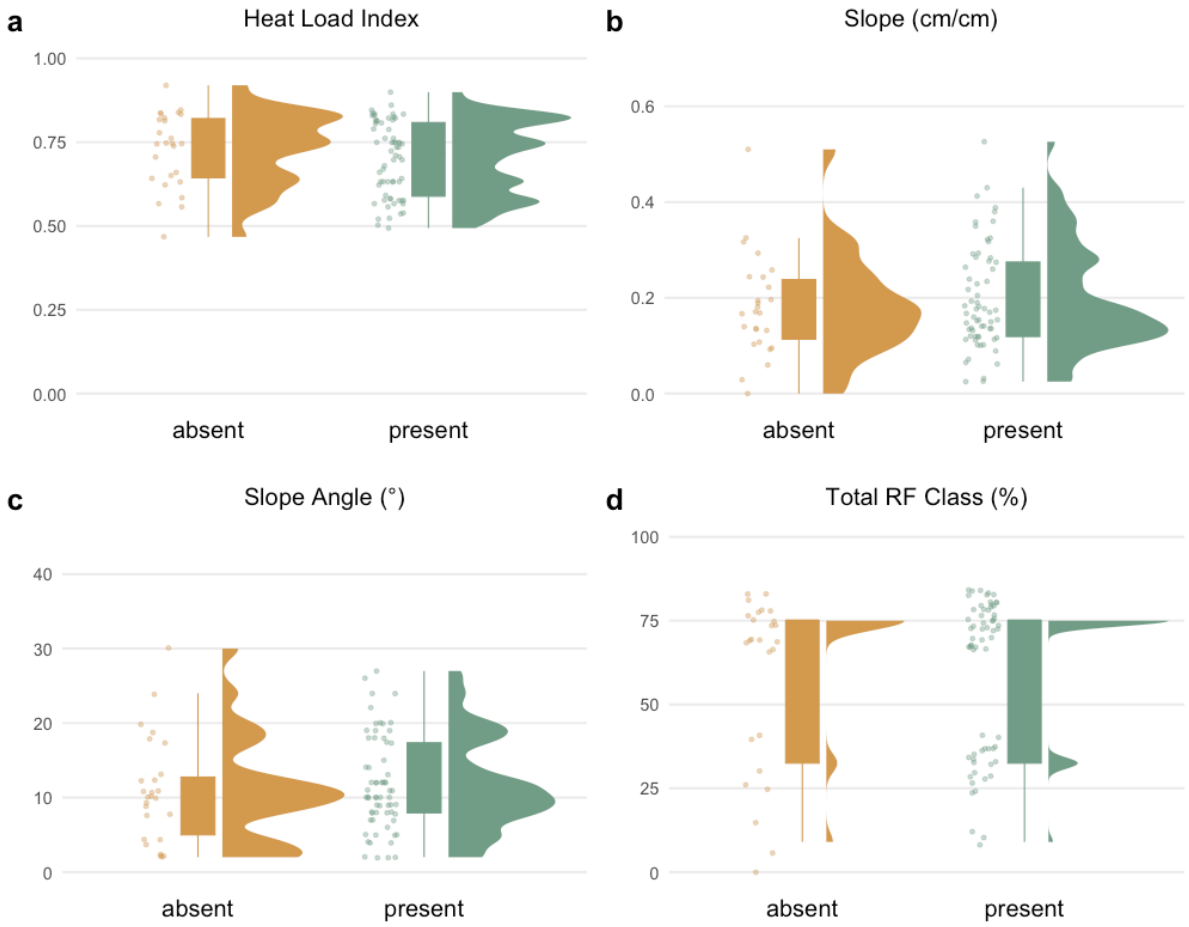


Figure 1.1.2 Raincloud Plots of Site Characteristics by *E. codium* Occurrence
Differences in continuous site variables between where *E. codium* is present and absent (n=90) including heat load index (A), slope (cm/cm) (B), slope angle (°) (C), and total percentage of rock fragment cover classification (D). Range of continuous habitat variables characterizes *E. codium* habitat. No significant differences were determined between continuous site variables (p = >0.05).

surface composition was not significantly different, there is lower maximum biocrust component where *E. codium* is absent (3%), while biocrust is present at a maximum of 20% where *E. codium* is present, indicating *E. codium* can successfully grow in areas where biocrust makes up almost a quarter of surface cover (Table A-2). Biocrust presence and abundance is not characteristic of the majority of *E. codium* habitat, as there is an overall low number of plots with biocrust where *E. codium* occurs (20% of plots) and low average mean cover (1%).

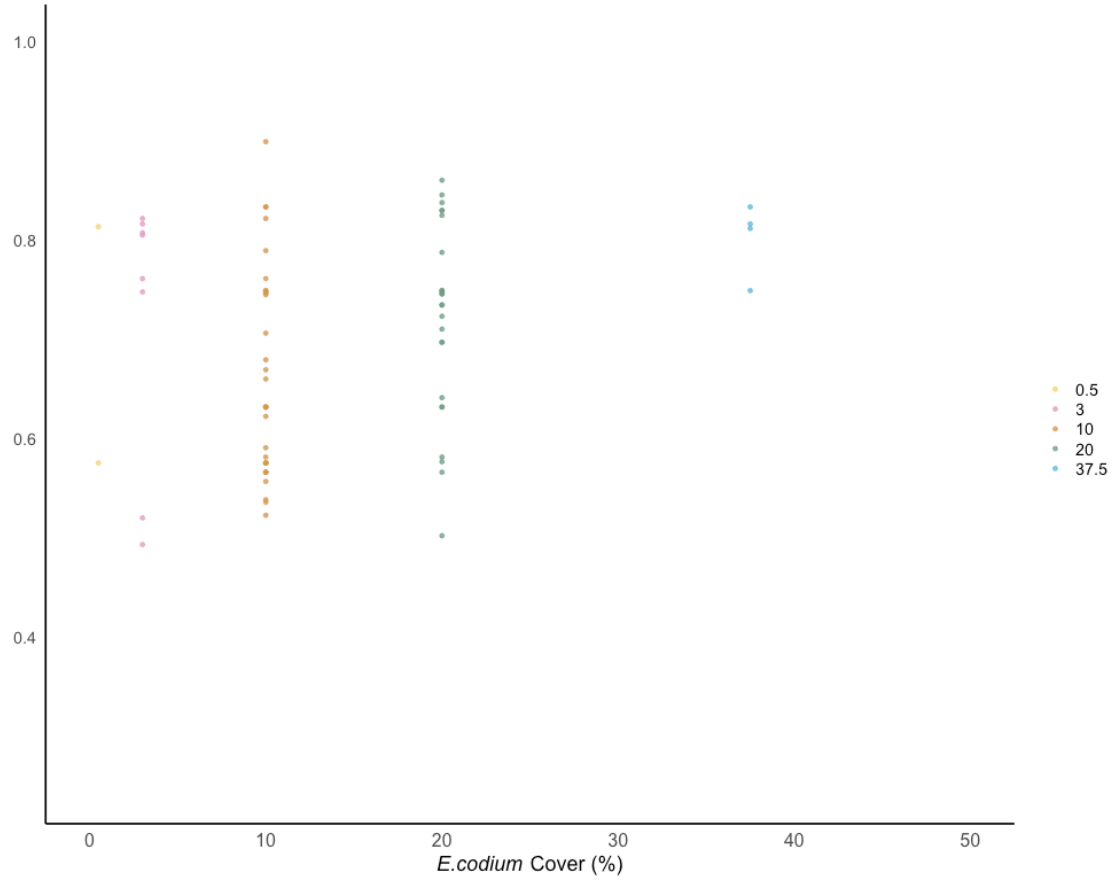


Figure 1.1.3 Scatterplot of Relationship between Heat Load Index and by *E. codium* Abundance
Significant (p = <0.05) relationship of heat load index and *E. codium* cover in areas where it is present (n= 72). Heat load index is > 0.7 for all plots where *E. codium* cover is 37.5%. Medium abundance areas had a range of HLI values from 0.5-0.9. Highest and lowest abundance of *E. codium* are both related to higher HLI values.

Vegetation Characteristics

Neither LAI or species richness were found to have significant relationships with either *E. codium* occurrence or abundance (Table 1.1.3). Although total cover was not found to have a significant relationship to *E. codium* occurrence, it was significantly related to *E. codium* abundance (p = 0.001) (Fig 1.6). Vegetation composition did strongly significantly differ both by *E. codium* occurrence (p = 0.001) and abundance in areas where *E. codium* was present (p = 0.001) (Table 1.1.3 and Fig 1.1.8).

Table 1.1.2 PERMANOVA of Soil Surface Characteristics Relationship to *E. codium* Occurrence and Abundance
Significant relationships are indicated by asterisks (* = significant, ** = strongly significant, ***= very strongly significant). Soil texture weakly significantly differed (p = 0.048) in relationships to *E. codium* occurrence. Differences in soil texture were reflected in the differences in mode soil texture (present: sandy loam, absent: loamy sand) , and is related to the presence of and sandy clay loam soil only where *E. codium* is absent.

Occurance and Abundance of *E. codium*

Soil Property	Soil Characteristic	n	Df	R^2	F	*Pr(>F)*	
***E. codium* Present/Absent**							
Soil Hydrology	Hydraulic Conductivity (K)	71	1	0.0085	0.62	0.448	
Soil Surface	Surface Texture	90	1	0.0483	4.47	0.057	*
Soil Surface	Surface Cover (%)	90	1	0.0018	0.15	0.811	
Soil Surface	Surface Rock Fragment Cover (%)	90	1	0.0048	0.43	0.769	
***E. codium* Abundance**							
Soil Hydrology	Hydraulic Conductivity (K)	61	1	0.0000	0.00	0.974	
Soil Surface	Surface Texture	72	1	0.0225	1.61	0.194	
Soil Surface	Surface Cover (%)	72	1	0.0366	2.66	0.090	
Soil Surface	Surface Rock Fragment Cover (%)	72	1	0.0190	1.35	0.249	

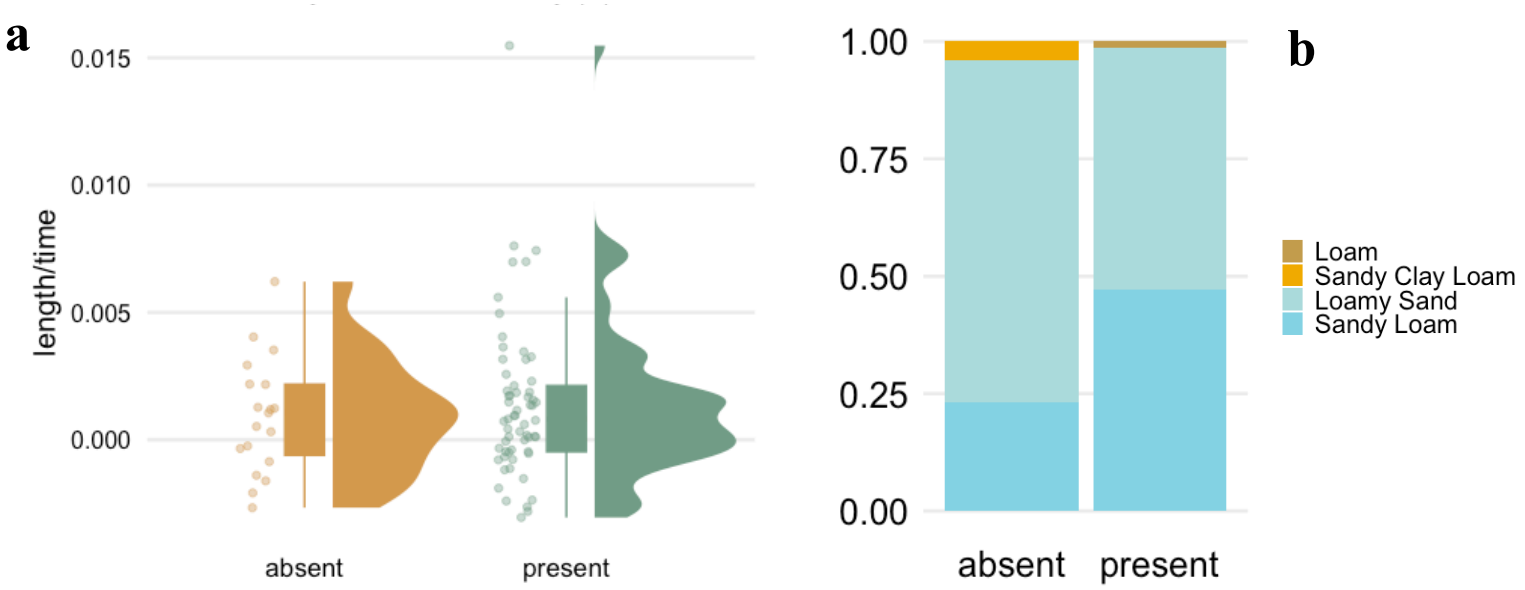


Figure 1.1.4 Raincloud Plot of Hydraulic Conductivity and Bar graph of Soil Surface Texture by *E. codium* Occurrence
Significant (p = 0.05) differences in surface soil texture (n= 90) (a) and similarities in soil hydraulic conductivity (n= 71) (b) between areas where *E. codium* is present and absent. Soil texture weakly significantly differed (p = 0.048) in relationships to *E. codium* occurrence. Differences in soil texture were reflected in the differences in mode soil texture (present: sandy loam, absent: loamy sand) , and is related to the presence of and sandy clay loam soil only where *E. codium* is absent.

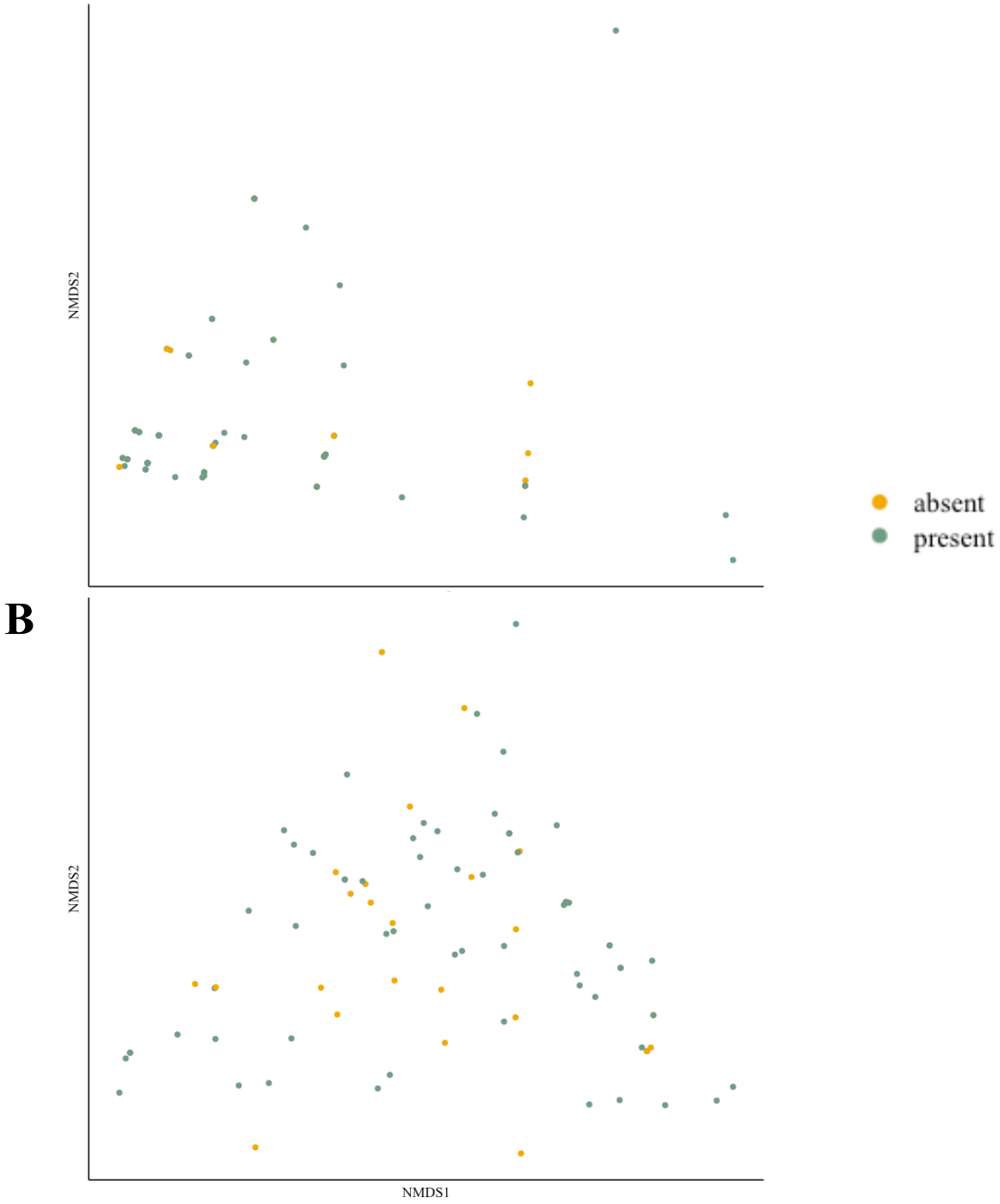


Figure 1.1.5 NMDS Ordination of Soil Surface and Soil Surface Rock Fragment Composition by *E. codium* Occurrence
Non-metric multidimensional scaling (NMDS) ordination of soil surface composition (A) (k = 2 , stress = 0.005) and soil surface rock fragment composition (B) (k = 3 , stress = 0.058). Points are coded by color to correspond to where *E. codium* is present (green) and absent (yellow). Each point represents a $1m^2$ plot. Points closer together are more similar to than those farther apart. Overlap between groups of points indicates the observed range of surface and rock fragment compositions are reflective of *E. codium* habitat.

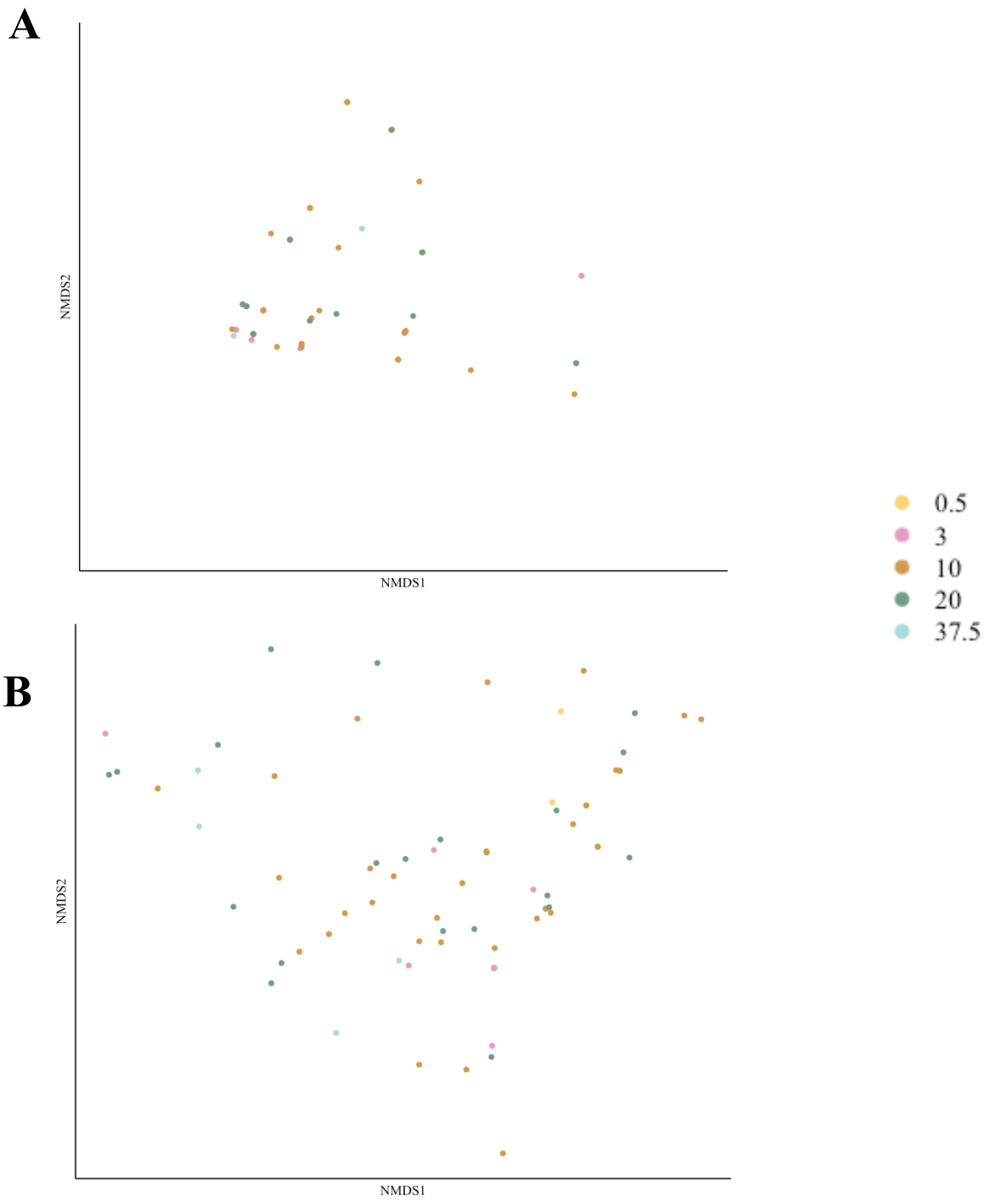


Figure 1.1.6 NMDS Ordination of Soil Surface and Soil Surface Rock Fragment Composition by *E. codium* Abundance
Non-metric multidimensional scaling (NMDS) ordination of soil surface composition (A) (k = 2 , stress = 0.004) and soil surface rock fragment composition (B) (k = 3 , stress = 0.039). Points are coded by color to correspond to *E. codium* cover (%). Each point represents a $1m^2$ plot. Points closer together are more similar to than those farther apart. Overlap between groups of points indicates the *E. codium* is equally abundant across the observed range of surface and rock fragment compositions.

While total cover was determined to significantly differ by *E. codium* abundance ($p = 0.001$), adjusted total cover did not significantly differ ($p > 0.05$) indicating the positive relationship between *E. codium* abundance and total cover is related to the increasing cover of *E. codium* itself (Table 1.1.3, Fig 1.6). Mean total cover was slightly lower in areas where *E. codium* was absent, further indicating *E. codium* is contributing to total cover values. Plots where *E. codium* was present never exceed 75% total cover, and the majority of plots consisted of 10-20% *E. codium* cover with 25-50% total cover. Mean total cover was 33% with a maximum cover of 70.5%, however mean of adjusted total cover indicates the mean cover of other species that are not *E. codium* is lower (~19%) and does not exceed 60.5%.

Table 1.1.3 PERMANOVA of Vegetation Characteristics Relationship to *E. codium* Occurrence and Abundance
Significant relationships are indicated by asterisks (* = significant, ** = strongly significant, ***= very strongly significant). Significant differences were not determined in LAI or species richness, indicating observed range is representative of *E. codium* habitat. Significant relationships between vegetation composition and *E. codium* occurrence and abundance indicated vegetation composition is the only measured habitat characteristic impacting both where *E. codium* grows and its abundance in the areas where it grows. Although a significant relationship was detected between total cover and *E. codium* abundance, the lack of this relationship in adjusted total cover indicates this is a circular relationship based on the inclusion of *E. codium* in vegetation cover totals.

Occurance and Abundance of *E. codium*

Vegetation Characteristics	Df	R^2	F	*Pr(>F)*	
ERCO Present/Absent (n=90)					
Leaf Area Index	1	0.0023	0.16	0.851	
Total Cover (%)	1	0.0217	1.95	0.179	
Total Cover Adjusted (%)	1	0.0332	3.03	0.091	
Species Richness	1	0.0102	0.91	0.405	
Vegetation Composition	1	0.2472	28.89	0.001	***
ERCO Abundance (n=72)					
Leaf Area Index	1	0.0088	0.43	0.444	
Total Cover (%)	1	0.2895	28.52	0.001	***
Total Cover Adjusted (%)	1	0.0001	0.01	0.942	
Species Richness	1	0.0065	0.46	0.512	
Vegetation Composition	1	0.5528	86.54	0.001	***

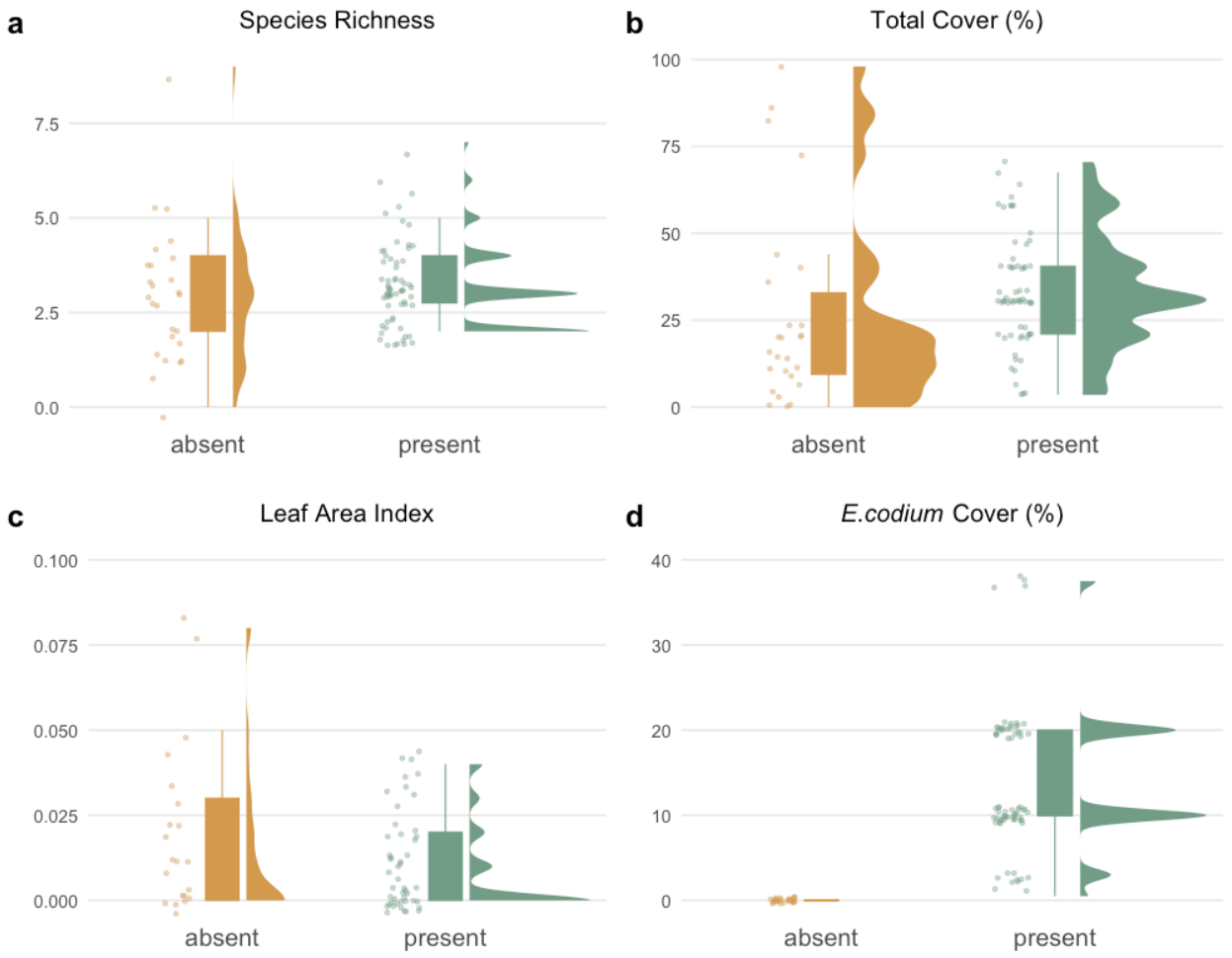


Figure 1.1.7 Raincloud Plots of Vegetation Characteristics by *E. codium* Occurrence
Differences in vegetation characteristics between where *E. codium* is present and absent (n= 90) including species richness (A), total cover (B), leaf area index (C), and *E. codium* cover (D). Significant differences were not determined for any vegetation characteristics except vegetation species composition (p = >0.05). Range of vegetation characteristics indicate *E. codium* prefers habitat with low abundance and diversity of other species.

NMDS of vegetation composition shows clear separation based on *E. codium* occurrence (Fig 1.1.8-A) and some, but not complete separation between vegetation communities where *E. codium* is ≤ 10% cover and where it is > 10% (Fig 1.1.8-B). PERMANOVA results indicated a significant negative relationship between shrub cover and *E. codium* occurrence (Table 1.1.4 and Fig 1.1.9). Where *E. codium* was present, shrub cover of any of the three shrub species growing at the site did not exceed 10% (Table 1.1.6). Perennial graminoid cover reached maximum of

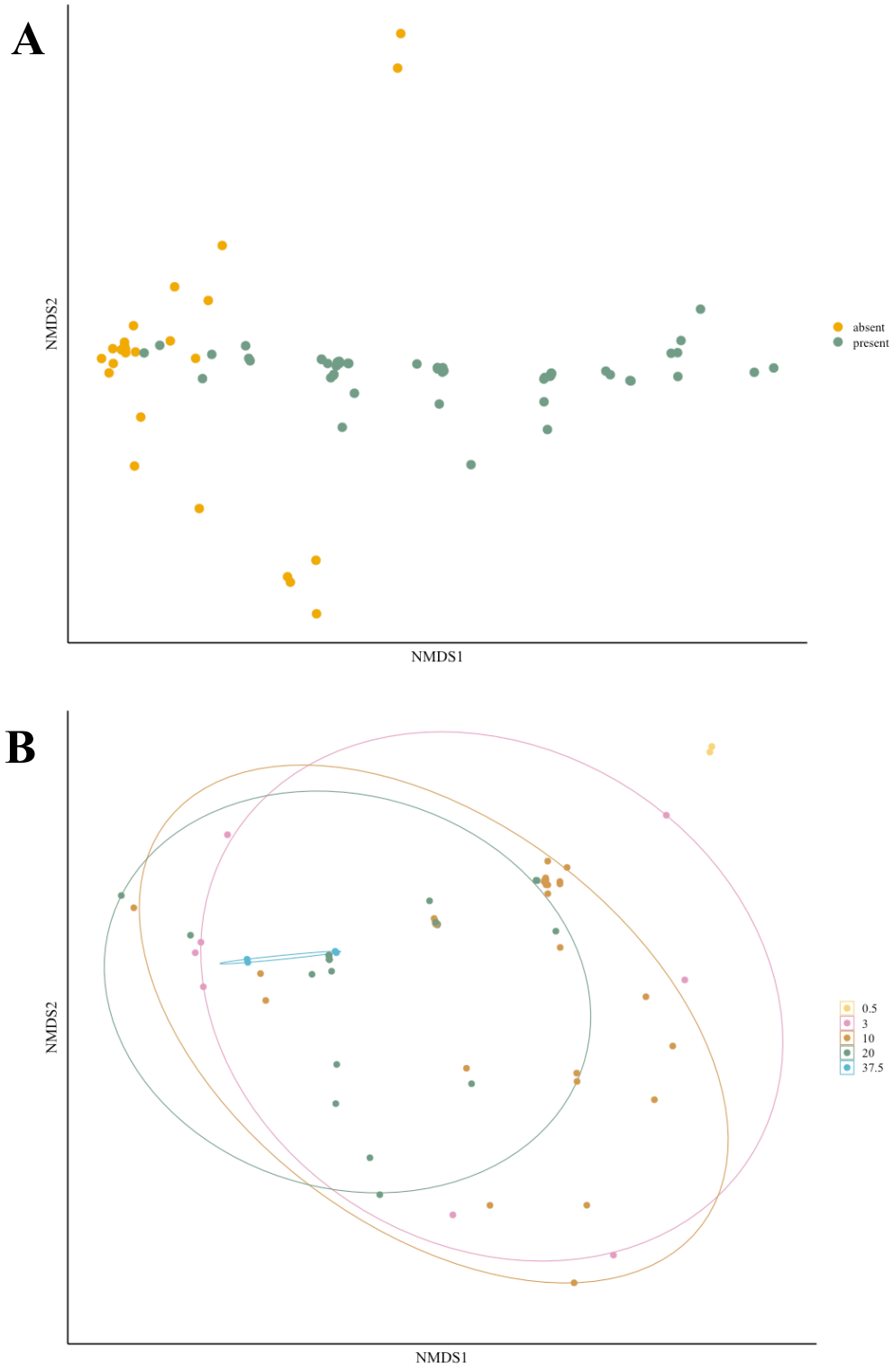


Figure 1.1.8 NMDS Ordination of Vegetation Composition by *E. codium* Occurrence and Abundance
Non-metric multidimensional scaling (NMDS) ordination of vegetation composition by *E. codium* occurrence (A) (k = 3 , stress = 0.057) and abundance (B) (k = 3 , stress = 0.094). Points are coded by color to correspond to where *E. codium* is present (green) and absent (yellow) (A) or to correspond to *E. codium* cover (%) (B). Each point represents a $1m^2$ plot. Points closer together are more similar to than those farther apart. Clear separation in vegetation composition is visible by *E. codium* occupancy. While some separation in vegetation composition is visible between the highest and lowest *E. codium* abundance, some overlap is also present between vegetation composition associated with 10-20% *E. codium* abundance.

almost 60% where *E. codium* was present, compared to a maximum cover of 40% where it was absent, with a slightly higher mean where it is present (17%) compared to where *E. codium* is absent (13%). The majority of total forb cover was below 10%, never exceeding 20%, and annual invasive graminoid cover was also similarly low, never exceeding 3% cover. In contrast, perennial graminoid cover reached maximum of almost 60% cover where *E. codium* was present, compared to a maximum cover of 40% where it was absent, as well as a slightly higher mean where *E. codium* was present (17%) compared to where it was absent (13%).

ISA analysis indicated *E. codium* was the singular diagnostic species of where it occurs ($p = 0.005$, IVij = 100), with an IVij of 100 indicating this species occurs in all plots of that group and in no plots of the other group (Table 1.1.5). Common Yarrow (*Achillea millefolia*) and Pursh's milkvetch (*Astragalus purshii*) both characterized the areas where *E. codium* did not grow. Of the twenty-seven total species recorded across the entire population, twenty-three species (85%) were recorded in plots where *E. codium* was present (Table 1.1.6). Of these

Table 1.1.4 PERMANOVA of Vegetation Functional Groups Relationship to *E. codium* Occurrence and Abundance
Significant relationships are indicated by asterisks (* = significant, ** = strongly significant, ***= very strongly significant). Only shrub cover is significantly impacting where *E. codium* occurs, with the presence of shrubs characterizing where *E. codium* is absent, indicating potential niche competition between *E. codium* and other woody species.

Vegetation Fuctional Group	Df	R^2	F	*Pr(>F)*	
ERCO Present/Absent (n=90)					
Shrub	1	0.1103	10.91	0.012	**
Forb	1	0.0311	2.83	0.095	
Annual Graminoid	1	0.0294	2.66	0.109	
Perennial Graminoid	1	0.0258	2.33	0.134	
ERCO Abundance (n=72)					
Shrub	1	0.0060	0.42	0.590	
Forb	1	0.0119	0.84	0.368	
Annual Graminoid	1	0.0030	0.21	0.624	
Perennial Graminoid	1	0.0011	0.08	0.815	

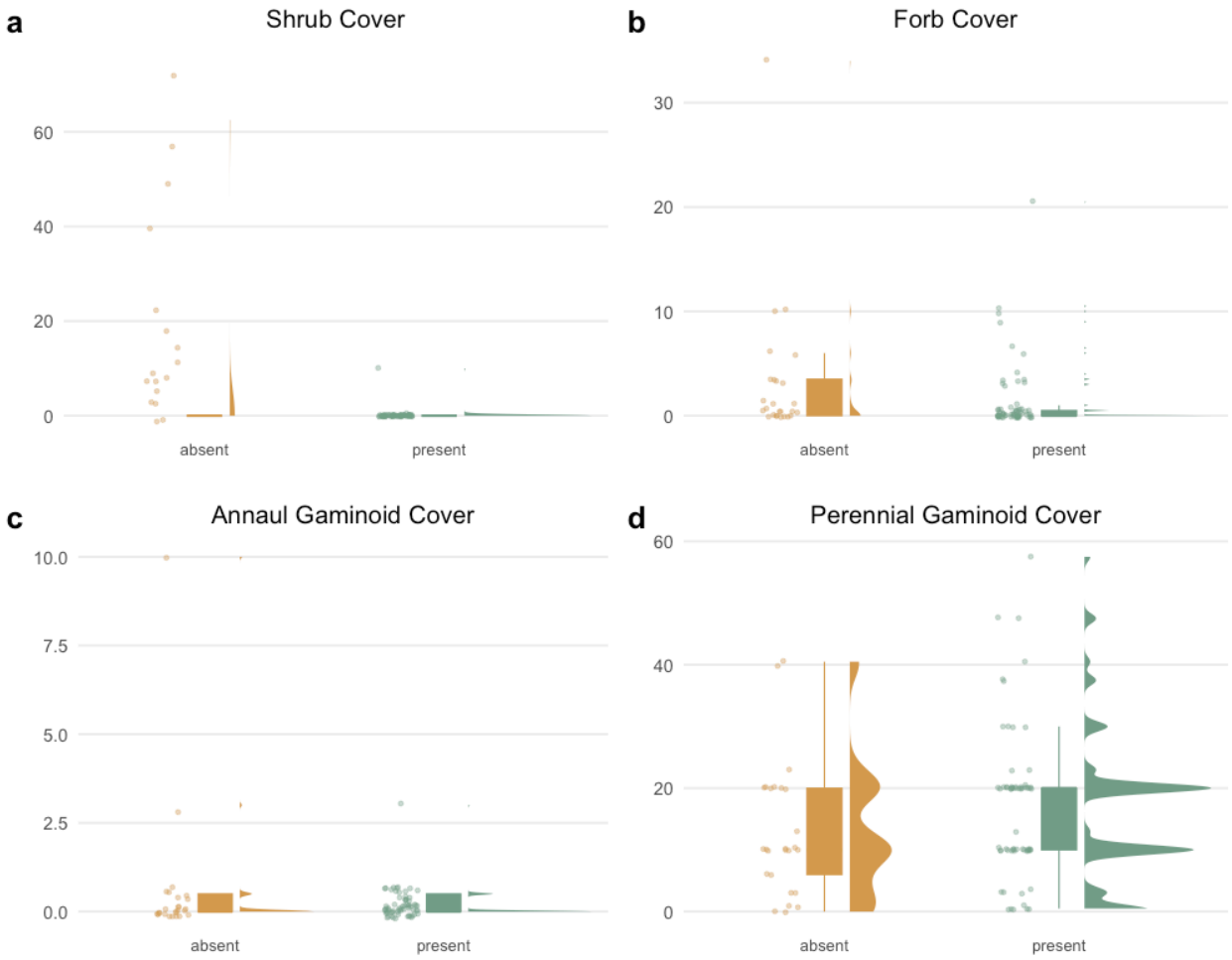


Figure 1.1.9 Raincloud Plots of Vegetation Functional Groups by *E. codium* Occurrence
Only shrub cover was significantly greater ($p = < 0.05$) where *E. codium* did not occur, indicating potential niche competition between *E. codium* and other woody species. Perennial graminoid cover is relatively greater than forb or annual graminoid cover, indicating *E. codium* forms a subshrub-perennial graminoid association.

species, thirteen species (57% of species present) were recorded in less than 5% of plots (1-3 plots total) while sixteen species (70% of species present) were recorded in less than 10% of the plots (maximum 6 plots total). Species that occurred in <5% of plots included woody shrubs Purple sage (*Salvia dorii*), Big sagebrush (*Artemisia tridentata*), and Yellow rabbitbrush (*Chrysothamnus viscidiflorus*). This group also included leafy perennial forb species such as Longleaf Phlox (*Phlox longifolia*) and Orange globe mallow (*Sphaeralcea munroana*) and spring

annuals including Rigid fiddleneck (*Amsinckia retrorsa*), Douglas' dusty maiden (*Chaenactis douglasii*), and Western tansymustard (*Descurainia pinnata*).

Species in <10% of plots included one spring annual, Thinleaf phacelia (*Phacelia linearis*), and two perennial forbs, Canby's biscuitroot (*Lomatium canbyi*) and Arrowleaf balsamroot (*Balsamorhiza sagittata*) (Table 1.1.6). Three species were recorded in ~10-15% of plots, including two native perennial *Astragalus* species *A. purshii* and Buckwheat milkvetch *(Astragalus caricinus)* and an invasive annual and known noxious weed Russian thistle (*Salsola tragus*). No species were recorded in 15% - ~30% of plots, while two graminoid species were recorded in ~30% of plots: Cheatgrass (*Bromus tectorum*) and Bluebunch wheatgrass (*Pseudoroegneria spicata*). Sandberg bluegrass (*Poa secunda*) was the only other perennial native bunch grass recorded at the native site, and the only species to occur in 100% of the plots occupied by *E. codium*.

Table 1.1.5 ISA of Vegetation Composition by *E. codium* Occurrence
Species characterizing areas where *E. codium* is present and absent (n= 90). IV_{ij} of 100 means species occurs in all plots. Significant relationships are indicated by asterisks (* = significant, ** = strongly significant, ***= very strongly significant). *E. codium* is the only significant indicator of its own vegetation habitat, suggesting it is the dominant species of its own unique habitat type.

Species	Group	IVij	*P*	
Achillea millefolia	absent	11.5	0.035	*
Astragalus purshii	absent	22.4	0.015	**
Eriogonum codium	present	100.0	0.005	**

Table 1.1.6 Summary of Vegetation Species Occurrence
Vegetation species in plots where *E. codium* is present (n = 72). Table includes number of times species presence was recorded (plot counts) and percentage of total plots surveyed in each subpopulation (I-V) and accumulatively across all subpopulations (whole site). Perennial native graminoid species Sandburg's Bluegrass (*Poa secunda*) and Bluebunch wheatgrass (*Pseudoroegneria spicata*) occurs the most often with *E. codium* indicating this species forms its own subshrub-perennial graminoid habitat type. Occurrence and abundance of all other species is low, indicating *E. codium* occupies vegetation community characterize by low diversity and productivity. The presence of invasive annual species in relatively high abundance should be the focus of future management efforts.

Species	Code	Class	Habit	Origin	Site (count)	plots (%)	1	%	2	%	3	%	4	%	5	%
Eriogonum codium	ERCO	subshrub	Perennial	Native	72	100.00	28	100.00	4	100	8	100.0	10	100	22	100.00
Poa secunda	POSE	graminoid	Perennial	Native	72	100.00	28	100.00	4	100	8	100.0	10	100	22	100.00
Pseudoegneria spicata	PSSP	graminoid	Perennial	Native	22	30.56	3	10.71	2	50	8	100.0	9	90	0	0.00
Bromus tectorum	BRTE	graminoid	Annual	Invasive	21	29.17	5	17.86	2	50	2	25.0	0	0	12	54.55
Astragalus purshii	ASPU	forb	Perennial	Native	8	11.11	5	17.86	0	0	2	25.0	0	0	1	4.55
Salsola tragus	SATR	forb	Annual	Invasive	8	11.11	5	17.86	1	25	2	25.0	0	0	0	0.00
Astragalus caricinus	ASCA	forb	Perennial	Native	7	9.72	3	10.71	0	0	3	37.5	0	0	1	4.55
Balsamorhiza sagittata	BASA	forb	Perennial	Native	6	8.33	2	7.14	0	0	2	25.0	1	10	1	4.55
Lomatium canbyi	LOCA	forb	Perennial	Native	6	8.33	0	0.00	0	0	1	12.5	2	20	3	13.64
Phacelia linearis	PHLI	forb	Annual	Native	5	6.94	4	14.29	0	0	1	12.5	0	0	0	0.00
Descurainia pinnata	DEPI	forb	Annual	Native	3	4.17	3	10.71	0	0	0	0.0	0	0	0	0.00
Balsamorhiza hookeri	BAHO	forb	Perennial	Native	2	2.78	2	7.14	0	0	0	0.0	0	0	0	0.00
Chaenactis douglasii	CHDO	forb	Annual	Native	2	2.78	0	0.00	0	0	1	12.5	1	10	0	0.00
Erigeron poliospermus	ERPO	forb	Perennial	Native	2	2.78	0	0.00	0	0	0	0.0	1	10	1	4.55
Phlox longifolia	PHLO	forb	Perennial	Native	2	2.78	0	0.00	0	0	1	12.5	1	10	0	0.00
Sphaeralcea munroana	SPMO	forb	Perennial	Native	2	2.78	2	7.14	0	0	0	0.0	0	0	0	0.00
Amsinckia retrorsa	AMRE	forb	Annual	Native	1	1.39	0	0.00	1	25	0	0.0	0	0	0	0.00
Artemisia tridentata	ARTR	shrub	Perennial	Native	1	1.39	1	3.57	0	0	0	0.0	0	0	0	0.00
Chrysothamnu viscidiflorus	CHVI	shrub	Perennial	Native	1	1.39	1	3.57	0	0	0	0.0	0	0	0	0.00
Cryptantha pterocarya	CRPT	forb	Annual	Native	1	1.39	0	0.00	0	0	1	12.5	0	0	0	0.00
Eriocoma hymenoides	ERHY	graminoid	Perennial	Native	1	1.39	1	3.57	0	0	0	0.0	0	0	0	0.00
Lomatium species	Lomati	forb	Perennial	Native	1	1.39	1	3.57	0	0	0	0.0	0	0	0	0.00
Salvia dorii	SADO	shrub	Perennial	Native	1	1.39	0	0.00	0	0	1	12.5	0	0	0	0.00

Part II: Similarities and Differences Between Subpopulations and Sampling Transects

Site Characteristics

The five subpopulations of *E. codium* occur as spatially segregated clusters along a discontinuous band on the edge of a U-shaped curve of Umtanum Ridge (Fig 1.3), and all measured site characteristics differed between subpopulations ($p = \leq 0.01$) except for slope shape ($p = 0.6$) (Fig 1.2.1, Fig 1.2.2, Table 1.2.1). Landscape position and slope also differed by sampling transect, indicating high spatial heterogeneity of the variables within and between subpopulations. Subpopulations I and II, III, IV, and V occupy significantly different landscape positions along the ridge ($p = 0.001$) (Fig 1.2.2-A and Table 1.2.1), and this spatial arrangement

Table 1.2.1 PERMANOVA of Site Characteristics Relationship by Subpopulation and Transect
All measured site characteristics differed between subpopulations ($p = \leq 0.01$) except for slope shape ($p = 0.6$). Only slope and landscape position also significantly differed within subpopulations by sampling transect. Significant relationships are indicated by asterisks (* = significant, ** = strongly significant, ***= very strongly significant).

Subpopulation Differences in Site Characteristics[1]

Site Characteristics (n=98)	**Df**	**R^2**	**F**	**Pr(>F)**	
Subpopulation (n=5)					
Heat Load	4	0.7030	37.72	0.001	***
Slope	4	0.3969	16.42	0.001	***
Slope Angle	4	0.3507	12.86	0.001	***
Aspect Degree	4	0.6292	38.30	0.001	***
Total Rock Fragment Class	4	0.1242	3.47	0.014	**
Landscape Position	4	0.7732	95.36	0.001	***
Slope Complexity	4	0.2380	7.31	0.001	***
Slope Shape	4	0.0278	0.64	0.651	
Transect (n=11)					
Heat Load	6	0.0128	0.46	0.848	
Slope	6	0.0774	2.13	0.056	*
Slope Angle	6	0.0561	1.37	0.229	
Aspect Degree	6	0.0134	0.54	0.807	
Total Rock Fragment Class	6	0.0976	1.82	0.109	
Landscape Position	6	0.0504	4.14	0.003	**
Slope Complexity	6	0.0535	1.09	0.379	
Slope Shape	6	0.0264	0.41	0.857	

[1] Subpopulation and transect effects analyized in a single model assesing terms independently and sequentially

was also reflected in the significantly different slope aspects of the different subpopulations along the ridge ($p = 0.001$) (Fig 1.2.2-D and Table 1.2.1).

Significant differences in site characteristics were determined between subpopulation I and V, (Fig 1.2.1 and Fig 1.2.2). Generally, across most measured site variables, subpopulation I was more homogenous with less variability occurring between plots than in subpopulation V, which encompassed a wider range of habitat variability. Subpopulation I occurred predominantly on the upper third of the ridge's shoulder, with sampling transect 1.3 extending upslope onto the upper third of the ridge summit (Fig 1.2.2-A), Fig J-2). While some of subpopulation V occurred on the upper third of the ridge's shoulder, it largely extended downslope to the shoulder's middle and lower thirds, and into the upper third of the backslope. While sampling transects 5.2 and 5.3 both extended from the middle third of the shoulder to the lower third of the shoulder, transect 5.1 traversed four landscape positions, crossing from upper third of the shoulder, across the middle and lower thirds into the upper third of the backslope (Fig J-2). Subpopulation I was predominantly western facing (west = 39%, southwest = 32%, northwest = 25%) with a small number of north (2%) and northeastern (2%) facing plots, while subpopulation V was predominantly eastern (70%) facing with a subset of areas facing southeast (11%), northeast (15%) and north (4%) (Fig 1.2.1-D).

Subpopulation I had a significantly lower slope and slope angle than all other subpopulations, likely due to it encompassing mostly the upper areas of the ridge's shoulder and summit (Fig 1.2.2-B-C and Table E-2). Subpopulation V encompassed a wider range of slopes and slope angles, including the second lowest minimum after subpopulations I, and the highest maximum values of any subpopulation. This is likely due to this subpopulation extending vertically along the slope across a number of different landscape positions and extending below

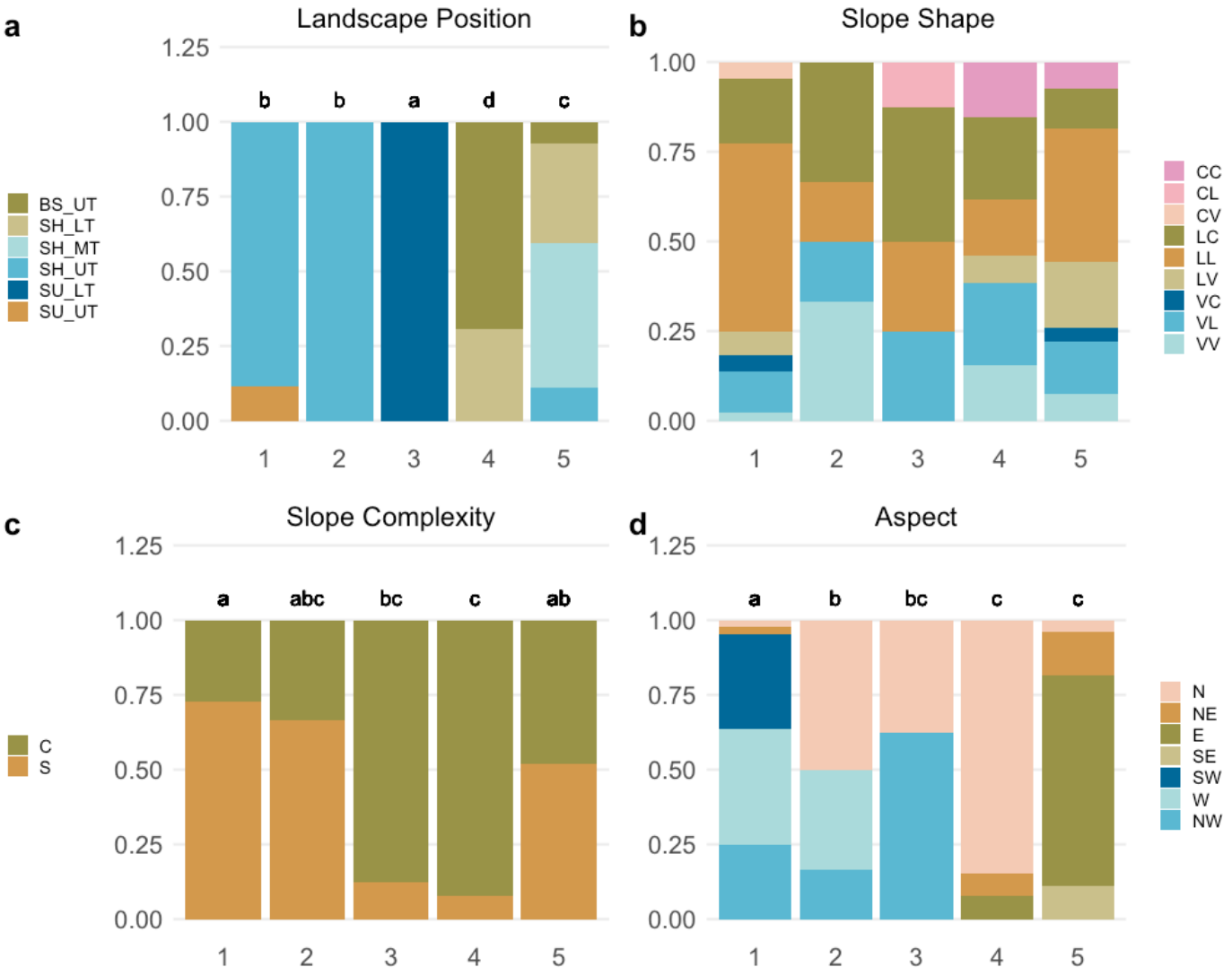


Figure 1.2.1 Bar Graph of Site Characteristics by Subpopulations
Differences in categorical site variables between subpopulations (n= 98) include landscape position (BS_UT = backslope- upper third, SH_LT= shoulder-lower third, SH_MT = shoulder-middle third, SH_UT= shoulder- upper third, SU_LT = summit-lower third, SU_UT = summit-lower third) (A), slope shape (CC= concave-concave, CL= concave-linear, CV = concave-convex, LC= linear-concave, LL= linear-linear, LV= linear-convex, VC= convex-concave, VL= convex-linear, VV= convex-convex (B), slope complexity (C= complex, S= simple) (C), and aspect (N = north, NE = northeast, E= east, SE= southeast, SW= southwest, W= west, NW= northwest) (D).

the summit and upper shoulder onto the steeper backslope (Fig 1.2.1-A). Subpopulation I contains a larger proportion of simple microtopography (73%), likely due to this subpopulation's position predominately on the upper shoulder of the ridge, while subpopulation V had a more

even distribution of simple and complex slope microtopographies (simple = 52%, complex = 48%) likely because it extends across a more topographically variable area including four landscape positions and three distinct hillslope positions (summit, shoulder, backslope) (Fig 1.2.4- A+C).

Subpopulation II occurred only on the upper third of the ridge's shoulder and showed similarities to subpopulation I in terms of its high ratio of simple (67%) to complex slope microtopography and its north (50%), northwest (17%) and north (33%) facing aspects (Fig 1.2.4- D). Despite their close physical proximity and similarities in site characteristics, both mean slope and slope angle values were significantly higher in subpopulation II than subpopulation I, mirroring differences between subpopulation I and the other three subpopulations (Table E-2). Although the range of slope angle values at subpopulation II mirrored subpopulation I the most, the range of slope values were the most similar to subpopulation III (Fig 1.2.2 B+C and Table E-2). Although the entire area of subpopulation II surveyed in this study occurs on the upper third of the ridge's shoulder, slope ranged from a minimum of 0.1 cm/cm to a maximum of 0.38 cm/cm and slope angle ranged from a minimum of 5° to a maximum of 20° with clustering around 10° or less and 20°. This wide range of values indicates a transition from a relatively flat area to a considerably steeper one over a small spatial distance.

Subpopulation III was characterized by its unique occupancy of the lower third of the ridge's summit, which was a significantly different landscape position than those occupied by all other subpopulations (Fig 1.2.2-A). Unlike the other subpopulations, subpopulation III was exclusively north (38%) and northwest (62%) facing with a similar proportion of north facing plots as subpopulation II (Fig 1.2.2-D). Mean slope and slope angle were both higher in

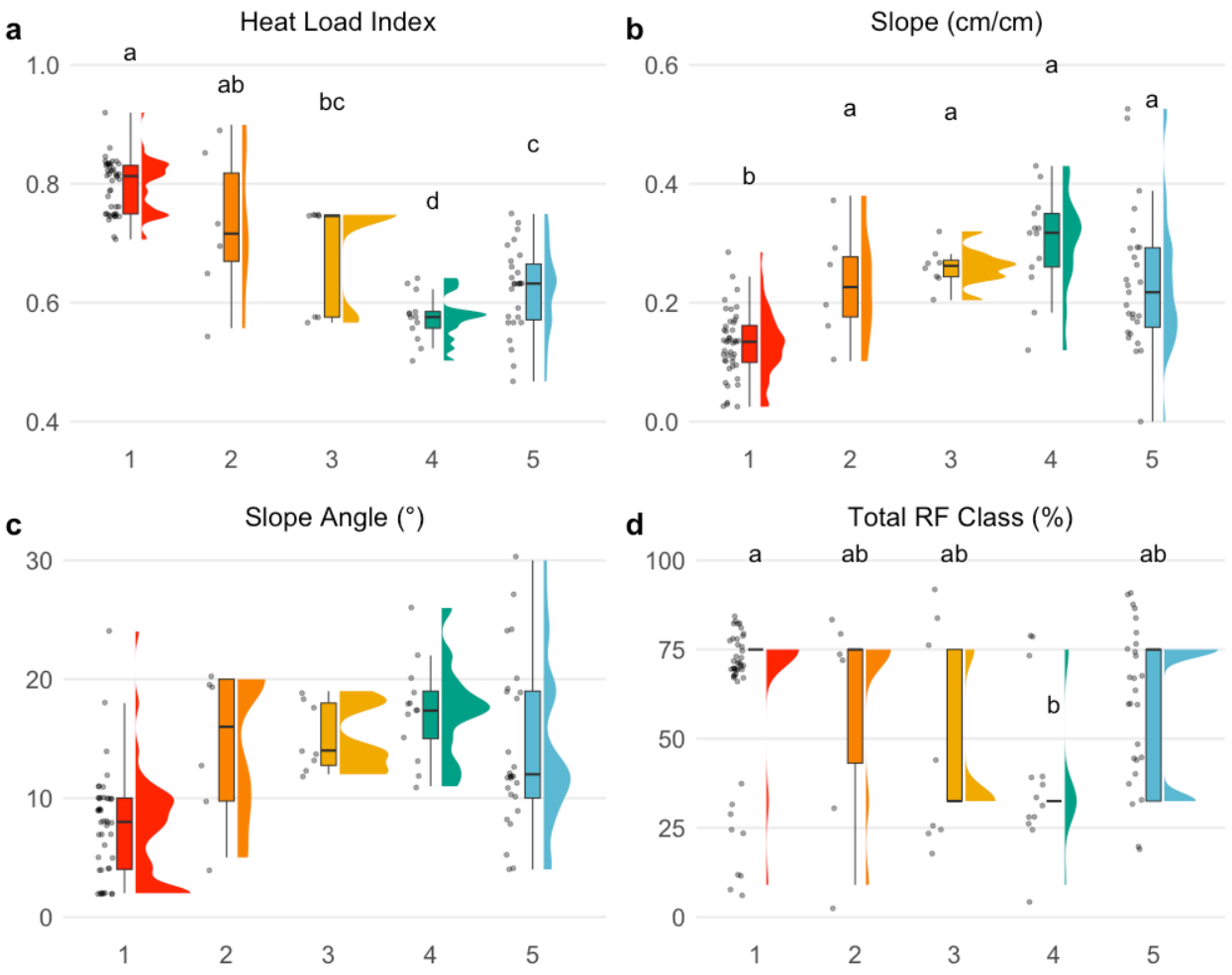


Figure 1.2.2 Raincloud Plots of Site Characteristics by Subpopulation
Differences in continuous site variables between subpopulations (n=98) including heat load index (A), slope (cm/cm) (B), slope angle (°) (C), and total percentage of rock fragment cover classification (D).

subpopulation III than subpopulation I, II or V, and subpopulation III contained a higher proportion of complex (88%) to simple and concave-concave microtopographic slope characteristics as well (Fig 1.2.1-B, Fig 1.2.2-B+C, Table E-2). Like subpopulation II, subpopulation III had the second lowest sample size (n=8) and length of transect (24m), but in contrast to subpopulation II, subpopulation III was characterized by the lowest variability in slope (sd = 0.03) and slope angle (n= 2.88) of all subpopulations over a distance twice the size of subpopulation II.

Subpopulation IV was the only subpopulation to exclusively occupy the lower third of the shoulder and upper third of the backslope, (Fig 1.2.1-A). Subpopulation IV has the highest mean slope (0.30 cm/cm) and slope angle (17.36°), and although the range of these values falls within the range of values observed at subpopulation V, subpopulation IV had a narrower range of values, higher minimum, and smaller standard deviation (Fig 1.2.2-B+C and Table E-2). Similar to subpopulation III, subpopulation IV was mostly north facing (N = 84%, NE = 8%, E = 8%) and contained the largest proportion of complex (92%) and concave-concave slope micro topographies (Fig 1.2.2-B and Table E-1).

Although no significant differences in slope shape between subpopulations was determined, subpopulations I and V had the highest number of different recorded slope shapes (7) (Fig 1.2.2-B and Table E-1). Subpopulation IV showed similar variation (6), suggesting higher microsite complexity within these subpopulations. Subpopulations II and III had the lowest variation (4) and lowest microsite complexity. In all subpopulations except subpopulation II, the majority of slope shapes were linear (I = 77%, II= ~50%, III= ~63%, IV = 47%, V= 67%). Subpopulations II and III had linear-linear and linear-concave shapes, while subpopulations I, IV and V had linear-convex in addition to linear-linear and linear-concave and shapes. Subpopulation I had the largest proportion of linear-linear plots (52%) followed by subpopulation V (37%). The remaining plots in subpopulation I were largely comprised of linear-concave (18%) and linear convex (7%) plots while the subpopulation V had the inverse (linear-convex = 19% linear-concave = 11%). While convex shapes comprised the second largest proportion of plots after linear shapes in all other subpopulations, subpopulation II had the most convex plots (I = 18%, II= 50%, III = 25%, IV = ~38%, V = 26%). Subpopulation III contained only convex-linear plots, while subpopulations II and IV were characterized by convex-linear

and convex-convex plots, and subpopulations I and V had all three convex-linear, convex-concave, and convex-convex plots, although convex-concave shaped plots totaled <5% in both subpopulations (I = 5% V = 4%). All subpopulations contained one type of concave shaped plot (I= 5% concave-convex, III= 12% concave-linear , IV =15% concave-concave, V =7% concave-concave).

Subpopulation I had a significantly higher mean HLI than subpopulation V (subpopulation I= 0.8 , subpopulation V= 0.63) (Fig 1.2.2-A and Table E-2). Subpopulation V showed more variability in HLI and had a wider range of HLI values, and maximum values overlapped with subpopulation I around 0.7 (subpopulation I range = 0.71-0.86, subpopulation V range = 0.47-0.75). Subpopulation II had the second highest mean HLI (0.73) and second highest maximum value (0.9) after subpopulation I. Mean HLI at subpopulation III (0.68) was similar to subpopulation V, but had a higher minimum value (0.57) with values clustering around 0.7 and 0.6 (Fig 1.2.4 and Table E-2). Subpopulation IV had a significantly lower mean and range of HLI index compared to all other subpopulations (mean= 0.53, range= 0.5-0.62). Standard deviation of HLI at subpopulation IV was similarly low, reflecting the narrower range of values and lower variability in HLI observed at all other subpopulations in comparison to subpopulation II.

Subpopulation I had a higher mean rock fragment cover classification than subpopulation V, and also had a wider range of values, with distinct clustering of values either below 50% cover (rubbly) or around 75% cover (very rubbly) (Fig 1.2.2-D and Table E-2). Subpopulation V had a slightly lower mean rock fragment cover class (59% = very rubbly) and a more even distribution of rock classification values between the maximum and minimum. However, subpopulation V also has a significantly higher minimum total cover then subpopulation I (I = 9% and V= 32%), despite subpopulation I having a slightly higher mean value (Table E-2).

Subpopulation IV had a significantly lower mean rock fragment classification (40.5%) than all other subpopulations. Although a few plots had values around 75%, most plots were clustered around 30% cover with comparatively low variability within the subpopulation (sd = 20.69). Subpopulation II and III had significantly similar patterns in mean rock fragment cover class that most closely resemble subpopulation V, although the values minimum and range (9-75%) better matched the ranges observed in subpopulations I and IV (Fig 1.2.4 and Table E-2).

Soil Characteristics

Significant differences were determined between subpopulations for all soil characteristics except hydraulic conductivity (K) (Table 1.2.3). No significant difference in hydraulic conductivity (K) was determined between subpopulations ($p = 0.6$) (Table 1.2.2) . The widest variation of K values was observed in subpopulations I and V, which encompassed the range of values observed at subpopulations II, III and IV. Minimum values in supopulations II and IV are >0 while minimum values in subpopulations I, III and IV are <0 (Fig 1.2.3 and Table E-3). Subpopulations I, II and V had the highest maximum range of values. Subpopulation I and II had similar maximum values close to 0.01, while the maximum value at subpopulation V was an outlier significantly larger than any other K values observed either within subpopulation V or at any of the other subpopulations (K = 0.015). Subpopulations I and V had the largest clustering of plots with K values between -2×10^{-3} and 2×10^{-3}. As higher K values indicate faster rates of water infiltration into the soil profile, and areas of maximum K values in subpopulations I and V, and subpopultion II, indicate areas with the fastest draingae. K values <0 likely indicates the rate in which water has stopped moving through the soil profile and become stagnant. Observed K values are consistant with Kv values asocaited with gravel (K = ~0.01), course to fine sand (K = 0.003- 0.01), and silty sand ($K = 1 \times 10^{-5} – 0.003$) (Maurya et al 2016).

Table 1.2.2 PERMANOVA of Soil Characteristics Relationship by Subpopulation and Transect
Significant differences were determined between subpopulations for all soil characteristics except hydraulic conductivity (K). Both soil surface and rock fragment compositions significantly differed within subpopulations by sampling transect. Significant relationships are indicated by asterisks (* = significant, ** = strongly significant, ***= very strongly significant).

Spatial Relationship of Soil Surface Characteristics[1]

Soil Property	Soil Variable	n	Df	R^2	F	*Pr(>F)*	
Subpopulation							
Soil Hydrology	Hydraulic Conductivity (K)	80	4	0.1123	2.57	0.060	
Soil Surface	Surface Texture	72	4	0.3466	8.90	0.001	***
Soil Surface	Surface Composition	98	4	0.3124	11.69	0.001	***
Soil Surface	Surface Rock Fragment Composition	98	4	0.4571	20.83	0.001	***
Transect							
Soil Hydrology	Hydraulic Conductivity (K)	80	6	0.1353	2.07	0.063	
Soil Surface	Surface Texture	72	6	0.0596	1.02	0.429	
Soil Surface	Surface Composition	98	6	0.1065	2.66	0.016	**
Soil Surface	Surface Rock Fragment Composition	98	6	0.0656	1.99	0.013	**

[1] Subpopulation and transect effects analyzed in a single model assesing terms independently and sequentially

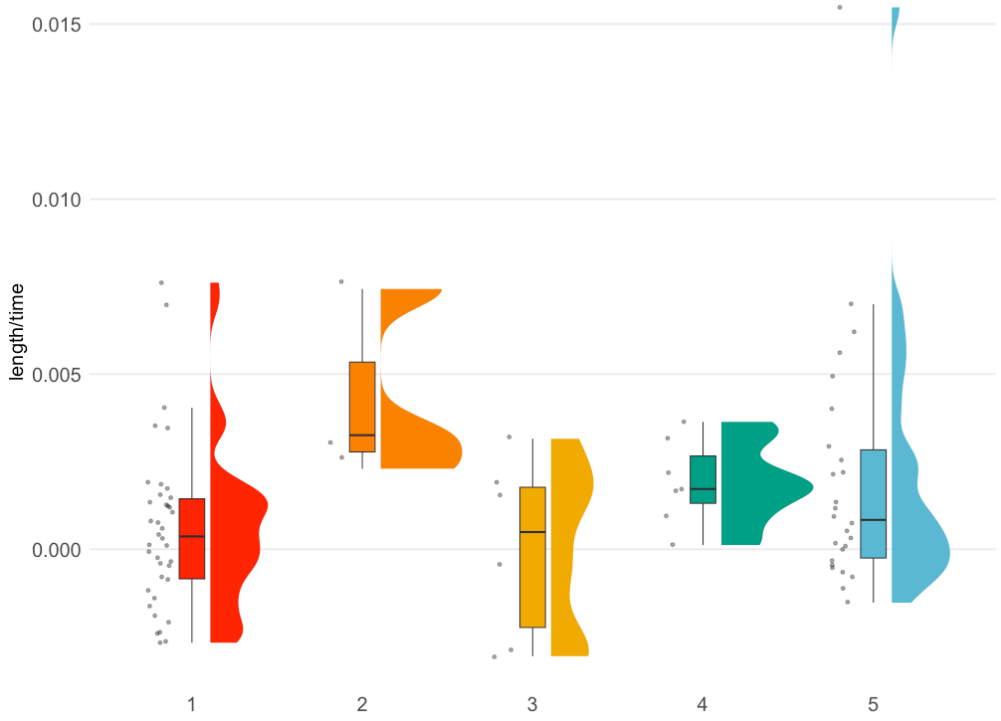


Figure 1.2.3 Raincloud Plot of Hydraulic Conductivity by Subpopulation
No significant difference in hydraulic conductivity (K) were determined between subpopulations ($p = 0.6$). Minimum values in subpopulations II and IV are >0 while minimum values in subpopulations I, III and IV are <0. Subpopulations I and V have the largest clustering of plots with K values between -2×10^{-3} and 2×10^{-3}.

Significant differences in soil texture were determined for all subpopulations (Table 1.2.2). The dominant surface soil texture at subpopulation I was loamy sand, with less than 25% of plots containing sandy loam, suggesting the presence of two distinct soil environments within this subpopulation (Fig 1.2.4). Inversely, almost 75% of plots at subpopulation V contained sandy loam, with ~5% of plots containing loam, and the remaining 20% containing loamy sand, indicating the subpopulation stretches across a gradient of loam derived soils. Although differences between subpopulations significantly accounted for ~35% of the variation in soil texture, an additional 11% was determined to be significantly related to landscape position (Subpopulation: $p = 0.001$, $F = 9.9$, $R^2 = 0.3$; Landscape position: $p = 0.018$, $F = 3.05$, $R^2 = 0.107$). Subpopulation III had similar proportions of loamy sand (75%) to sandy loam (25%) soils as subpopulation I, and like subpopulations I and III, the dominant soil surface soil texture at subpopulation II was loamy sand (Fig 1.2.4, Table E-1). However, unlike subpopulations I and

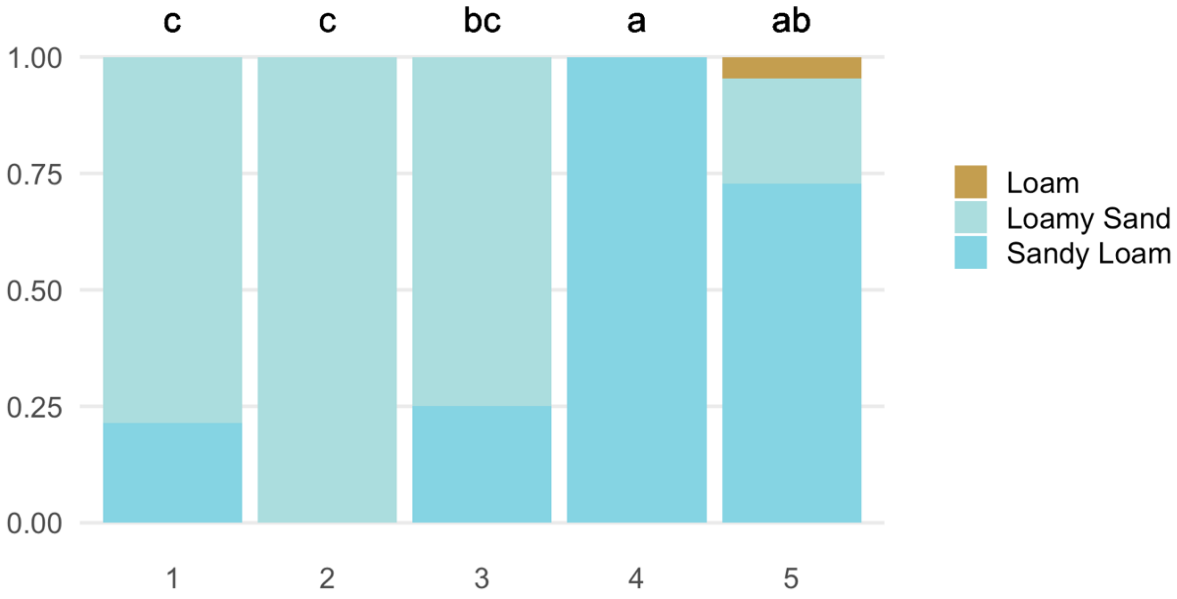


Figure 1.2.4 Bar Graph of Soil Surface Texture by Subpopulation
Weakly significant ($p = 0.05$) differences in surface soil texture were determined between subpopulations in the areas where *E. codium* is present (n= 72). Subpopulations I, III and V contained a mixture of loamy sand and sandy loam soils, while subpopulation contained only loamy sand soil and subpopulation IV contained only sandy loam soils. Subpopulation V was the only subpopulation to also contain loam soils.

III, sandy loam was not present. This indicates a spatial transition in soil texture and an increase in sand content moving east from subpopulation I along the ridge to subpopulation II. Subpopulation IV was the only site to exclusively have only sandy loam soil surface texture.

Significant differences in soil surface composition and surface rock fragment composition were determined between all subpopulations ($p = 0.001$) (Table 1.2.2), including very strong pairwise differences between subpopulations I and V (Fig D-1A and Fig D-2A), and within subpopulations by sampling transects (Fig D-1B and Fig D2-B). NMDS ordination of soil surface composition shows large areas of overlap between subpopulations I and V illustrating compositional similarities between the subpopulations, such as similarities in low mean, range and standard deviation of litter (Fig 1.2.5-A and Table E-4). Areas of separation between subpopulation I and V visible in the NMDS ordination reflect significant differences between these subpopulations due to the presence of biocrust cover (minimum = 0.5%) in subpopulation V that is not present at subpopulation I (minimum = 0%), and the ratios of rock and bareground cover at each subpopulation.

While both subpopulations had similar maximum rock cover, subpopulation I had significantly higher mean (81%) and minimum (38%) rock cover and smaller standard deviation than subpopulation V (mean = 66% , minimum = 20%) which had a lower mean and minimum rock cover but a higher standard deviation (Table E-4). This indicates subpopulation V had more consistent rock cover in areas where it is present, but with more variability in rock: bareground ratios than in subpopulation I, as areas with lower rock composition were more common in subpopulation V. While both subpopulations had similar minimum bareground cover, subpopulation V had significantly higher mean (20%) and maximum bareground (62%) cover than subpopulation I (mean = 4%, maximum= 20%). Standard deviation of bareground cover

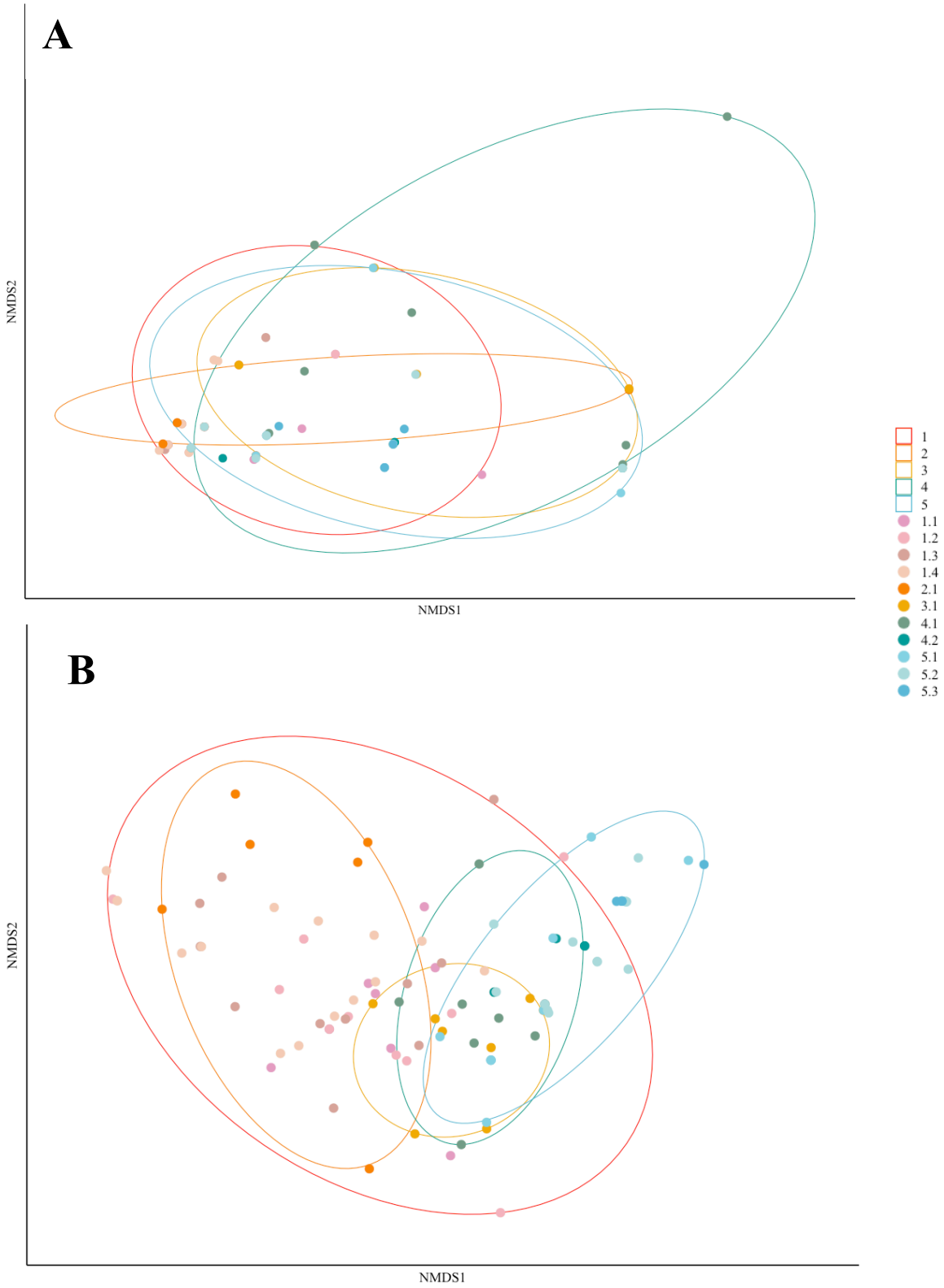


Figure 1.2.5 NMDS Ordination of Soil Surface and Soil Surface Rock Fragment Composition by Subpopulation and Transect
Non-metric multidimensional scaling (NMDS) ordination of soil surface (k = 2 , stress = 0.0045) and soil surface rock fragment (k = 3, stress = 0.057) (n= 98) compositions. Points are coded by color to correspond to transect. Hulls are coded by color to correspond to subpopulation. Each point represents a $1m^2$ plot. Points closer together are more similar to than those farther apart.

was significantly lower in subpopulation I (sd= 5) than in subpopulation V (sd= 13), indicating pattern of lower variation within subpopulation I and higher variation within subpopulation V. Overall, rock composition had the highest standard deviation in both populations, indicating it is the most variable surface composition component within both subpopulations.

Significant pairwise differences in soil surface composition was determined between subpopulations I and III, IV and V ($p = 0.001$) (Table D-1A). Subpopulations I and II showed similar surface composition ($p = 0.69$), while subpopulations III and IV likewise showed strong similarities ($p= 0.964$). Subpopulation V had similar surface cover to the other subpopulations II, III and IV. These relationships are illustrated in the NMDS ordination, which shows subpopulation III encompassed within subpopulation V, while subpopulation V extends beyond III, indicating all variation of subpopulation III is encompassed by the variation present in subpopulation V (Fig 1.2.5-A). Subpopulation II is encompassed with the variation of the four other subpopulations, particularly populations I and V on one side of the ordination space and subpopulation III on the other side. The variation of surface composition in subpopulation IV overlaps subpopulation V, and includes where subpopulation III and V overlap. However, the hull of subpopulation IV also extends beyond both subpopulations at the top of the ordination space. The clustering of subpopulations III, IV and V at the top of the ordination space is likely due to the presence of biocrust composition in these subpopulations in contrast to subpopulations I and II (Table E-4).

Subpopulation IV has significantly higher mean and maximum biocrust cover and significantly wider variation of biocrust composition throughout the subpopulation than occurred in subpopulations III and V (III: sd = 0.27, IV: sd = 5.42, V: sd = 0.96) (Table E-4). Subpopulations III, IV and V had significantly similar mean and minimum of bareground cover

Table 1.2.3 ISA of Soil Surface Composition by Subpopulation and Transect
Soil surface components that most characterize subpopulations and individual transects within subpopulations. IV_{ij} of 100 means species occurs in all plots. Significant relationships are indicated by asterisks (* = significant, ** = strongly significant, ***= very strongly significant).

ISA of Soil Surface Cover

Cover Class	Classical	Multiple Group	IVij	*P*	
Subpopulation					
Biocrust	4	—	54.3	0.005	**
Rock	1	—	23.8	0.005	**
Transect					
Bareground	—	1.1+ 1.2+ 1.3+ 3.1+ 4.1+ 4.2+ 5.1+ 5.2+ 5.3	94.5	0.005	**
Biocrust	4.1	—	31.1	0.030	*
Biocrust	—	4.1+ 4.2+ 5.3	55.0	0.005	**
Rock	1.2	—	10.8	0.050	*

(mean = 20-22%, minimum = 3%), but subpopulation III had almost 20% smaller maximum cover than subpopulation V while subpopulation IV had a slightly higher standard deviation, indicating subpopulation III had less variation in bareground than subpopulation V while subpopulations IV had more. This pattern continues in rock composition. Subpopulations III, IV and V had similar mean rock composition, with the highest cover occurring in subpopulation V and the lowest in subpopulation IV. Subpopulation IV also has lower minimum cover (20%) than subpopulations III and V and a higher standard deviation indicating more variability. Although subpopulations III and IV have the same higher mean litter cover (8%) than subpopulation V (3%), subpopulations III and V have the same range (0-20%) and lower maximum cover than subpopulation IV (maximum = 38%), which also had a larger standard deviation (III: sd= 6 , IV: sd= 10 , V: sd= 4).

These patterns indicate surface composition is more variable in subpopulation IV than subpopulation V and less variable in subpopulation III. Despite these differences in the compositional variation of litter and biocrust, subpopulations III, IV, and V have significantly

similar surface composition characterized by 55-65% rock composition, ~20% bareground composition, and the presence of biocrusts. In contrast, subpopulations I and II are characterized by their high mean rock cover (~80%), low mean cover of bare ground (4-7%), low mean litter cover (4%), and absence of biocrusts (Table E-4). Subpopulation I has higher maximum litter cover (I: 20%, II:10%) and standard deviation (I: 6, II: 4), while subpopulation II has higher standard deviation of rock cover (I= 12, II = 20), and maximum and standard deviation of bareground cover (I: mean= 4 sd= 5, II: mean = 7 sd= 15).

PERMANOVA results and pairwise comparisons determined there are no significant similarities in surface rock fragment composition between any of the five subpopulations, and each subpopulation was determined to have a unique rock fragment composition characterized and distinguished by different rock fragment size classes (Table 1.2.2 and Fig D-2). Overall, subpopulation I had the lowest overall variability in surface rock fragment composition (mean sd = 5.75), subpopulation IV has the highest variability (mean sd = 14.5) and subpopulations II, III and V had a "medium" variability (mean sd = 9.25-10.25) in-between the minimum and maximum variability established by subpopulations I and IV.

NMDS ordination of surface rock fragment composition shows both areas of overlap between subpopulations I and V in the center of the ordination, and areas of separation between them where each subpopulation's hull moves towards opposite sides of the ordination space (Fig 1.2.5-B). This is because while both subpopulations have similar mean cover of cobble, medium and very fine gravel components, they display different patterns in standard deviation and

Table 1.2.4 IS4 of Soil Surface Rock Fragment Composition by Subpopulation and Transect
Rock fragment components that most characterize subpopulations and individual transects within subpopulations. IV_{ij} of 100 means species occurs in all plots. Significant relationships are indicated by asterisks (* = significant, ** = strongly significant, ***= very strongly significant).

ISA of Soil Surface Rock Fragment Cover

Cover Class	Classical	Multiple Group	IVij	*P*	
Subpopulation					
Cobble	4	—	56	0.005	**
Course Gravel	5	—	29	0.005	**
Fine Gravel	1	—	11	0.005	**
Medium Gravel	3	—	96	0.005	**
Stone	2	—	30	0.040	*
Very Fine Gravel	2	—	89	0.005	**
Transect					
Cobble	4.2	—	96	0.010	**
Cobble	—	1.2+ 1.3+ 4.1+ 4.2+ 5.1	30	0.010	**
Course Gravel	5.3	—	56	0.005	**
Fine Gravel	1.4	—	11	0.010	**
Medium Gravel	3.1	—	89	0.015	**
Very Fine Gravel	2.1	—	29	0.005	**

minimum/maximum cover in other compositional components that distinguish each subpopulation (Table E-5). Although subpopulation I had a higher variation and maximum cover of the cobble, medium and very fine gravel components than subpopulation V, significant differences observed in surface rock cover are due predominantly to differences in the boulder, stone, coarse and fine gravel components. Subpopulation I is distinguished by the presence of boulders and significantly higher cover and variability of stone compared to subpopulation V. Subpopulation I also has significantly higher cover and variability of fine gravel (Table 1.2.4 and Table E-5). Subpopulation V is characterized by the absence of boulders and significantly lower cover of stones compared to subpopulation I, and higher cover and variability of coarse gravel.

In the NMDS ordination, all subpopulations except subpopulation V are fully encompassed within the variation present at subpopulation I (Fig 1.2.5-B). Subpopulations III

and IV form a gradient between where subpopulations I and V overlap, similar to their spatial arrangement along the ridge (Fig 1.3). The entire variation of subpopulation III is tightly clustered inside this overlap zone where subpopulation I and V come together (Fig 1.2.5-B). While subpopulation IV also overlaps in this area of the ordination space, it continues upwards into the area of subpopulation I that does not intermix with subpopulation III or V. In contrast, subpopulation II occupies a space overlapping with subpopulation I but spatially separated from the other subpopulations, mirroring its spatial arrangement as the most eastern subpopulation only closely situated to subpopulation I. In the ordination space, subpopulation II has wide vertical variability but extends within subpopulation I only on the left side of the ordination space, where it does not overlap with subpopulations III, IV and V.

Boulders were absent in all subpopulations except I. All subpopulations except subpopulation IV contained stone, with subpopulation II containing the highest mean stone cover and standard deviation (II: mean = 4%, sd= 8) (Table E-5). Subpopulation III contained similar mean stone cover and standard deviation to subpopulation I, while low cover (mean = 0, max = 3%, sd= 1) at subpopulation V reflected the general lack of stone in subpopulation IV. Subpopulation IV was characterized by its significantly higher mean, range and standard deviation of cobble cover (Table 1.2.4 and Table E-5). In contrast, subpopulation III had the lowest mean, maximum and standard deviation of cobble cover, while subpopulation II showed similar a mean, range and standard deviation as subpopulation V.

Subpopulations I, II, III/IV and V had significantly different mean coarse gravel cover, with subpopulation V characterized by significantly high mean and minimum values (Table 1.2.4 and Table E-5). While mean coarse gravel cover increased moving east to west along the ridge, subpopulations I and V both had higher maximum coarse gravel cover values than

subpopulations II, III and IV. Subpopulations III and IV had similar mean and variation of coarse gravel cover (subpopulation III mean = 2, sd = 11 and subpopulation IV mean = 2, sd = 13) indicting their similarity. Subpopulation II mean coarse gravel cover was the most similar to subpopulation I, although it was significantly lower and less variable that at subpopulation I due to there being lower maximum cover despite both subpopulations having the same minimum cover. Subpopulation III was characterized by significantly high mean cover of medium gravel, and a narrowest range of higher cover values (38-62%) across the subpopulation, despite having the same minimum cover and variation (sd = 13) as subpopulations IV (sd = 15) and V (sd = 14) (Table 1.2.4 and Table E-5). Subpopulations III, IV and V had low variability in medium gravel, as did subpopulation II (sd =34), which had the lowest mean cover (20%). Despite having the same mean cover as subpopulation III (29%), subpopulation I had a similar wide range of medium gavel cover values as subpopulation II (0-88%), but with lower variability (sd = 19).

Both subpopulations I and II where characterized by high mean cover of fine gravel (Table E-5). Subpopulation I had the highest mean cover (39%), widest range of cover (0-88%) and highest variability (sd= 19) of any subpopulation. Subpopulation II had the second highest mean cover of fine gravel (34%) but higher minimum and lower maximum (10-62%) and less variation (sd = 18) than subpopulation I (Table 1.2.4 and Table E-5). In contrast subpopulations IV and V had low mean cover, range and variation in fine gravel cover, while subpopulation III was characterized by its medium mean cover, range and variability of fine gravel. These patterns in fine gravel composition are the inverse of spatial patterns in coarse gravel, with decreasing fine gravel cover moving east to west along the ridge and subpopulation III representing a “medium” between the high and low ranges established by subpopulations I/II and IV/V. Subpopulation II is characterized by its significantly higher mean, maximum, and variation of

very fine gravel compared to all other subpopulations (mean = 45%, range = 0-88%, sd = 32). Fine and very fine gravel components made up the majority (80%) of the total mean cover of this subpopulation, in significant contrast to all other subpopulations including subpopulation I which had the second highest mean cover of these two components (45%). Mean cover of very fine gravel components did not exceed 10% in any other subpopulation, although subpopulation IV had a wide range of cover values (0-62%) and the second highest standard deviation (17) despite having low mean cover.

In summary, subpopulation I was characterized by a high proportion of fine gravel, the presence of all rock fragment types, and high overall variation in rock fragment composition (mean sd = 10.7) (Table 1.2.5 and E-5). Subpopulation II was characterized by a high proportion of fine and very fine gravel and higher cover of stone and very fine gravel components compared to all other rock fragment types and the highest overall variation in rock fragment composition (mean sd = 15.3). Subpopulation III is characterized by a high proportion of medium gravel and medium proportion of fine gravel and low variation in rock fragment composition (mean sd = 6.9). Subpopulation IV is characterized by a high proportion of cobble cover and high variation in rock fragment composition (mean sd = 10). Subpopulation V is characterized by a high proportion of coarse gravel and low variation in rock fragment composition (mean sd = 6.6).

Vegetation Characteristics

Although significant differences in *E. codium* cover were not found between subpopulations, some similarities and differences in mean, range and standard deviation highlight patterns reflected in other habitat characteristics (Fig 1.2.6, Table 1.2.5).

Table 1.2.5 PERMANOVA of Vegetation Characteristics Relationship by Subpopulation and Transect
PERMANOVA results and pairwise comparisons indicate no significant differences in vegetation composition between subpopulations I, II and V (p = >0.05) while significant differences were determined between subpopulations III and IV and all other subpopulations (p = < 0.05). Significant differences in *E. codium* cover were determined between sampling transect 1.3 in subpopulation I and sampling transect 5.1 in subpopulations V. Significant differences in leaf area index (LAI) were determined between subpopulations I and V (p= 0.01).

Subpopulation Differences in Vegetation Characteristics[1]

Vegetation Characteristics (n=72)	**Df**	**R2**	**F**	**Pr(>F)**	
Subpopulation					
Leaf Area Index[2]	1	0.0440	3.13	0.014	**
Species Richness	4	0.2919	8.01	0.001	***
Total Cover	4	0.2946	8.14	0.001	***
ERCO Cover	4	0.0287	0.59	0.679	
Vegetation Composition	4	0.2468	5.59	0.001	***
Transect					
Leaf Area Index[2]	5	0.0582	0.83	0.553	
Species Richness	6	0.1526	2.79	0.019	**
Total Cover	6	0.1538	2.83	0.016	**
ERCO Cover	6	0.2274	3.11	0.016	**
Vegetation Composition	6	0.0797	1.20	0.282	

[1] Subpopulation and transect effects analyized in a single model assesing terms independently and sequentially

[2] LAI analyized for Subpopulations 1 and 5 only (n=71)

Subpopulations I and II had highest mean cover, subpopulations III and V also had similarly high mean cover, and subpopulation IV had the lowest mean cover and the lowest standard deviation (Table E-6). All subpopulations had a maximum *E. codium* cover of 20% except subpopulation I, which has a maximum cover of 37.5%. Only subpopulations I and V had minimum cover values of 0.5%, and subpopulation I had the highest standard deviation, indicting the most variation in *E. codium* cover across the subpopulation. While subpopulation III had a minimum of 3% *E. codium* cover, subpopulations II and IV had minimums of 10% cover, making the total range of cover across both these populations extremely low. *E. codium* cover was consistent within subpopulations and between the majority of sampling transects (Fig J-1). However, significant

differences were determined between sampling transect 1.3 in subpopulation I and sampling transect 5.1 in subpopulations V (Table 1.2.5 and Fig J-1). This indicates that habitat characteristics at sampling transect 1.3 are the most optimal for *E. codium* growth and abundance, while habitat characteristics at sampling transect 5.1 are likely the "least-optimal" for *E. codium* growth.

Significant differences in leaf area index (LAI) were determined between subpopulations I and V (p= 0.01) (Table 1.2.5). Subpopulation I had significantly larger mean, maximum value and standard deviation, indicating larger variation within this subpopulation (Fig 1.2.7 and Table E-6). Mean and maximum LAI values from subpopulation V were extremely small, indicating little to no canopy cover across the subpopulation. LAI of subpopulation I was also small but consistent with the low LAI values around 0.03 – 0.53 typical in deserts and dryland

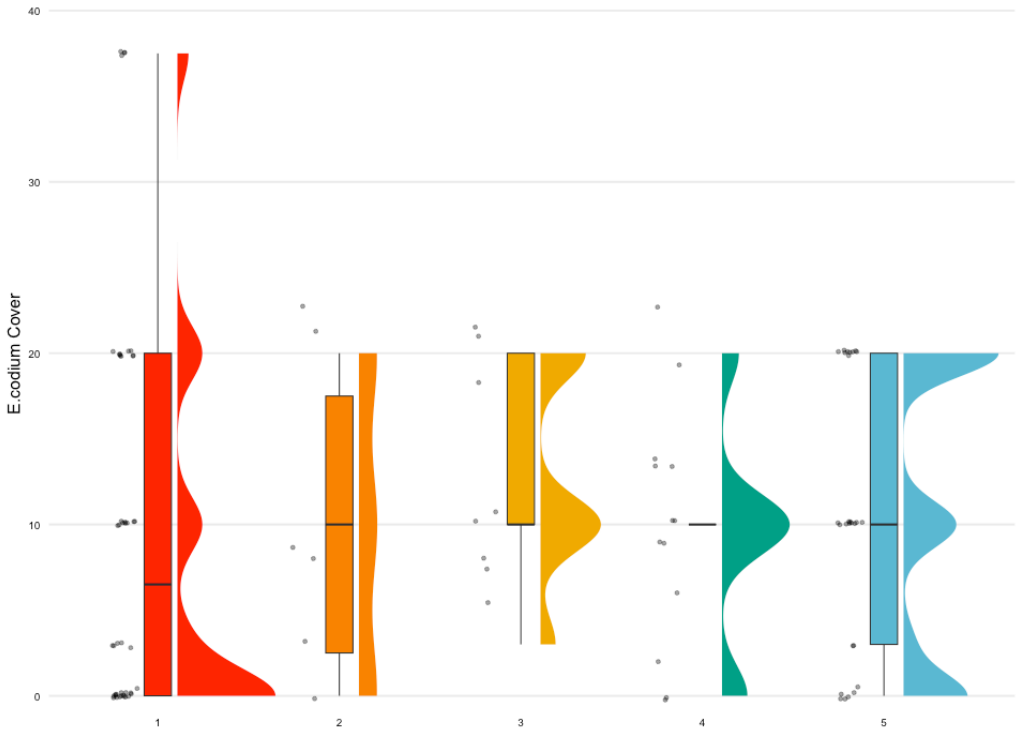


Figure 1.2.6 Raincloud Plot of *E. codium* Cover by Subpopulation
No significant differences in *E. codium* cover were determined between subpopulations. Subpopulations I and II had highest mean cover, subpopulations III and V also had similarly high mean cover, and subpopulation IV had the lowest mean cover and the lowest standard deviation.

systems and expected in low sagebrush and lithosol communities in the sage-brush steppe (Clark and Seyfried 2001). The majority of measured LAI values in subpopulation I are <0.05 with over half of the values <0.025, indicating the majority of the site had very sparse canopy cover similar to subpopulation V. However, the presence of two plots with LAI values >0.075 combined with the higher variation in LAI values between 0-0.05 suggests there is more variation in vegetation community productivity in subpopulation I than in subpopulation V (Fig 1.2.7 and Table E-6). During data collection of LAI at subpopulation V, the ceptometer would register a LAI reading of 0 even when cover and shading of plants was observed, indicating potential issues with the ceptometer and unreliable LAI data collected at subpopulation V. The extent to which the maximum LAI at subpopulation V may actually reflect maximum values at subpopulation I remains unclear.

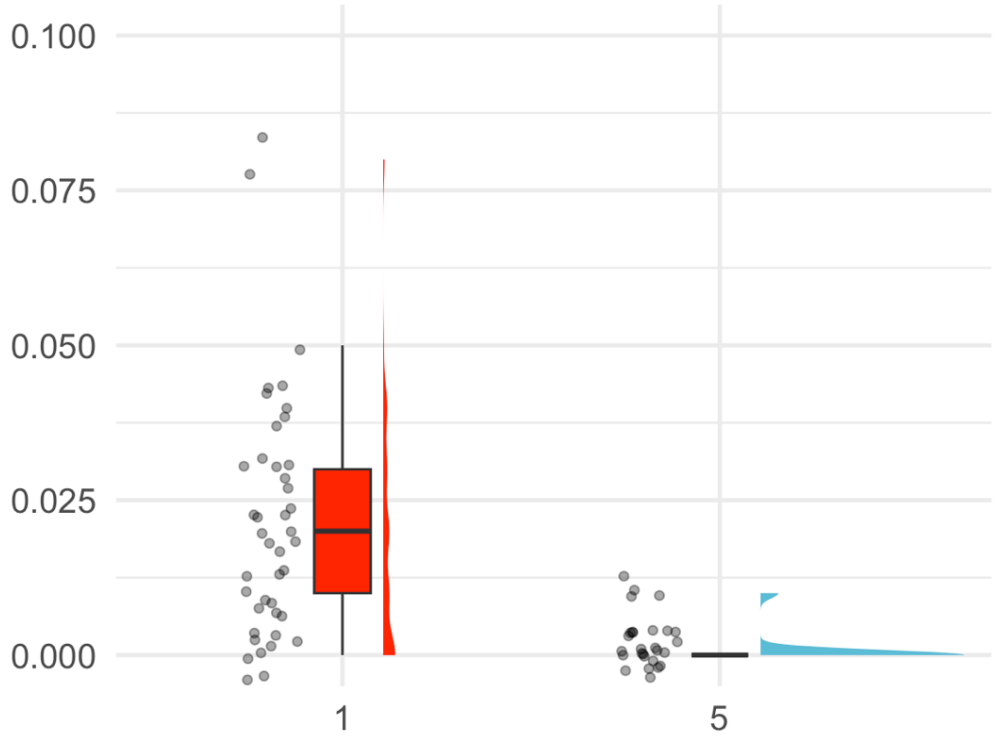


Figure 1.2.7 Raincloud Plots of Leaf Area Index (LAI) at Subpopulations I and V
Mean and maximum LAI values from subpopulation V were extremely small, indicating little to no canopy cover across the subpopulation. LAI of subpopulation I was also small but consistent with the low LAI values 0.03-0.53 typical in deserts and dryland systems and expected in low sage-brush and lithosol communities in the sage-brush steppe (Clark and Seyfried 2001).

PERMANOVA results and pairwise comparisons indicate no significant differences in vegetation composition between subpopulations I, II and V ($p = >0.05$) while significant differences were determined between subpopulations III and IV and all other subpopulations ($p = <0.05$) (Table 1.2.5 and Fig D-3). These patterns in vegetation composition mirror patterns in mean *E. codium* cover and relationships between subpopulations observed in site and soil habitat characteristics. NMDS ordination of vegetation composition shows the largest clustering of variation within all subpopulations inside the hull of subpopulation I, indicating all subpopulations to some extent reflect the wide range of "optimal" *E. codium* vegetation habitat that exists within subpopulation I (Fig 1.2.9). Both subpopulations III and IV extend beyond the hull of subpopulation I into separate but overlapping areas within the ordination space. This separation reflects the significant differences found between subpopulations III and IV, in contrast to the similarity of the other three subpopulations, represented in the ordination space by the clustering of subpopulations II and V within the hull of subpopulation I.

Despite significant differences in vegetation composition, species richness and total cover between all subpopulations ($p = 0.001$), pairwise comparisons found no difference between subpopulations I and V ($p = > 0.05$) (Table 1.2.5 and Fig D-3). Both subpopulations have a low mean species richness of approximately three species and low total cover around 30%, with maximum species richness ranging from five species in subpopulation V to seven species in subpopulation I (Fig 1.2.8 and Table E-6). Both vegetation communities were characterized by low species diversity and sparse vegetation cover, with subpopulation V only reaching a maximum cover of 40%. Although subpopulation I maximum cover (64%) and species richness is slightly higher than subpopulation V, it is accompanied by a larger standard deviation and the

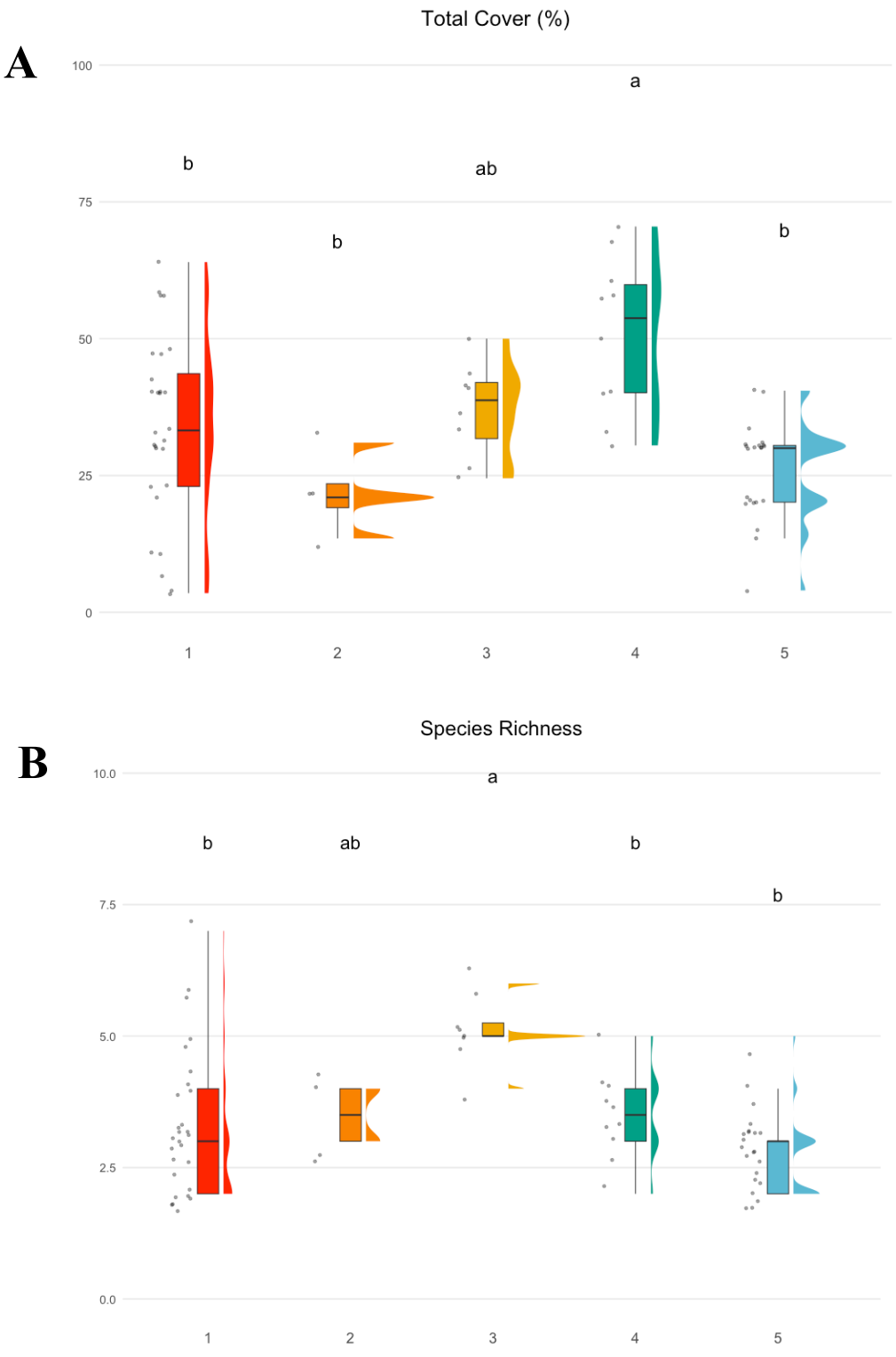


Figure 1.2.8 Raincloud Plots of Species Richness and Total Cover by Subpopulation
Differences in total cover (A) and species richness (B) by subpopulation where *E. codium* is present (n= 72). Subpopulation III is the only subpopulation to have both significantly higher mean spices richness and total cover than subpopulations I and V, indicating it is more productive, diverse, and "less-optimal". While subpopulation IV has the same species richness as subpopulations I, II and V, it has significantly higher cover than all other subpopulations including subpopulation III, making it the most productive, diverse and "least-optimal" vegetation habitat for *E. codium* within the native population.

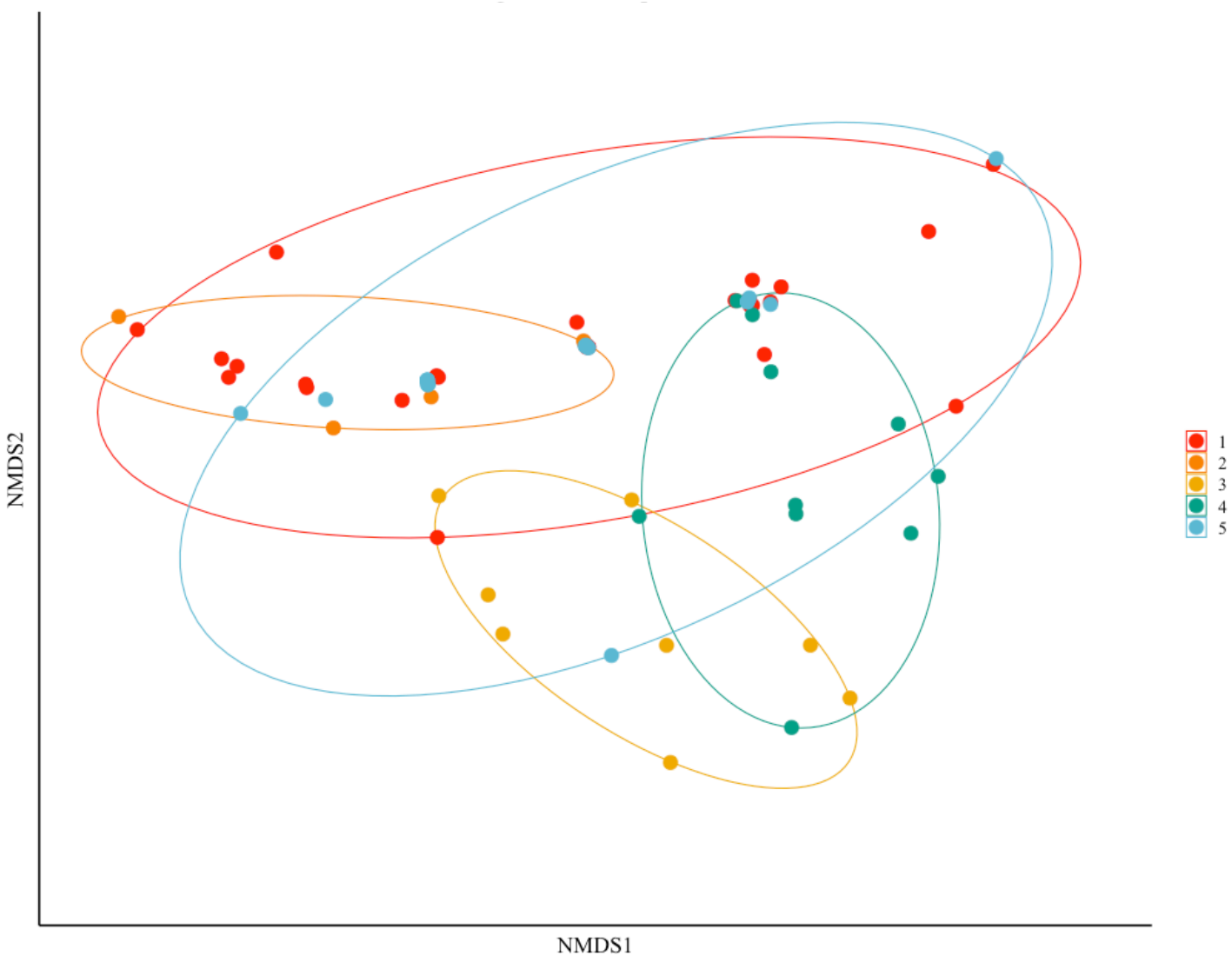


Figure 1.2.9 NMDS Ordination of Vegetation Composition by Subpopulation and Transect
Non-metric multidimensional scaling (NMDS) ordination of vegetation composition (k =3, stress = 0.057) where *E. codium* is present (n= 72). Points are coded by color to correspond to subpopulation. Each point represents a $1m^2$ plot. Points closer together are more similar to than those farther apart.

same minimum values as subpopulation V, indicating subpopulation I contains a wider range and variability of total cover and species richness.

These patterns are mirrored by patterns in *E. codium* cover. Mean *E. codium* cover ranges between 13-16% in both subpopulations, with higher maximum cover occurring in population (37.5%) than in subpopulation V (20%), reflecting WNHP population data for the species and known differences between the subpopulations (Fig 2, Fig 1.2.6, Fig 1.2.8 and Table 1.1, E-6).

Subpopulation V has a lower standard deviation and smaller range of cover values, while the variability of *E. codium* was higher in subpopulation I. ISA analysis indicated no individual species characterizes the vegetation communities at either subpopulation I or V, and *E. codium* is the only species to characterize the vegetation communities where it occurs (Table 1.1.5). *E. codium* makes up on average 46% of the mean total cover at subpopulation I and 51% at subpopulation V (Table E-6).

Subpopulations I and V each contained unique vegetation composition dynamics not observed in the other subpopulation. However, some of these dynamics were present at other subpopulations. These relationships are shown in the NMDS ordination of vegetation composition, in which the majority of subpopulation V's hull is encompassed by subpopulation I, but both hulls extend beyond their areas of overlap to encompass aspects of the other three subpopulations (Fig 1.29). More broadly, this indicates that the significantly different

Table 1.2.6 ISA of Vegetation Composition by Subpopulation and Transect
Vegetation species that most characterize subpopulations and individual transects within subpopulations where *E. codium* is present (n= 72). Subpopulations III and IV are characterized by the presence of the native perennial graminoid species Bluebunch wheatgrass (*Pseudoroegneria spicata*). Subpopulation IV is also characterized by the Sandburg's bluegrass (*Poa secunda*) despite this species co-occurring with *E. codium* in every sampled plot. Invasive annual graminoid Cheatgrass (*Bromus tectorum*) has invaded subpopulations II and V and should be the focus on management efforts. IV_{ii} values reported in Appendix G.

ISA of Vegetation Composition (n=72)

Species	Classical	Multiple Group	Simplified
Subpopulation			
Amsinckia retrorsa	2	—	—
Astragalus caricinus	—	—	3
Bromus tectorum	—	2+5	2+3+5
Poa secunda	4	—	—
Pseudoegneria spicata	3	3+4	2+3+4
Transect			
Astragalus caricinus	—	1.1+ 3.1+ 5.3	—
Bromus tectorum	5.1	2.1+ 5.1+ 5.3	—
Pseudoegneria spicata	3.1	3.1+ 4.1+ 4.2	1.1+ 2.1+ 3.1+ 4.1+ 4.2

variation in vegetation composition present at subpopulations II-IV constitute unique “vegetation community types” that are subsets of the variation in community composition present at subpopulations I and V. Subpopulation IV was distinguished by its significantly higher minimum (30.5%), maximum (70.5%) and mean total cover (50.8%) than all other subpopulations (Table E-6). While subpopulation IV has a similar mean and range of species richness (mean= 3.5, range =2-5) to subpopulations I, II and V despite having significantly higher mean cover, subpopulation III is the only subpopulation to have both significantly higher mean spices richness (5.12) and total cover (37.12%) than subpopulations I and V (subpopulation I: 3.36/33.79%, subpopulation V: 2.86/26.02%) (Fig 1.2.8).

Pairwise ADONIS results indicate that subpopulation II hosts the same “optimal” vegetation habitat type as subpopulations I and V in the areas *E. codium* is able to occupy (Fig D-3). This can be seen in the NMDS ordination where the entirety of subpopulation II’s vegetation composition is intermixed with a portion of the variation within subpopulation I, and a portion of this area is also intermixed with a portion of subpopulation V (Fig 1.2.9). Likewise, where subpopulation IV overlaps with subpopulations I and V is separated from where subpopulations I and V overlap with subpopulation II, indicating variation within subpopulations II and IV occupy different areas within the range of variation found within subpopulations I and V.

Part III: Defining "Optimal" and "Less-Optimal" Habitat Groups via Cluster Analysis

Six Cluster Analysis Groups Based on Composition of Vegetation Functional Group

Agglomerative, hierarchical cluster analysis was performed to identify groups of plots based on vegetation functional group composition: shrub, subshrub, perennial forb, annual forb, perennial graminid and annual graminoid cover (Fig 1.3.1). Visual assessment of a scree plot and dendrograms showed six groups (a-f) best characterized the variation in functional group composition between plots (Fig K-1). Mean, range and standard deviation of each vegetation functional group was determined for each cluster analysis grouping, and groups were characterized by mean and range of subshrub (i.e. *E. codium*) cover (Fig 1.3.2 and Table 1.3.1). *E. codium* abundance was significantly different between cluster groups ($p = 0.001$ $F = 41.8$ $R^2 = 0.374$) (Fig 1.3.2). Patterns of separation and branching within dendrograms indicate functional group similarities between groups "a" and "b", groups "c" and "d", and groups "e" and "f" (Fig 1.3.1).

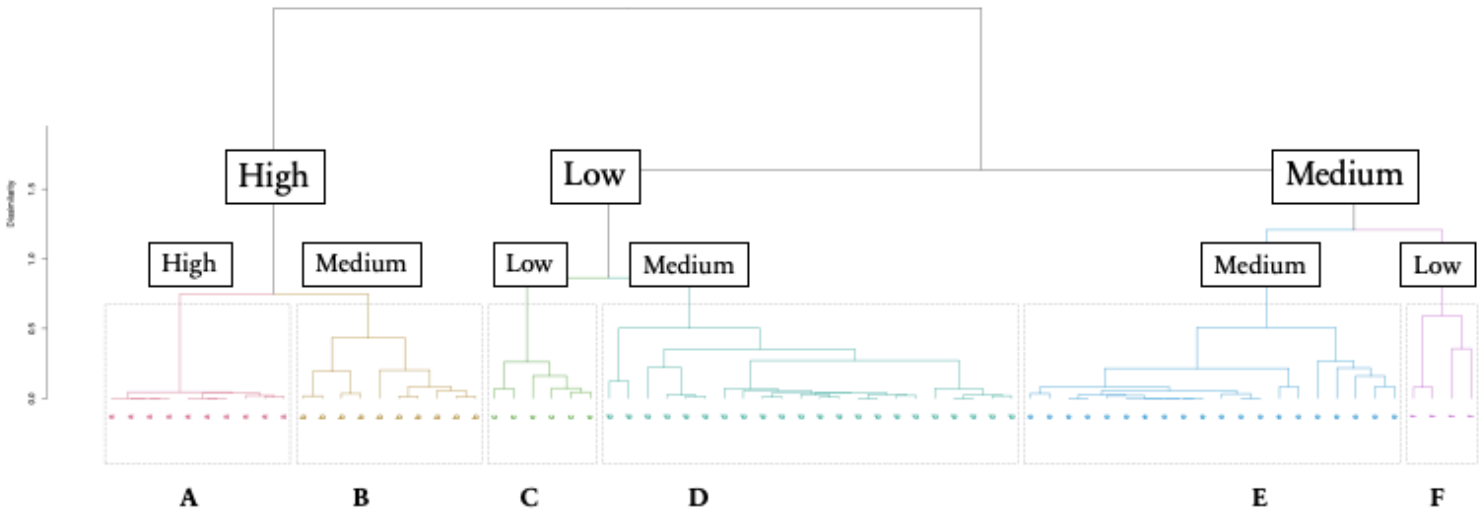


Figure 1.3.1 Dendrogram of Cluster Analysis Groups Based on Vegetation Functional Group Composition
Cluster analysis based on vegetational functional group composition resulted in three groups related to high, medium and low *E.* codium cover were created by agglomerating six cluster analysis groups of different high, medium and low "optimal" *E. codium* vegetation habitats. Group identity of relationship to *E. codium* abundance (high, medium, low) is indicated for six cluster groups (A-F). Three cluster analysis groups are labeled based on relationship to *E. codium* abundance (high, medium, low).

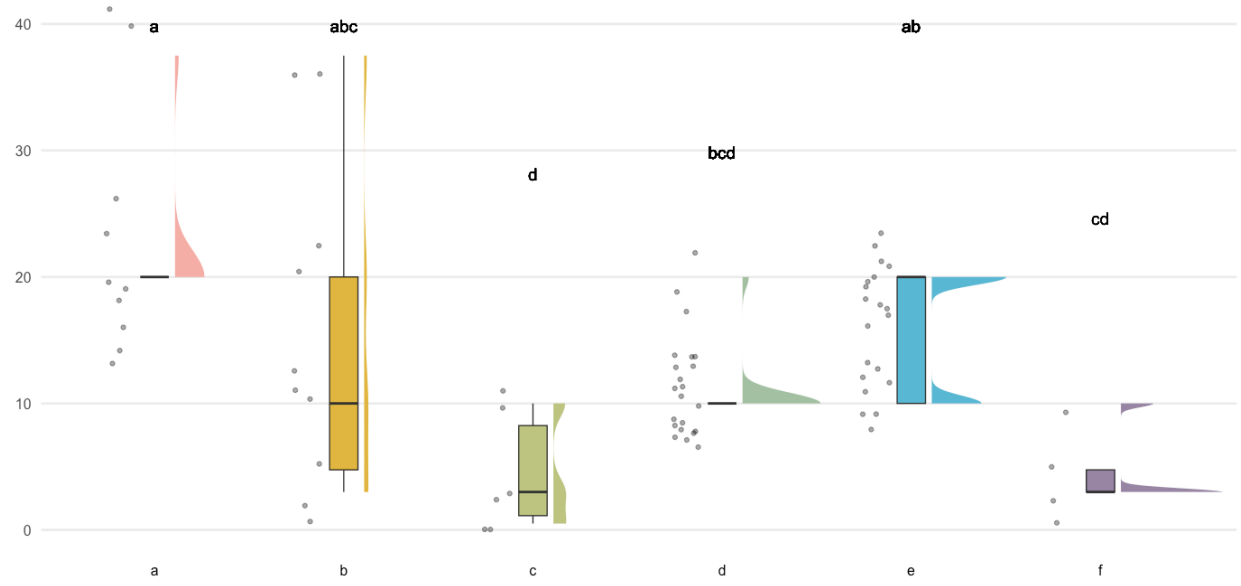


Figure 1.3.2 Differences in *E. codium* Abundance Between Six Cluster Analysis Groups Based on Vegetation Functional Group Composition
Six cluster analysis groups based on differences in veegation functional group composition were characterized by signincant differnecs in mean and range of subshrub (i.e. *E. codium*) cover. Groups (a-f) are asocaited with high (a), medium (b, d, e) and low (c, f) abundance of *E. codium*. Groups represent "optimal" and "less" optimal habitat types that occure within three distinct prennial gramminoid vegeation community types.

Group "a" accounted for 14% of plots, and was characterized as a "high" *E. codium* abundance group as it had the highest mean and minimum *E. codium* cover of all the cluster analysis groups (mean= 23.5%, min = 20%) and contained the largest number of plots with the highest maximum cover of *E. codium* recorded (37.5%) (Fig 1.3.2 and Table 1.3.1). This group represents the *E. codium* – perennial graminoid habitat association, containing <1% forb and annual graminoid cover and moderate perennial graminoid cover (mean = 12%, range = 10-20%), and best characterizes the most "optimal" habitat type for *E. codium* growth and abundance. Groups "b", "d" and "e" were characterized as "medium" *E. codium* cover groups, as these groups contained mean cover between 11-16%. Both groups "d" and "e" had higher minimum *E. codium* cover values (min = 10%) compared to group "b", and narrower cover ranges but lower maximum cover values (max = 20%). Groups "d" and "e" each accounted for ~30% of plots and together account for ~60% of plots surveyed. Group "b" accounted for 14%

Table 1.3.1 Summary of Vegetation Functional Group Cover Characterizing Six Cluster Analysis Groups
Differences in mean, minimum/maximum (range), and standard deviation (sd) of vegetation functional group cover between cluster analysis groups. Grouping of optimal *E. codium* vegetation habitat are separated into high, medium, low based on subshrub (i.e. *E. codium*) cover values. Groups a/b represent low perennial graminoid community types with a moderate to low perennial graminoid cover habitat type (group a) associated with high *E. codium* abundance, and a low/bare perennial graminoid cover habitat group (group b) associated with medium *E. codium* abundance. Groups c/d represent a high perennial graminoid community type with low perennial forb cover, with a group associated with medium *E. codium* cover and perennial graminoids cover <50% (group d) and a group associated with low *E. codium* cover and perennial graminoid cover <60% (group c). Groups e/f represent a moderate perennial graminoid community type with moderate perennial forb cover, with a group associated with medium *E. codium* cover and perennial forb cover <10% (group e), and a group associated with low *E. codium* cover and perennial forb cover <20% (group f).

		Shrub			Subshrub			Perennial Forb			Annual Forb			Perennial Graminoid			Annual Graminoid		
Grouping	n	Mean	Range	sd	Mean	Range	sd	Mean	Range	sd	Mean	Range	sd	Mean	Range	sd	Mean	Range	sd
a	10	0.00	0-0	0.00	23.50	20-37.5	7.38	0.05	0-0.5	0.16	0.05	0-0.5	0.16	12.05	10-20	4.19	0.25	0-0.5	0.26
b	10	0.00	0-0	0.00	15.40	3-37.5	13.20	0.00	0-0	0.00	0.05	0-0.5	0.16	3.25	0.5-10	3.75	0.15	0-0.5	0.24
c	6	0.00	0-0	0.00	4.50	0.5-10	4.40	1.17	0-3.5	1.63	0.17	0-0.5	0.26	29.67	10-57.5	18.50	0.08	0-0.5	0.20
d	22	0.91	0-10	2.94	11.36	10-20	3.51	0.84	0-3.5	1.38	0.57	0-10	2.12	25.75	20-47.5	8.37	0.11	0-0.5	0.21
e	20	0.03	0-0.5	0.11	16.00	10-20	5.03	1.40	0-10	2.63	0.50	0-6	1.34	15.45	10-30	5.77	0.15	0-0.5	0.24
f	4	0.00	0-0	0.00	4.75	3-10	3.50	10.00	3-20.5	7.65	0.00	0-0	0.00	11.62	0.5-30	13.39	0.75	0-3	1.50

of plots and shared the highest maximum cover of *E. codium* recorded (37.5%) with group “a” and had similar patterns of low (<1%) forb and annual graminoid cover and moderate perennial graminoid cover (range = 0.5 -10%). In addition to subshrub cover, minimum and mean perennial graminoid cover was also lower in group “b” than in group “a”.

In contrast, groups “d” and “e” represent *E. codium* habitat characterized by forb-perennial graminoid communities (Table 1.3.1). This included higher maximum cover values of both perennial and annual forbs than in groups “a” and “b”, combined with relatively high perennial graminoid cover. Mean and maximum perennial graminoid cover was particularly high in group “d”, which had a mean cover of 25% and a maximum cover of 47.5% Group “d” also had the highest maximum cover of annual forbs (max = 10%), while group “e” had a similarly high maximum cover of perennial forbs (max = 10%). Shrub cover was also only present in groups “d” and “e” and was highest in group “d” with a maximum cover of 10%. Groups “c” and

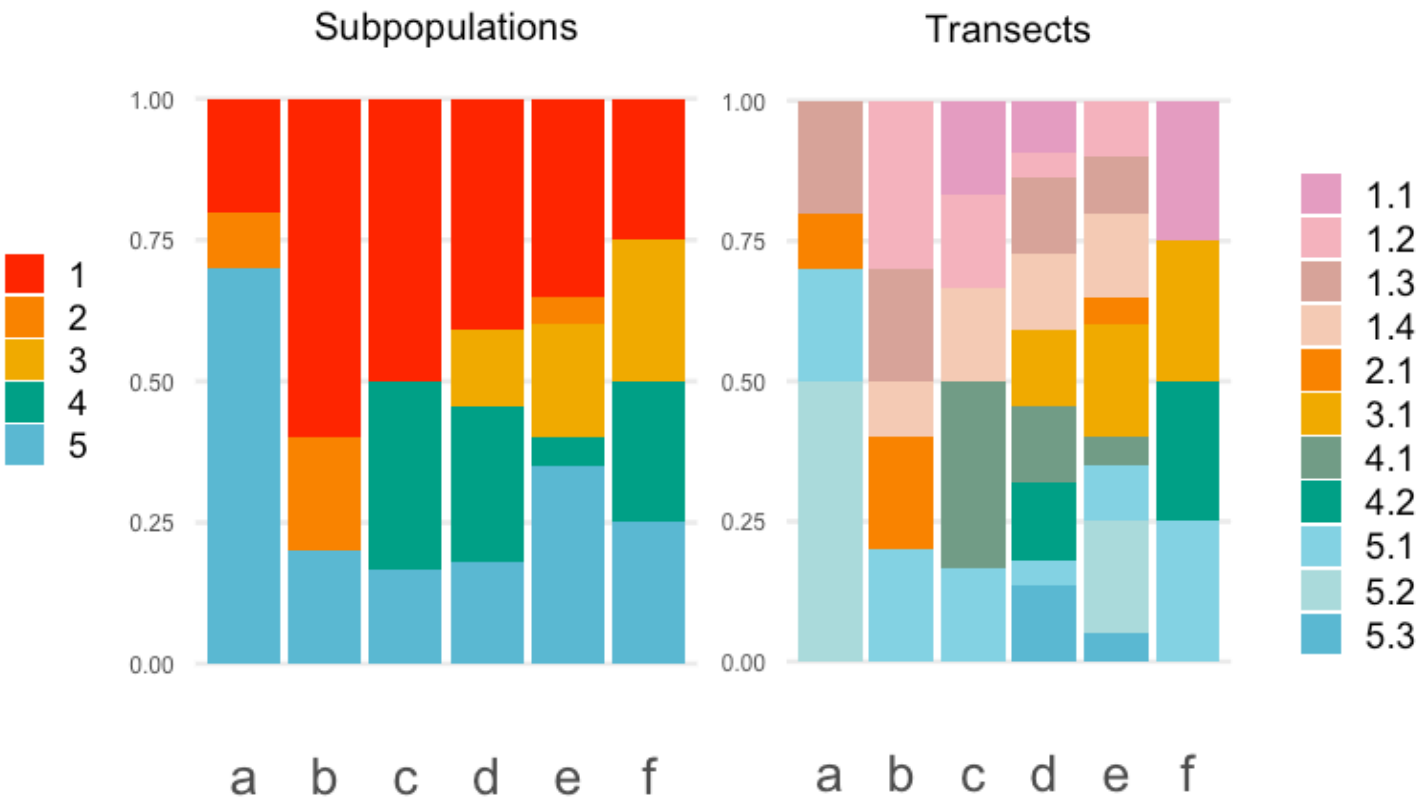


Figure 1.3.3 Differences in Subpopulation and Sampling Transact Identity Between Six Cluster Analysis Groups Based on Vegetation Functional Group Composition
PERMANOVA results indicate significant (0 = 0.01) differences in subpopulation identity while Tukey test was unable to determine any pairwise differences. Largest remaining subpopulations I and V include plots from all six habitat types, indicating high spatial heterogeneity within subpopulations and the presence of "optimal" and "less-optimal" microhabitats. Group a, associated with the highest abundance of *E. codium* is comprised of plots from subpopulations I, II and V. Groups associated with low cover contains plots from subpopulations I, III, IV, and V, indicating subpopulations III and IV host "less-optimal" habitat than subpopulations I, II, and V.

"f" were charactered as "low" *E. codium* cover groups as they had the lowest *E. codium* abundance, with mean cover of ~4% and maximum cover of 10%. The lowest number of plots are represented by these groups, with each group accounting for 8% or less of surveyed plots. Group "c" had the highest mean and maximum perennial graminoid cover (max = 57.5%) of any group, and a relatively high mean cover of perennial forbs while group "f" had moderate perennial graminoid cover and the highest mean and maximum cover of perennial forbs (mean = 10%, mx = 20.5%).

The proportion of plots from the five *E. codium* subpopulations were significantly different between cluster analysis groups ($p = 0.011$, $F = 3.58$, $R^2 = 0.18$), however, no pairwise

differences were determined (Fig 1.3.3). Groups “a” and “b” both exclusively contained plots from subpopulations I, II and V, with group “a” containing the highest proportion of plots from subpopulation V and while group “b” contained the highest proportion of plots from subpopulation I. Both medium *E. codium* abundance groups “d” and “e”, and low *E. codium* abundance groups “c” and “f” contained plots from subpopulation IV while only groups d-f contained plots from subpopulation III. Only group “e” contained plots from all five subpopulations including II, III and IV while group “c” contained plots from only I, IV, and V. Significant differences in the proportion of plots from the eleven different sampling transects was not determined ($p > 0.05$), although transect 1.1 was only included in the “medium” *E. codium* group “d” and the “low” *E. codium* groups “c” and “f”, while transect 5.3 was only present in “medium” groups “d” and “e”. Both transects 4.1 and 4.2 were included in the “medium” group “d”, while 4.1 was the only subpopulation IX transect included in the “low” abundance group “c” and 4.2 was the only transect included in the “low” abundance group “e”.

Three Cluster Analysis Groups Form “Optimal” E. codium Vegetation Habitat Types

Visual assessment of a scree plot and dendrograms showed that the six cluster analysis groups characterizing differences in functional group composition and *E. codium* abundance could instead be considered as three groups (1-3), each comprised of two of the six cluster analysis groups (Figure 1.3.1 and Fig K-1). By selecting a lower level of dissimilarity between cluster analysis groups, group identities based on differences (high, medium, low) in mean, minimum and maximum subshrub (i.e. *E. codium*) cover could be assigned and highly “optimal”, medium “optimal”, and low “optimal” vegetation habitat types could be compared (Fig 1.3.4-A and Table 1.3.2). The optimal-high group (cluster group 3) was comprised of cluster groups “a” or the

"high abundance" group, and group "b" a medium abundance group. The optimal- medium group (cluster group 1) was comprised of group "e" the medium abundance group and group "f" the low abundance group (Fig 1.3.1). The optimal- low group (cluster group 2) was comprised of the low abundance group "c" and the medium abundance group "d". The optimal-high group had the highest mean *E. codium* cover (20%), while the optimal-medium group had 14% cover and the optimal-low group had the lowest (10%) cover (Figure 1.3.4-B and Table 1.3.2). Significant differences in *E. codium* cover ($p = 0.05$ $F= 3.8$ $R^2 = 0.051$) were determined between cluster analysis groups and pairwise comparison of groups indicated significant differences between optimal-high and optimal-low groups, while the optimal-medium group reflected both high and low groups.

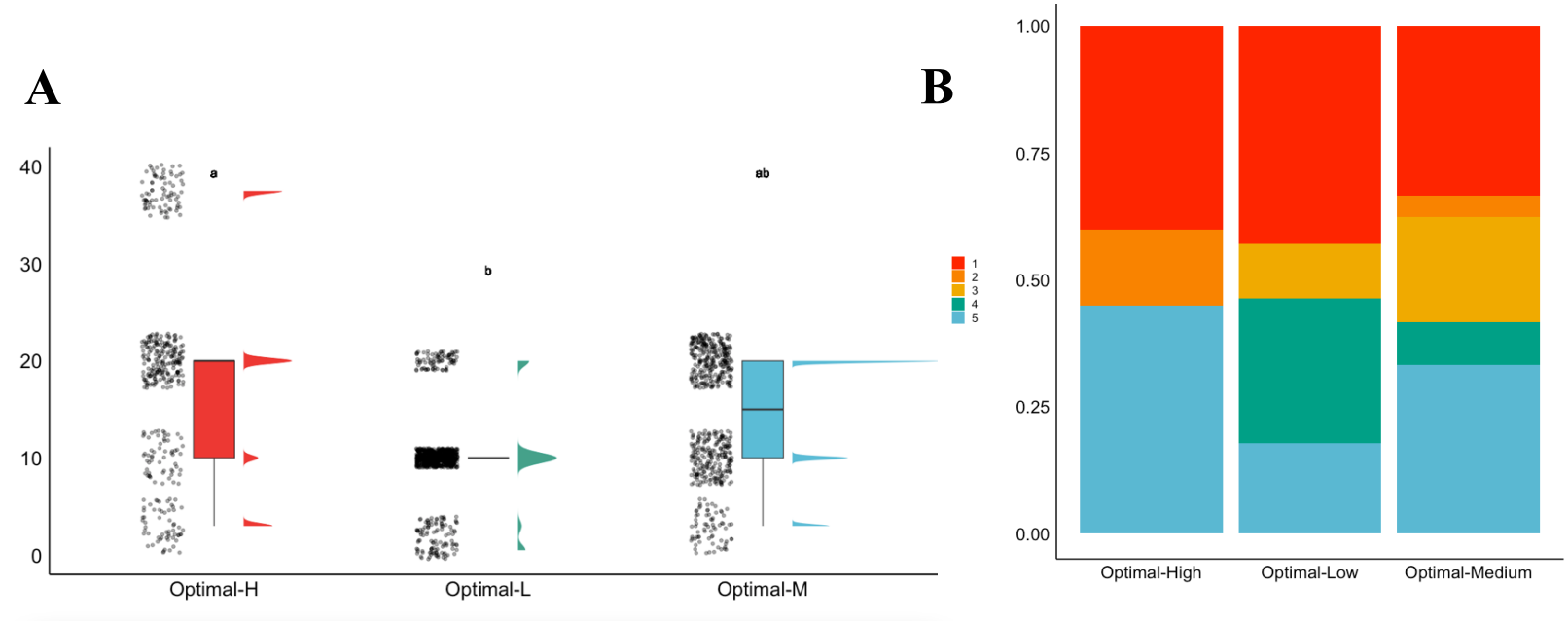


Figure 1.3.4 Differences in *E. codium* Abundance and Subpopulation Identity Between Three Cluster Analysis Groups Based on Vegetation Functional Group Composition
Raincloud plots of *E. codium* abundance asocaited with each group (A) and bar graph of cluster anlysis groups's subpopulation idenity (B). Three cluster analysis groups based on differences in vegation functional group composition were characterized by signincant differnecs in mean and range of subshrub (i.e. *E. codium*) cover (A). Groups (1-3) are associated with high (1), medium (3) and low (2) abundance of *E. codium*. Groups represent "optimal" and "less" optimal habitat types that occure within three distinct vegeation community types characterized by prennial gramminoid cover: High cover (group 2- low *E. codium* abundance), moderate cover (group 3- medium *E. codium* abundance), and low cover (group 1- high *E.* codium abundance). No significant difference in subppoulation idenity was determined between cluster anlysis groups, indicatng these groups best represent the habitat hertogenaity across the whole population (B).

The optimal-high group did not contain any shrub cover and mean and maximum shrub cover in the optimal-medium group was very low (mean = 0.02% max= 0.5%) (Table 1.3.2). The optimal-low group had the highest mean and maximum shrub cover (mean= 0.7% max= 10%) and the highest mean and maximum perennial graminoid cover (mean = 27%, max = 58%). Perennial graminoid cover was the lowest in the optimal-high group (mean = 7.7%, max= 20%). The optimal-high group has the lowest cover of all other vegetation functional groups, including mean perennial forb, annual forb and graminoid cover of <1% and a maximum cover of 0.5%.

The optimal-medium group has a higher mean and maximum perennial forb cover, a slightly higher mean and higher maximum annual graminoid cover, and similar mean and maximum annual forb cover as the optimal-low group (Table 1.3.2). PERMANOVA results indicated similarities in subpopulation identity between cluster analysis groups ($p = 0.119$, $F= 1.85$, $R^2= 0.01$). Boxplot of subpopulation identity indicated relatively even numbers of plots from subpopulation I and V in all cluster analysis groups (Figure 1.3.4-B). The optimal-low group has a larger number of plots from subpopulation I than optimal-high and optimal-medium groups, and a lower number form subpopulation V. The optimal-high group contains the largest number of plots from subpopulation II, with one plot from this subpopulation also assigned to the

Table 1.3.2 Summary of Vegetation Functional Group Cover Characterizing Three Cluster Analysis Groups
Differences in mean, minimum/maximum (range), and standard deviation (sd) of vegetation functional group cover between cluster analysis groups. Grouping of optimal *E. codium* vegetation community types are separated into high, medium, low based on subshrub (i.e. *E. codium*) cover values. The optimal-high *E. codium* habitat group represents a low cover perennial graminoid community type, the optimal-medium *E. codium* habitat group represents a moderate cover perennial graminoid community type, and the optimal-low *E. codium* habitat group represents a high cover perennial graminoid community type.

		Shrub			Subshrub			Perennial Forb			Annual Forb			Perennial Graminoid			Annual Graminoid		
Grouping	**n**	Mean	Range	sd	Mean	Range	sd	Mean	Range	sd	Mean	Range	sd	Mean	Range	sd	Mean	Range	sd
Optimal-High	20	0.00	0-0	0.00	19.45	3-37.5	11.21	0.03	0-0.5	0.11	0.05	0-0.5	0.15	7.65	0.5-20	5.95	0.20	0-0.5	0.25
Optimal-Low	28	0.71	0-10	2.62	9.89	0.5-20	4.63	0.91	0-3.5	1.41	0.48	0-10	1.88	26.59	10-57.5	10.98	0.11	0-0.5	0.21
Optimal-Medium	24	0.02	0-0.5	0.10	14.12	3-20	6.39	2.83	0-20.5	4.91	0.42	0-6	1.23	14.81	0.5-30	7.28	0.25	0-3	0.63

optimal-medium group. The optimal-low group contains the largest number of plots form subpopulation IV, while the optimal-medium group contains the largest number of plots from subpopulation III. Plots from subpopulations III and IV are not included in the optimal-high group. The 72 plots where *E. codium* was present at the native site utilized in this analysis were split relatively evenly between the three groups. The optimal-low group contained the largest number of plots (n= 28) while the optimal-high group contained the smallest number of plots (n= 20) and the optimal-medium group contained similar numbers of plots to both groups (n= 24).

Discussion

Part I: Relationship of Site, Soil, and Vegetation Habitat Characteristics to *E. codium* Occurrence and Abundance

Site Characteristics

The significant relationship determined between *E. codium* abundance and heat load index (HLI) may indicate *E. codium* is best able to grow in areas with higher soil temperatures and more direct incident radiation. This is possibly due to the decreased competition with other vegetation species these hotter and presumably drier microclimates afford. However, *E. codium* was less abundant in areas where HLI was closer to 0.9, which may indicate that *E. codium* abundance is most optimal within the higher range of HLI where soil temperature and moisture availability can negatively impact the growth of other species, but before HLI becomes too extreme and negatively impacts *E. codium* growth as well. Further study of the relationship of soil moisture and temperature to differences HLI at the native site, in combination with research aimed at determining *E. codium's* physiological range of tolerance to soil moisture and temperature, could help to further elucidate site HLI's relationship to *E. codium* survival and growth.

Soil Characteristics

The lack of a significant relationships between *E. codium* occurrence and soil hydraulic conductivity, soil surface composition, total rock fragment cover, or soil surface rock fragment composition could indicate these variables have no relationship to determining *E. codium* occurrence. However, as data collection was focused on the areas where *E. codium* is most abundant, and there is no significant relationship between any of these variables and *E. codium's* abundance, the measurements of these soil characteristics likely reflect the range of *E. codium's*

preferred soil "habitat". Although biocrust presence and abundance are not characteristic of the majority of *E. codium* habitat, if *E. codium* is able to tolerate growing with biocrusts, biocrusts are often indicators intact ecosystems not recently impacted by disturbances such as grazing or wildfire, and may be a potential indicator of suitable potential habitat for assisted migration of this species (Belnap and Eldridge 2001).

The weakly significant relationship of *E. codium* occurrence to the only measured soil physical property-surface soil texture- could potentially suggest the "specialist" theory of speciation associated with edaphic endemics at work. However, if this is the case, a stronger relationship (< 0.01) between abundance and soil physical properties would be expected. More extensive data comparing soil texture properties where plants occur to areas directly adjacent to the *E. codium* population where no plants occur is needed to better elucidate to what extent soil texture is impacting where *E. codium* can grow. The significant differences determined in surface soil texture due to the presence of a range of loam soils where *E. codium* is present and sandy clay loam soil where it is absent suggest that *E. codium* grows in loam soils, but grows best in a mixture of loam and sand across a range of ratios. The occurrence of sandy clay loam soils only where *E. codium* is not growing may indicate the presence of clay as an inhibiting textural component affecting *E. codium* occurrence. This would suggest larger soil profile textural patterns and horizonation may play an important role in determining *E. codium* suitable habitat, potentially further indicating an edaphic relationship between *E. codium* occurrence and soil physical properties such as soil texture. Lab based analysis of the soil surface or deeper into the soil profile that can provide quantitative information of the proportion of sand, silt and clay present at the native site that can help to better elucidate both the role of soil texture in determining *E. codium* occurrence and which textures *E. codium* grows best in. Greenhouse

studies aimed at studying varying ratios of loam and sand on *E. codium* germination, survival and growth may also help to better determine *E. codium's* tolerance to textural components and optimal soil texture range.

Vegetation Characteristics

The lack of significant relationships between LAI, species richness, total cover and *E. codium* occurrence indicates that the range of measured LAI, species richness and total cover values represent a low productivity vegetation "habitat" associated with *E. codium.* The significant relationship between vegetation composition and both *E. codium* occurrence and abundance suggests that differences in the species composition even between communities within the same range of LAI, species richness and total cover, are significantly impacting differences in where and how well *E. codium* can grow within its low productivity habitat. These findings suggest that vegetation community dynamics, and specifically competitive interactions between specific species, are likely contributing to patterns in *E. codium*'s occupancy and restriction to the lip of Umtanum Ridge. However, the lack of a significant relationship between *E. codium* occurrence, LAI, species richness, and total cover may indicate these relationships are not due to how diverse the vegetation community is or direct competition for above ground resources such as light, but instead may relate to below ground competition for limiting resources such as soil moisture, or to other species-specific interactions.

Scatter plots visualizing the significant relationship between total cover and *E. codium* abundance ($p = 0.001$), indicate a positive relationship between *E. codium* abundance and total cover (Fig 1.6-C). However, as *E. codium* cover is included in the calculations of total cover for each plot, this relationship is circular and does not constitute a truly significant relationship. Scatter plots comparing total cover and total cover *adjusted* to remove *E. codium* cover from

total cover calculated of all other species present, provides a clearer picture of the relationship between *E. codium* and the "competitive" total cover of other species (Fig 1.6- C+D). When *E. codium* is at an abundance of 10- ~40% cover, there is a negative relationship between adjusted total cover and *E. codium*, indicating increasing cover of other species, and the encroachment and competition from an increased presence of these other vegetation species,

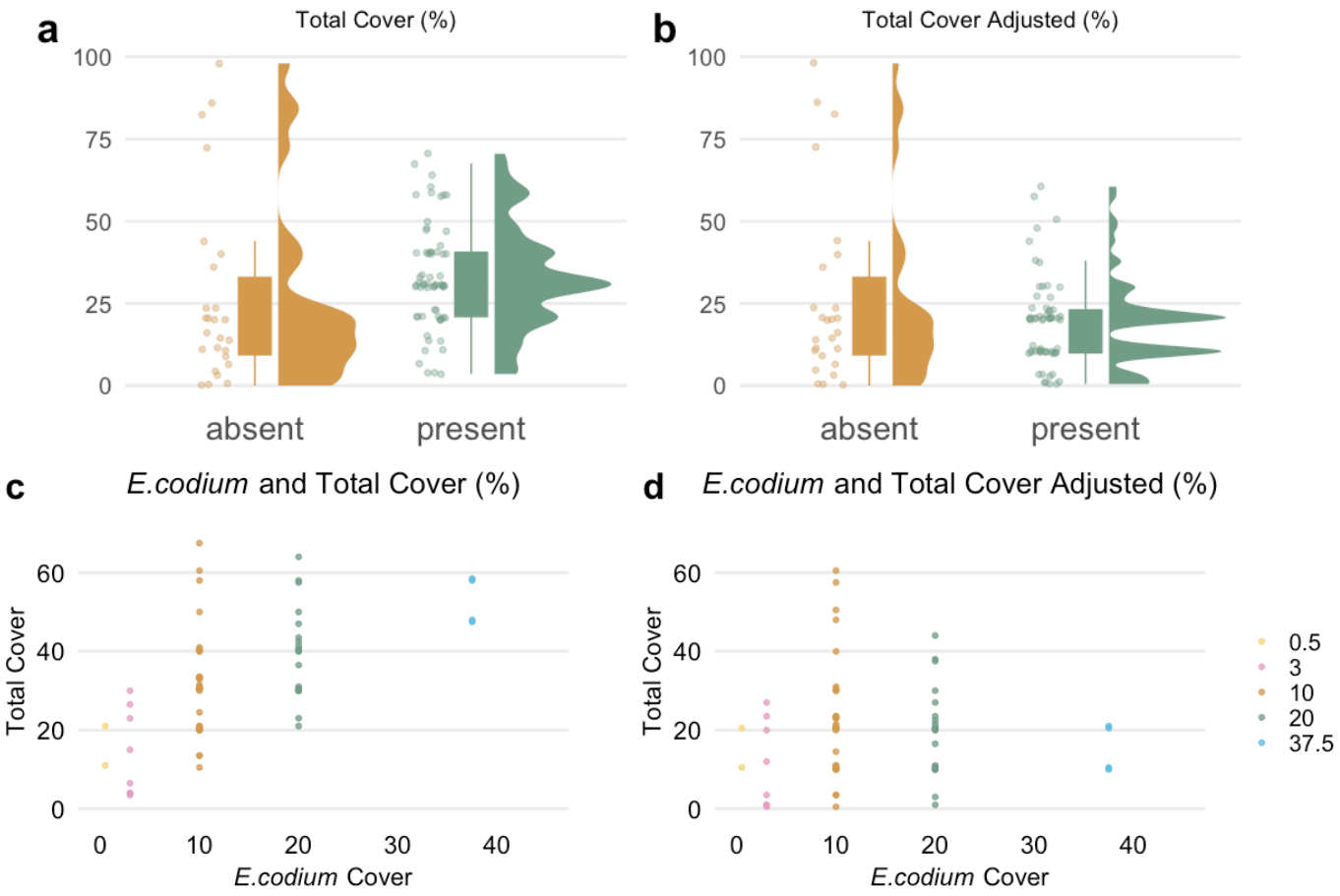


Figure 1.6 Differences in Relationships Between Total Cover and Adjusted Total Cover and *E. codium* Occurrence and Abundance Differences in the relationships of total cover to *E. codium* occurrence (a-b) indicate that the maximum and range in adjusted total cover of other species excluding *E. codium* is slightly lower than the range of values when *E. codium* cover is considered, although neither total cover or adjusted total cover significantly differed where *E. codium* is present vs absent. Differences in the relationships of total cover to *E. codium* abundance indicates that while total cover significantly increased with increasing *E. codium* cover ($p = 0.001$), adjusted total cover and competition with other species is not significantly negatively related to *E. codium* abundance ($p > 0.05$). A relationship between the lowest cover of other species and both the highest and lowest abundance of *E. codium* suggests *E. codium* occupies an extreme habitat niche characterized by low competition of other species.

negatively impacts *E. codium*'s abundance in the already low productivity habitat it currently occupies. Cover of other vegetation species is likely a key driver of *E. codium's* restricted spatial distribution to the most marginal habitats with the lowest inter-species competition, reflecting the generalist theory of speciation and edaphic rarity at work.

Interestingly, the lowest cover of *E. codium* (0.5-3% cover) is also associated with the lowest total cover values, analogous to total cover where *E. codium* is the most abundant (37.5% cover). This pattern of convergence in habitat characteristics between where the highest and lowest abundance of *E. codium* occurs, in contrast to characteristics in the medium abundance range, is consistent and reflected in other habitat variables measured in this study such as the relationship between *E. codium* abundance and heat load (Fig 1.1.3). This pattern further indicates the generalist theory of speciation, as it likely reflects *E. codium's* preference for an extreme environmental niche to minimize interspecies competition. In these areas, *E. codium* is likely able to reach highest abundance under favorable abiotic and biotic conditions that do not exceed its range of physiological tolerance, leading to the highest abundance of *E. codium* cover in these areas.

However, if *E. codium* is unable to tolerate the extreme environment conditions that characterize this extreme, low competition habitat niche, or changing environmental conditions start to push this species beyond its range of tolerance, the same conditions resulting in low inter-species competition likely negatively impact *E. codium* growth and abundance. While occupying an area with low total cover and competition with other species is ideal for maximum abundance, it does not appear to be able to support the majority of the *E. codium* population. The majority of the population appears to be located on areas with varying cover of other species and inter-

species competition, generally limiting *E. codium* abundance to 10-20% cover, but allowing the species to minimize environmental stress enough to persist and survive.

Patterns in low total cover where *E. codium* grows reflect patterns in the NMDS ordination of vegetation composition. Ordinations showings clear separation based on *E. codium* occurrence combined with some separation between vegetation communities where *E. codium* is ≤ 10% cover and where it is > 10% suggests different vegetation communities characterize "more-optimal" and "less-optimal" vegetation communities. However, on the left side of the ordination, plots with <10% *E. codium* cover (0.5%, 3%) and points >10% (20% and 37.5%) are intermixed, indicating some compositional overlap between the lowest and highest abundance groups. This separation in vegetation composition of the highest and lowest abundance groups from the abundance groups in the mid 10-20% cover range mirrors similar patterns in the relationship between heat load index and *E. codium* abundance. This may indicate *E. codium* is able to grow to highest abundance in an extreme habitat niche that is either highly suitable or inhospitable, possible due to site characteristics such as heat load.

The low number of taxa generally observed growing where *E. codium* is present, and the even smaller number of taxa growing to moderate abundance (>15%) where *E. codium* is present, explain ISA results indicating *E. codium* is the singular diagnostic species of where it occurs. The most common species growing with *E. codium* were also ubiquitous across vegetation habitats at Umtanum Ridge. Many species observed outside of *E. codium*'s limited distribution also occurred within *E.* codium's current population in plots where *E. codium* was absent. This further suggests *E. codium* is not growing in specialized edaphic habitat characterized by communities of specially adapted species, but an area where competition with more commend and widespread species is likely minimized.

These results, combined with low cover of woody shrubs, perennial and annual forbs, and annual graminoids in areas where *E. codium* is present, suggest *E. codium* may be the defining species of its own habitat type in a way similar to how sagebrush (*Artemisia*) species or other Buckwheat (*Eriogonum*) species are used to define shrub-steppe communities and habitat types in the Columbia Plateau (Franklin and Dryness 1973, Bryce and James 1997). *Eriogonum* species and their associations with perennial graminoids in particular, are known to characterize communities in other areas in the Columbia Plateau with low diversity and productivity, typically in association with shallow and rocky soils. The *E. codium-P. secunda* habitat types is likely a singular example and a unique form of an *Eriogonum* dominated habitat, fitting into a larger patchwork of *Eriogonum* dominated habitats that characterize this bioregion specifically and the Western U.S more generally.

Sandberg's bluegrass (*Poa secunda*) is one of two perennial native bunchgrass species recorded at the site, and the only species to occur in 100% of the plots occupied by *E. codium* and is likely associated to some extent with "optimal" *E. codium* habitat. The presence of Bluebunch wheatgrass (*Pseudoroegneria spicata*), a perennial native bunch grass, in 30% of plots indicates it also likely associates with *E. codium* and its characteristic habitat type. *E. codium* habitat is likely characterized by its relationship to both native bunch grass species, forming an *E. codium- P. secunda* and an *E. codium- P. secunda-P. spicata* vegetation community and habitat types. However, while the presence of *P. spicata* indicates it likely associates with *E. codium* and its characteristic habitat type to a lesser extent than *P. secunda* , this species is relatively abundant across both the ridge and bioregion in general. The areas where *E. codium* grows in association with *P. spicata* likely constitute the edge of the more productive surrounding vegetation community, where it transitions to the more barren habitat

that *E. codium* occupies. This area may constitute a "less-optimal" habitat for *E. codium* occupancy than areas where *E. codium* only grows in association with *P. secunda.*

E. codium likely favors growing in association with *P. secunda* as this species is commonly found on dry, rocky and marginal lithosol soils, and is a relatively shallow rooted bunch grass, likely minimizing the competition with *E. codium*s' deep woody taproots. *E. codium- P. secunda- P. spicata* likely forms a secondary, less common, and potentially less "optimal" habitat type. Because *P. spicata* is also known to root deeply in order to access underground reserves of water, potentially putting it into competition with *E. codium* (Canadell et al 1996, Harris and Goebel 1976, Zlatnik 1999). While beneficial relationships between deep rooted perennial bunchgrasses such as *P. spicata* and woody shrubs have been recorded for other woody shrub and subshrub species including other *Eriogonum* species, this does not seem to be the case of *E. codium* (Callaway 2007, Brooker 2008). Further field and greenhouse studies exploring the relationships between and effects of co planting with both *P. secunda* and *P. spicata* on *E. codium* establishment, growth and survival may help to better determine to what extent these grass species may positively associate with *E. codium*.

There was a significant negative relationship between *E. codium* occurrence and shrub cover. This relationship suggests that niche overlap and the resulting competition with other species, especially other long lived woody species, could be one of the most important species interactions determining where *E. codium* can grow. Species that occurred in <5% of plots included woody shrubs Purple sage (*Salvia dorii*), Big sagebrush (*Artemisia tridentata*), and Yellow rabbitbrush (*Chrysothamnus viscidiflorus*) which reflects these species' significant negative relationship to *E. codium* occurrence as they likely compete with the vegetation community niche *E. codium* has evolved to fill.

Similarly, species in <10% of plots include one spring annual Thinleaf phacelia (*Phacelia linearis*) and two perennial forbs Canby's biscuitroot (*Lomatium canbyi*) and Arrowleaf balsamroot (*Balsamorhiza sagittata*), both of which are deeply tap rooted species adapted to a variety of moisture limited habitats across the Columbia Plateau and may be competing with *E. codium* as well. Species that occurred in <5% of plots also included leafy perennial forb species such as Longleaf Phlox (*Phlox longifolia*) and Orange globe mallow (*Sphaeralcea munroana*) and spring annuals including Rigid fiddleneck (*Amsinckia retrorsa*), Douglas' dusty maiden (*Chaenactis douglasii*), and Western tansy mustard (*Descurainia pinnata*) which all likely compete with *E. codium* for belowground resources such as vernally available moisture. Ricegrass (*Eriocoma hymenoides*) likewise was recorded in one plot, likely because its cespitose rooting habit competes with *E. codium* for the same spatial niche and resources.

Further data collection aimed at distinguishing what species are present in the areas where *E. codium* is growing in comparison to the adjacent surrounding areas where it does not occur will help to better elucidate to what extent shrub and forb competition may be driving *E. codium* occupancy, and which species pair with *E. codium* to form distinct vegetation and habitat types. Assessment either in the field or a greenhouse setting of the effects of species competition and both above and below ground niche overlap on *E. codium* survival and success are important next steps for better understanding this specie's tolerance to other vegetation species, communities of species, and vegetation functional groups.

ISA results indicating Common Yarrow (*Achillea millefolia*) and Pursh's milkvetch (*Astragalus purshii*) both characterized areas where *E. codium* did not grow, further suggest competition from species specific niche overlaps may be impacting *E. codium's* current confinement to Umtanum Ridge. These interactions are likely apart of more complex interactions

occurring between vegetation community primary productivity and soil characteristics. *E. codium* may be intolerant of the increased competition encountered when growing in the deeper, richer and moistier soils, and the resulting more productive vegetation communities, favored by *A. millefolia*. *E. codium* could also be limited by challenges competing with a high abundance of faster growing perennials such as *A. purshii,* which has a similar mat forming growth habit and thus an above ground spatial niche overlap with *E. codium.*

Finally, the presence of two *Astragalus* species, *A. purshii* and Buckwheat milkvetch *(Astragalus caricinus)* in 10-15% of plots where *E. codium* also occurs, despite *A. purshii* characterizing areas where *E. codium* did not occur, further highlights patterns of common and widespread species growing both in low abundance with *E. codium* and in higher abundance in other vegetation habitats at Umtanum Ridge. This suggests *E. codium* can tolerate these species at relatively low abundances when total cover does not exceed 10% (ASCA and ASPU maximum cover = 10%), but struggles to compete with these more widely adapted species in higher abundance. As *A. purshii* characterized the plots where *E. codium* was absent, but also occurred with a very limited number of other species where *E. codium* was present, it is likely that the relationship between these species is not mutualistic. Growing with *A. purshii* may constitute a less than optimal, and potentially even barley tolerable, habitat type for *E. codium.* These species are likely associated with *E. codium*'s preferred habitat, as both species are known to occur on barren, rocky soils in the arid shrub steppe habitats (NPIP 2020, Slitcher 2023). Their presence may indicate the presence of the low vegetation competition habitat preferred by *E. codium*, and the extent to which *E. codium* can successfully co-exist with them in low productivity habitats should be the focus of further study.

The presence of known noxious weed Russian thistle (*Salsola tragus*) as one of only two species to occur in 15% of plots is concerning as this species is known to compete with and negatively impact native vegetation communities, invading and taking over habitats in the wake of disturbances such as wildfires. *S. tragus* likely invaded in the wake of extensive habitat degradation due to wildfires destroying the original surrounding native vegetation, and is likely currently either invading what was formerly areas of bare ground and/or areas degraded by wildfire. Like *S. tragus*, the presence of Cheatgrass (*Bromus tectorum*) in 30% of plots where *E. codium* occurs indicates the native population is being invaded by this noxious and invasive annual grass as well. This is especially concerning as *B. tectorum* is similar to *S. tragus* in competing with native forbs for vernal moisture and quickly invading and taking over degraded areas. *B. tectorum* also completes its annual life cycle, dies, and dries out by early summer, acting as the fine fuel that feeds and spreads destructive wildfires. As a significant portion of *E. codium's* single population has already been detrimentally affected by wildfire in the past 25 years, the continued presence of *B. tectorum* within the remaining population is concerning. Its presence and cover should be closely monitored, and management should focus on removing this species from the site.

Part II-I: Implications of Similarities and Differences Between Subpopulations and Sampling Transects on *E. codium*'s Current Confinement to Umtanum Ridge

Patterns in E. codium Abundance Across a Range of Habitat Characteristics

The lack of significant variation in *E. codium* cover (mean cover = 9.2-12.8%) between subpopulations indicates the range of variation in habitat characteristics found across all five subpopulations represents *E. codium* "habitat". However, although significant differences in *E. codium* cover were not found between subpopulations, differences in patterns of *E. codium* cover between subpopulations suggest subpopulations I and V may be more "optimal" areas of *E. codium* habitat. Over the past twenty-five years, the population of individual plants at the native site has decreased by 45%. Of the remaining population, subpopulations I and V are the largest and most extensive in terms of number of remaining plants and the total area covered (Table 1.1). These subpopulations are thus thought to be the most productive areas for *E. codium* growth and survival, and likely represent the most "optimal" habitat currently available for study. Subpopulation I had the highest mean (15.5%) and maximum (37.5%) *E. codium* cover and is thought to be the most extensive and abundant of the remaining subpopulations. Although subpopulation V has the second highest mean cover (13.02%) after subpopulations I and II, subpopulation V is significantly larger then subpopulation II, and is thus thought to be a more "optimal" habitat due to the larger total size of the population and the larger number of remaining plants.

The areas within subpopulations II, III, and IV assessed for this study represent remnants of formerly larger and more extensive areas of *E. codium* occupancy (Fig 1.3 and Table 1.1). Although all observed areas where plants occurred across the entirety of subpopulations II and III were not completely surveyed for this study due to time constraints and limited access to the site, WNHP records indicate that subpopulations II, III and IV all extended beyond what is

currently present at the site. The site and soil characteristics of these three subpopulations reflect spatial changes moving east to west along the ridge that also account for some of the habitat differences observed in subpopulations I and V (Fig 1.3). While subpopulations I and V likely remain the most intact representations of "optimal" *E. codium* vegetation habitats and the accompanying range of site and soil characteristics that can host its "optimal" vegetation community type, subpopulations II, III, and IV may be transition zones between these "optimal" habitat types and the inhospitable habitat occupying the majority of the ridge and surrounding the five disjointed subpopulations. Furthermore, as subpopulation IV was formerly joined to subpopulation V by plants that have since disappeared, IV may be a unique habitat type occupied by *E. codium* that formerly gradated into a less "optimal" but still formerly habitable ecotone with subpopulation V as the subpopulations crossed a number of distinct landscape positions. It appears that this ecotone has since become inhospitable to *E. codium* occupancy, possibly in response to lasting effects of wildfires that killed a substantial number of plants and altered the surrounding native vegetation. In this way, subpopulation IV may represent both a less "optimal" but tolerable *E. codium* habitat type occurring in a transition zone between more "optimal" habitats at subpopulations I and V.

While subpopulations I and II had highest mean cover, subpopulations III and V also had similarly high mean cover in contrast to subpopulation IV, which had the lowest mean cover and the lowest standard deviation of all subpopulations. All subpopulations had a maximum *E. codium* cover of 20% except subpopulation I, but while subpopulations I and V both had minimum cover values of 0.5% and thus a wide range of cover values across the subpopulations, subpopulation III had a minimum cover value of 3% while subpopulations II and IV had minimums of 10% cover, making the total range of *E. codium* cover across these subpopulations

extremely low. It is possible that this lack of lower cover values and small range observed in subpopulations II, III and IV could indicate the absence of smaller and thus younger *E. codium* individuals in these subpopulations. This is significant, as the occurrence of younger individuals indicates the subpopulation may have supported *E. codium* seedling germination, growth and survival in the recent past, and may still have the capacity to be colonized by seedlings and young plants in the future under the right conditions. In contrast, the possible presence of only older, larger, mature individuals in subpopulations II and IV especially may indicate the conditions at these subpopulations have not been conducive to successful germination and survival of young seedlings for a long time.

If these subpopulations are no longer hosting young plants and their continued existence is reliant on the survival of adult individuals, then it is likely an important aspect of this habitat has changed in at least the last 100 years to make these areas less hospitable to *E. codium* seedlings survival and long-term occupancy. This further suggests the current conditions at these subpopulations may be less "optimal" habitat for *E. codium* and may not be ideal to mimic for successful assisted migration. Instead, these remanent subpopulations may need to be at the forefront of management efforts at the native site to restore the "optimal" habitat conditions *E. codium* requires for long term success. Demographic studies are an important next step that can help to better elucidate the age structure of the remaining subpopulations, and can guide managers in identifying which subpopulations are most imperiled from long term lack of seedling recruitment and which subpopulations are hosting the youngest plants and thus likely contain the habitat type likely to support the long-term survival of young plants.

Subpopulations I and V Establish a Range of Site and Soil Characteristics That Likely Host "Optimal" E. codium Habitat

E. codium exists across a range of different site and soil habitat conditions. Differences across the range of characteristics that likely constitute "optimal" *E. codium* habitat is highlighted by differences in site and soil surface characteristics at subpopulations I and V. Observed gradients in rock fragment cover and the textural proportions of loam to sand content in surface soils are likely both based on differences in the location and position of these subpopulations on the ridge slope. Differences in site and soil characteristics point to the likelihood of differences in underlaying geology, soil profile composition, and horizonation patterns shaping distinct habitat characteristics found in each subpopulation. While all subpopulations at the native site exist on the same underlaying geological components of rock, silt, sand and clay, their varying distribution across Umtanum Ridge has likely resulted in variable soil profiles that have either directly or indirectly impacted *E. codium* current occurrence across the site. As soil texture was significantly related to *E. codium* occurrence in the areas where it is currently growing, the differing habitats that have evolved at each subpopulation in response to their interaction with site topography, geology, and climatic conditions likely have important evolutionary implications for *E. codium*'s current distribution. Understanding site and soil habitat differences between subpopulations may provide insight into the larger evolutionary drivers of why *E. codium* is only found in certain isolated areas along Umtanum Ridge.

Although no relationship was determined between rock fragment cover classification and soil surface texture where *E. codium* is present ($p > 0.05$, $R^2 = 0.0185$, $F= 0.5902$), a significant relationship was determined between landscape position and soil surface texture, even after variation by subpopulation was accounted for. Spatial differences between subpopulations

account for the ~35% of the variation in soil texture significantly related to subpopulation, while the spatial differences in landscape position accounted for an additional 11% (Subpopulation: $p = 0.001$, $F = 9.9$, $R^2 = 0.347$; landscape position: $p = 0.18$, $F = 3.1$, $R^2 = 0.107$). There is a significant relationship between surface cover and landscape position (14% of variation explained) even after the variation explained by subpopulation (31% of variation) was accounted for (Subpopulation: $p = 0.001$, $F = 12.7$, $R^2 = 0.312$; landscape position: $p = 0.001$, $F = 5.51$ $R^2 = 0.135$). While subpopulation accounted for only 12% of the variation in rock fragment cover classification and no significant relationship to landscape position was determined, the remaining 88% of the variation is still likely due to patterns in soil properties and/or underlaying geology. Ultimately, a better understanding of landscape position, the habitat variability it represents, and its relationship to soil characteristics such as soil texture and rock fragment cover is important for better understanding the variability of habitat characteristics *E. codium* can tolerate.

Significant differences in soil surface texture patterns indicate that subpopulation I may be characterized by the presence of at least two distinct soil habitats, while subpopulation V likely stretches across a gradient of loam derived soils. The overall higher mean rock fragment cover classification, wider range of cover values, and distinct clustering of values either below 50% cover (rubbly) or around 75% cover (very rubbly) suggests two spatially distinct areas with "higher" (~75%) and "lower" (<50%) rock cover at subpopulation I. This could indicate the presence of two "micro-site" habitats within this subpopulation, likely consisting of a rockier habitat type in close proximity to a less rocky ecotone, both of which *E. codium* seems to tolerate growing in. Qualitative observations of variation in habitat characteristics within and around the subpopulation suggest this ecotone likely exists adjacent to a third "habitat type" that does not support *E. codium* growth, and the area that includes subpopulation I likely constitutes a gradient

of key characteristics that range from most optimal to least optimal for *E. codium* growth. In contrast, subpopulation V had a slightly lower mean rock fragment cover class (59% = very rubbly), a significantly higher minimum cover value, and an overall more even distribution of rock classification values between the maximum and minimum, suggesting subpopulation V has a more uniformly "rocky" habitat extending across a variety of landscape positions that distinguishes it from surrounding inhospitable habitat.

Overall, subpopulation I was characterized by a high proportion of rock cover, and more specifically, a high rock to bareground ratio with low overall variability in soil surface composition. Within the rock component of soil surface composition, subpopulation I had significantly high variability of rock fragment composition, including a number of different rock fragment components ranging from large rock fragments such as boulders and stones to small rock fragments including fine and very fine gravel. In contrast and likely due to the wider range of landscape positions encompassed within the subpopulation, subpopulation V had a high bareground to rock ratio and a higher overall variability in soil surface composition. Despite this, subpopulation V was characterized by a more consistent rock fragment composition comprised mostly of coarse gravel, a notable absence of boulders, and significantly lower cover of stones and fine gravel compared to subpopulation I. These findings suggest areas on the upper third of Umtanum ridge's shoulder and summit are likely more constantly rocky with lower ratios of bareground (i.e. subpopulation I), becoming less rocky and more interspersed with bareground moving downslope into the shoulder and backslope of the ridge (i.e. subpopulation V).

While these differences affirm that *E. codium* is able to grow and persist across a range of soil surface and rock fragment characteristics, similarities between subpopulations I and V in mean cover of cobble, medium and very fine gravel components, as well as the dominance of

both rock and bareground at both subpopulations, suggest these soil surface compositional components likely play important roles in determining suitable habitat for *E. codium,* despite the different patterns in variation and minimum/maximum cover that statically distinguish subpopulations I and V. Follow up studies exploring the relationship between changes in soil texture and soil surface and rock fragment cover and composition, on *E. codium* occurrence and abundance along a gradient from where *E. codium* is absent to where it is present would help to better elucidate to what extent rock to bareground ratios, changes in rock fragment composition, and ratios of sand to loam content in soils distinguish *E. codium's* habitat from the surrounding ridge, and if observed "higher" and "lower" rock fragment cover groups are spatially segregated within subpopulations along an ecotone gradient. Exploring relationships between *E. codium* abundance, landscape position, and soil's physical and chemical characteristics[15] can help to further elucidate which of these variables may be impacting *E. codium's* occurrence and determining its suitable habitat.

Subpopulation I had a significantly higher mean HLI than subpopulation V, which is significant as HLI was determined to impact *E. codium* abundance where it occurs. In addition to lower mean and minimum HLI values, subpopulation V also had a wider range of HLI values, which is likely due to differences in aspect. Subpopulation V is predominantly eastern facing, while subpopulation I is predominantly western facing. This suggests subpopulation V receives less direct solar irradiance for most of the day, potentially indicating it may be cooler than subpopulation I with lower average soil temperatures and possibly better soil moisture retention. It is possible that subpopulation V represents a "moister-cooler" "optimal" habitat type while

[15] Variables warranting further exploration include soil profile textural composition and horizonation patterns, soil chemistry (macro/micronutrients and trace elements), soil organic content, and rock fragment composition, and seasonal and annual fluctuation in soil moisture and temperature.

subpopulation I represents a “hotter-drier” “optimal” habitat type. Furthermore, subpopulation I contained a larger proportion of simple microtopography (73%), likely due to this subpopulations position predominately on the upper shoulder of the ridge, while subpopulation V had a more even distribution of simple and complex slope microtopographies across the subpopulation. As microtopographic features have important implications for how water flows and collects as it moves down slope and infiltrates into soil during precipitation and snow melt events. , these results combined with differences in HLI, could further indicate subpopulation I is hotter and drier than subpopulation V. As a significant relationship was determined between the higher HLI values observed at subpopulation I and the highest recorded abundance values of *E. codium* also recorded there, site and soil characteristics that indicate a potentially “hotter-drier” habitat at subpopulation I and “cooler-moisture” habitat at subpopulation V likely have significant implications for understanding what drives *E. codium* occupancy at both sites, and how “optimal” they are.

Although no significant difference in slope shape was determined between subpopulations, patterns in slope shape across the native population and differences in frequency of certain slope shapes within specific subpopulations could likewise indicate important characteristics of how water moves and collects in the areas where *E. codium* is currently growing. Linear and convex micro topographies often shed water while water collects in concave micro topographies. However, the low proportion of concave slope shapes across the entire native population suggests the microtopography where *E. codium* occurs may not be ideal for slowing run off and retaining moistures around *E. codium* plants. While subpopulation I had the largest proportion of linear-linear plots (52%) followed by subpopulation V (37%), the remaining plots in subpopulation I were largely comprised of linear-concave (18%) and linear

convex (7%) plots while subpopulation V had the inverse (linear-convex = 19% linear-concave = 11%). In contrast to observed patterns in HLI and slope complexity, these differences in slope shape suggest subpopulation I may have slightly better microtopographic water retention after precipitation and snow events than subpopulation V, which could potentially account for why *E. codium* achieved higher maximum cover values in this subpopulation compared to subpopulation V. If subpopulation I is hotter, drier, rockier, but also better suited to percolate moisture down into rocky soils, this may favor the deep tap roots that characterize *E. codium's* growth habitat, while selecting against shallower rooted forb and graminoid species. Overall, the general lack of microtopographic variation and soil surface concavity at both subpopulations may be contributing to dry soil moisture and marginal habitat for other vegetation in these areas. However, the lack of a significant relationship between slope shape and *E. codium* suggest any microtopographic effects on moisture availability that may be happening are likely not strong enough to have measurable effects on *E. codium* occurrence or abundance within the areas where it currently grows.

Across the native site, a significant relationship was determined between slope shape and hydraulic conductivity ($p = 0.049$, $F= 2.5483$, $R^2 = 0.199$) indicating microtopography is likely having some impact on the dynamics of how water is moving through the soil profile. A majority of linear and convex slope shapes intermixed with smaller ratios of concave shapes may indicate the presence of dynamic moisture infiltration patterns in some areas, where water is shed from linear and convex areas and collects in concave microsites. These patterns are likely reflective of the soil and geological characteristics of the soil profile, and it is possible that the patterns underlaying the relationship between slope shape and hydraulic conductivity vary at much finer spatial scales than captured by the sampling design of this study. Recorded slope shapes are

based on patterns in the fine-scale micro-topographic variability that are then generalized across each $1m^2$ plot, and qualitative observations made during data collection suggest a high variability of water infiltration dynamics at scales finer than $1m^2$. A better understanding of microtopographic variability and differences in hydraulic conductivity within each $1m^2$ plot, and their relationship to soil horizonation and profile composition, would help to better elucidate these dynamics. However, as neither of these variables showed significant relationships to *E. codium* abundance at the 2-5m scale sampled by this study ($p => 0.05$), to what extent these variables may be impacting *E. codium's* ability to occupy potential habitat at finer spatial scales is unclear.

Similarities and Differences Between Subpopulations II, III and IV Help Define Site and Soil Characteristics Associated with "Optimal" and "Less-Optimal" E. codium Habitat

Through the comparison of site and soil characteristics at different subpopulations with patterns in vegetation community and *E. codium* abundance, conclusions can be drawn about which habitat characteristics may contribute to creating more "optimal" *E. codium* habitat. Like the outlined differences in site and soil characteristics at subpopulations I and V, outlining differences between these subpopulations and subpopulations II, III and IV can further illustrate the range of habitat characteristics *E. codium* can grow on with varying success. By contrasting what is likely more "optimal" habitat characteristics found at subpopulations I and V where *E. codium* is most abundant with habitat characteristics found in the formerly more productive habitat remnants represented by subpopulations II, III and IV, how variation in habitat conditions effect *E. codium's* occupancy of an area may be elucidated. Although these similarities and differences ultimately reflect the dynamic spatial arrangement of these subpopulations along the ridge, understanding the relationships between habitat characteristics at these different

subpopulations can help illustrate the types of evolutionary processes that may be responsible for *E. codium's* current confinement to these locations. Differing patterns of variation in site, soil and vegetation characteristics between subpopulations highlight both the differences that suggest subpopulation IV may be its own unique "less optimal" habitat type outside the range of "optimal" variation established by subpopulations I and V, and the similarities that equally indicate subpopulations II, II and IV are transition zone between the variation observed at subpopulations I and V. Ultimately, as subpopulations II, III, and IV are likely transitions zones encompassing the variability in site and soil characteristics that distinguishes more "optimal" habitats in subpopulations I and V, these subpopulations can provide insights into how *E. codium* responds to the range of habitat conditions that result in less suitable areas for occupancy.

Subpopulation II had the lowest sample size (n=6) and length of transect (12m) but the highest variation in site characteristics over the smallest spatial area. Subpopulation II showed some similarities to subpopulation I in aspect and microtopography, but also mirrored differences between I and the other three subpopulations in terms of rock fragment cover and slope characteristics. Subpopulation II was characterized by differences in HLI compared to all other subpopulations, and had the second highest mean HLI (0.73) and second highest maximum value (0.9) after subpopulation I. Like subpopulations I and III, the dominant soil surface texture was loamy sand, but unlike I and III sandy loam was not present. This suggests a spatial transition in soil texture and an increase in sand content moving east from subpopulation I along the ridge to subpopulation II. The higher overall proportion of plots with sand soils despite the wide range of site characteristics may account for *E. codium*'s higher mean cover at subpopulation II than subpopulations III, IV and V where sandy loam soils are also present. However, more work is

needed to better understand relationships between ratios of sand and loam in site soils, and patterns in *E. codium* site occupancy and abundance.

High topographic variability is likely responsible for the high variability of site characteristics and forms an interesting contrast to the relatively low variability in *E. codium* cover observed. These contrasting patterns affirm patterns observed in subpopulation V indicating *E. codium* can exist consistently at a relatively high abundance across a range of site characteristics. Because subpopulation II contains so much variability over such a small area and *E. codium* cover is particularly high there, it is an important subpopulation for further studies aimed at determining what habitat characteristics differentiate areas of *E. codium* occupancy. As this subpopulation shows contrasting similarities to both subpopulation I and V, it highlights *E. codium's* ability to occupy the range habitat characteristics observed across subpopulations I and V, even when these characteristics are combined in news ways not seen in either subpopulation. Further study of the spatial variability at subpopulation II with a larger sample size could help to better elucidate what is determining *E. codium's* habitat requirements there.

Subpopulation III is characterized by its unique occupancy of the lower third of the ridge's summit and contained a high proportion of complex (88%) to simple and concave-concave microtopographic slope characteristics, suggesting this subpopulation may have better moisture retention. This is also supported by hydraulic conductivity measurements, which show subpopulation IV is one of only two subpopulations where K values <0, indicating soil infiltration at rates expected for the well-draining rock -sandy loam-loamy sandy substate occurring at subpopulation IV. The clustering of slope angle values around 12° (minimum) and 19° (maximum) combined with a low standard deviation indicates that while this subpopulation does not encompass the large slope transitions observed in subpopulation II and V, it does

encompass a smaller topographic transition zone with plants likely running parallel to the ridge along two lines of elevation within the lower third of the summit.

Mean HLI at subpopulation III was similar to subpopulation V, but HLI values clustered around 0.7 and 0.6, further suggesting the existence of two topographically distinct but adjacent areas within this subpopulation. As 0.7 is within the HLI range shared by subpopulations I, and previous results indicate HLI in this range may be significantly related to higher abundance of *E. codium*, these two topographic areas may represent a more "optimal" habitat area adjacent to a less "optimal" area that *E. codium* has historically been able to exploit. This similar pattern has also been observed at subpopulations I and may be a significant insight for understanding *E. codium*'s evolutionary strategy and what determines patterns in site occupancy. It appears *E. codium* is seemingly able to exploit more "optimal" and slightly "less-optimal" adjacent habitat types, resulting in a patchwork of small subpopulations occupying small areas of "optimal" and "less optimal" habitat, surrounded by inhospitable habitat. Further study of subpopulations III is especially important for understanding if and how the range and diversity of site characteristics, and the ways these different characteristics gradate to form ecotones, impact *E. codium* site occupancy and subsequent productivity after site colonization.

As subpopulation III had both unique site characteristics and those similar to both subpopulations I, II, IV, and V, it is the most likely of all the subpopulations to be a transition zone between the differing "optimal" habitats found at subpopulations I and II to the east and habitats found in subpopulation IV and V to the west. This is especially illustrated by the similar proportion of loamy sand (75%) to sandy loam (25%) soils as subpopulation I, despite this subpopulation's large number of similarities in other site characteristics to subpopulation V. Subpopulation III showed similar pattens in mean, range and standard deviation of rock fragment

cover class as subpopulation V. Characterizing subpopulation III as a slightly less optimal but still habitable transition zone between subpopulations I and V may also account for why the range of *E. codium* cover is above the minimum cover values observed in subpopulations I and V, but below the maximum cover observed at subpopulation I, and has a mean cover value (13%) similar to subpopulation V and lower than subpopulations I and II.

Subpopulation IV is the only subpopulation to exclusively occupy the lower third of the shoulder and upper third of the backslope, reflecting its relationship to and former connectivity with subpopulation V, which extends from the shoulders upper third to the upper third of the backslope. It is also the only site to exclusively have only sandy loam soil surface texture. Subpopulation IV has the highest mean slope (0.30 cm/cm) and slope angle (17.36°), and although the range of these values falls within the range of values observed at subpopulation V, subpopulation IV has a narrow range of values, higher minimum, and smaller standard deviation, indicating subpopulation IV is slightly steeper habitat type comprised within the topographic variation observed in subpopulation V. While the majority of slope shapes were linear in all subpopulations except subpopulation II, subpopulations I, IV, and V had higher numbers of different recorded slope shapes than subpopulations II and III. This suggests there may be higher microsite complexity within these subpopulations, and further suggests that water retention may be more dynamic in these areas. In contrast, subpopulations II and III had the lowest variation in slope shape, and likely lowest microsite complexity, which may result in lower microsite variation and more homogenous patterns of moisture infiltration across these two subpopulations.

Subpopulation IV is most likely the coolest, wettest, and least rocky subpopulation occupied by *E. codium*, although further work comparing soil temperature and moisture

differences between subpopulations is important to verify this. While subpopulation IV shows some similarity in site and soil characteristics with subpopulations III and IV, its significantly distinct patterns of variables know to relate to *E. codium* occurrence and abundance (HLI and soil texture) distinguish it as a unique habitat type. Subpopulation IV also has the lowest mean *E. codium* cover (12%) of all subpopulations, high minimum cover (10%), and a narrower range of cover values (maximum = 20%) than subpopulations I and V, and low variation in cover across the subpopulation (Fig 1.2.1 and Table E-6). The combination of increased soil moisture due to low HLI and microtopographic conditions conducive to water retention, and the presence of only sandy loam soils in contrast to all other subpopulations, suggest subpopulation IV may be a slightly less environmentally extreme habitat type than that found in the drier and rocker subpopulations such as subpopulation I. Moister conditions combined with richer soils provide the habitat conditions for more productive vegetation communities which could account for the slightly lower abundance of *E. codium* there, further indicating subpopulation IV is a "less-optimal" but still tolerable habitat type distinct from subpopulation V.

Relationship Between Rock Fragment Composition and E. codium Cover

Overall patterns in rock fragment composition, illustrated by patterns of separation and overlap in the NMDS ordination, highlights ways subpopulations II, III, and IV are transition zones reflecting spatial changes in underlaying geology and site conditions moving east to west along the ridge (Fig 1.2.6-B). In contrast, differences in variability between subpopulations I, IV, and III/V are likely more indicative of larger trends delineating differences between *E. codium* habitat types. This mirroring of the ordination space and geographic space indicates patterns in rock fragment composition are likely reflecting underlaying patterns in geology and topography,

making rock fragment composition potentially a good non-destructive indicator of horizonation patterns occurring deeper in the soil profile.

All subpopulations except subpopulation IV were dominated by some form of gravel: fine gravel at subpopulation I, fine and very fine gravel at subpopulation II, medium and fine gravel at subpopulation III and coarse gravel at subpopulation V. As mean *E. codium* cover was highest in these subpopulations, the presence of gravel in general and especially high cover of fine gravel in particular, could be positively linked to *E. codium* cover. Moving spatially east to west along the ridge, increasing larger gravel sizes dominate subpopulations rock fragment composition, except for at subpopulation IV which breaks this pattern as it contains the highest proportion of cobbles. However, as subpopulation IV occupies a lower landscape position on the mountain slope, it is probable changing patterns in dominant gravel size are present moving vertically east to west along the ridge, while changes in composition of lager rock fragment size classes such as boulder, stone and cobble occurs vertically along elevation gradients.

This indicates that in addition to *E. codium*'s ability to occupy sites dominated by a range of rock to bareground ratios, it can also occupy habitats dominated by a range of different gravel sizes or larger cobbles, although cobbles may be a "less-optimal" habitat. Further study of the effects of different gravel size classes compared to cobble sized rock fragments on *E. codium*'s growth and habitat preference can help to better elucidate to what extent *E. codium* prefers the rock fragment sizes or ratio of sizes found at different subpopulations. The high proportions of gravel components at subpopulations I and V of coarse and fine gravel respectively, may indicate this species prefers rocky soil habitats derived from a range of gravel sizes. However, gravel fragment size may be less important than the interactions of rock fragments below 250mm and other site characteristics such as heat load index, or the dominant

rock fragment composition's impacts on shaping vegetation community dynamics. Controlled greenhouse studies aimed at understanding both the singular effects on gravel size on *E. codium* growth and survival, and interactive effects of rock fragment size on soil temperature and soil moisture, would help to clarify the roles these dynamics play.

Although rock fragment composition was not found to have a direct relationship on *E. codium* abundance ($p = <0.05$), this may be due to the bias of the data collection towards the range of rock fragment compositions found within that bounds of the existing subpopulations that are the most hospitable to *E. codium* occupancy. Additional studies aimed at better comparing differences in rock fragment composition where *E. codium* occurs to areas outside of the existing populations could help better elucidate how directly or indirectly rock fragment composition is diagnostic of "optimal" *E. codium* habitat. The similarities in observed patterns of variation between soil surface rock fragment composition and vegetation composition, such as high variation in subpopulation I in contrast to lower variation in subpopulation V, suggest that there may be a relationship between them. It is likely variation in rock fragment composition is influencing the structure and productivity of the vegetation communities in conjunction with other soil physical and chemical properties, which may be mediating its direct measurable impact on *E. codium* occurrence and abundance in its "optimal" habitat.

Site, Soil and Vegetation Interactions Influencing "Optimal" E. codium Habitat

By adapting to specific areas with high HLI and low spices richness and total cover as a means of avoiding competition, *E. codium* has likely evolved to occupy an extreme HLI niche. This is highlighted by patterns in mean rock fragment cover class and qualitative observations at subpopulation I that suggest *E. codium* occupies an "optimal" habitat type characterized by high HLI, rock cover and low vegetation productivity, adjacent to a "less-optimal" ecotone that

borders habitat unhospitable to *E. codium* growth. Subpopulation I thus likely represents a range in the growth response of *E. codium* to variations in interactions between soil surface cover, rock fragment composition, and vegetation community within its preferred extreme HLI niche. The "optimal" habitat type at this subpopulation is likely a lithosol community on rocky soil that is conducive to simple and sparse vegetation communities dominated by *E. codium*. However, this may ultimately be a risky evolutionary strategy, as occupancy of this extreme environmental niche may be negatively impacting *E. codium's* continued growth and survival in the face of drought and rapid climatic warming. In contrast to the high variability of *E. codium* observed within a narrow range of HLI values at subpopulation I, subpopulation V had a lower standard deviation and smaller range of *E. codium* cover values indicating a more consistent range and distribution of *E. codium* cover across a wider range of HLI values. Patterns in variation at subpopulation V indicate the subpopulation spans across several site and soil conditions that all support a similar, "optimal" vegetation community. Higher mean cover of bareground combined with lower mean total cover, species richness, and *E. codium* cover suggest subpopulation V is less conductive to vegetation cover than subpopulation I. These contrasting patterns shed light on the role HLI plays on creating the extreme environmental conditions *E. codium* has likely evolved to occupy.

HLI was determined to have a weaky significant relationship with vegetation composition when tested both in the areas where *E. codium* is present and absent ($p= 0.02$ $F= 2.66$ $R^2 = 0.027$ $n= 98$) and in the areas where it is only present ($p = 0.45$ $F = 3.04$ $R^2 = 0.042$ $n=72$). As a significant relationship was also determined between *E. codium* cover and HLI, the relationship between HLI and vegetation composition is likely important in shaping habitat suitability for *E. codium* and defining its "optimal" habitat. However, as the higher variability in

vegetation composition at subpopulation I is not reflected in the lower variability of HLI, it is likely the remaining observed variation in vegetation community may be related to interactions with additional habitat variables. Ultimately, observed patterns in vegetation communities are likely responding to complex interactions between HLI and soil properties such as soil surface and rock fragment composition.

TITIAN analysis of soil surface, rock fragment and vegetation compositions relationships to HLI indicate specific components of all of these habitat characteristics are associated with either higher or lower ranges of HLI values. These relationships are consistent with patterns of higher rock to bareground ratios in subpopulation I hosting slightly more productive and diverse vegetation communities and higher maximum *E. codium* cover, while higher bareground to rock ratios observed in subpopulation V hosted slightly less productive and diverse communities, and lower maximum *E. codium* cover. Similarly fine gravel, which also characterized subpopulation I, was determined to be a HLI "decreaser", occurring predominantly in areas with HLI values of 0.65 and below 0.78, while coarse gravel, associated with subpopulation V, was determined to be a HLI "increaser" occurring predominantly in areas with HLI values were around 0.75 and above 0.7. The native perennial forb Canby's biscuitroot (*Lomatium canbyi*) and *E. codium* associated native perennial graminoid *P. spicata* were both determined to be HLI increases above 0.58 and 0.63 respectively.

These significant relationships link *E. codium* variability and abundance to complex interactions between HLI, soil surface, rock fragment and vegetation composition, suggesting that "optimal" and "less-optimal" *E. codium* habitats exists within distinct "lower" and "higher" HLI habitat niches. These HLI niches are likely highly influenced by the synergistic impacts on vegetation composition and productivity interactions between HLI, rock and bareground surface

cover, and the rock fragment components present within the rock cover have. These relationships may also explain why the range and variation of *E. codium* cover and vegetation composition occurred at subpopulation I within a narrow and extreme range of HLI values (0.7-0.9), while the lower maximum and smaller range of *E. codium* cover values at subpopulation V occurred within a wider range of less extreme HLI values (0.5-0.8). As it is likely the interactive effects of these variables are responsible for the low productivity that characterizes *E. codium's* preferred vegetation habitat, *E. codium* may be able to occupy areas where HLI is lower, more variable, and less extreme, but only when soil surface and rock fragment compositions decrease site productivity for other species. The lack of competitive pressures afforded by higher HLI values in these areas may make *E. codium* less successful, constituting habitable but "less-optimal" habitat. Future work should focus on better understanding patterns in surface cover, rock fragment composition and HLI and their interactive relationship to vegetation composition and *E. codium* cover and in areas where *E. codium* is both present and absent. Understanding these complex interactions can help to better determine to what extent these relationships are directly impacting *E. codium* site occupancy and abundance.

Part II-II: Vegetation Characteristics Distinguish "Optimal" and "Less-optimal" *E. codium* Habitat, Supporting the "Generalist" Model of Species' Evolution

Similarities in Vegetation Structure and Composition Between Subpopulations I, II and V Likely Constitute "Optimal" E. codium Habitat

Although differences in site and soil characteristics between subpopulations I and V suggest the existence of two distinct "types" of optimal habitat for *E. codium*, subpopulation I and V are both examples of the same optimal vegetation habitat type required by *E. codium*. Similarities determined in vegetation composition indicate that measured variations in site and soil characteristics between subpopulations I and V represents the range of conditions hospitable to the "optimal" vegetation habitat associated with and dominated by *E. codium*. As significant differences between subpopulations I and V were determined for all site and soil characteristics, this contrasting pattern to their similarities in vegetation characteristics indicates "optimal" *E. codium* habitat is most likely defined by the similar vegetation communities that exists across the range of measured site and soil characteristics present at subpopulations I and V. The vegetation compositional overlap between subpopulations I and V likely constitutes the most "optimal" *E. codium* vegetation habitat, exemplify both the vegetation community associated with *E. codium* and the habitat type defined by *E. codium* occurrence. Further study and focus on these areas within both subpopulations could help to better define the commonalties that make them so optimal for *E. codium* occupancy.

High variability in vegetation community characteristics and *E. codium* abundance at subpopulation I make it an especially good example of the range of vegetation habitat conditions *E. codium* can exist in and their effects on *E. codium* abundance. Subpopulation V had less variable vegetation composition and a more consistent vegetation habitat "type" that is encompassed within the variability of vegetation composition dynamics present at subpopulation

I. At both subpopulations, patterns in *E. codium* abundance mirror larger patterns in vegetation composition, which is significant as vegetation composition was the only measured variable to have a relationship with both *E. codium* occurrence and abundance. Ultimately, these results suggest similar patterns in variability of vegetation composition, and related factors such as species abundance and total cover, are linked to variation in *E. codium* cover. Similarly, subpopulation II had the highest mean cover of *E. codium* after subpopulation I and similar vegetation composition to subpopulations I and V. Site and soil habitat patterns at subpopulation II also consistently reflected characteristics of both "optimal" habitats at subpopulations I and V, suggesting *E. codium*'s ability to reach its highest abundance at subpopulation II is directly linked to the existence in subpopulation II of this preferred "optimal" vegetation habitat type characterized by where subpopulations I, II and V overlap in the NMDS ordination space ().

Differences in Vegetation Structure and Composition Between Subpopulations III and IV Likely Constitute "Less-Optimal" E. codium Habitat

The vegetation composition characterizing the areas of the NMDS ordination space occupied by only subpopulations III and IV likely constitute distinct "less-optimal" but still habitable vegetation types *E. codium* can tolerate but does not thrive in. Although subpopulation IV reflects some of the habitat similarities that characterize subpopulations I and V, significant differences in species composition and the lowest mean *E. codium* cover indicates it is likely characterizing a distinctive vegetation habitat type that is "less-optimal" but still habitable for *E. codium*. The significantly different vegetation composition found at subpopulation IV is consistent with observed differences in key site and soil habitat characteristics and the distinct vegetation habitat "type" likely reflects these unique patterns. Compositional differences in vegetation community seem to reflect the higher moisture retention indicated by the

disproportionately high biocrust (moss) cover characterizing this subpopulation and unique patterns in HLI, soil texture, rock fragment cover and composition, and slope microtopography observed (Fig 1.2.4).

WNHP records show extensive population loss of *E. codium* on both sides of subpopulation IV, indicating the current incarnation of this subpopulation likely occupies the most hospitable remnant habitat in what was presumably formerly a more extensive hospitable area surrounding it. This suggests the area surrounding what is currently subpopulation IV, and especially between subpopulations IV and V, may be comprised of one or several ecotones gradating between what is now two distinct remnant hospitable habitat types: drier/rockier (subpopulation V) and wetter/less rocky (subpopulation IV). Potentially moistier and richer soil conditions at subpopulation IV indicate these potential ecotone areas, while tolerable to *E. codium* occupancy under the right conditions, are also productive enough to support other vegetation communities less adapted to the extreme HLI and high rock composition associated with "optimal" *E. codium* habitat at subpopulations such as I. These ecotone areas seem to have since transitioned away from hosting *E. codium*, likely in the wake of disturbances caused by the two wildfires known to have negatively impacted both *E. codium*'s occupancy at the native site, and the overall integrity of the original surrounding native sagebrush steppe community. It is possible the continuing disappearance of *E. codium* from these areas is a response to post-fire invasion by other vegetation better able to compete for soil moisture such as native perennial or invasive annual species, and thus directly related to wider changes in the surrounding native vegetation. If this is the case, it is important to better understand the variability and range of habitat characteristics such as HLI, soil texture, rock cover and composition, and vegetation composition know to impact *E. codium* occurrence and abundance in these areas. Further study

at both at subpopulations IV and V and the areas between these subpopulations where *E. codium* no longer occurs is important for determining to what extent interactions between wildfire disturbance and competition with other more common, widely adapted, and potentially invasive species may be impacting *E. codium'*s remaining occupancy and associated vegetation habitat. Ultimately, these results highlight the ability of *E. codium* to exist on and exploit different vegetation habitat conditions within a range of key site and soil characteristics.

Significant differences in vegetation composition observed between subpopulation III and the other subpopulations are likely due to this subpopulations position as a transition zone between the range of site and soil habitat characteristics at subpopulation I, IV and V. In particular, the similarities in aspect and slope microtopography that make subpopulation III similar the distinct and "less-optimal" habitat characteristics at subpopulation IV are likely contributing to make subpopulation III's vegetation habitat "less-optimal" as well. Despite this, mean *E. codium* cover is still similar to subpopulation V, likely because of the commonalities in habitat characteristics subpopulation III shares with subpopulation V in particular and subpopulations I and II more generally, including overlaps in vegetation composition. The result is a uniquely "less-optimal" vegetation habitat type somewhere between the "least-optimal" habitat type in subpopulation IV and the "most-optimal" habitats in subpopulations I and V. In the NMDS ordination space, areas of variation within subpopulation V that is separate from subpopulation I is intermixed with subpopulation III, suggesting some of the variation within subpopulations III does exist within the "optimal" range of vegetation composition established by subpopulation V. The overlap in variation between subpopulations III and V may explain why these subpopulations had similar mean *E. codium* cover values despite subpopulations III and V having significantly different vegetation composition. Ultimately, these results suggest there are

likely at least three unique vegetation habitat types defined by *E. codium* occurrence, one that is most "optimal" and two that are "less-optimal".

Although subpopulations III and IV both have unique vegetation compositions, subpopulation III maintains an abundance of *E. codium* similar to subpopulation V despite differences in species richness and total cover. In contrast subpopulation IV has lower mean and range of *E. codium* abundance despite its similarities to subpopulations I, II, and V in spices richness. This is likely due to the lower total cover at subpopulation III compared to subpopulation IV, suggesting that the 17-25% increase in mean total cover that distinguishes subpopulation IV from subpopulations I and V is more impactful on *E. codium* abundance alone than the 3-11% increase in mean total cover combined with the increase in species richness that distinguishes subpopulation III. These results further suggest the generalist model of speciation, and more specifically *E. codium's* apparent need to still minimize competition by growing in areas with low competing cover regardless of how low species richness is.

Total Cover and Species Richness Play Important Roles in Determining "Optimal" and "Less-Optimal" E. codium Habitat

E. codium makes up on average 46% of the mean total cover at subpopulation I and 51% at subpopulation V, both dominating and characterizing the vegetation communities found there. The dominance of *E. codium* in the areas where it grows, in combination with the low overall total cover and species richness that characterizes its "optimal" habitat in both subpopulations I and V despite their site and soil level differences, indicating *E. codium* both is what characterizes its own unique vegetation community type, and requires this unique community type to survive. Occurrence of *E. codium* is characterized by low species richness, with only six other species recorded in 10% or more of plots. Total cover is likely the more important aspects of vegetation

composition determining "optimal" *E. codium* habitat. The observed differences in "optimal" vegetation habitat at subpopulations I, II and V and "less-optimal" vegetation habitats at subpopulations IV and V appear to be mostly related to differences in the total cover of native species associated with *E. codium* habitat.

Prior to extensive wildfires over the past 25 years, the surrounding area was formerly dominated by sage-brush steppe communities characterized by *Artemisia* species. By occupying an extreme ecological and spatial niche challenging for other woody species to occupy, *E. codium* was likely able to avoid competition with them. By utilizing its tolerance to harsh conditions to dominate an area not otherwise occupied by these more widely adapted species, it came to also distinguish its own vegetation community and habitat type. As one of the three species included in mean species richness is *E. codium* itself, *E. codium* only associates on average with two other species in its "optimal" habitat. At most it occurs with between 6-7 other species at a time but often with only one other species (*P. secunda*) especially in subpopulation I. *E. codium's* association with simple and relatively sparse vegetation communities indicate the generalist theory of evolution in which *E. codium* is confined to the areas where environmental conditions allow for low competition with other vegetation species. Subpopulation IV is distinguished by its significantly higher minimum (30.5%), maximum (70.5%) and mean total cover (50.8%) than all other subpopulations, and this significantly higher total cover is likely reflective of the cooler, moister and more productive habitat that likely exists there. Observed patterns in lower *E. codium* occupancy and abundance at subpopulation IV further support the generalist model of speciation, with higher total cover indicating higher competition between other vegetation species and *E. codium*, decreasing *E. codium's* productivity and abundance.

Species Specific Interactions with E. codium

Of six other species recorded in 10% or more of plots where *E. codium* occurred, composition differences between "optimal" and "less-optimal" vegetation habitats were related to significant differences in the cover of the two native perennial graminoid species most closely associated with *E. codium*: *P. secunda* and *P. spicata* (Table G-1). *P. secunda* is the species most closely associated with *E. codium* occurrence and the co-dominate species of its habitat type (Table 1.1.6). While *P. secunda* reached maximum cover (37.5%) in both subpopulations I and IV, cover in subpopulation IV was significantly higher ($p = 0.001$, $F= 27.4$, $R^2= 0.62$) than in all other subpopulations including almost twice the mean cover of subpopulation I (subpopulation I: 15.7%, subpopulation IV: 27%) (Table G-1). *P. secunda* cover at subpopulation IV was so much greater that classical ISA analysis indicated *P. secunda* characterized subpopulation IV's vegetation composition despite this species occurring in all plots at every subpopulation.

Although subpopulation III had similar abundance of *P. secunda* as subpopulations I and V, the highest maximum cover of *P. spicata* (20%) was recorded in both of the "less-optimal" vegetation habitats at subpopulations III and IV and was significantly higher in these subpopulations ($p = 0.001$, $F= 27.4$, $R^2= 0.62$) (Table G-1). *P. spicata* occurred in 11% of plots at subpopulation I, 50% of plots at subpopulation II , and was not recorded in subpopulation V, reaching the highest mean cover (0.32%) in subpopulation I. In contrast it was recorded in 100% of the plots at subpopulation III and 90% of the plots in subpopulation IV. Both subpopulations had similar mean cover (subpopulation III = 8.62%, subpopulation IV, = 8.35%) and multigroup ISA analysis indicated *P. spicata* characterized both subpopulation III and IV's vegetation composition. These results indicate "less-optimal" *E. codium* habitat is characterized by >3% *P. spicata* cover as seen in subpopulation III or both >3% *P. spicata* cover and >20% *P. secunda*

cover as seen in subpopulation IV. This increased cover of both *P. secunda* and *P. spicata* at subpopulation IV is likely why this subpopulation had the lowest mean cover of *E. codium* and affirms that the *E. codium- P. secunda* habitat association is more optimal than the *E. codium- P. secunda- P. spicata* association.

In addition to *P. secunda* and *P. spicata*, *E. codium* seems to be able to tolerate low abundance and occurrence of two native and common forb species in the *Astragalus* genus. *A. purshii* was recorded at subpopulation V in only 5% of plots at extremely low abundance (mean cover = 0.02%), but in higher occurrence (18-25% of plots) and abundance (0.6-0.4% cover) at subpopulations I and III respectively, indicating may associate with *E. codium* in its "less-optimal" vegetation habitat (Table G-1). *A. purshii* is a low growing species that sprouts from a central caudex, and in low abundance may poses minimal above ground competition to *E. codium* cespitose growth habit due to its low and compact growth habit (Oregon Flora). However, this species also produces a woody tap root which may be posing below ground competition with *E. codium*, especially in high abundance (>3%). The occurrence *A. carcinus* at a maximum cover of 3% is both subpopulations I, III and V suggest *E. codium* is likewise able to tolerable the occurrence and low cover of this species in its "less optimal" habitat type. Although this species grows erect and can obtain heights of 30 cm tall when growing in optimal conditions, this species is likewise likely able to co-exist with *E. codium* only in low abundance when its competition for *E. codium*'s above ground and below ground spatial niche is minimal (Oregon Flora). However, its taller and more erect growth habitat compared to *A. purshii* may mean it is a less optimal associate. Although no differences in *A. carcinus* cover was determined between subpopulations, this species occurs in only 5-10% of plots in "optimal" habitats at subpopulations I and V but occurs in 38% of plots in subpopulation III and was identified as

characterizing subpopulation III via simplified ISA analysis. This indicates that while its cover is still low at subpopulation III it has a much higher population density than may be "optimal" for *E. codium*. Although this species is likely not impacting *E. codium* abundance due to its low cover, its increased occurrence at subpopulation III may be contributing to what makes this site "less-optimal" and to why this subpopulation is so much smaller. It also highlights *E. codium's* preference and ability to exploit areas where site and soil conditions restrict growth of other native species. *E. codium* seems able to grow on a continuum with highest productivity in sites with the lowest productivity of any other species and lower productivity in areas productive enough for other species to also grow in considerable quantities.

Classical ISA analysis indicates subpopulation II is significantly characterized by the native annual forb Rigid fiddleneck (*Amsinckia retrorsa*) and was the only subpopulation where this species was present (Table G-1). Although mean cover was only 0.13%, cover ranged from 0-10% indicating *A. retrorsa* site occupancy mirrors the high variability of other measured site and soil conditions at subpopulation II. *E. codium's* ability to occupy this area indicates it can tolerate a range of *A. retrorsa* cover below 10%, but this high variability of cover may also be why this subpopulation, like subpopulations III and IV, has a more restricted occurrence than subpopulations I and V where it is absent. As an early spring annual, *A. retrorsa* likely competes with *E. codium* for vernally available soil moisture which is why *E. codium* may be unable to tolerate more than 10% cover of this species. Although established adult plants may be able to compete with *A. retrorsa*, it is possible competition for moisture in the early spring may be negatively impacting seedling survival after germination. Greenhouse studies exploring the impacts of *P. secunda, P. spacata, A. carcinus, A. purshii* and *A. retrorsa* on *E. codium* survival and productivity under controlled conditions could help to better elucidate whether these

relationships are mutualistic or purely antagonistic, and what abundance thresholds of each species start to negatively impact *E. codium* growth and survival.

The increased presence of native species characterizing the smallest remnant populations while no species except *E. codium* dominates in the two largest and most abundant subpopulations affirms both the generalist model of speciation and that *E. codium* is the dominant species of its own habitat type. While *E. codium* can tolerate ecotones between the barren, rocky areas that characterize its "optimal" habitat and the more productive native shrub steppe communities surrounding it, this habitat is less optimal. *E. codium* appears to only able to truly dominate in large areas where competition from all other species, even the perennial graminoids it associates with, is very low. This is likely why this species is found in the drier conditions afforded by extremely high HLI. Ultimately, it appears all competition and increased cover, even in species *E. codium* can associate with in low frequency and abundance, pose inhospitable competition in more productive areas where these species can reach higher abundance. *E. codium* seems to be both reliant on and defining feature of its own habitat type with an evolutionary strategy to seek the most extreme habitat niche available to avoid competition with other more widely adapted species, resulting in its current confinement to the most extreme dry and rocky habitat niche on the edge of Umtanum Ridge.

Habitat Threats to the E. codium Population

Although seeking an extreme habitat niche to avoid competition may have historically worked enough for *E. codium* to dominate a small and restricted range, the effectiveness of this strategy is under threat from shifting vegetation conditions. The last two species occurring in >10% of plots where *E. codium* occurs are both invasive annuals whose increased presence in the Columbia Plateau bioregion has been linked to the widespread loss of native shrub steppe

vegetation communities. *S. tragus* appears to be spatially segregated to the eastern side of the *E. codium* population, as it was recorded in 18% of plots in subpopulation I and 25% of plots in both subpopulations II and III. This could also indicate the lower occurrence of *E. codium* in subpopulations II and III could be related to their closer proximity to native vegetation and more rapid invasion by *S. tragus*. Although *S. tragus* occurred in 7% less plots in subpopulation I than subpopulations II and III, it has a slightly higher mean (subpopulation I = 0.18%, subpopulation II and III = 0.13%) and maximum cover (subpopulation I = 3%, subpopulation II and III = 0.25%) indicating that while it may be experiencing as less rapid invasion, *S. tragus* is growing in higher abundance and may be invading subpopulation I more aggressively. Furthermore, vegetation composition was recorded in mid-June before *S. tragus* had finished growing to its maximum size and completed its life cycle, which occurs in late summer to fall. *S. tragus* is known to grow to a maximum of three feet (0.9 m) tall and six feet (1.8 m) in diameter forming a large, persistent tumbleweed once dead. This large and aggressive growth habitat could pose a significant competitive pressure on *E. codium* for limited resources like soil moisture.

B. tectorum occurs across the entire extent of the *E. codium* population, in all subpopulations except IV (Table 1.1.6). Multigroup ISA analysis indicates *B. tectorum* characterizes both subpopulations II and V, which had the highest frequencies of plots where it occurred (subpopulation V= 55% of plots, subpopulation II = 50% of plots), indicating this invasion is likely coming predominantly from the inhospitable vegetation communities surrounding the *E. codium* population on both sides (Table 1.2.6). Like *S. tragus, B. tectorum* also occurs in 25% of plots in subpopulation III and has the lowest frequency in subpopulation I (18% of plots). The presence of both of these invasive annual species in subpopulations I, II and III is especially concerning as their combined impacts on the low cover that characterizes *E.*

codium's habitat could be detrimental to its continued survival. This is especially true for subpopulation I, which is the largest and most productive remaining continuous area of the *E. codium* population.

Qualitative observations made during data collection in 2021, 2022 and 2023 and population data from WNHP indicate ~23% decline is occurring across the entire population including in subpopulation I. This may be related to increased competition with these novel invasive species to which *E. codium* is likely not adapted to. Anticipated future increases in summer and winter temperatures and decreases in precipitation and winter snowfall related to global climate shifts will likely exacerbate any competitive stress *E. codium* is already experiencing from the presence of these annual invasive species within its population (Littell et al 2009). This scenario could detrimentally impact future survival and reproduction of *E. codium*, becoming an increasing threat over time as the growing season available for *E. codium* decreases with decreasing available moisture and increasing temperatures. Increases in the fine fuel loads left by these annual species will likewise increase the frequency and intensity of larger fires, fueling continued destruction of the remaining *E. codium* plants and cycles of continued invasion.

Despite co-occurring in three out of five subpopulations, both *S. tragus* and *B. tectorum* were only recorded as co-occurring in 5% of plots in subpopulation I (two plots of 44 sampled), potentially indicating they occupy different environmental habitat niches within the range *E. codium* is able to tolerate. This may be positive in terms of ensuring both species don't co-occur and create a negative synergistic effect on *E. codium* worse than either would do separately, however, it may also indicate that these species could each aggressively invade different parts of *E. codium*'s habitat, further restricting the extent of available habitat more than either would do if

growing together in an isolated area of the population. Greenhouse studies examining the effects of varying levels of competition of *S. tragus* and *B. tectorum*, both individually and in tandem, on *E . codium*'s growth and survival could help to better elucidate the extent to which these invasive annuals may negatively impact the existing *E. codium* population or attempts at establishing additional populations in other locations. This study did not assess the full extent of how abundant *S. tragus* and *B. tectorum* are in the areas where *E. codium* occurs, how similar or different their composition is to the areas around the *E. codium* subpopulation, and how much of a threat these species pose to *E. codium*'s continued occupancy of Umtanum Ridge. Further work assessing the full extent of *S. tragus* and *B. tectorum* occupancy within the *E. codium* population, and management work focused on removing these species from these areas are important to ensure *E. codium* is able to continue occupying its current range into the future.

The higher abundance and cover of *B. tectorum* in subpopulations II and V (Table 1.2.6) indicates the eastern and western edges of the *E. codium* population are at the highest risk from wildfire in the future. *B. tectorus* usually dies back and dries out once its seeds have fully matured in early summer. This remaining dry material is highly flammable and as it matures long before native perennial species mature and enter summer or autumn dormancy, its presence in native shrub steppe communities is altering the timing and occurrence of wildfires with long lasting negative consequences for native plant communities. Although *B. tectorum* growth remains low across the entire population (mean cover < 0.5%), its higher occurrence in subpopulations II and V, and higher mean and maximum cover in subpopulation V especially, indicates wildfire will be most likely to spread from the *B. tectorum* in the surrounding vegetation to both sides of the *E. codium* population, putting these areas at highest risk. As subpopulation V is the only other substantially large area where *E. codium* occurs continuously

besides subpopulation I, and it is the area where *E. codium* is adapted to a wide range of site and soil habitat characteristics, it is important that management of this species focuses on protecting this subpopulation and any genetic diversity it may hold.

Interestingly, subpopulation IV is the only subpopulation where no invasive annual species were recorded despite having the lowest mean cover of *E. codium* and least extreme HLI. This may be due to the higher cover of biocrust and especially the higher moss component which has been linked to decreased annual grass invasion in other drylands systems in the western US (Peterson 2013). If increase biocrust/moss cover is able to help subpopulation IV resist *B. tectorum* invasion and maintain low species richness even as surrounding vegetation becomes unhabitable, then subpopulation IV may characterize a less optimal but still tolerable target habitat for assisted migration. As *B. tectorum* is a widespread and extremely common species that has invaded most areas in the Columbia Plateau, having a model vegetation habitat resistant to *B. tectorum* invasion could help assisted migration efforts. By targeting sites with similar habitat characteristics and 3-20% biocrust and/or moss surface cover be, managers may be able to successfully establish an *E. codium* population away from that native site that is more resilient to *B. tectorum* invasion than subpopulations I and V currently are. Work better understanding *E. codium's* response to moss cover and its impacts on *B. tectorum* could be useful first steps to better understanding biocrusts as an invasive species management tool.

Part III: Defining Optimal *E. codium* Habitat Types

Patterns in Vegetation Functional Group Composition Classify Habitat Differences by Perennial Graminoid Cover and E. codium Abundance

Through the use of agglomerative, hierarchical cluster analysis, observed similarities different in vegetation functional group composition observed across *E. codium's* five subpopulations can be classified, characterized and explored. By assessing the habitat similarities between subpopulations, establishing habitat groupings based on these similarities, and comparing the abundance of *E. codium* and associated habitat characteristics between these groups, "optimal" and "less-optimal" habitat types can be described and utilized as reference habitat to inform habitat selection for assisted migration.

The overarching structure of the cluster analysis groupings are based on the segregation of plots into three classifications, with each corresponding to a different "perennial graminoid community type" characterized by varying abundance of perennial graminoid cover. The second level of structure is based on the segregation of the three "perennial graminoid community types" into two groups based on abundance of *E. codium*, for a total of six groups or "habitat types". Each of the three "graminoid community types" contain one "habitat type" with a significantly higher abundance of *E. codium* and a "habitat type" with a significantly lower abundance of *E. codium*. Each of the six total "habitat types" can be classified as containing either a "high", "medium" or "low" abundance of *E. codium,* i.e. representing high, medium or low "optimal" *E. codium* habitat*. E. codium* habitat is thus comprised of three graminoid community types, each characterized by two distinct habitat types, one which is "more-optimal" and one which is "less-optimal" for *E. codium* abundance.

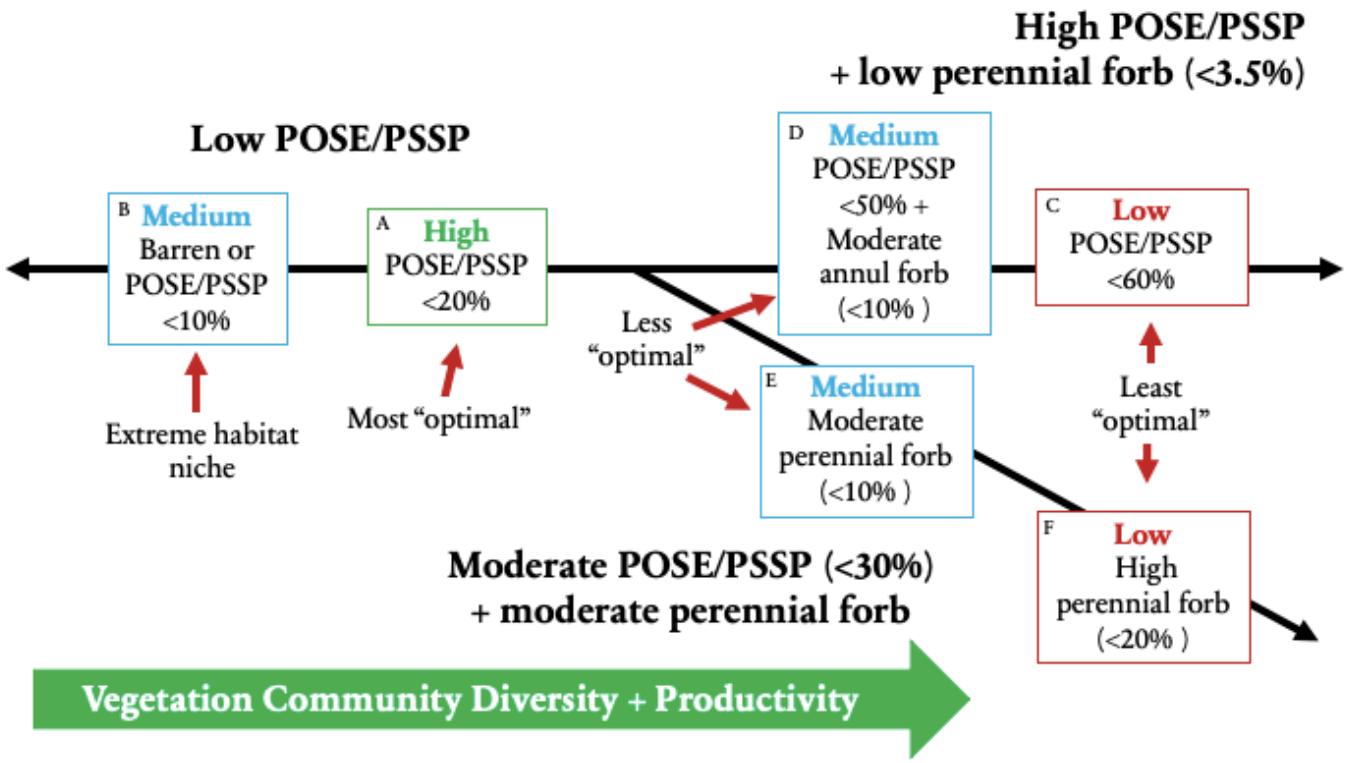


Figure 1.7 Vegetation Community and Habitat Types Occupied by *E. codium*
Cluster analysis of vegetation functional group composition in the areas were *E. codium* is present (n = 72) distinguished three groups (1-3) associated with three distinct perennial graminoid community types: low perennial graminoid community type, moderate perennial graminoid + moderate perennial forb community type, and high perennial graminoid + low perennial forb community type. Sandburg's Bluegrass (*Poa secunda)* (POSE) and Bluebunch wheatgrass (*Pseudoroegneria spicata)* (PSSP) are the main species of perennial graminoids included in perennial graminoid cover. Each community type is composed of two habitat types associated with the six cluster analysis groups A-F, and three levels of *E. codium* abundance (high, medium, and low). Cluster group A is part of the low POSE/PSSP community type, is characterized by moderately low perennial graminoid cover <20%, and is associated with the highest abundance of *E. codium* (i.e. "high" abundance) and represents the most optimal *E. codium* habitat. "Medium" abundance groups in all POSE/PSSP community types represent "less-optimal" *E. codium* habitats associated with either a barren/extreme habitat niche (B), higher perennial graminoid and low annual forb cover (group D), or moderately higher perennial graminoid and forb cover (group E). Habitat suitability decreases with increasing vegetation community diversity and productivity, and habitat types with the highest cover of either perennial graminoid (C) or perennial forb (F) species were associated with the lowest abundance and least optimal *E. codium* habitat types.

"Optimal" E. codium Habitat is Characterized by Low Perennial Graminoid Cover

The "habitat" type associated with the highest abundance of *E. codium* (group A) is a habitat type classified within the "low perennial graminoid cover" community type (Fig 1.7). The "low perennial graminoid cover" community type is characterized by the dominance of *E. codium* in association with low perennial graminoid cover and the relative absence of all other vegetation types. The "low perennial graminoid" community type contains two habitat types, a "high" *E. codium* abundance habitat characterized by "moderately-low" perennial graminoid

cover (<20%) and a "medium" abundance habitat characterized by either "very-low" perennial graminoid cover (<10%) or the complete absence of all other vegetation (group "B"). In contrast to this low perennial graminoid community type, habitat groups in the other two perennial graminoid community types are classified as either "medium" (groups D and E) or "low" (groups C and F) abundance habitats. This indicates the "low perennial graminoid cover" community types is overall the most "optimal" community type where *E. codium* can reach highest abundance, and this "optimal" habitat is characterized by a relative lack of all other vegetation and minimal inter-species competition (i.e. generalist model of evolution).

However, the habitat type associated with the highest abundance of *E. codium* is not the one with the lowest maximum perennial graminoid cover, but the one with moderately low mean perennial graminoid cover ranging from 10-20%. *E. codium* is likely unable to reach highest abundance in the most barren areas because the same extreme environmental conditions that limit competition in these areas likely also make them challenging for *E. codium* to grow in. *E. codium* is able to grow to its highest abundance where conditions are marginal enough to restrict competition with the majority of surrounding species, but not extreme enough to stress plants beyond their physiologically range of tolerance. While the very low perennial graminoid "habitat type" represents one of the most "optimal" perennial graminoid "community types", it likely also constitutes an extreme habitat niche associated with the most challenging environmental conditions on the edges of *E. codium's* physiological range of tolerance, such as extremely high heat load.

The highly optimal "moderately-low" perennial graminoid habitat type was only recorded in 14% of plots, indicating the amount of remaining "optimal" habitat where this species can reach its greatest abundance represents a small amount of its overall remaining habitat.

Furthermore, the most barren "very-low" perennial graminoid habitat type also occurred at an equal frequency (14% of surveyed plots). This indicates *E. codium* is equally tolerating the most marginal and barren "very-low" perennial graminoid habitat type as often as it is able to grow in the slightly more productive "moderately-low" perennial graminoid habitat type it prefers within the low perennial graminoid, high rock and bareground habitat it has adapted to. Combined, both the "high" and "medium" optimal habitat groups within the "low perennial graminoid cover" community type account for almost a third (28%) of *E. codium* habitat measured in this study, further indicating *E. codium's* ability to exploit this marginal habitat and associated extreme environmental conditions are a key evolutionary strategy contributing to its current confinement to Umtanum Ridge

The decline of the population over the past twenty-five years is likely reflective of a general decline in habitat conditions and increasing stress experienced by individuals in these marginal habitat areas. Increased solar radiation and decreased precipitation and winter snowfall resulting from anthropogenic induced climatic shifts have likely further exacerbated the marginal to extreme environmental condition in these habitats, pushing individuals beyond their range of physiological tolerance to key environmental variables. While *E. codium* is currently dominating areas that few other plants can tolerate growing in, these areas are of particular conservation concern as they represent areas of the native population most vulnerable to the adverse impacts of changing environmental conditions such as increasing drought and climatic warming.

"Less-optimal" E. codium habitat is characterized by moderate to high perennial graminoid cover and moderate to low presence of forbs

The "low perennial graminoid cover" community type contained the only "high" abundance habitat group, while the "moderate" and high" graminoid cover community types

each contained habitat types associated with “medium” and a “low” *E. codium* abundance, indicating these two graminoid community types constitute “less-optimal” habitat *E. codium* is able to tolerate but likely does not thrive in (Fig 1.7). Each graminoid community types is characterized by varying abundance of perennial graminoid cover >20% and the presence of forb species largely absent from the “optimal” habitat. “Optimal” and “less-optimal” *E. codium* habitat appears to exist along a continuum of site productivity and vegetation community diversity, with the more optimal habitat types providing moderate to low competition with perennial forbs and graminoids, and the least optimal habitats associated with the highest abundances, and thus greatest competition, with perennial forbs and graminoids. This likely indicates high and low “optimal” vegetation habitat groups occupy similar marginal habitats areas. Variation in localized conditions likely at fine spatial scales results in either successful *E. codium* occupancy and high abundance when perennial graminoid competition is low or less successful *E. codium* occupancy and lower abundance when perennial graminoid competition is higher.

These two graminoid community types can be classified as a “high perennial graminoid (<60%) and low perennial forb (<3.5%)” community type, and a “moderate perennial graminoid (<30%) and moderate perennial forb (<20%)” community type (Fig 1.7). The segregation of *E. codium* into “high” “moderate” and “low” perennial graminoid communities exhibit *E. codium’*s ability to tolerate habitats primarily within a range of perennial graminoid cover below 60% and secondarily within a certain set of vegetation community structures with perennial forbs in moderate to low abundance (<20%), although it is unable to reach its highest abundance in these areas. While *E. codium* is able to best thrive when competition is almost completely minimized, it can tolerate habitats with perennial graminoid cover two to three times more abundant than

what is present in its most "optimal" habitat, as long as cover of perennial forbs remains very low (<3.5%). Similarly, *E. codium* is able to tolerate habitats with higher perennial forb cover orders of magnitude more abundant than in its "optimal" habitat, as long as cover of perennial graminoids remains moderate (<30%).

Differences between "medium" and "low" *E. codium* abundance "habitat types" corresponds to differences in maximum and mean perennial graminoid cover in the "high" perennial graminoid community type (group C= "low" and group D= "medium") and in maximum and mean perennial forb cover in the "moderate" perennial graminoid community (group E= "medium" and group F= "low") (Fig 1.7). Highest mean and maximum cover of either perennial graminoids or perennial forbs was associated with "low" *E. codium* abundance groups in both the high and medium perennial graminoid community types, indicating that while *E. codium* can tolerate growing in vegetation communities with other species to some extent, inter-species competition is directly related to habitat quality, which degrades with increasing vegetation community productivity and complexity. While "medium" abundance groups represent vegetation community compositions that *E. codium* can likely tolerate and survive in, albeit not thrive in, the "low" abundance groups indicate that beyond certain thresholds in cover, inter-species competition can push *E. codium* beyond its range of tolerance and adversely affect its ability to successfully compete and survive.

E. codium appears to have a higher tolerance for interspecies competition with perennial graminoids than perennial forbs, which accounts for why its grows in an association with only *P. secunda* and *P. spicata* and not regularly with any one forb species, and why it is able to tolerate perennial graminoid cover up to 50% while it is unable to tolerate perennial forb cover >20%. However, a trade-off does seem to be occurring between perennial graminoid and perennial forb

competition, in which *E. codium* is able to tolerate higher competition with perennial graminoids only when there is little to no presence of perennial forbs (<3.5%). Similarly, it appears *E. codium* is likewise only able to tolerate growing with a low to moderate abundance of perennial forbs (<10%) only when perennial graminoid cover is moderate (<30%), suggesting the combined pressures of perennial graminoid cover >30% and forb cover >20% are actively restricting where this species can grow.

Ultimately, in conditions with very low perennial forb cover, 50% perennial graminoid cover appears to be *E.* codium's threshold for perennial graminoid competition, with significant decreases in *E. codium* abundance occurring when perennial graminoid cover is between 50-60%, and no plants occurring in habitats with >60% perennial graminoid cover. Likewise, when perennial graminoid cover is moderate and remains <30%, *E. codium* is able to tolerate moderate to low competition (<10% cover) with perennial forbs, with significant decreases in *E. codium* abundance occurring when perennial graminoid cover is between 10-20%, with no plants occurring in habitats with >20% perennial graminoid cover. Interestingly, mean abundance of annual forb species was highest in the high perennial graminoid community /medium abundance habitat type characterized by <50% graminoid cover and <10% annual forb cover. While *E. codium* can tolerate the low abundance of annual forbs in the context of a perennial graminoid vegetation community, growing in mixed communities with both annual and perennial forb species likely results in levels of competition beyond this species' tolerable limits. Mean and maximum *E. codium* abundance was lower in the high perennial graminoid/ annual forb community than in the moderate perennial graminoid/moderate perennial forb community, indicating *E. codium* is best able to tolerate competition with moderate cover of mixed perennial graminoid/forbs communities, than it is able to tolerate competing a high abundance of perennial

graminoids growing with a low to moderate abundance of annual forbs and low abundance of perennial forbs.

E. codium Principally Occupies "Less-Optimal" Habitat Types

The high perennial graminoid community/medium abundance habitat type and the moderate perennial graminoid community/medium abundance habitat type each accounted for 30% of plots surveyed, meaning 60% of surveyed habitat occurred in the more moderately productive but "less-optimal" habitat associations between perennial graminoids, forbs and *E. codium.* In contrast, 10% of surveyed habitat was comprised from the "low" abundance groups in both the high perennial graminoid community and moderate perennial graminoid community types, indicating that these areas of increased productivity and competition are barley tolerable for *E. codium* habitation and not a habitat type it can easily establish in. Although the barren/very low perennial graminoid habitat type and the moderate perennial graminoid/moderate perennial forb habitat type had similar mean *E.* codium cover, the moderate perennial graminoid/moderate perennial forb habitat type had a higher frequency of plots with *E. codium* cover values >10%, although the barren/very low perennial graminoid habitat type had two plots with significantly higher maximum cover values. This indicates that while in the barren/very low perennial graminoid habitat type *E. codium* is sometimes able to reach highest abundance due to minimized competition, but in general, the marginal habitat conditions in these barren areas is less tolerable than the levels of competition faced in the moderate perennial graminoid/moderate perennial forb habitat type. This suggests that while the moderate perennial graminoid/moderate perennial forb habitat type is not the most "optimal" *E. codium* habitat, it may be the best model habitat for assisted migration. If this habitat is productive enough to support other species but barren enough to minimize competition, it may represent a happy medium between the pressures

of inter-species competition, changing environmental conditions, and habitat likely to actually occur at outplanting locations that could likely support species introduction.

Vegetation Habitat Groups Reflect Habitat Heterogeneity at Fine Spatial Scales Across Subpopulations

The six habitat groups significantly reflected vegetation differences between the "optimal" vegetation habitats observed in subpopulations I, II and V and the "less-optimal" vegetation habitats observed in subpopulations III and IV. The "moderately low perennial graminoid" community comprised of the only "high" *E. codium* abundance habitat group and the barren "medium" habitat group only occurred in subpopulations I, V and II, confirming earlier observations that these populations contain the most "optimal" habitat, in contrast to "less-optimal" subpopulations III and IV. Similarly, the majority of sampled plots from subpopulation III were classified in the "medium" abundance habitat types in both the "moderate" and "high" perennial graminoid community types, and reflected the relatively higher perennial forb cover observed there. Similarly, the majority of plots in subpopulation IV were classified in the "high" perennial graminoid community type, in the "medium" abundance habitat type, and to a lesser extent, the "low" abundance habitat type as well, reflecting the relatively higher cover of perennial graminoids observed there. However, high spatial variation in vegetation community habitat type across all subpopulations is also evident. Especially in the largest subpopulations I and V, all six distinct habitat types are represented, demonstrating the heterogenous nature of microhabitats in this system.

This is further highlighted by significant spatial differences in the habitat groups within individual sampling transect. The low perennial graminoid/high *E. codium* abundance habitat type only occurs in sampling transect 1.3 at subpopulation I, at subpopulation II, and at transects

5.1 and 5.3 at subpopulation V. While the low perennial graminoid/medium *E. codium* abundance habitat type occurs at transect 1.3 at subpopulation I, it also occurs in surrounding transects 1.2 to the west and 1.4 to the east on either side. This indicates transect 1.3 is the heart of the most "optimal" *E. codium* habitat within these subpopulations, with increasingly extreme and "less-optimal" low perennial graminoid habitat expanding on either side. This indicates conservation concern and further work on this species should focus on this area of subpopulation I to protect this important, highly optimal habitat. All subpopulation I sampling transects also contained areas with both the high and medium perennial graminoid/ medium abundance habitat types, and the majority of transects were divided between both these medium abundance habitat types. This further indicates subpopulation I likely has such high overall abundance of *E. codium* because it is primarily comprised of a core of "high" abundance habitat type surrounded by "medium" abundance habitats all three perennial graminoid community types. Mainly transect 1.1 was classified in the low abundance habitats in both the high and moderate perennial graminoid community types, indicating this transect is occupying "least-optimal" habitat on the edge of the edaphic island zone it occupies.

Similarly, sampling transect 5.2 at subpopulation V exclusively contained the low perennial graminoid/high *E. codium* abundance and the moderate perennial graminoid/ medium abundance habitat types, indicating this area is the heat of "optimal" habitat in this subpopulation, and raising the same conservation concerns and research interests as at subpopulation I. Sampling transect 5.3 contains both medium and low abundance habitat types in the moderate perennial graminoid/ medium abundance habit types, indicating habitat quality in this area, though not as optimal as in transect 5.2, is likely largely tolerable for *E. codium*. However, sampling transect 5.1 contained all six habitat types over a 30 m areas, showing high

variation in microhabitat variation across a relatively small spatial scale. The spatial variation between highly optimal, less optimal and least optimal habitat types within relatively small spatial scales illustrate the ways in which fine-scale variation in a key habitat characteristic likely shaping the localized distribution of *E. codium* along Umtanum Ridge. The high variation in high, medium and low abundance habitat types across sampling transects 2.1, 3.1, 4.1 and 4.2, which range from 10-20 m long, highlight how heterogenous key vegetation habitat characteristics are.

Habitat variation at subpopulation II ranged was divided between the low perennial graminoid community type and the moderate perennial graminoid community type/ moderate abundance habitat type, highlighting how the range of optimal and slightly less optimal habitat together can support relatively high abundance of *E. codium*. The majority of subpopulation III contained medium *E. codium* abundance habitat types in both the high and moderate perennial graminoid community types, although some plots were classified as moderate perennial graminoid /low abundance habitat type. This supports previous observations that indicated subpopulation III represents a "less-optimal" but tolerable vegetation community with moderate cover of perennial forbs adjacent to a "less-optimal" but tolerable high perennial graminoid community type. In contrast, the largest portion of sampled plots at subpopulation IV belonged to the low abundance groups in both high and moderate perennial graminoid community types, further supporting observations that subpopulation IV contains the least optimal *E. codium* habitat. The majority of transect 4.1 contained medium or low abundance habitat types in the high perennial graminoid community type, further reflecting observations of relatively higher cover of perennial graminoids in this subpopulation, contrasting the other subpopulations. Interestingly, transect 4.2 had a mixture of plots classified as high perennial graminoid/ medium

abundance community type, combined with plots classified as moderate perennial graminoid/ low abundance community type. While ecologically these habitat groups exist on a continuum related to graminoid and forb abundance, spatially these groups may exist in highly fragmented patchworks reflecting the highly heterogenous edaphic factors these communities have developed in response to. Continuing to quantify and map habitat differences at fine scales reflective of the microhabitat variation present can help managers better understand the impacts this variation is having on *E. codium* occupancy and abundance at this site.

Three Perennial Graminoid Community Types Reflect "High", "Medium" and "Low" "Optimal" E. codium Habitat Groups

While the six distinct habitat types best reflect habitat variation both within and across the five subpopulations, the three perennial graminoid community types best capture the spatial heterogeneity of vegetation habitats at across the *E. codium* population. While differences by subpopulation were not significant when vegetation habitat is classified by perennial graminoid community type, these three habitat groups did significantly reflect differences in *E. codium* abundance. The low perennial graminoid community type remained reflective of the most abundant and "optimal" *E. codium* habitat, categorized as "high-optimal" *E. codium* habitat. Averaging *E. codium* cover across both "medium" and "low" abundance groups in each of the high and medium perennial graminoid community types delivers insight into which of these community types provide "less-optimal" and "least-optimal" *E. codium* habitat. The moderate perennial graminoid/ moderate perennial forb community group had mean *E. codium* abundance significantly higher than the high perennial graminoid/low perennial forb group, which had the lowest *E. codium* abundance. This indicates that overall, *E. codium* is more tolerable of moderate perennial graminoid and forb cover combined than high perennial graminoid cover, even when

forb cover is low. The moderate perennial graminoid/ moderate perennial forb community group is thus categorized as a "medium-optimal" *E. codium* habitat group, while the high perennial graminoid cover/ low forb cover is categorized as a "low-optimal" *E. codium* habitat. Together, these three habitat groups provide habitat benchmarks to compare assisted migration locations to, that reflects the heterogenous micro-habitat spatial arrangements observed across the five subpopulations.

Differences in Site, Soil and Vegetation Characteristics Between Three "Optimal" E. codium Habitat Groups Highlight Key Variables Likely Impacting Habitat Suitability

While comparison of the site, soil and vegetation characteristics of the three "optimal" *E. codium* habitat groups is conducted in Chapter 2 in conjunction with analysis of habitat differences in assisted migration locations, key differences in habitat characteristics highlight key variables likely impacting patterns in habitat suitability at the native population (Table 1.2). Although majority of site, soil and habitat characteristics were not significantly different between optimal habitat groups, significant differences were determined in site characteristics hillslope slope position, slope shape, aspect, heat load, and slope. Differences were also observed in soil texture and perennial forb cover. A greater number of similarities in habitat characteristics was determined between the optimal-high group- associated with the greatest abundance of *E. codium*- and optimal-low group- associated with the lowest abundance of *E. codium*- in contrast to the optimal-medium group, despite this group being associated with *E. codium* cover lower than the optimal-high group but higher than the optimal-low group. Overall, the optimal-medium group had the most measured variables distinguishing it from the other two groups. It is likely that the differences distinguishing the optimal-medium group from the similarities observed

Table 1.2 Differences Between the Optimal *E. codium* Habitat Groups Associated with High, Medium and Low *E. codium* Abundance
Summary table of similarities and differences in site, soil and vegetation characteristics between the three "optimal" *E. codium* habitat groups. Significant similarities are indicated by an X and differences are indicated by blank spaces or + and – icons. The + icon indicates that habitat variable is higher or increases in that habitat group, while – icon indicates that variable is lower or decreased in that habitat group. Total number of differences in variables are calculated for each habitat group and type of habitat characteristic (site, soil, vegetation). The majority of habitat differences are between the high/low and medium group, while differences in vegetation characteristics define each group.

Differences Between Optimal *E. codium* Habitat Groups

	High	Medium	Low
Site Characteristics	**1**	**3**	**1**
Landscape position	X	X	X
Hillslope Position	-	X	X
Slope (rise/run)	X	-	X
Slope (°)	X	X	X
Slope Shape	X		X
Slope Complexity	X	X	X
Aspect	X	X	
Heat Load	X	-	X
Rock Fragment Class	X	X	X
Soil Characteristics	**1**	**0**	**0**
Hydraulic Conductivity (K)	X	X	X
Soil Texture		X	X
Soil Surface Composition	X	X	X
Soil Surface Rock Fragment Composition	X	X	X
Vegetation Characteristics	**4**	**4**	**4**
Vegetation Composition			
Species Richness	X	X	X
Total Cover	X	X	X
Shrub	X	X	X
Subshrub	+		-
Perennial Forb		+	
Annual Forb	X	X	X
Perennial Graminoid			+
Annual Graminoid	X	X	X
Total	**8**	**5**	**7**

between the high and low groups highlight *E. codium's* evolutionary strategy and provide important insights into what habitat characteristics create "optimal" habitat.

Differences in ISA analysis of vegetation functional group composition illustrate important similarities between the optimal-high and optimal-low groups in contrast to the optimal-medium group. The optimal-high group is distinguished by subshrub (i.e. *E. codium*) cover and the optimal-low group by perennial graminoid cover, while ISA analysis did not distinguish the optimal-medium group by any one functional group. While the associated *E. codium* habitat type is comprised largely of only *E. codium* and the two perennial graminoid species *P. secunda* (primary) and *P. spicata* (secondary), the similarities and differences in vegetation functional group composition between the optimal high and low groups continue to highlight the trade-off occurring between *E. codium* and perennial graminoid cover that was first described in the six optimal habitat groups. This trade-off is especially illustrated by the significant differences in subshrub and perennial graminoid cover between the optimal-high and optimal-low groups, in which mean, minimum and maximum cover of subshrubs are higher in the optimal-high group and lower in the optimal-low group, and perennial graminoid cover is higher in the optimal-low group and lower in the optimal-high group.

While the optimal-medium group provides a midpoint in subshrub and perennial graminoid cover between the high and low groups, the optimal- medium group has significantly higher perennial forb cover. This higher perennial forb cover at the midpoints in subshrub and perennial forb cover between the high and low groups, reflects key vegetation community differences structuring compositional similarities between the six optimal habitat groups. While a trade-off is occurring between *E. codium* and its associated perennial graminoid species, a trade-off is also occurring between *E. codium* and perennial forb species at the same time. *E. codium*

can exploit and grow well in areas with a moderate abundance of both perennial graminoids and perennial forbs, although it is unable to reach its highest abundance in these areas due to simultaneous competition with both vegetation functional groups.

In total, the optimal-high group was distinguished from the other habitat groups by four measured variables- one site characteristics, one soil characteristics and two vegetation characteristics. The optimal-high group did not include any areas of the native *E. codium* population that grow on the backslope of the hillslope, suggesting the backslope of Umtanum Ridge, though tolerable, is less optimal for *E. codium* than the summit and shoulder of the hillslope. The optimal-high group also contained a larger proportion of plots with loamy sand soil texture, and contained one plot with loam soils in contrast to the medium and low groups which contained higher proportions of sandy loam and did not contain loam soils. These results confirm patterns observed in chapter 1 indicating *E. codium* grows best on loamy sand soils, but can still thrive on loam derived soils (loam, sandy loam) under the right site and vegetation conditions. Furthermore, ISA analysis indicted the optimal-high group is distinguished by the rock component of soil surface composition and more specifically the very fine gravel component of soil surface rock fragment composition, suggesting disproportionately higher very fine gravel cover is either directly related to conditions that allow *E. codium* to achieve its maximum abundance, and/or characterizes underlaying geology, soil nutrient and moisture retention dynamics that are likely impacting maximum *E. codium* abundance. The association of very fine gravel with the highest abundance of *E. codium* may be due to the ability of very fine gravel to allow moisture from rain and snowfall to percolate into the soil profile where *E. codium's* tap root can access these moisture reserves. Very fine gravel in particular, is likely a

rocky substates that quickly percolates moisture during precipitation events, that *E. codium* can fairly easily establish deep, woody taproots into with minimal difficulty or resistance.

The optimal-low group was distinguished from the high and medium habitat groups by three measured variables- one site characteristic and two vegetation characteristics. The optimal-low group had the largest proportion of north and southwest facing plots and the smallest proportion of northeast and east facing plots. This suggests the increased afternoon solar radiation of southwest slopes may be less optimal for *E. codium* growth than the morning solar radiation of northeast and eastern facing slopes. The association of north facing slopes, which receive the least amount of daily solar radiation, with the lowest *E. codium* abundance group may be related to interactions between shading and increased vegetation productivity in extreme arid environments. As it is likely *E. codium* does not compete well with both native and invasive species for space or resources, the increased vegetation productivity associated with north facing slopes could be negatively impacting *E. codium* abundance in these areas. These findings suggest differences in habitat characteristics including hillslope position, the composition of sand to loam in soils, and aspect may have significant impacts on how optimal an area is for *E. codium* survival and growth, and for distinguishing which areas with similar habitats are high-optimal vs low-optimal.

Six variables, including three site characteristics and three vegetation characteristics, distinguished the optimal-medium group, including slope, slope shape, and HLI. The optimal-medium group contained the largest proportion of linear-linear and linear-concave slope shapes, did not contain any plots with a convex-linear shape and contained one plot with a linear-convex shape. Mode of both optimal-high and optimal-medium groups was linear-linear, in contrast to the optimal-low group which had a mode of convex-linear. Despite this, the optimal-low group

shared more of an overall compositional similarity to the optimal-high group as it had more convex-shaped plots and less concave shaped plots than the optimal-medium group. Ultimately, this further confirms observations that *E. codium* likely grows best on linear-linear or fairly flat and even slope shapes, where incoming moisture from rain and snowmelt shed relatively evenly down the slope. It appears *E. codium* is also able to exploit and grow well on more concaved slopes that trap and retain moisture, although these areas do not necessarily support the highest abundance of this species, and are likely related to the high cover of perennial forbs that characterize this vegetation habitat group. These findings suggest more convex slopes may be able to provide the drier conditions with minimum vegetation competition that support the highest abundance of *E. codium* under the right conditions, but this lack of moisture may also inhibit *E. codium*'s own growth under other conditions such as extreme heat or drought. Slightly moistier habitats, while requiring more competition with native perennial forbs, may provide an alternative- although less optimal- habitat *E. codium* can persist in.

Similarly, mean HLI in the optimal-medium group was the same as the optimal-high group and lower than in the optimal-low group. However, minimum HLI was higher in the optimal-high and optimal-low groups while the optimal-medium group had the lowest minimum but the second highest maximum value after the optimal-high group. These results suggest that *E. codium* is able to exploit a range of heat loads above 0.5 under a range of conditions, and can do relatively well in these areas. However, it is only able to grow to the highest abundance in the higher and more extreme ranges of HLI under certain conditions, likely when vegetation competition is minimal. However, its exploitation of this higher HLI niche can also inhibit its growth under different conditions, likely when direct competition with other species is higher. This dynamic is further mirrored in the significant differences in slope between the optimum-

medium group vs optimum-high and optimum-low groups. The optimum-high and optimum-low groups have similar mean and range of slope values, in contrast to the optimal-medium group, which has a higher mean and wider range of values. Once again *E. codium* is able to exploit a slightly steeper and more extreme range of slope values, and do relatively well in these areas, but not well enough to grow to its highest abundance. While able to grow to higher abundance in areas with a slightly less extreme range of slope values under the right set of habitat conditions, it may also be inhibited from these more favorable site conditions by competition with other species under a different set of habitat conditions. Overall, these findings suggest slope shape, heat load, and slope, and the relationships between these variables and solar irradiation, erosion, and moisture retention dynamics, may be significantly impacting what characterizes optimal *E. codium* habitat. These site level habitat characteristics are likely key to shaping the significant differences in vegetation community and functional group composition observed between the optimal *E. codium* habitat groups.

Differences Between Three "Optimal" E. codium Habitat Groups Indicate Influence of Habitat Variables on E. codium Abundance and Range of Tolerance

Differences in mean values between the optimal-high and optimal-low groups in contrast to the optimal-medium group are likely variables that *E. codium* can tolerate above or below its optimal range but which contribute to inhibiting it from reaching maximum abundance when conditions do not fall within its optimal range. Variables positively associated with the optimal-medium group are *highest* in this group and are likely variables that cause stress to *E. codium* when in *excess* of *E. codium's* optimal range of tolerance (Fig 1.8). These variables include species richness, the perennial forb and annual graminoid components of vegetation functional group composition, slope (rise/run), and the medium gravel component of soil surface rock

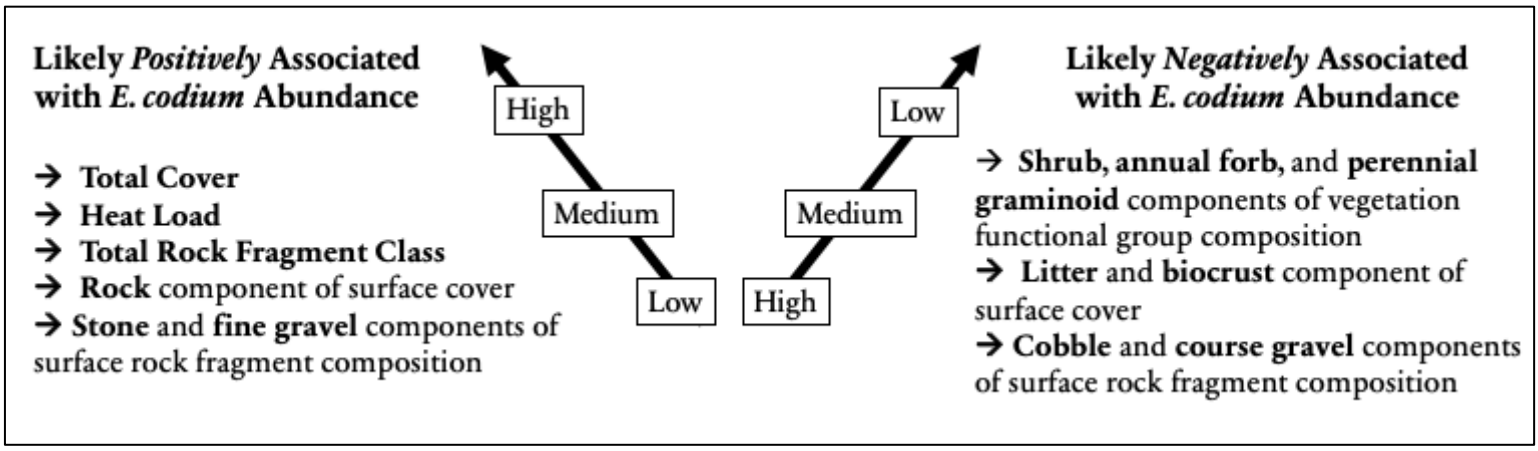


Figure 1.8 Positive and Negative Associations of Site, Soil and Habitat Characteristics with *E. codium* Abundance
Positively associated habitat variables are those that increase in variable strength (i.e. mean value) from the low to high group with increasing *E. codium* abundance and include total cover, heat load, total rock fragment class, the rock component of surface cover, and the stone and fine gravel components of surface rock fragment composition. Negatively associated habitat variables are those that decrease in variable strength (i.e. mean value) from the low to high group with increasing *E. codium* abundance and include the shrub, annual forb, and perennial graminoids components of vegetation functional group composition, litter and biocrust component of surface cover, and the cobble and coarse gravel components of surface rock fragment composition.

fragment composition. While the optimal-high and optimal-medium groups have higher mean annual graminoid cover than the optimal-low group, the maximum cover values in both the optimal-high and optimal-low groups are below 1%, while maximum cover in the optimal-medium group reaches 3%. Variables negatively associated with the optimal-medium group are *smallest* in this group and are likely variables that cause stress to *E. codium* when they are *lacking* below *E. codium*'s optimal range of tolerance (Fig 1.8). These variables include slope angle, the bareground component of soil surface composition, and the very fine gravel component of soil surface rock fragment composition.

Although the majority of measured site, soil and vegetation characteristics were similar between these three groups, differences between the high, medium and low optimal groups in which variable strength (mean value) was greatest in the high, then medium, and then low group, indicate variables that are likely positively associated to some extent with *E. codium* abundance. These variables include heat load index, total rock fragment classification, the rock component

of soil surface composition and the stone and fine gravel components of soil surface rock fragment composition. Differences between high, medium and low optimal groups, in which variable strength (mean value) was weakest in the high group, increased in strength in the medium group, and was strongest in the low groups, are likely negatively associated to some extent with *E. codium* abundance. These variables include total cover, the shrub, annual forb, and perennial graminoid component of vegetation functional group composition, the litter and biocrust components of soil surface composition, and the cobble and coarse gravel components of soil surface rock fragment composition. Mean annual forb cover in particular, is lower in the optimal-high group compared to the optimal-medium and optimal-low groups, which have similar mean values.

Conclusion

Umtanum Desert Buckwheat and the Generalist Model of Speciation

Observations of habitat characteristics at the single native population of *E. codium* indicate that the generalist model of evolution, and more specifically the tolerance of marginal habitat to avoid competition, is likely driving *E. codium*'s evolution and habitat preference. Only vegetation composition was determined to significantly impact *E. codium*'s occurrence and abundance, as vegetation dynamics are likely shaping where *E. codium* is able to grow as opposed to a single specific and unique site or soil characteristic. *E. codium* is likely confined to its current location on the edge of Umtanum Ridge due to its ability to exploit an extreme abiotic habitat niche that also hosts distinct vegetation composition from the surrounding habitat characterized by low competition. *E. codium* appears to only grow in vegetation communities characterized by low species richness, total cover, leaf area index and inter-species competition, especially with other long lived woody perennial species such as shrubs. As only *E. codium* and two native perennial graminoid species *P. secunda* and *P. spicata* occurred in >30% of surveyed habitat, *E. codium* is likely the dominant species characterizing its own optimal vegetation community and habitat type in association with these perennial graminoid species.

Differences in site and soil characteristics between subpopulations indicate *E. codium* can likely exist within a range of abiotic environmental conditions. A range of site and soil habitat characteristics were observed between subpopulations, contrasting similarities in vegetation composition at subpopulations I, II, and V while mirroring differences in vegetation composition between subpopulations III, IV and all other subpopulations. *E. codium*'s seeming ability to occupy a wide range of abiotic conditions in contrast to requiring specific biotic conditions reflect observations made in other studies of both rare edaphic endemic species, and of common

and rare species within the *Eriogonum* genus. Research conducted on Crosby's buckwheat (*E. crosbyae*), anther rare *Eriogonum* species also believed to an edaphic endemic, was unable to identify a specific soil characteristic tied to site occupancy across its distribution in Nevada, despite the presence of extreme and unique soil priorities in the areas where it currently grows (McClinton 2020). Utilizing observations both in the field and from seedlings grown experimentally in soils from both occupied and unoccupied outcroppings, researchers did not observe any significant differences in soil properties or greenhouse plant growth based on site occupation, with soil physical and chemical characteristics acting as poor predictors of site occupancy.

While the soils in *E. crosbyae's* current habitat were generally characterized by deficiencies of available nitrogen and phosphorus and high levels of K, Mg, Na, SO_4-S, and KCl extractable- Al, indicating they are likely marginal and may even be toxic for most species to grown on, variation in soil properties were observed between sampling locations. Researchers demonstrated that this species is both able to occupy a range of marginal soil properties, and that significant associations between soil variation and plant form exist in both the field and in the controlled conditions of the greenhouse. *E. crosbyae* responded to variation in soil properties in different ways at different life stages, with certain morphological responses associated with specific soil properties (Faucon et al 2017, Sánchez et al 2017).

The polyphyletic evolutionary convergence on the adjustments of morphological and physiological traits in response to variability within the environment is characteristic of the genus as a whole, with this type of phenotypic plasticity disconnected from a single phylogenetic lineage typical the generalist model of evolution at work (Ellis 2009, Gardy 2012, Lemon 2017, Pearman 2021). Ultimately, widespread adaptability of common species to diverse and marginal

environments serves as a key driver of patterns in site specialization, with the consequential isolation and speciation of these populations resulting in rare and isolated species in multiple clades simultaneously.

The hypothesis that the adaptation of greater tolerance to marginal habitats and soil substrates results in a trade-off with competitive ability is increasingly becoming a prominent evolutionary theory in the study of edaphic endemic species (Rajakaruna 2017, Grady 2012). Recent genetic work on a number of different edaphic endemics further substantiates that *Eriogonum* species specifically, and edaphic endemics more broadly, likely do not associate with specific soil types because they have specifically co-evolved with that soil type (i.e. specialist model of evolution) (Harper 1997a, Harper 1997b, Grady 2012, Lemon 2017, Rajakaruna 2017, Pearman 2021). The integration of molecular phylogenies with both descriptive and experimental ecological information is beginning to reveal discrepancies between current understandings of speciation based on morphology and habitat and emerging genetic patterns indicating current taxonomy may better reflect morphological adaptions to specific climate and soil environments than district evolutionary lineages.

Serpentine endemics have been found to face less competition from invasive species when growing on serpentine soils and to be poor competitors on high-nutrient soils (Rice 1989, Harrison 1999, Jurjavcic et al 2002, Gram et al 2004, Going et al 2009, Vallano et al 2012). Resent work with serpentine endemics noted trade-offs between competitive ability and tolerance to serpentine soils (Brady et al 2005, Kay et al 2011, Anacker and Harrison 2012, Fernandez-Going et al 2012). Research showed that while species did not experience a physiological "cost" for tolerance to the extreme soil properties that characterize serpentine soils, they are typically stress-tolerant and thus generally more slow-growing than fast-growing but less stress tolerant

species typically considered competitively superior in more productive habitats. While the relationships between an edaphic endemic species' reduction in fitness and the direct physiological trade-offs associated with tolerances to different soil properties remains unclear for the majority of species, it is likely edaphic endemic species are not only adapted to a particular textural and/or chemical property, but to environmental stressors generally, including drought, low nutrients, high light, and poor soil structure (Harper et al 1997a , Harper et al 1997b, Rajakaruna 2017.)

It is likely that a suite of adaptive traits that under "normal" habitat conditions and in nutrient rich soils would require a metabolic "cost" that decreases a species competitive fitness, can instead confer a species with higher abiotic tolerances, and thus a competitive advantage, in barren and marginal habitats where competition is inherently reduced by the challenging growth environment (Smith and Macnair 1998, Cacho and Strauss 2014). Evolutionary shifts to specialized soil environments appear to occur not form other species adapted to other specialized soils, but from species adapted to barren microhabitats (Armbruster 2014). Adaptations to conditions in bare habitats, such as increased tolerance to water stress, are thus likely precursors for tolerance of more specialize conditions, with adaptive plasticity, competitive ability, and lineage history all contributing to the phenotypic divergence, edaphic niche specialization, and limited range distributions characteristics of rare edaphic endemic species (von Wettberg et al 2014, Strauss and Cacho 2013, Cacho and Strauss 2014).

Umtanum Desert Buckwheat Subpopulations and Defining Optimal Habitat Groups

Areas where *E. codium* occurs along Umtanum Ridge can be grouped into highly optimal to less optimal habitat types, illustrating its ability to persist with varying levels of success in a range of different vegetation habitat types. Subpopulations I, II and V, contained the largest

number and/or highest abundance of *E. codium,* and in contrast to patterns of variation in site and soil characteristics, are all examples of the same optimal vegetation habitat required by *E. codium.* The higher variability in vegetation community characteristics and *E. codium* abundance at subpopulation I makes it a better example of the range of vegetation habitat conditions *E. codium* can exist in and their effects on *E. codium* abundance. The high variability in site and soil characteristics in combination with the low variability of vegetation community characteristics and *E. codium* abundance at subpopulation II and V make them better examples of the range of site and soil conditions that can support the optimal vegetation habitat both required and dominated by *E. codium.* While subpopulations III and IV also contained significant variation in site and soil characteristics, vegetation habitats at each subpopulation were distinct and a lower occurrence and abundance of *E. codium* was observed*,* indicating these subpopulations represents two distinctly less optimal but still tolerable habitat types for *E. codium.*

Contrasting patterns indicating higher levels of variation in site and soil characteristics than in vegetation characteristics at all subpopulations, combined with varying similarities and differences in habitat characteristics between and within subpopulations, indicated *E. codium* abundance is likely related to the exploitation of fine scale and spatially heterogeneous microhabitats. Through the use of agglomerative cluster analysis using vegetation functional group composition, six vegetation habitat types based on differences in high, medium, and low *E. codium* cover were identified. Relationships between the six habitat types were based on similarities and differences in perennial graminoid cover, with the only high and one medium abundance group forming a low perennial graminoid vegetation community type, and one low and one medium of the remaining four habitat types together forming one of two additional vegetation community types associated with moderate and high perennial graminoid cover

respectively. By averaging habitat variables across the high and medium habitat types in the low perennial graminoid community type, and the low and medium habitat types in both the moderate and high perennial graminoid community types, “high”, “medium” and “low” optimal *E. codium* habitat groups were determined, with “optimal” habitat inversely related to abundance of perennial graminoid species and the “medium-optimal” group characterized by the relatively higher abundance of perennial forbs. Site, soil and vegetation community differences between groups were assessed to describe habitat characteristics influencing the most optimal and least optimal habitat types.

Studying habitat at the single existing population of *E. codium* can help provide insights into why this species is confined to a single population at a single location, while helping managers develop a habitat profile or “reference ecosystem” that can be used to target suitable habitat for assisted migration attempts. However, to fully capture the range of habitat characteristics a species is able to tolerate requires numerous observations of species across multiple environmental and ecological gradients. *E. codium* represents an extreme example of the challenges mangers face attempting to conserve extremely rare species with very limited distributions and remaining populations. While the habitat characteristics and growth responses observed at the only population available for assessment are likely reflective in some capacity to the “habitat” *E. codium* is most adapted to, the ability to knows if observed habitat conditions represent the full range of adaptions within the species, or only a range of responses to highly site- specific habitat conditions, is extremely limited. It is unclear if observed conditions within this single population are characteristic of the species or just represent the responses of a limited and genetically isolated group of individuals confined to a single location. Ultimately, due to the limited number of remaining individuals and continuing decline of the existing population, some

of these uncertainties are likely unknowable. However, future work aimed at understanding the reaming functional trait diversity within the species combined with experimentally determining this species range of tolerance, can help mangers better articulate what "optimal" habitat is for this species.

Importance of Understanding Umtanum Desert Buckwheat's Range of Tolerance to Environmental Conditions

Significant variation in site and soil characteristics suggest subpopulations reflect a variety of abiotic habitat characteristics *E. codium* can tolerate. Site and soil characteristics likely interact to shape vegetation communities and inter-species competition, thus having synergistic effects on *E. codium* distribution and habitat occupancy. Heat load, high ratios of rock and bareground, and variation in soil texture and rock fragment composition are important site and soil habitat characteristics creating the extreme environment conditions responsible for vegetation composition characterized by low productivity and inter-species competition that *E. codium* has adapted to. In order to exploit this marginal habitat, *E. codium* has developed the ability to tolerate a range of these environmental variables and their impacts on *E. codium* occurrence may be more related to their impacts on vegetation composition and productivity than directly inhibiting *E. codium* growth. However, gaining a better understanding of these abiotic habitat characteristics and their relationships to vegetation community characteristics, especially the physical and chemical properties that characterize the native population's soil environment, are important next steps to understanding how habitat characteristics shape *E. codium* abundance.

While descriptive ecological studies are important for establishing baseline habitat conditions associated with a particular species, there are numerous limits to field-based habitat

studies as they have limited ability to demonstrate or explain causal relationships between habitat variables and a species' growth response. To understand *E. codium's* habitat requirements, a batter understanding of this species' range of tolerance and adaptative responses to environmental conditions is necessary. This work can only be done experimentally in a controlled environmental setting such as a greenhouse to ensure the synergistic effects of many habitat variables simultaneously can be isolated and their individual impacts explored.

Because *E. codium's* occupancy of an extreme habitat niche is reliant on its ability to adapt to and tolerate these abiotic conditions as a means of avoiding competition, changes in these variables due to climate change and drought may be negatively impacting *E. codium's* growth and survival. Especially as *E. codium* is a long-lived perennial species that can persists for >100 years, it is likely that when current adult plants initially germinated and established as far back as the early 19th and possibly even late 18th centuries, abiotic conditions working as selective pressures on the species were undoubtably much different. It is possible that the abiotic site and soil conditions that best characterize *E. codium's* current habitat may be negatively impacting its ability growth and survive where it current occurs, especially in the face of drought and warming conditions. Understanding *E. codium*'s morphological and physiological responses to key habitat characteristics such as soil, heat load and available moisture can help managers better understand the impacts the extreme, and in some cases inhospitable, abiotic habitat conditions are having on the survival of adult plants and seedlings, as well as help managers predict the response of the population to expected trends in global climatic warming.

Identifying assisted migration sites with soil properties representing "average" soil characteristics within a water and nutrient "range of tolerance" may help prevent inadvertently choosing sites too environmentally extreme or high in competition from other species for *E.*

codium survival. As a species of acute conservation concern, future research into *E. codium* should be aimed at gaining a better understanding of the impacts on growth and survival of both biotic factors such as interspecies competition while also understanding impacts of fluxes in abiotic conditions such as soil nutrient and water availability. Through pairing analysis of interspecies competition with information on environmental and soil properties, future studies can elucidate how important these limiting factors are on shaping habitat suitability for current and future populations. Gaining a better understanding of the relationships between abiotic soil and climatic variation and *E. codium*'s growth and reproduction can help elucidate which mechanisms are the most important drivers of habitat distribution, seedling survival and successful establishment of new individuals.

Wildfire, Invasive Species, and Habitat Protection at the Native Site

The spare vegetation community that *E. codium* has come to dominate along the edge of Umtanum Ridge is under eminent threat from the loss of the surrounding native shrub-steppe communities to multiple wildfire events, and the subsequent invasion by fast growing and highly invasive annual species. *E. codium* likely co-evolved in proximity to the low productivity interspaces between larger "islands of fertility" around shrubs such as *A. tridentata* and *C. viscidiflorus* that characterize native shrub steppe habitats (Steven 2017, Burgess 2020). These lower productivity interspaces were likely dominated by perennial graminoids such as those associated with *E. codium*, and microhabitat variation of their abundance and cover along gradients relating to soil moisture, nutrient content, rock cover, and heat load likely allowed *E. codium* to exploit some of these more marginal areas and dominate them with its own sparse vegetation association.

Cyclical wildfires combined with anthropogenic impacts from work conducted by the Department of Defense at Hanford Nuclear Facility, have resulted in severe degradation of the surrounding native vegetation, destroying much of the structural complexity characteristics of shrub steppe communities. The resulting vegetation conditions is now more homogenous with regrowth after wildfire resulting in the dominance of perennial and annual forbs and invasive non-native annual species as *B. tectum* and *S. tragus* (Davies et al 2011, Davies et al 2012, Miller 2013). Aside from the damage wildfires have directly caused to the remaining population, this change in vegetation composition is likely contributed to the observed declines in population after wildfire events in 1997 and 2017, as well as completely isolating the remnants of the main population from what may have previously been a more extensive habitat area or even other formerly adjacent populations.

Repeated wildfire burns have been found to shift vegetation composition from shrub-dominated to native forb dominated communities both directly following and 15 years after wildfire events (Davies et al 2011, Ellsworth 2020). These effects are especially pronounced when sites burn multiple times, with aboveground biomass of twice-burned sites comprised of 71% herbaceous species, compared to 44% at once-burned sites (Ellsworth 2020). While known responses of native graminoid species *P. secunda* and *P. spicata* have been known to vary, and multiple studies have not observed changes of *P. spicata* in response to wildfire events, there is evidence that this is changing, especially as sites experience repeated connective wildfire events at 15-25 year intervals (Blaisdell 1953, Wright and Klemmedson 1965, Young and Evans 1978, Akinsoji 1988, Miller 2013, Ellsworth 2020). While multiple studies have similarly not observed changes in *P. spicata* cover following wildfire in the first year, increases in cover after two or

three years have been observed, with a 143% increase in high severity burn areas (Blaisdell 1953, Conrad and Poulton 1966, Uresk et al 1976, Hosten and West 1994, Miller 2013).

These shifts in vegetation composition are likely negatively impacting *E. codium*'s habitat conditions by decreasing the cover and extent of its primary associated graminoid species *P. secunda*. While *E. codium* likely associates with *P. secunda* 100% of time because it is a small, shallow rooted graminoid that poses minimal competition to *E. codium, P. spicata* is a robust and deeply tap rooted perennial graminoid that *E. codium* only associates with ~30% of the time and is in highest abundance in *E.* codium's "less-optimal" habitats. The combined increases in the productivity of both *P. spicata* and perennial forbs following wildfire have likely created conditions that *E. codium* is unable to successfully compete with.

The USFWS recovery plan calls for populations to be adequately protected from wildfire, requiring the plant's habitat to have less than 1% nonnative vegetation cover (U.S. Fish and Wildlife Service 2022). Currently, *B. tectorum* is one of the most abundant species growing in association with *E. codium* as it occurred in 30% of recorded habitat-higher than any forb species. Current invasion is recorded in subpopulations II, III, and V, and while mean cover is <1% in all subpopulations, maximum cover reached 3% in subpopulation V. Especially as *E. codium* occupies an extremely arid habitat niche, the invasion of species such as *B. tectorum* is more likely, however, this species poses a direct threat to *E. codium*'s continued existence both through direct competition for limited resources and by fueling future wildfires within the boundaries of the population (Bagchi et al 2013). Similarly, invasive annual forb *S. tragus* occurred in subpopulations I, II, and III and in 11% of recorded habitat. Although *S. tragus* also accounted for <1% of mean cover in these subpopulations, subpopulation I had a maximum cover of 3%. These species are both known to invade sites and increase in abundance after

cyclical wildfires events, and their presence should be managed, especially within subpopulations I and V.

The lack of *B. tectorum* and *S. tragus* in subpopulation IV is likely related to the increased cover of native perennial graminoids and forbs in the high perennial graminoid and moderate perennial forb *E. codium* habitat groups recorded there, as well as the relatively high biocrust cover recorded there. Both perennial graminoids and forbs, as well as biocrusts, are known to limit *B. tectorum* invasion by limiting the size and connectivity of gaps between vegetation, and limiting invasions within gaps (Reisner 2013, Beckstead and Auspburger 2004, Chambers et al 2007, Condon et al 2011, Mazzola et al 2011). Consideration of this habitat type for as a model for invasive species resilient habitat for *E. codium* should be considered by managers. However, the tension between *E. codium*'s need to limit competition and the presence of associated native species in increasing habitat resiliency is a line that will require considerate management planning.

The destruction of the area between current subpopulations IV and V that contained *E. codium* individuals was likely impacted by these post wildfire shifts in vegetation community, as better fire adapted species likely rapidly increased in the years following the 2017 fire. Ultimately, the destruction of the native shrub steppe community and associated habitat complexity to which this species evolved, and the resulting increase in inter-species competition, is likely combining with the lasting effects of direct damage from wildfires and increasing stress from changing abiotic conditions to push this species beyond its physiological limit for stress tolerance.

Genetic Bottlenecks and the Evolutionary Liability of the Generalist Model

Population genetic and phylogenetic analyses of a number of different species with a range of edaphic[16] associations indicate that while the tolerance to extreme edaphic conditions has been gained numerous times within various clades of angiosperms, this trait has then been subsequently lost in some of these groups, potentially making edaphic evolution "evolutionarily labile" (Mengoni et al 2001, Mengoni et al 2003, Nyberg Berglund et al 2004, Pauwels et al 2005, Anacker et al 2011, Bennett et al 2013, Klein and Kadereit 2015, Bresowar and McGlaughlin 2015, Rajakaruna 2017). The direction of edaphic endemic evolution within a genus is always originally from a non-tolerant species to a tolerant species (Anacker et al 2011). However, the reversal of edaphic tolerance observed in some species could indicate edaphic endemism is an evolutionary "dead-end", as confinement to an isolated soil habitat may result in inbreeding depression that inhibits successful survival of offspring (Anacker et al 2011, Rajakaruna 2017).

When high phenotypic plasticity in response to environmental conditions is combined with geographic isolation, the resulting limitations of genetic exchange between populations can result in high levels of speciation and the restriction of a specie's distribution to unique soil conditions can ensue .The presence of genetic variance is necessary for widespread species to evolve a tolerant ecotype[17] of unique and often challenging soil substrate, and resulting speciation ensues from processes of hybridization and polyploidy. A lack of necessary genetic variance can potentially define the limits of a species' ability to adapt to marginal soils, and these

[16] Serpentine tolerant, metallophytes, halophytes, calciphiles, gypsophiles are examples of edaphic endemic groups recently studied.
[17] An ecotype, also known as ecospecies, is a geographical variation, population, or race that belongs to a species and is genotypically suited to a particular environment.

differences appear foundational to a species' ability to form ecotypes (Bradshaw 1991, Macnair and Gardner 1998).

Multiple studies analyzing gene regions from distinct populations of a single *Eriogonum* species have found high rates of polyploidy, while high rates of polyploidy have been observed within other species from the *Eycycla II* clade which *E. codium* belongs to (Gardy 2012, Lemon 2017, Pearman 2021). The generally high rates of polyphyly found within currently described subgenera of common and widespread *Eriogonum* species, combined with the high variability of morphological characteristics observed across the genus, indicates polyploidy and haplotype diversity may be conserved within species as a means of conserving a range of phenotypically adaptable traits while providing opportunities for hybridization with other members of *Eriogonum* when opportunities become available in the face of fluctuating climate. The conservation of polyploidy and haplotype diversity within the *E. codium* genome is likely important for maintaining this species adaptability to a range of habitat conditions and potentially even the marginal habitat it is currently occupying on the edge of Umtanum Ridge.

Due to *E. codium's* small population and highly restricted range, it is likely that this species is either currently experiencing or is at high risk of genetic stochasticity. It is possible that observed low rates of reproductive success are indicators of inbreeding depression, in which the limited number of reproducing individuals may have extremely low genotypic variability, resulting in low fecundity and seedling survival. The genetic variability between individuals and subpopulations, and any potential relationships between observed rates of high seedling mortality and low genetic variability, are currently unknown as no population wide genetic work has been done on this species. Understanding the levels of genetic diversity and polyploidy conserved within the remaining individuals is a necessary and important management step that can help

establish *E. codium*'s capacity for adaptation to new environments and changing habitat conditions. For a more detailed discussion of stochasticity within the single *E. codium* population, see Appendix AD.

Ultimately, an evolutionary trade off that results in the occupancy of the most marginal habitat conditions combined with an intolerance for comparatively low levels of inter-species competition, becomes less of a successful evolutionary strategy as the conditions that make the habitat marginal begin to push a species beyond its range of abiotic tolerance. The key to this adaptive stagey is the maintenance of high levels genetic polyploidy and haplotype diversity, translating into high morphological and physiological plasticity. This maintenance of genetic diversity if key to ensure a species has numerous adaptable traits to utilize as environment and habitat conditions change. *E. codium* likely serves as a potent example of the effects of isolation to a uniquely marginal habitat can have on a species' fitness, as the synergic effects of isolation and low genetic exchange have potentially resulted in a genetic bottleneck and declining rates of adaptable traits.

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Chapter 2

Assessment of Habitat Differences Between the Single Native Population of Umtanum Desert Buckwheat (*Eriogonum codium*) and Assisted Migration Locations

Introduction

Assisted Migration as a Strategy for the Conservation of Rare Species

To keep pace with rates of global climatic change and anthropogenic habitat fragmentation, many species are required to disperse rapidly through highly fragmented, human- dominated landscapes (Dawson et al 2011). Assisted migration is an ex-situ conservation approach aimed at reducing biodiversity loss by facilitating the survival of selected species via translocation beyond their recent and historical ranges to locations otherwise unattainable by autonomous dispersal (Pedlar et al 2012, Tichelmann 2014, Mendoza-Maya et al 2022, Clifton et al 2024). Through assisted migration, humans serve as effective vectors for long-distance dispersal as they can navigate anthropogenic landscapes and thus do not require contiguous habitat to establish or maintain connectivity between populations. Often utilized as a means for protecting species from human-induced extinction, "species rescue assisted migration" aims to translocate vulnerable species to suitable habitats outside their native ranges where they can reproduce and compete successfully (McLane and Aitken 2012).

While assisted migration has been utilized in various forms and applied to numerous species both common and rare, "species rescue assisted migration" is the approach considered in this study (hereafter referred to as "assisted migration") (Pedlar et al 2012, Iverson et al 2013). Although assisted migration can be a time- and resource-intensive intervention strategy, enabling otherwise impossible translocations of species outside their native range can greatly reduce the

extent to which a vulnerable species or population is at risk of decline, genetic loss, or extinction (Hoegh-Guldberg et al 2008, Dawson et al 2011).

Species selected for assisted migration tend to have ecological or physiological constraints limiting their distributions, including low dispersal ability, high habitat specificity, and narrow climate niche (Hunter 2007, Early and Sax 2011, Loss et al 2011, Sté-Marie et al 2011, Pedersen 2015, Clifton et al 2024). These species have little ability to adapt to changing climatic conditions, occur in areas with high levels of habitat fragmentation, and/or have little potential to migrate across natural or man-made barriers. Processes driving population responses to climate change can interact with climate variables and a species life history in complex and context-specific ways, and the vulnerability of a given species depends on a variety of factors. Ecophysiology, life history, and microhabitat preferences also influence a species need for assisted migration, with more sensitive species likely to experience greater reductions in survival and/or fecundity in response to smaller changes to climate variables (Parmesan 2006, Dawson et al 2011). *E. codium*'s current distribution is confined to a single, small population surrounded by fragmented habitat degraded by wildfire events and anthropogenic activity, resulting in the limited ability of this species to adapt to rapid climatic warming and increased drought. Therefore, assisted migration is an important conservation tool in its recovery.

Modeling Habitat for Rare Species

"Ecological niche modeling" or "species distribution modeling" (SDM) can be used to define a species critical habitat, and has become an important tool for both understanding current species distributions and for designing management and conservation strategies such as assisted migration (McLane and Aitken 2012, López-Tirado and Hidalgo 2016, Ongaro et al 2018, Sofaer et al 2019, Volis and Tojibaev 2020, Mendoza-Maya et al 2022). SDM seeks to characterize a

species distribution in “ecological space” by linking key habitat characteristics to their potential distributions in “geographic space”, and can be utilized at a variety of spatial scales including to define current distributions of rare species at local or regional scales (Peterson 2006, McCune 2016). SDM has been used to evaluate future impacts of climate change on species distributions by utilizing statistical relationships between current climate variables and the geographic patterns of a species’ distribution to define an “environmental space”, which is than incorporated into models of climate change projections to generate maps of a species’ future range (Botkin et al 2007, Jeschke and Strayer 2008, Ledig et al 2010, Dawson et al 2011**,** Pinedo-Alvarez et al 2019, Mendoza-Maya et al 2022). A number of SDM methods have been developed with applications from identifying new rare species occurrences to predicting future impacts of climate change and invasive species (Elith et al 2006, Guisan et al 2006, Schwartz et al 2006, Loarie et al 2008, Underwood et al. 2004, Gogol-Prokurat 2011). Currently, the majority of climate modeling studies are based on assumptions that species distributions will shift in an attempt to track their current climatic niche, while ignoring barriers to dispersal such as edaphic and anthropogenic constraints (Lesica 2015).

Numerous critiques of both SDM in general and its use in climate modeling in particular center on the correlative nature of these models, their scale dependency, and their failure to account for key ecological and evolutionary processes that influence species ability to persist in heterogeneous landscapes (Dormann 2007**,** Wiens et al 2009**,** Willis and Bhagwat 2009). Despite their ubiquitous use in management-often due to their power in explaining modern distributions-their ability to accurately assess extinction risk, delineate suitable future habitat, and predict ecological outcomes is largely unproven (Lesica 2015). The accuracy and applicability of SDM is extremely limited by the quantity and quality of distributional information available for a

species. To accurately characterize and predict the realized niche of a species, data collection in the field is necessary to ensure habitat constraints can be identified. Recording abiotic data paired with information on a species' occupancy across its geographic range is important, ideally paired with habitat information on unoccupied areas beyond the range of the current populations (Henrys et al 2015, Rowe et al 2015, Smart et al 2015). As this method depends on adequate data of a species' realized niche across its entire distribution, accurate modeling is often restricted by the scarcity of this type of fine-scale data sampled across the entirety of each species' biogeographic range (Smart et al 2015).

While SDM can be utilized with species with few recorded populations, such as *E. codium*, resulting habitat descriptions will likely be ecologically incomplete (Gogol-Prokurat 2011, Smart et al 2015). Especially as the most vulnerable species are often the rarest, getting a robust set of the spatial data and habitat information required for accurate modeling can be impossible (Volis and Tojibaev 2020). However, as legal land protection, species recovery plans, and management efforts require defining critical habitat for species of concern, SDM is still an important tool guiding conservation of rare and endangered species. Ultimately, when SMD is combined with localized and fine-scale knowledge of a species and its current habitat, it can be an immensely important tool for guiding management decisions such as site selection for assisted migration.

The Importance of Spatial Scale in Habitat Modeling

The scale at which an SDM is generated is an important consideration impacting both the accuracy and applicability of the model (Abbitt et al 2000, Wu and Smeins 2000, Scott et al 2002, Crain et al 2015). Generally, SDM utilizes data on environmental conditions and geographic species distributions to predict habitat suitability across the landscape (i.e. at a

landscape-scale) (Austin 2002, Thuiller et al 2003, Thuiller et al 2004b). However, within many rare species populations, the spatial distributions of plants reflect microhabitat requirements occurring in small patches across heterogenous landscapes. To be useful for local conservation planning, SDMs for rare species with patchy distributions and low mobility must be able to identify suitable habitat at spatial scales close to the patch size of the species, which can often be within the range of tens of meters (Gogol-Prokurat 2011). Furthermore, for SDM to be useful for guiding the selection of areas for assisted migration, models need to be able to predict the important spatial variation affecting seedlings within even smaller spatial ranges. Three important model features have been identified to optimize the use of SDM in conservation planning for rare species with patchy distributions (Fielding and Bell 1997, Engler et al 2004, Gogol-Prokurat 2011):

i. High discrimination between suitable and unsuitable habitat at a fine scale applicable to local conservation planning (site-level).
ii. Habitat quality ranked as a measure of the likelihood a species is present or by population abundance.
iii. Suitable habitat areas are identified with high levels of accuracy while the frequency of habitat incorrectly classified as unsuitable is minimized.

To be useful for conservation planning, it is particularly important SDMs are able to differentiate between suitable and unsuitable habitat at the site-level, and field collection of occupancy data from species populations within fine spatial scales must be used to train and test the model (Marage et al 2008). To date, while only a small number of SDMs have been developed to model habitat variation of rare plants at spatial scales ranging from 25–250 m, these

studies have proven successful at finding new occurrences of rare plant species where habitat suitability was predicted to be high (Elith and Burgman 2002, Engler et al 2004, Guisan et al 2006, Marage et al 2008, Williams et al 2009). The success of these models indicates that SDMs have the capacity to be extremely useful conservation tools at the fine spatial scales best reflecting on the ground patch size of rare plant populations.

Most edaphically unique sites with high levels of soil heterogeneity and microclimatic features also contain fine-scale variation in environmentally significant variables **(**Rossington 2018, van der Ent et al 2018, Corlett 2020). However, the accuracy of niche modeling for rare species is generally limited by the availability of accurate, high-resolution and fine scale habitat data, and SDM at coarse spatial scales often result in extremely imprecise and often overly optimistic approximations of a true habitat (Gogol-Prokurat 2011, Hengl et al 2017, Cramer 2019, Corlett 2020). As coarse scale data inevitably omits some important aspects contributing to species variability in a given location, a species actual realized niche is usually smaller than that predicted by the model (Volis and Tojibaev 2020). Often, key missing habitat data include a lack of modeling for biotic interactions, either due to the lack of relevant ecological information about the species and/or fine scale vegetation data reflective of on-the-ground changes in vegetation communities.

A general lack of fine scale data, ground truthing of model assumptions, and assessment of model fit against field observations can significantly affect the accuracy of SDMs and their ability to support conservation planning, resulting in planning errors at best and failure of management goals at worst (Vaughan and Ormerod 2005, Lobo et al 2008). Ultimately, understanding the unique threats faced by *E. codium*, and adequately developing management strategies to ensure its resiliency to stochastic events, anthropogenetic development and climatic

change will require modeling and assisted migration protocols adapted to the fine scale and often abrupt variations that characterize edaphic island environments and habitat variability across the Columbia Plateau. By focusing on linking this information to an understanding of the limits of a species tolerance to changing conditions, managers can better assess the potential success of assisted migration to new locations.

WNHP 2020 Potential Suitable Habitat Model

In 2020 the Washington Natural Heritage Program (WNHP) developed a potential suitable habitat model for *E. codium* based on the environmental characteristics of the single naturally occurring population on Umtanum Ridge (Fig 2.1). The model depicts areas of low to moderate to high potential habitat in central Washington and is based on the intersection of a variety of climate, geology, vegetation, and landform/relief variables including mean January, April, July, and October precipitation, temperature, elevation, relief, ecological system and surficial geology from the WA state geology database (1:100,000 scale). Prior to this study, the model had not been ground-truthed and the scale in which habitat characteristics relevant to *E. codium*'s survival and success spatially change at the native site was unknown. Gaining more information about the habitat characteristics present at the single native population and potential assisted migration sites is needed to develop successful assisted migration strategies for this species. Determining which habitat characteristics are relevant for this species growth and survival is necessary to better refine where assisted migration attempts are made. This includes understanding changes in relevant habitat characteristics both at the coarse scale used to refine the habitat model guiding assisted migration site selection, and at finer scales reflective of the microhabitat realities determining the survival of young plants.

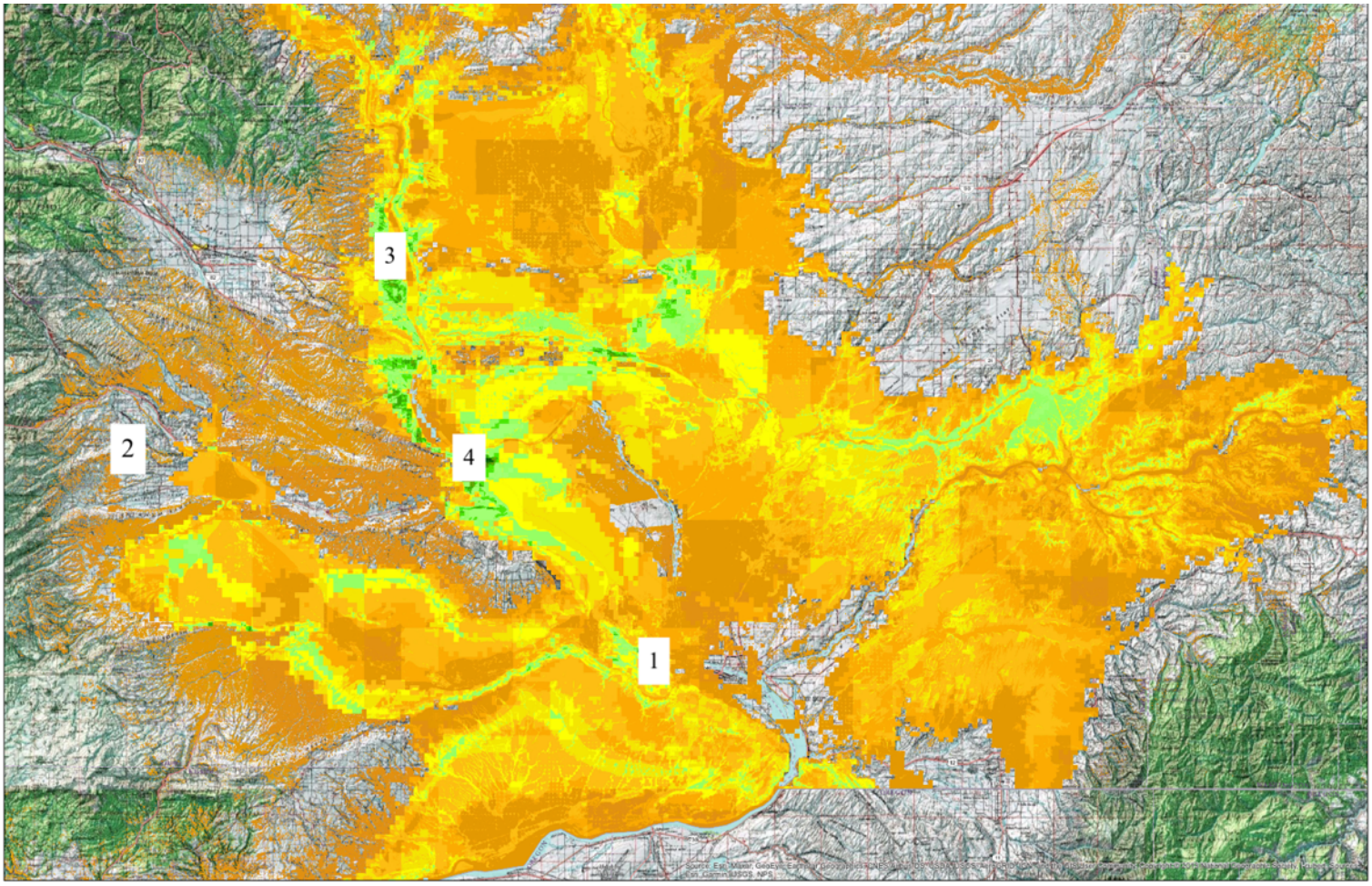


Figure 2.1 WNHP Suitable Potential Habitat Model for Umtanum Desert Buckwheat
Numbers one and two indicate locations where assisted migration attempts have occurred: (1) Badger Mountain (BM) in the most southern portion of the model and (2) Snow Mountain (SM) in the most western portion of the model. Area of suitable potential habitat for future assisted migration attempts at (3) Gingko Petrified Forest State Park (GSP) and the single native population at the (4) Native Site (NS) are also indicated. Habitat suitability ranges from low (orange) to moderate (yellow) to high (green). Highest suitability is indicated by dark green.



Figure 2.2 Locations of the *E. codium* Native and Assisted Migration Sites
Map shows where assisted migration attempts have occurred including Badger Mountain (BM) and Snow Mountain (SM), site of suitable potential habitat for future assisted migration attempts at Gingko Petrified Forest State Park (GSP) and the single native population at the Native Site (NS). Ridges of the Yakima Fold Belt can be seen running west to east, including Umtanum Ridge where NS is located as well as Snow and Badger Mountains.

Past Work on Umtanum Desert Buckwheat Assisted Migration

The recovery aims of assisted migration include increasing the number of wild populations of *E. codium*, determining if plants can survive in similar habitats away from its native site on Umtanum Ridge, and demonstrating the feasibility of assisted migration as a conservation strategy for this species (USFW 2019, Fertig 2021). 115 acres of suitable habitat was identified by the 2020 WNHP model, including other areas of Umtanum Ridge, the Saddle Mountains, Frenchman Hills, Rattlesnake Hills, Yakima Ridge, Naches Heights, and Badger Mountain. To date, Saddle Mountains, Yakima Ridge, Snow Mountain Ranch, and Badger Mountain have been used for experimental assisted migration attempts.

From 2010 to 2016, experimental assisted migration attempts were conducted at Hanford Reach National Monument in an attempt to establish plants close to but outside of the native population. Plants were propagated in north Richland and beginning in 2011 a total of 548 first-year seedlings were planted at 11 sites (102 plants at three sites on Yakima Ridge and 446 plants on Saddle Mountain) (Arnett and Goldner 2017). At Yakima Ridge, only 10 of the original cohort were still alive (9.8% survival) after 20 months, and less than five plants survived for as long as 32 months. By July 2016, only 3 stressed plants were still alive (2.9%). A subsequent fire has presumably killed any remaining plants and made the site inaccessible due to road damage (Fertig 2021). Although suitable habitat may still exist in similar or adjacent areas of Yakima Ridge as selected sites appeared to have comparable aspects and elevations to the native site, the area is not currently being monitored or replanted (Newsome and Goldie 2017, Fertig 2021). Starting in November 2012, 100 seedlings were planted at one site on Saddle Mountain, with an additional 386 seedling plugs planted from 2013-2017 at an additional three sites on the mountain (Newsome and Goldie 2017). In 2017 only 9% of seedlings were still alive, with only 4 surviving more than 21 months. In 2019, 88 seedling plugs were added to two previous assisted migration sites that survived fires in 2017 and 2018. As of 2019, 21 plants were still alive (23.8%) with some individuals growing large enough to flower (Newsome 2020).

In March 2020, one year old seedlings were introduced at Badger Mountain Centennial Preserve south of Richland (Newsome and Abel 2021) in the most southern portion of the habitat model (Fig 2.1). Twenty-nine one year old plugs were planted on the south side of the mountain.

In fall 2020, sixty seedlings were planted at three new sites at Snow Mountain Ranch (Cowiche Canyon Conservancy) in the western most portion of the habitat model (Newsome and Abel 2021). 264 additional seedlings were added to all three sites in fall of 2021 and monitoring

of both 2020 and 2021 seedlings survival was conducted by the USFWS in July 2022 (USFWS). Additional seedlings were added to additional sites in the fall of 2022 and assisted migration attempts at this location are ongoing.

Current Work

The aim of this study was to compare habitat characteristics measured at the single native population of *E. codium* with those present at sites identified by the WNHP habitat model as suitable habitat for assisted migration. This includes comparing sites where experimental assisted migration attempts have occurred (Badger Mountain) or are ongoing (Snow Mountain), and potential future assisted migration locations (Gingko Petrified Forest State Park) (Fig 2.2). By utilizing assessments of site, soil surface, and vegetation community characteristics, this study aims to determine to what extent these habitat characteristics reflect the area where *E. codium* currently grows.

The accuracy of the WNHP habitat model at predicting habitat similarities and differences important to assisted migration planning and implementation are explored at two spatial scales. In part one, a coarse "site-level" spatial scale reflective of the spatial variability considered by managers when making decisions about assisted migration site locations is explored. Site- level habitat characteristics at the Native Site, "highly suitable" habitat at Gingko State Park and three "moderately suitable" assisted migration sites at Snow Mountain are compared. In part two, a fine "outplanting transect-level" spatial scale reflective of the spatial variability considered by managers when selecting areas to plant seedlings within assisted migration sites is explored. "High", "medium", and "low" "optimal" habitat groups derived from differences in vegetation functional group composition observed at the Native Site are compared to variation in habitat characteristics at eleven outplanting transects where assisted migration of

seedlings occurred at Badger and Snow Mountains from 2020-2021. “Optimal” habitat groups are utilized to better compare varying micro-habitat conditions within *E. codium's* native population to the variation of micro-habitat conditions affecting seedlings during initial establishment at assisted migration locations.

The fundamental research questions of Chapter 2 are:

Part 1: Comparisons of the *E. codium* Native Site, Three Past, and One Potential Future Assisted Migration Sites

Goal: Ground truth model of suitable habitat for introduced efforts.

- How similar are “site-level” site, soil and vegetation habitat characteristics at the Native Site where *E. codium* currently grows to habitat characteristics at current and potential assisted migration locations identified by the WNHP habitat model?
- How accurately is the WNHP habitat model able to predict “site-level” similarities between the Native Site and assisted migration sites?

Part 2: Comparison of Three “Optimal” *E. codium* Habit Groups and 2020-2021 Seedling Outplanting Transects at Assisted Migration Sites

Goal: Determine the best augmentation and reintroduction methods in suitable habitat.

- How similar are “transect-level” site, soil and vegetation habitat characteristics at past assisted migration locations to “high”, “medium” and “low” optimal habitat groups identified at site where *E. codium* currently grows?
- How do seedling responses and survival rates between 2022-2023 to small-scale habitat variation illustrate *E. codium's* evolutionary strategies?

Methods

Field Methods

Study Locations

Data was collected at the **Native Site (NS)** located at Hanford Reach Nuclear Facility within the 1.9 acre area of the single *E. codium* population along the north facing edge of Umtanum Ridge (Fig 2.2 and 2.3). The population is located along the edge of the basalt cliff overlooking the Columbia River. For this study only the largest area of remaining plants was targeted for data collection. The existing population occurs as clusters of plants spatially separated by areas of unhospitable habitat. The five clusters with the largest number of remaining plants were assessed independently as subpopulations I-V (Fig 2.3). The largest remaining subpopulations are I and V. For more detailed information on the *E. codium* Native Site, see Chapter 1 "Methods".

Snow Mountain (SM) was selected as a "current" assisted migration site as it was the primary location for USFWS assisted migration attempts between 2020-2022 (Fig 2.2 and 2.4). It is located on the western edge of the region of likely habitat identified by the model, and is deemed an area of moderate potential habitat (Fig 2.1). Snow Mountain is at the highest elevation of the locations assessed in this study and receives higher average rainfall than the Native Site (Table 2.1 and Newsome 2021). Assisted migration attempts at this site provide a potential case study for *E. codium's* response to colder, moister and more productive conditions. In 2020 and 2021, year old seedlings were outplanted at three sites (SM 1-3) with different mapped soil series, site level topography, aspect and elevation (Fig 2.4 and Table 2.1).

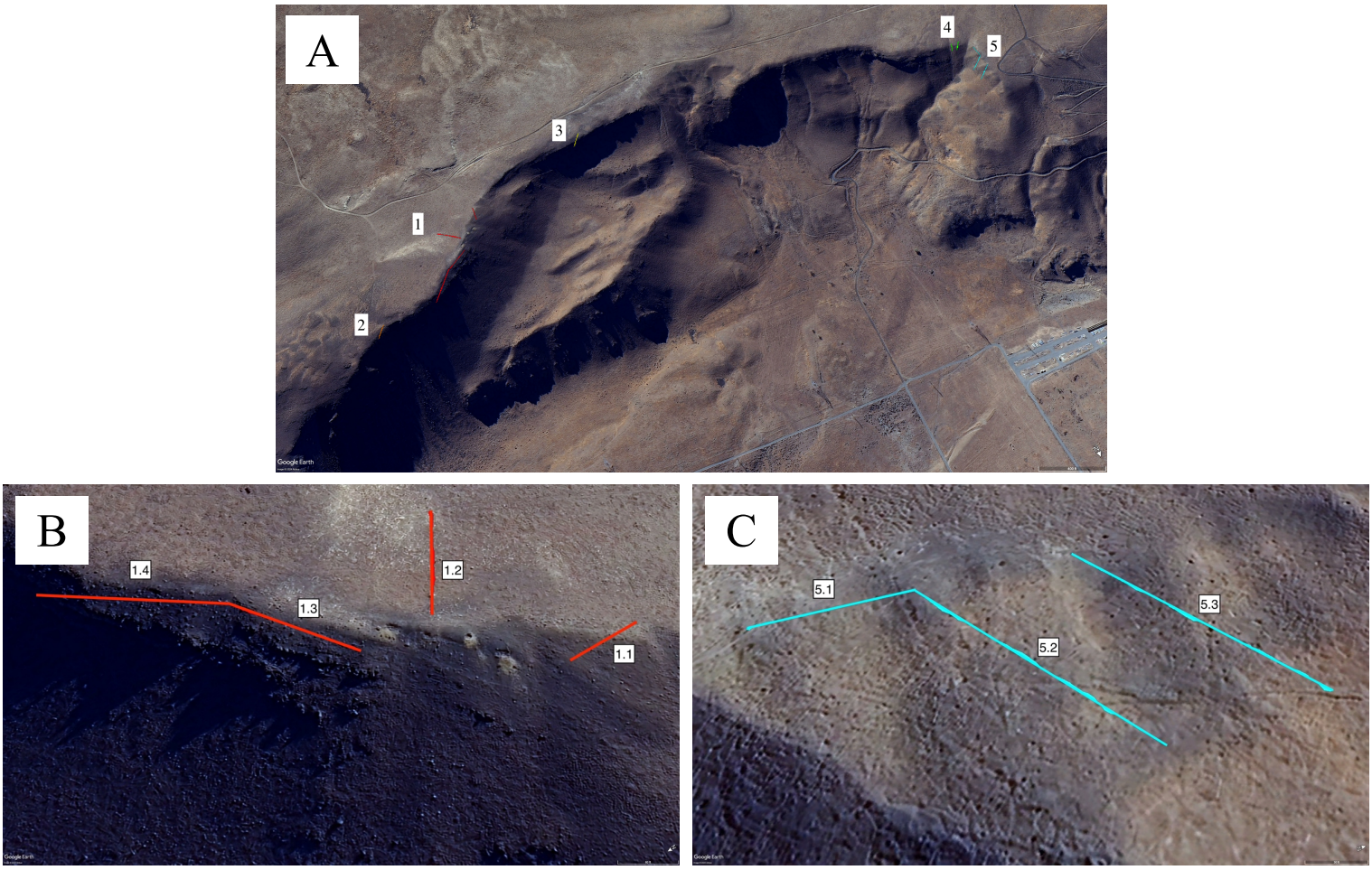


Figure 2.3 Single population of Umtanum Desert Buckwheat at Umtanum Ridge
Images show the five subpopulations (1-5) of *E. codium* along the edge of Umtanum Ridge (A) and sampling transects within the two largest subpopulations I and V (B and C). Images are facing south from the Columbia River up towards the top of Umtanum Ridge.

In late October 2020, USFWS and the Cowiche Canyon Conservancy outplanted one year old seedlings at each site along a five meter transect running east to west. 10 plants were placed on either side of the transect with approximately 0.5 meter (~20 inches) spacing between plants for a total of 20 plants at each site (Figure 2.9 and Table 1.2). Rocky areas were targeted for planting and plant locations were adjusted horizontally along the transect midline when digging into rocky soil was impossible. In early November 2021, additional seedlings were added to each site. Seedlings were planted in blocks, with each block containing forty-four seedlings on the north side of a 10 meter transect line. Seedlings were outplanted into eleven

rows with four plants in each row, with plants spaced approximately one meter apart on all sides except when locations were adjusted due to challenges with digging into the rocky soil. Sites 2 and 3 had the most challenging soils to dig into. One block of forty-four seedlings was added to both sites 1 and 2, for a total of 64 seedlings planted at each site between 2020-2021 (transect 2020= 20 and transect 2021= 44) in two transect configurations (5 meters and 10 meters) (Fig 2.6 B-C). At site 3 one block of forty-four seedlings was added in 2021 upslope of the 2020 transect containing twenty seedings (transect 1= 2021 planting, transect 2 = 2020 plantings) (Fig 2.6 D). Three additional blocks each containing forty-four seedlings were also added downslope of the 2020 transects (transects 3-5) for a total of 176 seedlings outplanted in 2021 in addition to the 20 outplanted in 2020 (total = 196) .

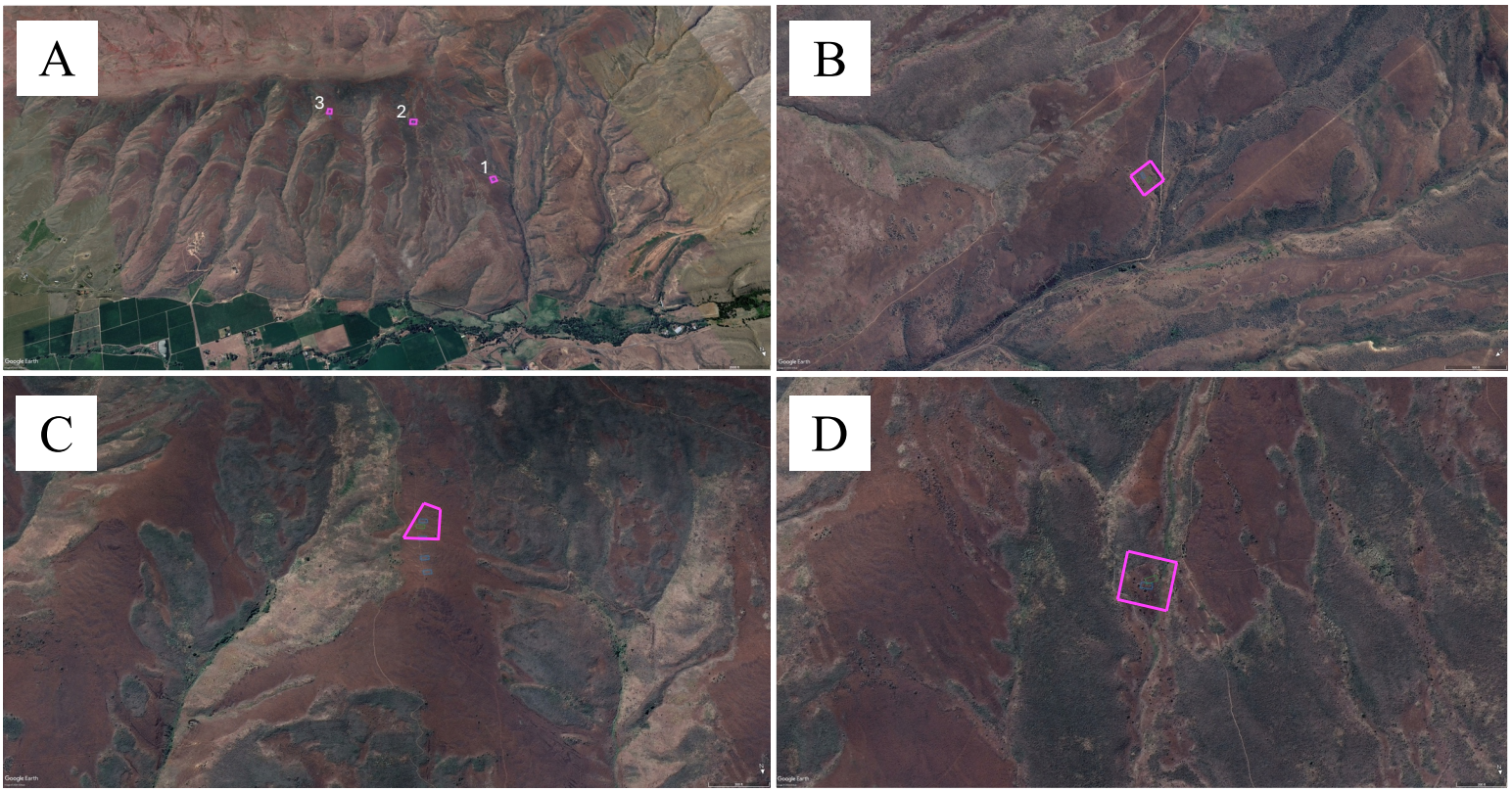


Figure 2.4 Location of the Assisted Migration Attempt at Snow Mountain
Images shows location of study sites 1-3 (purple) on the north side of Snow Mountain (A). Sites 1-3 are located at increasing elevations on the North side of the mountain: Site 1 (B) at 2100 ft, Site 2 (D) at 2480 ft and Site 3 (C) at 2700 ft. Sites are located in rocky outcroppings surrounded by deeper soils and more productive vegetation communities. Numbers indicate Snow Mountain site ID number (A).

Due to observations of wild seedling loss at the native site and outplanted seedling loss at assisted migration sites from apparent water and drought related stress, introduced seedlings received supplemental watering. Seedlings outplanted in 2020 received minimal watering during the 2021 growing season while 2021 seedlings received supplemental watering from June – September 2022. Sites 1 and 2 received supplemental watering six times during this period as they are lower elevation sites and easier to access than site 3, which only received supplemental watering three times during this period. Survival of young plants was monitored by USFWS personnel July 2022 and by UW personnel in May 2023. During the 2023 monitoring, some dead plants were dug up to check whether the roots had grown into the surrounding soil after outplanting. Plants outplanted in 2020 did not survive to July 2022 and were not monitored in 2022 or 2023.

Badger Mountain was selected as a "past" assisted migration site as an attempt was made in 2020 (Fig 2.2). Plants were introduced at two sites with different mapped soil series (USDA soil map), site level topography and aspect. Only one site on the southern side of the mountain (site 1) was utilized in this study (Fig 2.5). Badger Mountain is located in the southern range of the region of likely habitat identified by the model, and is deemed an area of high potential habitat (Fig 2.1). As Badger Mountain has the lowest elevation after the native site, is the only site on a south facing aspect and occurs in the most southern range of the locations assessed in this study, assisted migration attempts provide a potential case study for *E. codiums*'s response to hotter and drier conditions (Table 2.1). Twenty-nine one year old seedlings arranged in six clusters were outplanted as bareroots in spring 2020 (Fig 2.10). Plants were watered during

the growing season until at least June 2022, although it is unknown how often watering occurred or if/when it stopped. Survival was monitored in May 2023.

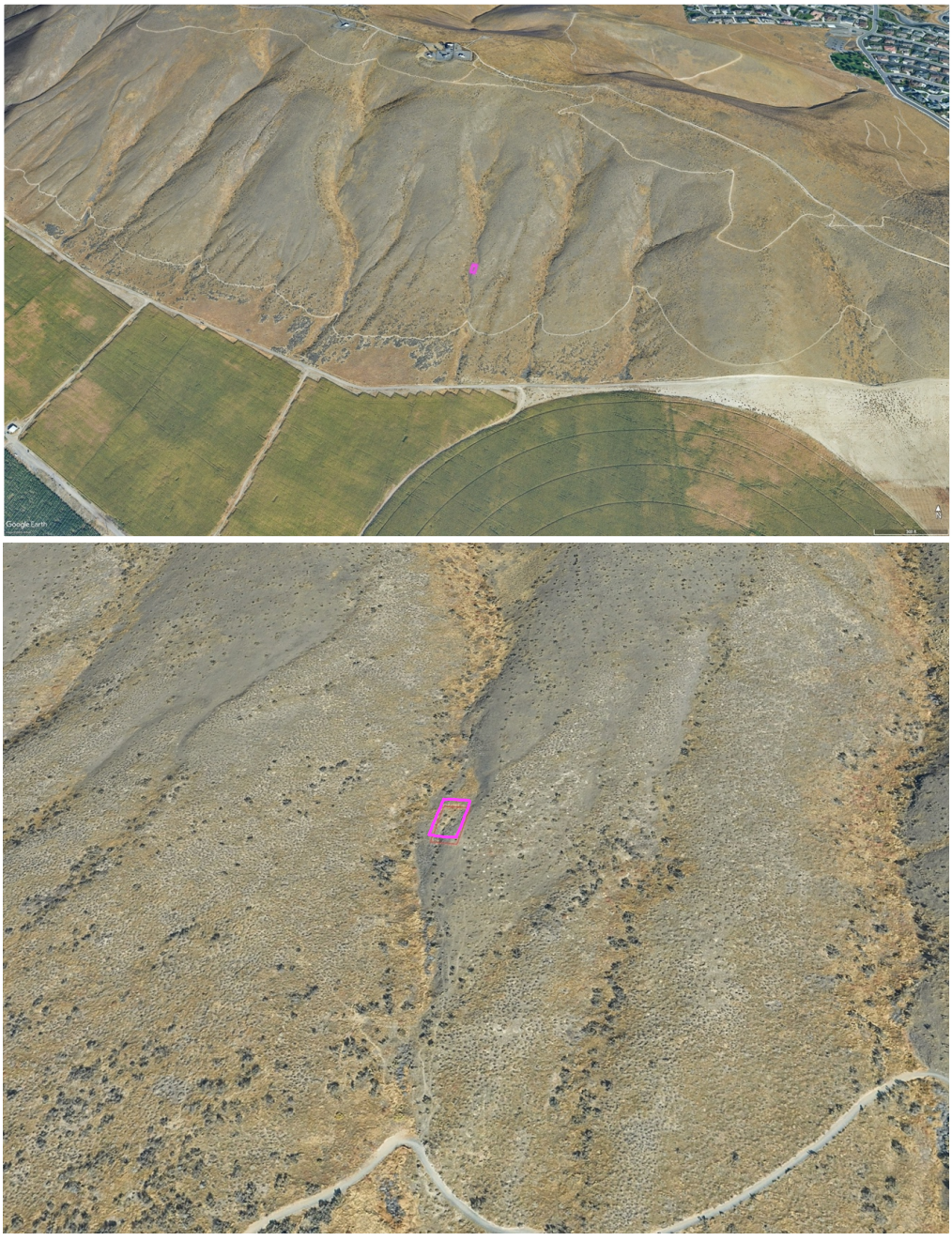


Figure 2.5 Location of the Assisted Migration Attempt at Badger Mountain
Images shows location of experimental assisted migration attempt (purple) on the south side of Badger Mountain (top). Outplanting location (purple) was determined based on visual assessment of higher surface soil rock composition in the folds of the mountain's topography in contrast to the visually deeper loams surrounding this area and covering most of the mountain side (bottom).

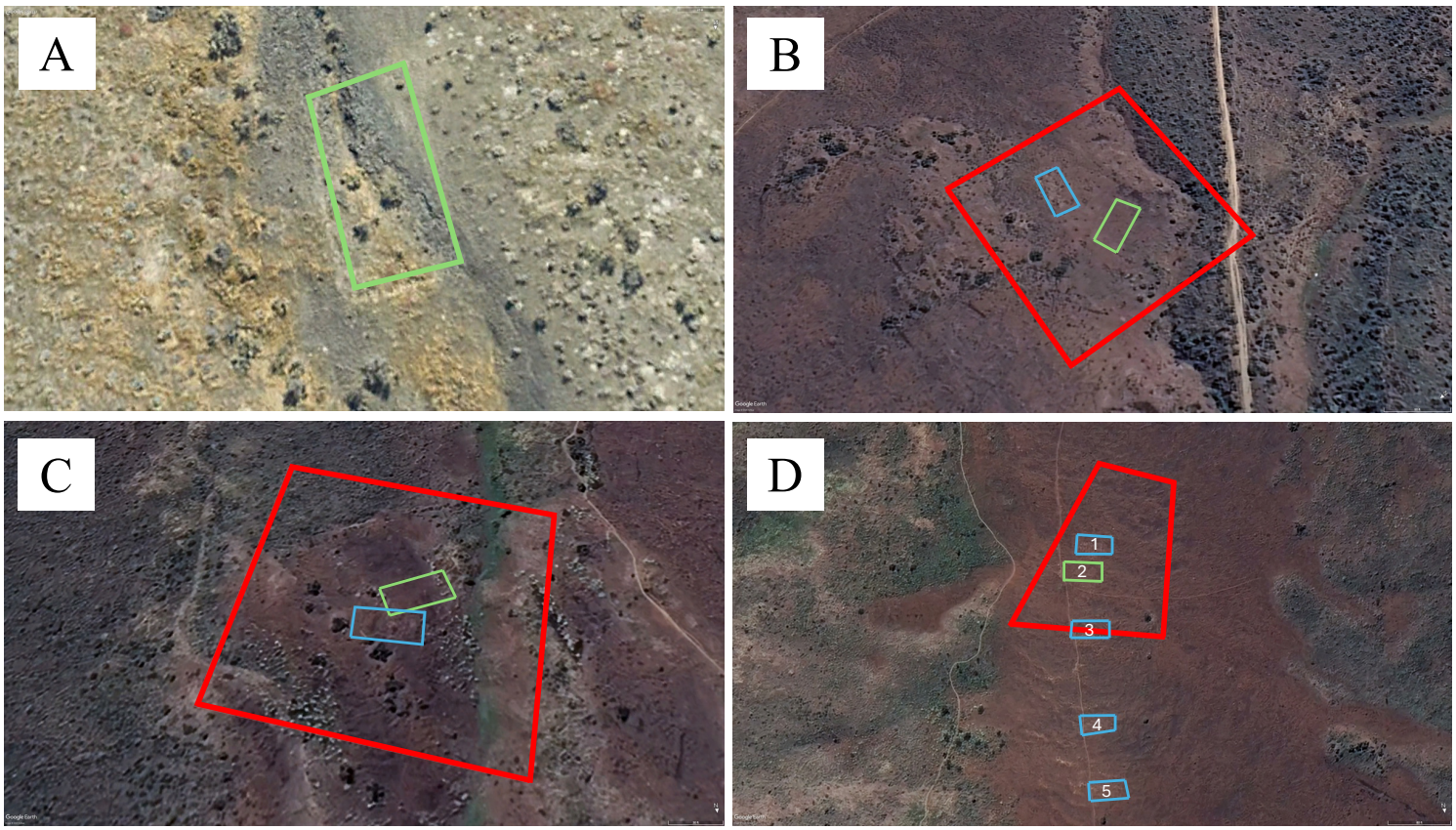


Figure 2.6 Locations of Assisted Migration Outplanting Transect Sampling Grids at Snow and Badger Mountains
Images show the outline of site-level sampling grides (red) (B-D) and transect-level sampling grides (A-D) surrounding the location of experimental *E. codium* outplanted seedling. The outline of transect-level grides surrounding seedlings outplanted in 2020 are green and grides surrounding 2021 seedlings outplanting locations are blue. Numbers at Snow Mountain Site 3 (D) indicate transect level ID numbers.

Gingko State Park was selected as a "potential future" assisted migration site because it is deemed an area of high potential habitat by the model and is located in the northern range of the likely habitat identified (Fig 2.1 and 2.2). Assisted migration attempts here could make this location a potential case study for *E. codium*'s ability to expand its range north into higher elevation areas and to the hillslopes on the opposite side of the Columbia River. Five areas of highest potential habitat were identified as areas of interest for inclusion in this study (Fig 2.7). Ultimately area 2 was selected for further study due to the relatively easier access to this area of the park, and two adjacent sites were selected based on visual assessments of aspect, topography, and the high percentage of soil surface rock present (Fig 2.7 and 2.8).

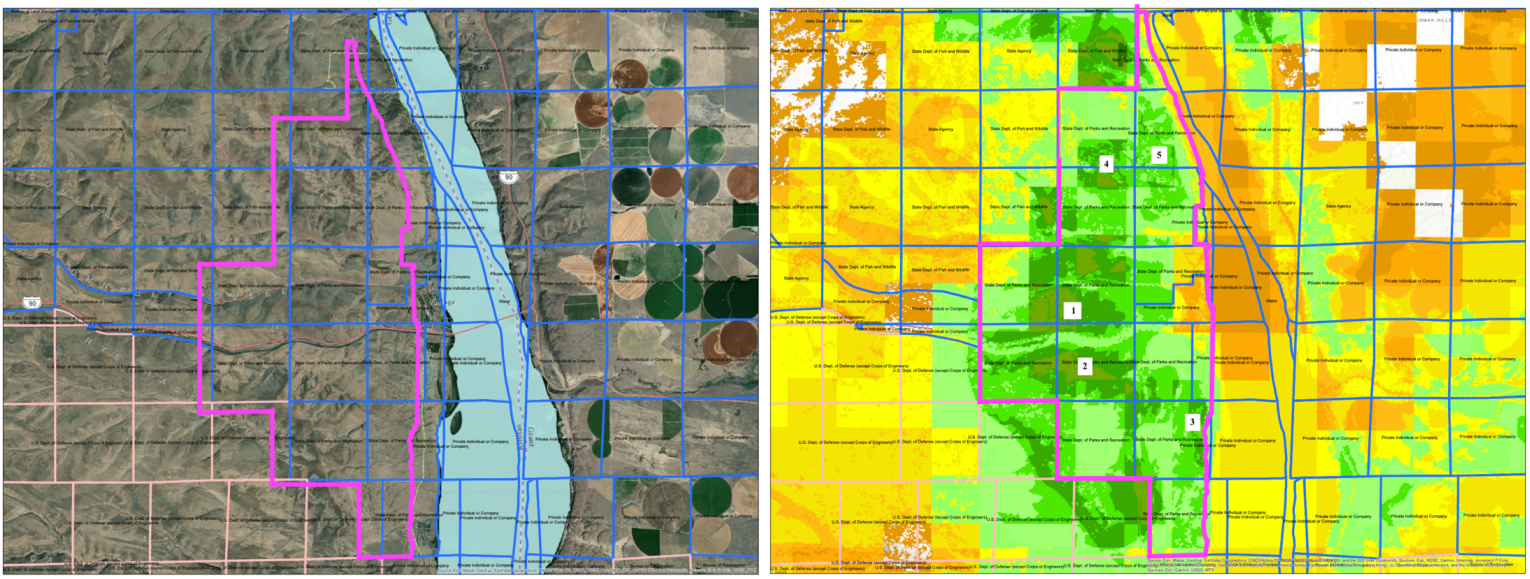


Figure 2.7 Gingko State Park Zones of WNHP Suitable Potential Habitat
Maps show boundaries of GSP (purple). The park is dissected by the Hwy 90 through the center and boarded by the Columbia River to the east (left). Major topographic features include Rocky Coulee north of Hwy 90 and Ryegrass Coulee south of Hwy 90. Five areas of highest potential suitable habitat were identified and area two was selected for study (right). This area includes the northern slope of Ryegrass Coulee. Map is oriented with the top facing North.

Study Design

All data at the Native Site (NS) were collected on June 15-16th 2023. Data were collected from eleven temporary transects between 12 and 75 meters long established with the five subpopulations (Fig 1.5). Transects were laid in accordance with sampling methods outlined in Chapter 1 “Methods”. GPS coordinates of each plot center was recorded using the Google Maps application on an iphone 6s.

At each Snow Mountain site (SM1-3) and both sites at Gingko State Park (GSP 1-2), a 60 x 60 meter square “site”-level sampling gird was constructed (n=5) (Fig 2.9A). At Snow Mountain, the site-level sampling grids (n=3) were laid so both 2020 and 2021 transects were centered inside the grid and equally distant from center (Fig 2.6 B-D). At Gingko State Park, site-level sampling girds were centered on a ribbon of rocky soil running vertically along the slope



Figure 2.8 Location of the Potential Future Assisted Migration Site at Gingko State Park
Images show location of study site (purple) on the north side of Ryegrass Coulee (top). Hwy 90 is visible north of the coulee and the Columbia River borders it to the east. Two adjacent study areas approximately 15 meters apart were selected and surveyed separately (purple) (bottom). Study areas were combined for analysis as one assisted migration site. Future work assessing habitat differences between the two study areas can be used to better elucidate spatial variability of suitable habitat characteristics within this potential assisted migration site.

Table 2.1 Known Site and Soil Differences Between the Native and Assisted Migration Sites
Table shows information about known site characteristics (elevation and mountain side position) and mapped soil series at each site. Soil series are in accordance with USDA soil mapping information (SoilWeb). There is currently no available soil information for the location of the single *E. codium* population at the native site. Soil series from approximately 650 m west of the western edge of the native population were obtained, and two most likely series based on observed soil surface and upper horizon (>4 inches) characteristics.

Location	Site #	Mountain Side	Elevation/ Avg Rain	Soil Series Code	Soil Series Name	Assisted Migration Site?
Badger Mountain						
Average annual precipitation: 24cm/9.6 inches	Site 1	South Side	1227ft	WdE3	Warden silt loam (WdE3) (15- 30 % slopes), severely eroded H1 - *0 to 2 inches:* silt loam H2 - *2 to 12 inches:* silt loam H3 - *12 to 60 inches:* stratified very fine sandy loam to silt loam	Yes 2020 n= 29
Snow Mountain						
Average annual precipitation: 35.5mm/14 inches	Site 1	North Side	Lowest: 2104ft	109/110	Intersection of two series: Rock Creek-Clint-Simcoe complex 110: 0 - 45 % slopes 109: 0 - 30 % slopes H1 - *0 to 2 inches:* very stony silt loam H2 - *2 to 10 inches:* very cobbly clay H3 - *10 to 14 inches:* unweathered bedrock	Yes 2020 n = 10 2021 n= 44
	Site 2	North Side	Middle: 2408ft	109/110	Intersection of two series (same as above)	Yes 2020 n= 10 2021 n= 44
	Site 3	North Side	Highest: 2664ft	109	109: Rock Creek-Clint-Simcoe complex, 0 - 30 % slopes	Yes 2020 n= 10 2021 n= 176
Gingko State Park						
Average annual precipitation: 30.5mm/12 inches	Site 1	North Side	Lower: 1505ft	755/695	Intersection of two series 755: Nevo-Fortyday complex, 3 to 15 % slopes H1 - *0 to 2 inches:* very cobbly loam H2 - *2 to 8 inches:* very gravelly clay loam H3 - *8 to 18 inches:* unweathered bedrock 695: Drino-Sohappy-Fortyday complex, 30 to 60 % slopes H1 - *0 to 3 inches:* very gravelly loam H2 - *3 to 7 inches:* very gravelly loam H3 - *7 to 19 inches:* very gravelly loam H4 - *19 to 38 inches:* extremely cobbly loam H5 - *38 to 48 inches:* unweathered bedrock	Potential Future Site
	Site 2	North Side	Higher: 1537ft	755	755: Nevo-Fortyday complex, 3 to 15 % slopes	Potential Future Site
Native Site						
Average annual precipitation: 25.5mm/10 inches	---	North side	1141ft	3/68	Possible soil series based on mapped soils in similar landscape position approximately 650m west of subpopulation V on Umtanum Rdige: 3: Bakeoven very cobbly silt loam, 0 to 30 % slopes H1 - *0 to 4 inches:* very cobbly silt loam H2 - *4 to 10 inches:* very gravelly clay loam H3 - *10 to 14 inches:* unweathered bedrock 68: Lickskillet very stony silt loam, 5 to 45% slopes H1 - *0 to 3 inches:* silt loam H2 - *3 to 20 inches:* very cobbly loam H3 - *20 to 24 inches:* unweathered bedrock	No. Location of single known native population.

so sampling maximized the number of $1m^2$ plots that fell within this target substrate (Fig 2.8 and Fig L-2). Thirteen $1m^2$ plots were sampled within the grid (Fig 2.9A). GPS coordinates were recorded at plot center using a Trimble Geo 7x handheld GPS unit.

At each Snow Mountain site, 14 x 7m rectangular "outplanting transect" -level sampling grids were constructed to encompass outplanting transects (Fig 2.9 B-C). Eight $1m^2$ plots were sampled within each grid. Sampling grids were centered on outplanting transects to ensure at least one plot was sampled directly on top of *E. codium* seedlings in each 2020 outplanting transect (Fig 2.9 B) and at least two plots were sampled directly on top of *E. codium* seedlings in each 2021 outplanting transect (Fig 2.9C). The same 14x7m rectangular sampling grid was also used at Badger Mountain, but the sampling grid was centered on the ribbon of rocky soil running vertically along the slope so it would encompass all six clusters of seedlings (Fig 2.10). GPS coordinates were recorded at plot centers using a Trimble Geo 7x handheld GPS unit.

Data Collection

Seedling Survival

Survival was tracked for individual outplanted seedlings in 2022 (n = 264) and 2023 (n= 293). In 2023, USFWS personnel recorded information on survival (alive/dead) and status (healthy, stressed, very stressed) of the 2021 seedling cohort at Snow Mountain. In 2023, UW personnel monitored the 2021 seedling cohort at Snow Mountain at the 2020 seedling cohort on the south side of Badger Mountain. Information was collected on survival (alive/dead), percentage of foliage (1-100%), visible stem protruding from soil surface (yes/no), microtopography classification (flat, convex, concave), if micro topography information was

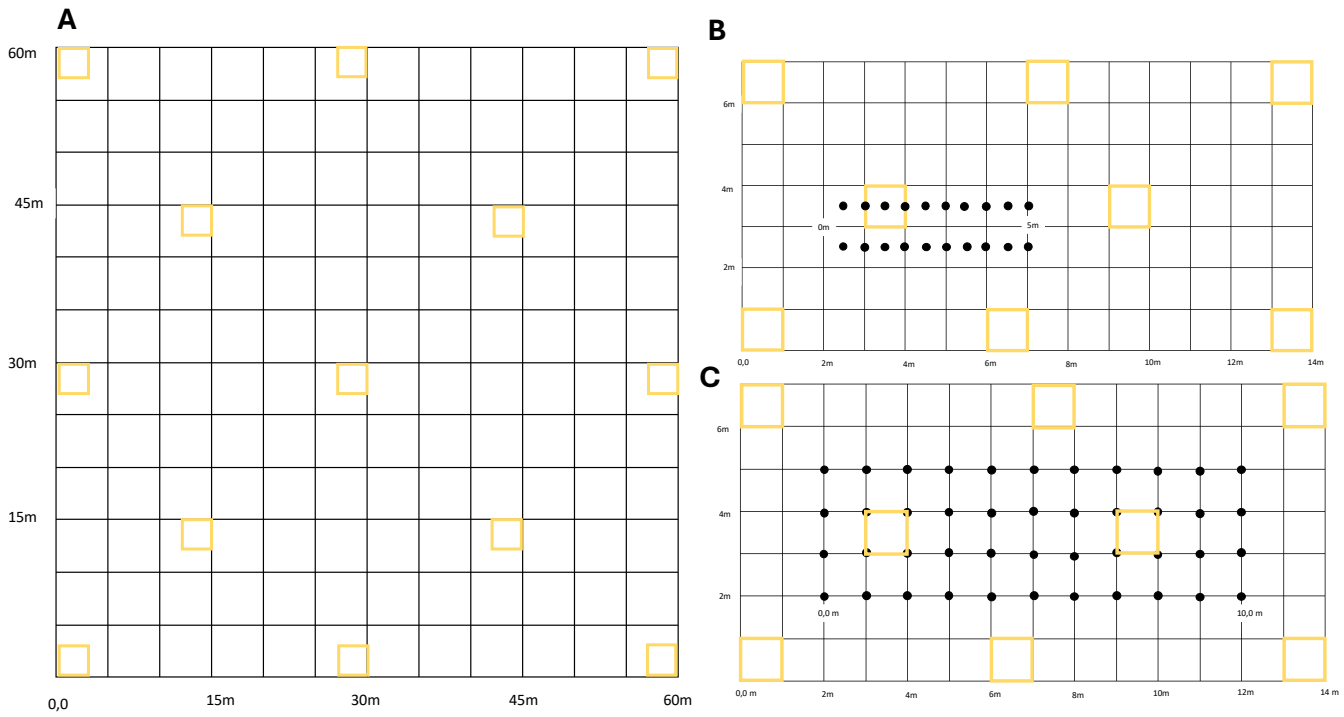


Figure 2.9 Design of Data Collection Methods Used at Snow Mountain and Gingko State Park
Figure includes site-level sampling scheme used to compare Snow Mountain sites 1-3 (n=3) and two adjacent sites at Gingko State Park (n=2) (A). Thirteen plots were sampled at 30m spacing within each 60x60m grid. At Snow Mountain 60x60 meter sampling grids were laid so both 2020 and 2021 transects were centered inside the grid and equally distant from center (30m, 30m). At Gingko State Park sampling girds were centered on the ribbon of rocky soil running vertically along the slope so sampling maximized the number of $1m^2$ plots that fell within this target substrate. Figure includes transect-level sampling scheme used to compare where outplanting occurred at Snow Mountain (n= 9) (B-C). Eight plots were sampled at 7m spacing within each 14x7m rectangle. Sampling scheme of 2020 (B) and 2021 (C) outplanting attempts illustrate the relationship of the sampling grid to seedling locations (black dots). Plot coordinates indicate location of outplanting transects. Yellow squares indicate locations of $1m^2$ plots.

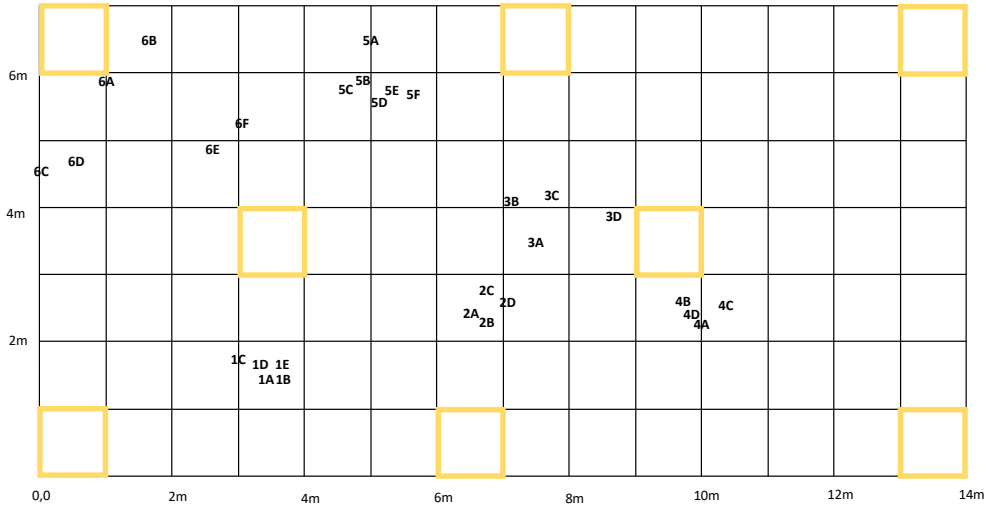


Figure 2.10 Design of Data Collection Methods Used at Badger Mountain
Figure includes transect-level sampling scheme used to compare where outplanting occurred at Badger Mountain (n= 1). Eight plots were sampled at 7m spacing within each 14x7m rectangle. Sampling scheme illustrates the relationship of the sampling grid to seedling locations, which are indicated by number and letter combos. Seedlings were planted in six clusters (1-6) with two to six plants within each cluster (A-F) (1: n= 5, 2: n= 4, 3: n= 4, 4: n= 4, 5: n= 6, 6: n=6). Yellow squares indicate locations of $1m^2$ plots.

concave, then depth of concavity (cm), and soil surface rock fragment composition. Information was collected in a 50cm^2 frame centered around each outplanted seedling that was still alive. Due to the extremely low survival rates observed in 2023 (n= 10 survived), only information on survival rate was considered.

Habitat Characteristics

In each 1m^2 plot, information on site characteristics, soil surface characteristics, soil hydrology, and vegetation characteristics was collected. Unless otherwise noted, all data were measured and recorded in accordance with sampling methods outlined in Chapter 1 “Methods”. Site characteristics included spatial location (GPS point), aspect, landform, slope position, hillslope position, slope shape, slope complexity, slope rise, slope run, and slope angle.

Soil surface characteristics included soil surface composition, (SSC), soil surface rock classification (SSRFCL), soil surface rock fragment composition (SSRFC) and soil texture. Due to ongoing negotiations between The Department of Defense and The Confederate Tribes and Bands of the Yakima Nation, no data collection that required disturbance or removal of soil was conducted at the Native Site. Soil surface texture was determined through a qualitative in-field hand texturing method (Thein 1979). Soil texture at assisted migration sites was determined by removing a 6”x6” cubic square of soil from each 1m^2 plot center. Soil was collected in all site-level grid plots at Snow Mountain sites. At Gingko State Park, soil was only collected from the three plots along each of the 0m, 30m, and 60m horizontal grid lines (Fig 2.9A), for a total nine plots in each GSP-1 and GSP2 respectively, and a total of eighteen plots across the entire site. At outplanting transect sampling grids, soil was only collected from the four corners of each grid (Fig 2.9 B-C). Soil was air dried, homogenized and >2mm rock fragments removed using metal

sieves (Gilson) at UW laboratory facilities. 50g of soil was sent to laboratory facilities at Kansas State University for textural analysis using a hydrometer particle size distribution method with a hexametaphosphate solution (Gee and Bauder 1986, Gavlak et al 2005).

Measured soil hydrology characteristics include hydraulic conductivity based on soil water infiltration rate. Soil water infiltration rate was determined using a Mini Disk Infiltrometer (Meter) to measure the volume (mL) of water infiltrating through the soil every 30 seconds for 330-390 seconds. Hydraulic conductivity was calculated from water infiltration rate in accordance with protocols outlines by meter utilizing R script developed by Jon Bakker (Meter 2020-2021, Appendix AB). For plots where recording continuous infiltration over six minutes required stopping the run to refill the minidisk infiltrometer, multiple runs were consolidated into a single continuous six-minute run (0-360 seconds) (Appendix AA).

Vegetation characteristics include vegetation composition and cover (VCSC), and photosynthetically active radiation (PAR) (measured in μmol / m2 / s). At the Native Site, measurements were only taken in subpopulations I and V on June 15th and 16th 2023 respectively between 10am and 3pm. At assisted migration sites, PAR was only measured during site-level data collection at Snow Mountain and Gingko State Park (SM: n=3 and GSP: n=2). PAR was recorded in one day at each site between July 26th and August 30th 2022 between 10am and 3pm. PAR was not collected from transect-level sampling grids.

Statistical Methods

Software and R Packages

Entry, review, organization, of all study data, and the correction of mini disk infiltrometer raw data, were completed using Excel (Microsoft Office). All data analysis, calculations made from raw data values, corrections and manipulations including the filling of missing values, were completed using R version 4.4.0 (R Core Team 2024).

Packages used for all analyses include “dplyr” version 1.1.4 and “tidyverse” version 2.0.0.
Packages used for data preparation included “broom” version 1.0.5, and “here” version 1.0.1.
Packages used for statistical analyses include “corrplot” version 0.92, “dendextend” version 1.17.1, “indicspecies” version 1.7.14, “labdsv” version 2.1.0, “stats” version 4.4.0, and “vegan” version 2.6.4.
Packages used for creating tables include “gt” version 0.10.1, “gtExtras” version 0.5.0, “ggdist” version 3.3.2, , “modeest” version 2.4.0 and “tibble” version 3.2.1.
Packages used for graphing data include “ggplot2” version 3.5.1, “ggdist” version 3.3.2, “ggforce 0.4.2”, gghalves “version” 0.1.4, “ggpubr” version 0.6.0, “multcompView” version 0.1.10, “systemfonts” version 1.0.6, “ unpivotr” version 0.6.3, “reshape” version 0.8.9, and “wesanderson” version 0.3.7.
Package “soiltexture” version 1.5.3 was used for graphing soil textural classifications onto USDA-NCSS soil textural triangles and converting soil textural data (% sand-silt-clay) to USDA-NCSS soil textural classifications.

Data preparation

Site and Outplanting Transect Identity

To accomplish the first study objective, "site-level" comparisons were made between the Native Site (n= 1) and assisted migration sites at Gingko State Park (GSP) (n=1) and Snow Mountain (SM) (n=3) for a total of five sites (n= 5). Data from all subpopulations at the Native Site were agglomerated under a single siteID (NS) (n= 98). Vegetation composition data from the Native Site were subset by only plots where *E. codium* is present (n= 72). All data collected within the *E. codium* subpopulations at the Native Site, irrespective of whether *E. codium* was present in the $1m^2$ plot, were used to compare site and soil characteristics at the site-level. This is because soil texture was the only site characteristics determined in Chapter 1 to significantly differ by *E. codium* occupancy, and together the complete dataset best represents the variation occurring across the site. Data collected at Gingko State Park from adjacent 60x60m site-level sampling grids (GSP-1 and GSP-2) were agglomerated under a single siteID (GSP) (n= 26) to best show the site level variation across the entire area identified as potentially suitable for future assisted migration. Data collected in 60x60m site-level sampling grids at each Snow Mountain site (SM1-3) were agglomerated with the data collected in the 7x14m outplanting transect-level grids under a single siteID SM1-3 (SM1: n = 29, SM2: n = 29, SM3: n = 53) to best capture the range of variation across the site and where *E. codium* assisted migration occurred. Although statistical methods provide analysis of differences and similarities between all study sites, only relationships between each assisted migration site (GSP, SM1, SM2, and SM3) and the Native Site (NS) were interpreted. Relationships between assisted migration sites at the same location (i.e. Snow Mountain) are not reported and are only considered to make general observations about Snow Mountain as it differs to Gingko State Park and the WNHP suitable habitat model.

To accomplish the second study objective, "transect-level" comparisons were made between three "optimal" *E. codium* habitat groups[18] (high, medium, low) described in Chapter 1, and assisted migration outplanting transects at Snow and Badger Mountains. All data from the Native Site were subset by only plots where *E. codium* is present (n= 72) to best captures the microhabitat *E. codium* occupies. Each outplanting transect at Snow Mountain sites 1-3 were considered individually (SM1: 2, SM2: 2, SM3: 5) including three transects where assisted migration attempts occurred in 2020 (SM1-2020, SM2-2020, SM3-2) and six transects where attempts were made in 2021 (SM1-2021, SM2-2021, SM-1, SM-3, SM-4, SM-5). Data collected at Badger Mountain from a single "outplanting transect" sampling grid were considered as a single sampling unit with the identity BM-1. In total 13 "transect-level" units were compared across three locations (NS, SM, and BM) and four assisted migration sites (BM, SM-1, SM-2, SM-3). Although statistical methods provide analysis of differences and similarities between all groups (3 optimal habitat groups and 10 outplanting transects n= 13), only relationships between each attempted assisted migration outplanting transect (BM-1, SM1-2020/2021, SM2-2020/2021, SM3-1-5) and the "optimal" *E. codium* habitat groups (high, medium, low) were interpreted. Relationships between assisted migration outplanting transects are not reported or considered unless to make general observations about site level spatial heterogeneity and outplanted seedling survival. Relationships between "optimal" habitat groups are described in Chapter 1 "Discussion" although data values are reported in the "Results" of this chapter.

[18] For a more detailed description of "optimal" *E. codium* habitat groups and their differences, see Chapter 1 Part 3: "Defining 'Optimal' E. codium Habitat Types".

Site Characteristics

Aspect (N, NE, E, SE, S, SW, W, NW) was recorded as a categorical factor and converted into a continuous numeric variable by replacing each factor with its associated aspect degree (0º, 45º, 90º, 135º, 180º, 225º, 220º, 315º). Aspect degree was utilized to compute heat load index. Missing continuous values were filled by taking the average value from the transect in which the plot occurred.

Heat load index was calculated using the heatload() function developed by Zeleny and Lin (2021) based on equations published by McCune and Keon (2002) and revised by McCune (2007) (Fig AB). Equation 2 was used as recorded slope angle values are below 60º (maximum slope recorded was 30º).

Missing values were filled for slope aspect (n= 3) and slope (n=1) at the Native Site. Missing categorical values at the Native Site were filled by taking the mode of the plot's transect and was filled for aspect (n=3).

Because the Native and assisted migration sites are located on a variety of landforms (mountain top, mountain flank, mountain base), categorical factors for landform and slope position for each plot were combined into the category "landscape position" with six levels:

Mountain Top-Upper Third (MT_UT)

Mountain Top -Middle Third (MT_MT)

Mountain Top -Lower Third (MT_LT)

Mountain Flank-Upper Third (MF_UT)

Mountain Flank -Middle Third (MF_MT)

Mountain Base-Upper Third (MB_UT)

Soil Characteristics

Soil textural data collected at assisted migration sites were converted from a multivariate data set of percentage of sand-silt-clay to a categorical soil texture classification according to the USDA-NSCC system of soil classification (Moeys et al 2024). This allowed soil textural data from 6 inches (15cm) in the soil profile to be compared to soil textural classifications of the soil surface determined by hand texturing method at the Native Site.

Soil/Vegetation Characteristics

Recorded cover classes (0-7) were converted to percentage cover values by using the mid-point of each cover class (1= 0.5%, 2= 3%, 3= 10%, 4= 20%, 5 = 37.5%, 6 = 62.5%, 7 = 87.5% for VCSC, SSC and SSRFC; 0= 0%, 1= 0.05%, 2= 1.55%, 3 =9%. 4 = 32.5%, 5 = 75% for SSRFCL).

Vegetation Characteristics

Total cover of all species in each plot (total cover) and number of total species in each plot (species richness) was calculated using VCSC data.

Vegetation Functional Group Cover and Composition

Data collected on vegetation composition were used to calculate the total cover of each vegetation functional group within each $1m^2$. Vegetation composition data from the Native Site were subset by only plots where *E. codium* is present (n= 72). For more information on the creation of vegetation functional group cover and composition data see Chapter 1 “Methods”. All shrubs and subshrubs were perennial, and therefore are referred to here only by their life-form. All *Eriogonum* species were classified as “subshrubs” due to their physically and functionally unique combination of long-life span, woody growth, and low, cespitose growth habit.

Separating all *Eriogonum* species into the category "subshrub" allows for differentiation between upright, long lived woody shrubs in other families, and the common, widespread, low growing, long lived woody subshrubs that characterize the genus *Eriogonum* and are the most functionally analogues to *E. codium* ecologically. In total six vegetation functional groups were used: shrub, subshrub, perennial forb, annual forb, perennial graminoid and annual graminoid.

Statistical Tests

A Euclidean distance metric was used for all data except vegetation species composition. A Euclidean distance metric was used because the data is continuous and symmetric (Bakker 2024). A Bray-Curtis distance metric was used for vegetation species composition data (VCSC) as the data are continuous and asymmetric. Distances matrices were created to analyze sets of multivariate responses of soil surface composition, soil surface rock fragment composition, and vegetation species composition data. All multivariate response data were relativized by row total before conversion to a distance matrix to better represent how the totals are distributed among compositional components.

Cluster Analysis

Hierarchical cluster analysis (stats, R Core Team 2024) was used to identify groups and classify plots from the *E. codium* Native Site based on similarities in vegetation functional group composition (n = 72). This approach utilizes an iterative agglomerative process to consolidate plots into "clusters" based on their dissimilarity (Singh et al 2011, Bakker 2024). For more information on the use of cluster analysis see Chapter 1 "Methods". Three cluster analysis groups were selected to represent "optimal habitat groups" based on differences in "high" (n= 20),

"medium" (n= 24) and "low" (n= 28) *E. codium* cover. See Chapter 1 "Results" and "Discussion" for a consideration of the variation within and among these groups.

Permutational Multivariate Analysis of Variance (PERMANOVA) and Post-Hoc Tests (Tukey Test and Pairwise ADONIS)

Permutational multivariate analysis of variance (PERMANOVA) (vegan "Community Ecology Package", Oksanen et al 2022) was used to address all analysis objectives. For more information on PERMANOVA see Chapter 1 "Methods". Post hoc pairwise comparisons of significant differences between groups were conducted using a Tukey test (stats, R Core Team 2024) for univariate responses, and pairwise ADONIS for sets of multivariate responses (Bakker 2024). Results of Tukey tests are included in associated bar graphs and raincloud plots, while results of pairwise ADONIS are visualized with heat maps in which color is linked to statistical strength of differences between groups (p-value).

To address the first objective and explore "site-level" habitat characteristics of the Native Site and assisted migration sites, plots were grouped based on site identity (siteID) into a total of 5 levels (NS: n= 98 for site and soil characteristics and n= 72 for vegetation characteristics, GSP: n= 26, SM1: n = 26, SM2: n = 26, SM3: n = 53). siteID was run as the explanatory variable against categorical and continuous variables characterizing site characteristics (landscape position, hillslope position, aspect, slope shape, slope complexity, heat load index, slope, slope angle, SSRFCL), soil characteristics (hydraulic conductivity, SSC, SSRFC, soil texture), and vegetation characteristics (total cover, species richness, VCSC, LAI).

To address the second objective and explore "outplanting transect-level" habitat characteristics of optimal *E. codium* habitat groups (n= 3) and outplanting transects (n = 10), plots were grouped based on transect identity (tranID) into a total of 13 levels (high: n= 20,

medium: n = 24, low: n= 28, BM1-1, SM1-2020: n = 8, SM1-2021: n = 8, SM2-2020: n = 8, SM2-2021: n = 8, SM3-1: n = 8, SM3-2: n = 8, SM3-3: n = 8, SM3-4: n = 8, SM5-1: n = 8). tranID was run as the explanatory variable against categorical and continuous variables site characteristics (landscape position, hillslope position, aspect, slope shape, slope complexity, heat load index, slope, slope angle, SSRFCL), soil characteristics (hydraulic conductivity, SSC, SSRFC, soil texture), and vegetation characteristics (total cover, species richness, and VCSC).

Differences and similarities in vegetation functional group composition between "site-level" and "transect-level" groups was addressed by analyzing the cover of each vegetation functional group as six independent univariate responses (shrub, subshrub, perennial forb, annual forb, perennial graminoid, annual graminoid) and as a multivariate data frame containing the total cover of each functional group. siteID and tranID were each run as explanatory variables against each vegetation functional group's cover and their composition.

Data Visualization: Bar Graphs, Raincloud Plots, Scatter Plots and NMDS Ordinations)

Differences between site and transect-level groupings in mean and variation of continuous variables were visualized with raincloud plots using raw data values. Raw values of vegetation functional group cover were calculated and graphed using raincloud plots as well. Differences in categorical variables were visualized using bar graphs and the mode for each grouping determined. Seedling survival rates between 2020-2023 were visualized using a scatter plot. Raw soil textural data (% sand-silt-clay) collected at assisted migration sites were visualized by graphing values into USDA-NSCC soil textural triangle. Ordinations of multivariate response matrices were created using non-metric multidimensional scaling (NMDS) (vegan "Community Ecology Package", Oksanen et al 2022). For more information on the use of NMDS ordination see Chapter 1 "Methods"

Data Summary Tables

Summary tables of site, soil and vegetation characteristics were created for site and transect-level groupings explored in this study. For each group, mean, range (minimum/ maximum) and standard deviation were calculated for continuous univariate habitat characteristics, and mode determined for categorical univariate site and soil characteristics. Mean, range and standard deviation of the compositional components of soil surface composition (rock, bareground, litter biocrust) and soil surface rock fragment composition (bedrock, boulder, stone, cobble, coarse gravel, medium gravel, fine gravel, very fine gravel) were determined. To better understand differences in species composition, the occurrence (total number of plots recorded) for all vegetation species were calculated for each site- level groupings. Differences in mean, range and standard deviation of each vegetation functional group's cover was determined for both site and transect-level groupings.

Indicator Species Analysis

Indicator species analysis (ISA) (indicspecies, De Cáceres and Legendre 2009, De Cáceres et al 2012) was used as a follow up test to assess which vegetation species, soil surface, and rock fragment types were associated with significant relationships with site and transect-level groupings explored in this study (De Cáceres et al 2012, Bakker 2024). For more information on the use of ISA see Chapter 1 "Methods". While this technique has originally developed to work with vegetation composition data, it can be applied to any type of multivariate compositional data (Bakker 2024).

Results

Part I: Differences in Site, Soil and Habitat Characteristics Between the Native Site and Assisted Migration Sites

Site Characteristics

Significant differences (p = <0.05) in all site characteristics were determined between study sites except for slope shape and complexity (p = >0.1) (Table 2.1.1). Mode of slope complexity was linear-linear (LL) at all sites (Fig P-1). All sites have similarly equal ratios of simple to complex slopes, although GSP has <50% plots with complex slopes (Fig 2.1.1-D). Mode slope at SM2 and SM3 was complex while GSP, NS and SM1 had simple slops in the majority of plots.

The majority of plots at NS were located on the upper, middle, or lower thirds of the mountain top, with <5% of plots occupying the mountain flank (Fig 2.1.1-A). In contrast, all assisted migration sites except SM1 were located exclusively on the upper or middle thirds of the mountain flank, while SM1 was located on the upper third of the mountain-base. The majority of

Table 2.1.1 PERMANOVA of Differences in Site Characteristics Between the Native Site and Assisted Migration Sites
Significant differences (p = <0.05) in all site characteristics were determined between study sites except for slope shape and complexity (p = >0.1). Significant relationships are indicated by asterisks (* = significant, ** = strongly significant, ***= very strongly significant.

Site-Level Differences

Site Characteristics (n=235)	**Df**	**R^2**	**F**	**Pr(>F)**	
Heat Load	4	0.1285	8.48	0.001	***
Slope	4	0.0996	6.36	0.001	***
Slope Angle	4	0.2183	16.06	0.001	***
Aspect	4	0.0477	2.88	0.024	*
Total Rock Fragment Class	4	0.1387	9.26	0.001	***
Landscape Position	4	0.8716	390.30	0.001	***
Hillslope Position	4	0.3372	29.26	0.001	***
Slope Complexity	4	0.0134	0.78	0.548	
Slope Shape	4	0.0290	1.72	0.140	

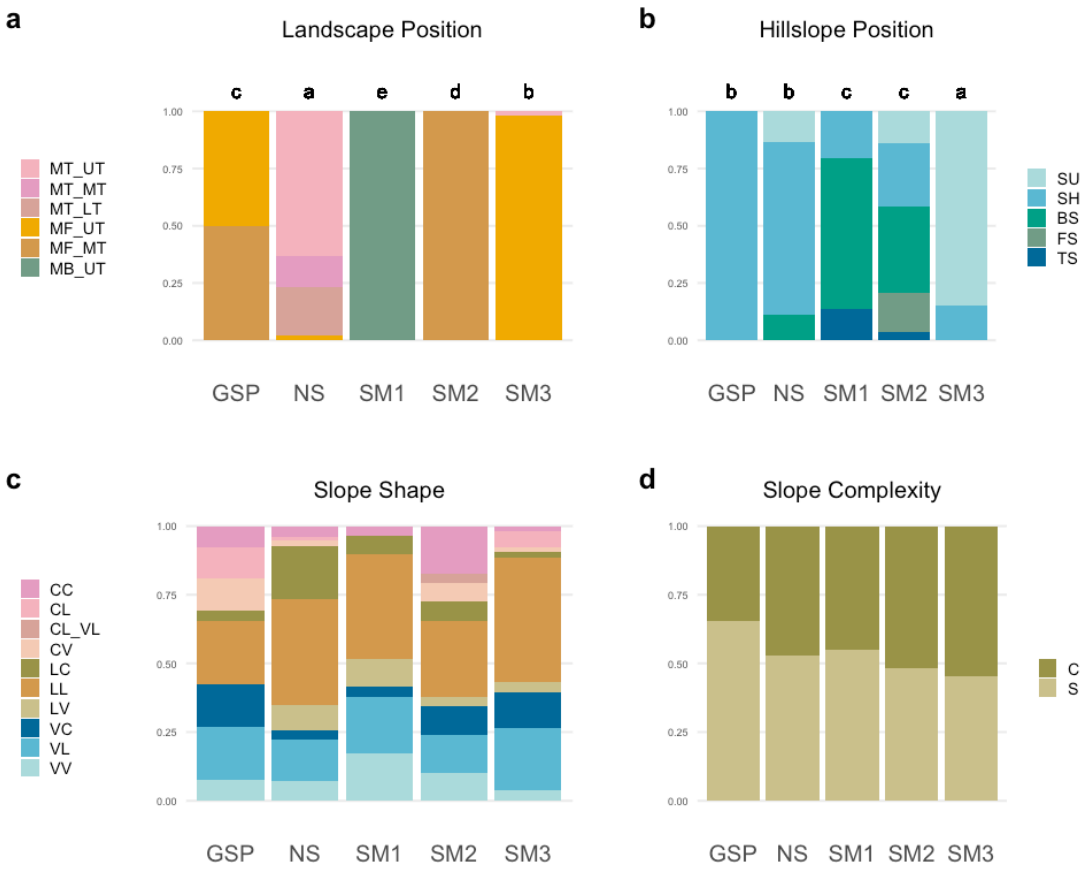


Figure 2.1.1 Bar Graphs of Site Characteristics at the Native Site and Assisted Migration Sites
Differences in categorical site variable at the native site (NS), Gingko State Park (GSP) and Snow Mountain sites 1-3 (SM1-3) including landscape position (a) (MT_UT = mountaintop- upper third, MT_MT = mountaintop- middle third, MT_LT = mountaintop- lower third, MF_UT= mountain flank_ upper third, MF_MT= mountain flank_ middle third, MB_UT= mountain base_ upper third), hillslope (b) (SU= summit, SH= shoulder, BS= backslope, FS= foot-slope, TS= toe-slope), slope shape (c) (CC= concave-concave, CL= concave-linear, CV = concave-convex, LC= linear-concave, LL= linear-linear, LV= linear-convex, VC= convex-concave, VL= convex-linear, VV= convex-convex and slope complexity (d) (C= complex, S= simple). Significant differences ($p < 0.05$) were determined in landscape position between the native and all assisted migration sites, and in hillslope position between the native site and sites at Snow Mountain (1-3). All assisted migration sites have similar slope shape and complexity to the Native site, and Gingko State Park had similar hillslope position.

plots at NS and GSP occupied the shoulder of the hillslope, while the majority of plots at SM3 occupied the summit of the hillslope and the majority at SM1 and SM2 occupied the backslope. In addition to the shoulder, NS also occupied the summit and backslope. Although some proportion of all assisted migration sites occupied the shoulder, SM2 is the only assisted migration site to occupy the summit, shoulder and backslope similar to NS. SM2 also occupied the foot and toe slopes, encompassing the widest range of hillslope positions and distinguishing

it from NS. While a portion of SM1 also occupied the back slope and a portion of SM3 also occupies the summit, neither encompassed the summit, shoulder and backslope like NS.

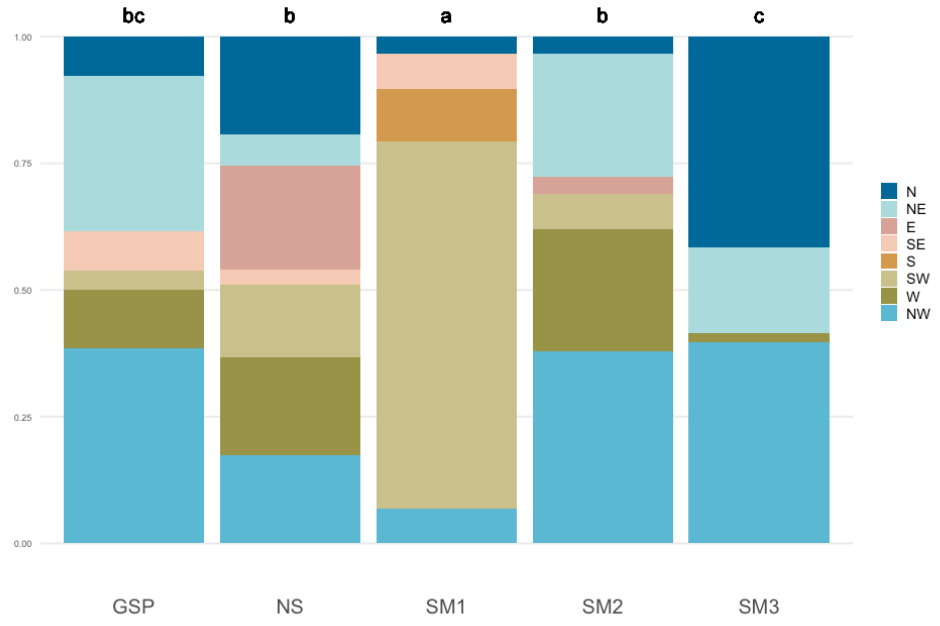


Figure 2.1.2 Bar graph of Aspect at the Native Site and Assisted Migration Sites
Differences in aspect at the native site (NS), Gingko State Park (GSP), and Snow Mountain sites 1-3 (SM1-3) (N = north, NE = northeast, E= east, SE= southeast, SW= southwest, W= west, NW= northwest). Significant differences ($p < 0.05$) were determined between the Native Site and Snow Mountain sites 1 and 3. Aspect is similar at the Native Site, Gingko State Park and Snow Mountain 2.

While all sites contained portions of plots with north, northeast, northwest and western facing slopes, NS had a larger proportion of eastern facing slopes than any of the assisted migration sites (Fig 2.1.2). Mode aspect of NS was east, while mode of the assisted migration site's aspects were north or northwest except SM1 which had a mode aspect of southwest (Fig P-1). NS has similar slope (rise/run) to SM1 and SM2 (NS: mean= 0.20, SM1: mean= 0.22, SM2: mean= 0.24) and a similar slope angle (degree) to all other sites except SM3 (Fig 2.1.3 B-C and Fig P-2). While GSP and SM3 both had significantly lower mean slopes than NS (GSP: mean = 0.15 , SM3: mean =0.13), GSP also had a lower maximum slope while SM3 had a higher maximum slope (NS: max= 0.53, GSP: max = 0.35 , SM3: max =0.9). Similarly, mean, range

and standard deviation of slope angle was significantly smaller at SM3 than NS (NS: mean= 12, SM3: mean= 5) (Fig 2.1.3 and Fig P-1). All assisted migration sites had the same mean heat load index (HLI) as NS except SM1, which had higher mean, minimum and maximum values (NS: mean = 0.71, SM1: mean = 0.82) (Fig 2.1.3-A and Fig P-1). Although SM 2 and 3 had similar HLI as NS (range: 0.47-0.92), SM2 has a smaller minimum value (0.33) and SM3 had a smaller maximum value (0.76). GSP has a narrower range of HLI values (rage: 0.55-0.89) encompassed within the range of values at NS .

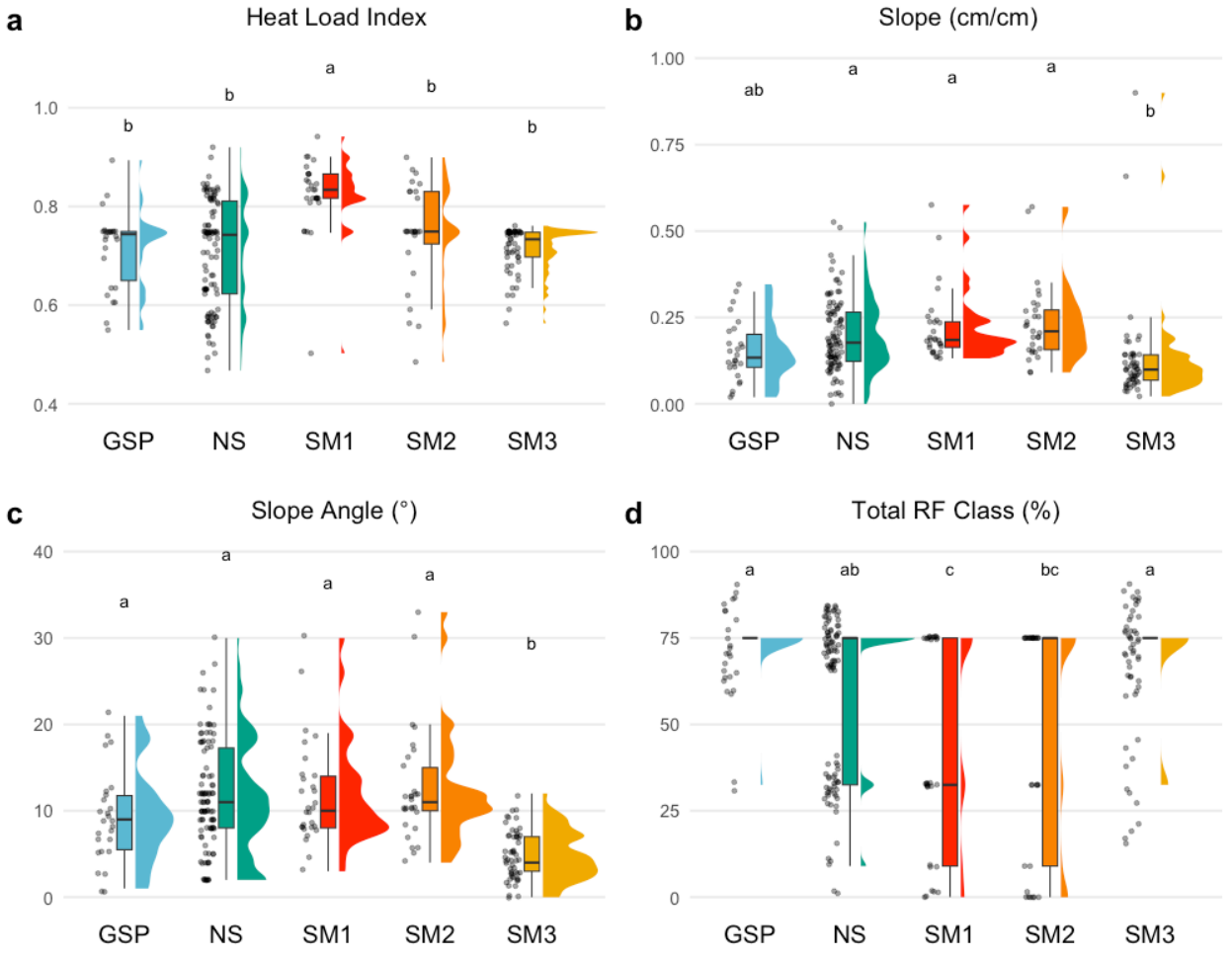


Figure 2.1.3 Raincloud Plots of Site Characteristics at the Native Site and Assisted Migration Sites
Differences in continuous site variables between the native site (NS), Gingko State Park (GSP), and Snow Mountain sites 1-3 (SM1-3) including heat load index (A), slope (cm/cm) (B), slope angle (°) (C), and total percentage of rock fragment cover classification (D). Significant differences ($p < 0.05$) in heat load were determined between the Native Site and Snow Mountain. Significant differences in slope and slope angle were determined between the Native Site and Snow Mountain 3. Significant differences in total rock fragment class were determined between the Native Site and Snow Mountain 2.

NS rock fragment cover classifications showed clustering above 50% around 75% and below 50% around 30% (Fig 2.1.3-D). GSP and SM3 showed similar patterns of clustering around rock fragment cover classification above 50%. Mean and minimum values were higher at GSP and SM3 (GSP: mean= 71.73% min= 32%, SM3: mean= 66.18% min= 32%) than at NS (mean = 57% min= 9%) and had lower standard deviations (NS: 23.12, GSP: 11.55, SM3: 17.4), while SM1 and SM2 had lower mean and minimum values and higher standard deviations than NS (SM1: mean= 42%, min= 0%, sd=30.2, SM2: mean=45%, min=0%, sd=33.22) (Fig P 2).

Soil Characteristics

Significant differences in hydraulic conductivity, soil texture, soil surface composition and surface rock fragment composition were present between study sites (p = 0.001), and very strong pairwise differences were found between NS and SM 1-3 (p =<0.001) (Table 2.1.2 and Fig O-1). While pairwise comparison determined similarities in soil texture and soil surface composition between NS and GSP (p = >0.05), surface rock fragment composition was different (p = <0.01).

Table 2.1.2 PERMANOVA of Differences in Soil Characteristics Between the Native Site and Assisted Migration Sites
Significant differences (p= 0.001) were determined in all measured soil characteristics, indicating key habitat differences between *E. codium* and assisted migration sites. Significant relationships are indicated by asterisks (* = significant, ** = strongly significant, ***= very strongly significant).

Site Differences in Soil Characteristics

Soil Characteristics	n	Df	R^2	F	*Pr(>F)*	
Hydraulic Conductivity (K)	217	4	0.1438	8.90	0.001	***
Soil Texture	227	4	0.1220	7.71	0.001	***
Surface Composition	235	4	0.3387	29.45	0.001	***
Surface Rock Fragment Composition	235	4	0.2279	16.97	0.001	***

Significant differences in hydraulic conductivity were determined between NS and all assisted migration sites (Table 2.1.2 and Fig 2.14). NS had significantly higher mean and maximum K values and a wider range of values (Fig P-3). While all K values observed at assisted migration sites fell within the range of observed values at NS, SM-3 best reflects the faster rates of infiltration observed at NS (i.e. K> 0).

Soil texture at NS was largely comprised of loamy sand soils, with the second largest proportion of plots containing sandy loam soil, and a very low occurrence of loam and sandy clay loam soils (Fig 2.1.5). Soil texture at GSP was determined to be similar to soil texture at NS despite only sandy loam and loam soils occurring there, although mode soil texture indicated sandy loam soils were the most prevalent (Fig 2.1.5 and Fig P-1). In contrast, although SM2

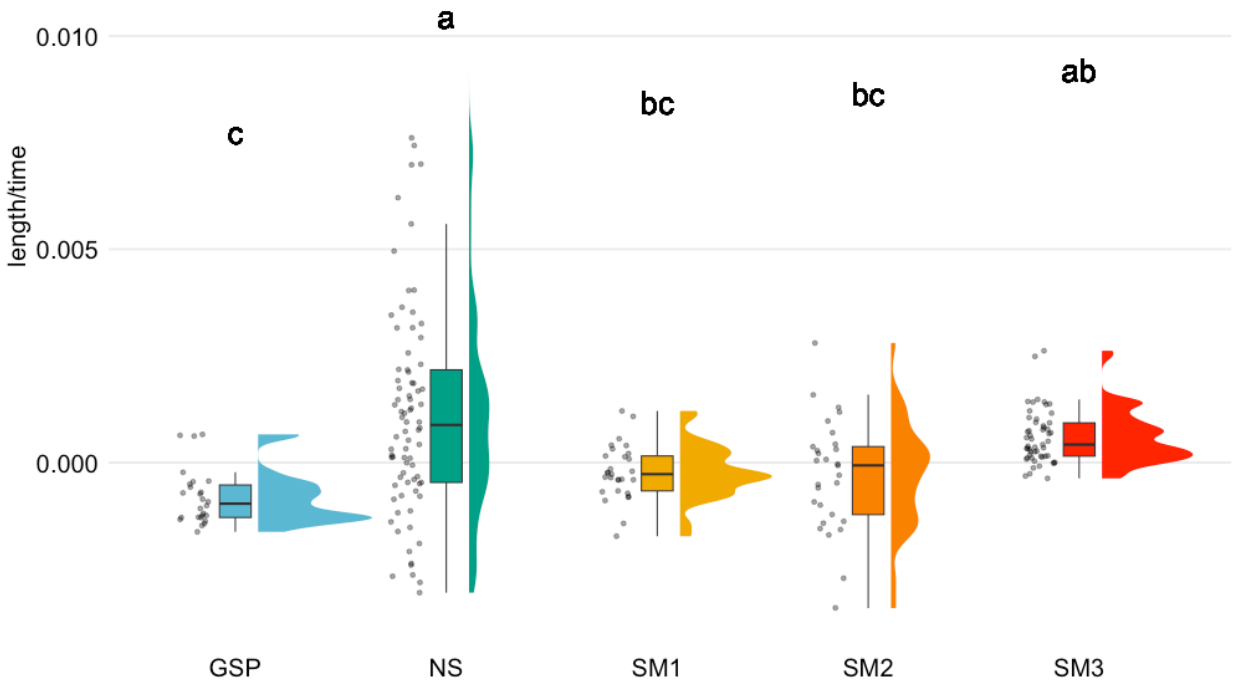


Figure 2.1.4 Raincloud Plots of Hydraulic Conductivity (K) at the Native Site and Assisted Migration Sites
Differences in hydraulic conductivity (K) at the native site (NS), Gingko State Park (GSP), and Snow Mountain sites 1-3 (SM1-3). Infiltration rates are significantly ($p < 0.05$) slower than the Native Site at all assisted migration sites except SM3. Infiltration rates at the Native Site vary more widely than at assisted migration sites.

was the only assisted migration site to have three of the four soil types present at NS, including a small proportion of loamy sand. Despite these similarities, SM1 and SM3 were dominated by loam soils, making them distinct from NS, despite sandy loam soil occurring at both sites. One plot with silt loam soil, which did not occur at NS, was also detected at SM3.

NMDS ordination of soil surface composition shows clustering of both NS and GSP in the left of the ordination space illustrating their similarity (Fig 2.1.7-A). While there is some overlap between NS and SM3 in the bottom left of the ordination space, these areas are separated from the large clustering of plots primarily of SM 1-2 but also from SM3 and GSP in the center of the ordination space. The area of the NMDS ordination where NS and GSP plots do not overlap with site SM 1-3 is likely due to similarities between NS and GSP in the rock and litter components of their soil surface composition. All assisted migration sites at SM have lower mean and minimum rock cover than NS (NS: mean= 71% min= 20% SM1: mean= 33% min=

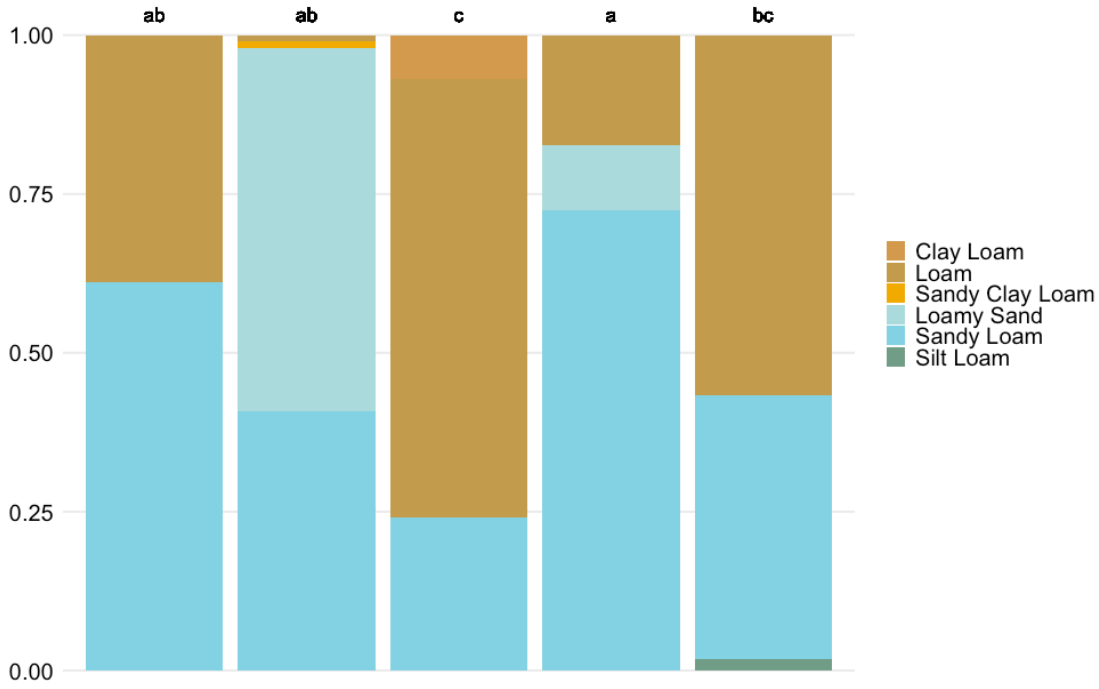


Figure 2.1.5 Bar Graph of Soil Texture at the Native Site and Assisted Migration Sites
Differences in top 15cm of soil profile at assisted migration sites Gingko State Park (GSP) and Snow Mountain sites 1-3 (SM1-3) and surface soil texture at the native site (NS). Significant differences ($p < 0.05$) were determined between the Native Site and Snow Mountain Sites 1-2.

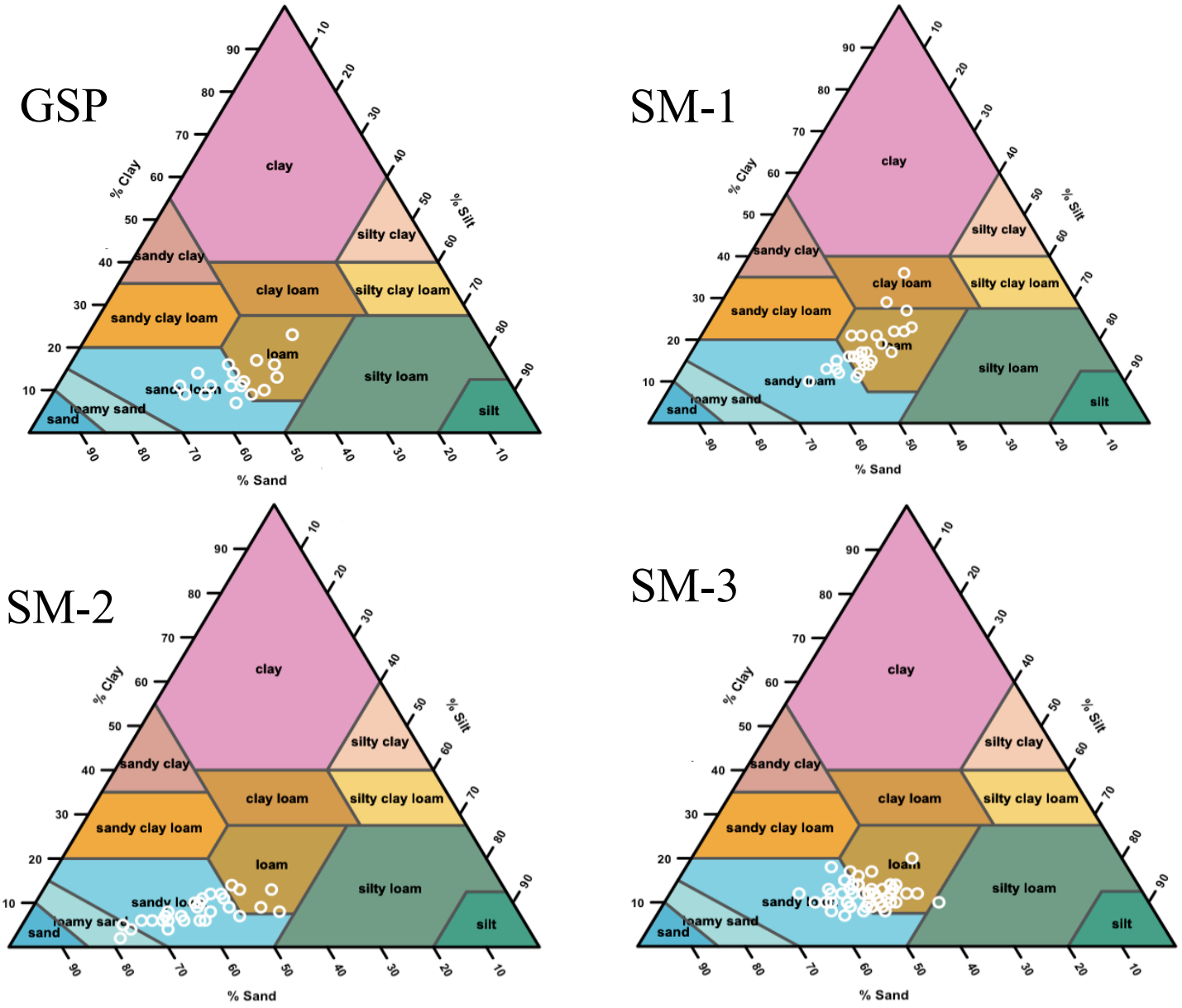


Figure 2.1.6 USDA-NCSS Soil Textural Triangles of Assisted Migration Sites
Soil textural classification of top 15cm of soil at assisted migration sites Gingko State Park (GSP) (n= 18) (A) and Snow Mountain sites 1-3 (SM1-3) (n= 111) (B-C). White circles indicate individual 1m^2 sample plots. Native Site soil texture (ratio sand-silt-loam) could not be mapped onto texture triangle because soil could not collect or removed from site.

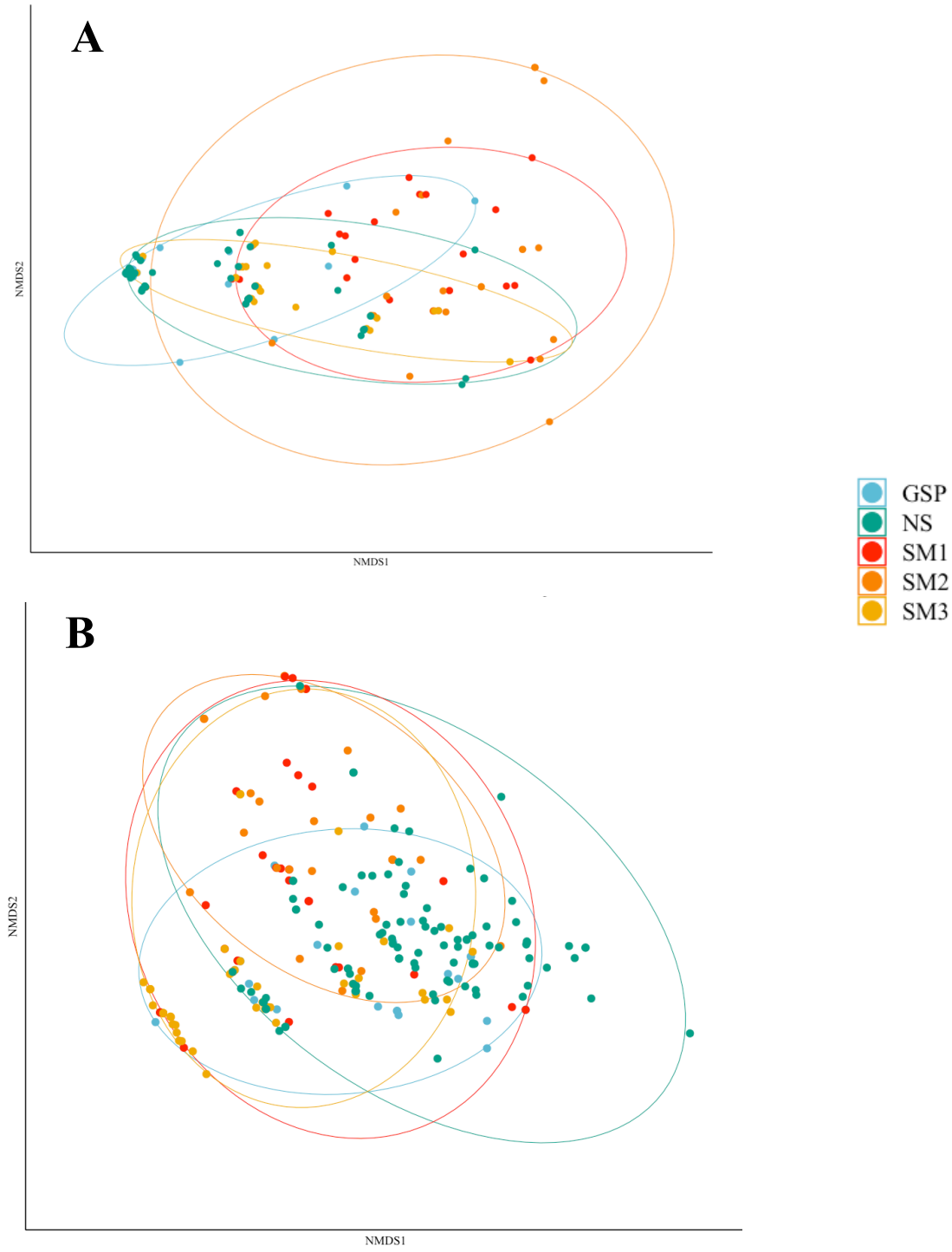


Figure 2.1.7 NMDS Ordination of Soil Surface and Soil Surface Rock Fragment Composition at the Native Site and Assisted Migration Sites
Non-metric multidimensional scaling (NMDS) ordination of soil surface (A) (k = 3 , stress = 0.021) and soil surface rock fragment (B) (k = 3, stress = 0.058) compositions. Points and ellipses s are coded by color to correspond to site . Each point represents a $1m^2$ plot. Points closer together are more similar to than those farther apart. Separation of soil surface composition (A) at the Native Site (green) and Snow Mountain sites illustrate significant differences ($p < 0.05$), while overlap with Gingko State Park (blue) highlights similarities between these sites. Extension of the rock fragment composition (B) at the Native Site (green) into the right side of the ordination space away from assisted migration sites illustrate differences related to the high composition of fine and very fine gravel at the Native Site.

0%, SM2: mean= 30% min= 0%, SM3: mean= 56% min= 10%) although SM 2-3 have the same maximum cover values as NS (88%) (Fig P-4). Only GSP has similar mean rock cover to NS (NS: 71%, GSP: 74%), however minimum cover is higher at NS (NS: 20% GSP: 0%). NS and GSP have the lowest and second lowest mean litter respectively (NS: 5%, GSP: 7%), the same range of litter cover (0-38%) and similar standard deviations (NS: 6, GSP: 8). Although SM3 has significantly lower mean litter cover than SM 1-2 (SM1: 20%, SM2: 24%, SM3: 9%), the mean is almost twice that at NS and the minimum is higher (NS: 0%, SM3: 3%).

Despite significant similarities of soil surface composition between NS and GSP, GSP has lower mean and maximum bareground than NS (NS: mean= 13% max= 62%, GSP: mean= 8% max= 38%) and higher mean and maximum biocrust cover (NS: mean= 0% max= 20%, GSP: mean= 6% max= 62) (Fig P-4). Bareground cover at NS is between the range of mean values at GSP (lower) and SM3 (higher) (SM3: 21%) while all assisted migration sites had higher mean biocrust values than NS although SM-1 and SM-3 has similar ranges (0-20%). ISA analysis of soil surface composition indicates unique patterns in the rock component of surface composition ($p = 0.005$) distinguish the NS from all assisted migration sites (Table 2.1.3). SM2 is likewise distinguished by its uniquely high mean and maximum cover of litter and bareground while SM3

Table 2.1.3 ISA of Soil Surface Composition at the Native Site and Assisted Migration Sites
Soil surface components that most characterize the native and assisted migration sites. IV_{ij} of 100 means soil surface component occurs in all plots. Significant relationships are indicated by asterisks (* = significant, ** = strongly significant, ***= very strongly significant). The Native Site is distinguished from all other sites by the higher composition of the rock portions of soil surface composition.

Site	Cover Class	IVij	*P*	
NS	Rock	28.1	0.005	**
SM2	Litter	37.2	0.005	**
SM2	Bareground	32.5	0.005	**
SM3	Biocrust	33.6	0.005	**

is distinguished by its biocrust cover, with the highest mean and second lowest standard deviation indicating consistently higher cover across the site (mean= 10%, sd= 6) (Table 2.1.3 and Table P-4).

In the NMDS ordination of surface rock fragment composition, NS overlaps to some extent with all assisted migration sites (Fig 2.1.7-B). This includes areas primarily of overlap with SM3 in the bottom left of the ordination space, but also overlaps with SM2 in the center of the ordination space. SM1 and GSP are intermixed with NS throughout these areas, indicating similarities between these sites, NS and SM 2-3. However, NS also extends right into the ordination space beyond points corresponding to GSP and SM 1-3. This illustrates the areas of NS that are different in rock fragment composition from the assisted migration sites. ISA analysis of rock fragment composition indicates areas of the ordination space occupied only by NS are characterized by unique patterns in fine and very fine gravel components ($p = 0.005$) (Table 2.14 and Fig P-5). NS is distinguished by its significantly higher mean, maximum

Table 2.1.4 ISA of Soil Surface Rock Fragment Composition at the Native Site and Assisted Migration Sites
Soil surface rock fragment components that most characterize the native and assisted migration sites. NS is distinguished by higher cover of fine and very fine gravel components. GSP and SM3 are both characterized by course and medium gravel. The Native Site is distinguished from all other sites by the higher composition of fine and very fine gravel portions of rock fragment composition. IV_{ij} of 100 means soil surface component occurs in all plots. Significant relationships are indicated by asterisks (* = significant, ** = strongly significant, ***= very strongly significant).

Site	Cover Class	IVij	*P*	
GSP	Medium Gravel	29.3	0.005	**
GSP	Stone	14.2	0.020	*
NS	Fine Gravel	44.3	0.005	**
NS	Very Fine Gravel	96.9	0.005	**
SM2	Bedrock	13.8	0.005	**
SM2	Cobble	28.3	0.025	*
SM3	Course Gravel	34.2	0.005	**

and a standard deviation of fine gravel (mean= 25%, range= 0-88% , sd= 22) and is the only site where a significant quantity of boulders (mean = 1%) or very fine gravel (mean = 8%) was recorded. In contrast, GSP was distinguished by patterns in higher stone (mean = 3%) and medium gravel (mean = 35%) composition, while SM2 and SM3 are characterized by patterns in high cobble (SM2 mean= 38%) and coarse gravel (SM3 mean= 61%) cover respectively ($p < 0.05$). Multigroup ISA analysis indicates that all assisted migration groups are distinguished from NS by higher cobble cover (Fig R-1). Although GSP has the same mean cobble cover as NS (9%), GSP has a lower maximum and standard deviation (GSP: max= 38%, sd= 10), indicating cobbles are likely more consistently distributed across GSP, in contrast to NS which has a higher maximum cover and standard deviation (NS: max= 62%, sd= 15) (Fig P-5).

Vegetation Characteristics

Significant differences ($p = <0.01$) in LAI, total cover and species richness were determined between study sites (Table 2.1.5). Pairwise comparison determined significant differences in LAI and species richness between NS and SM1 and SM2, in contrast to GSP and SM3 (Fig 2.1.8 and Fig 2.1.9-A). Differences in total cover were determined only between NS and SM3 (Fig 2.1.9-B). Mean and standard deviation of LAI was significantly lower at NS than all assisted migration sites and was highest at SM 1-2 (NS: 0.03 , GSP: 0.1, SM1: 0.2, SM2: 0.4 SM3: 0.1) (Fig P-6). All sites had similarly low minimum LAI (0-0.02) and NS had a higher maximum value than GSP and similar maximum values to SM1 and SM3 (NS: 0.78 , GSP: 0.53, SM1: 0.76, SM2: 1.35 SM3: 0.71). SM1 and SM2 also had the highest stranded deviations (SM1: 0.2, SM2: 0.4), while LAI varied less at NS and SM-3 (NS: 0.9, SM3: 0.2) (Fig 2.1.8 and Fig 2.1.9-A).

Table 2.1.5 PERMANOVA of Differences in Vegetation Community Characteristics Between the Native Site and Assisted Migration Sites
Significant differences were determined between the Native and assisted migration sites. Differences in total cover and species richness between the Native Site and Snow Mountain sites reflect key habitat differences accurately predicted by the WNHP habitat model. Significant relationships are indicated by asterisks (* = significant, ** = strongly significant, ***= very strongly significant).

Site Differences in Vegetation Characteristics

Vegetation Characteristics	n	Df	R2	F	Pr(>F)	
Leaf Area Index	136	4	0.2946	13.68	0.001	***
Species Richness	209	4	0.0863	4.82	0.002	**
Total Cover	209	4	0.1287	7.53	0.001	***
Vegetation Composition	209	4	0.4099	35.42	0.001	***
Vegetation Functional Group	209	4	0.4205	37.00	0.001	***

At all SM sites (1-3) species richness values were clustered around >10 species and <5 species while at GSP species richness values were clustered around >5 species and <5 species (Fig 2.1.9-A). In contrast, species richness values at NS were clustered around <5 species with a few plots extending to <10 species, reflecting the lower mean range and standard deviation of species richness there (Fig P-6). SM 1 and 2 had the highest mean and minimum species richness values (mean= 7, min = 2), while SM-3 had the highest maximum value (22). Despite higher species richness at SM 1-2 than the NS, these sites did not differ in total cover (Fig 2.1.9-B). Mean total cover was lower at GSP (24%) and SM3 (15%) than at NS despite that both minimum and maximum total cover was higher at GSP (9-76%) and maximum total cover was higher at SM3, although minimum total cover was significantly lower (0.5-84%) (Fig P-6). Mean total cover was the most similar between NS and SM 1-2 (NS: mean = 33%, SM1: mean= 40% , SM2: mean= 32%) although minimum cover was higher at NS and maximum cover was much higher at SM 1-2 (NS: 4-71%, SM1: 1-105%, SM2: 1-116%).

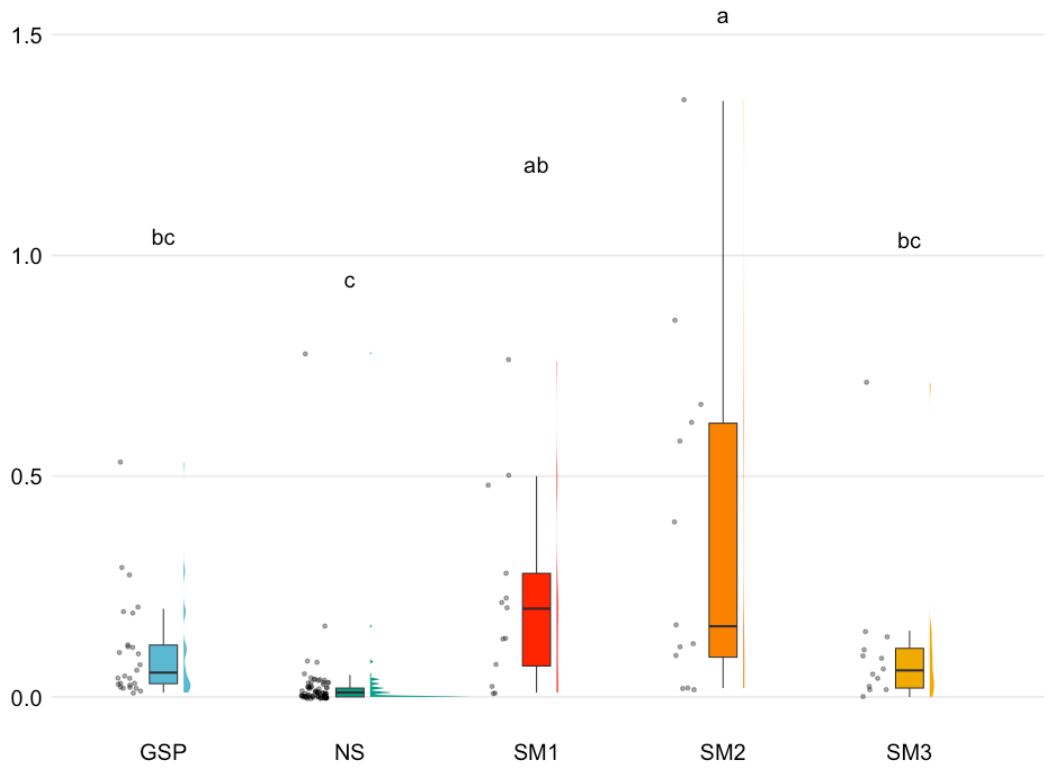


Figure 2.1.8 Raincloud Plot of Leaf Area Index (LAI) at the Native Site and Assisted Migration Sites
Differences in LAI at the Native Site (NS), Gingko State Park (GSP), and Snow Mountain sites 1-3 (SM1-3). Significant differences between the Native Site and Snow Mountain sites 1-2 indicate they are more productive and diverse vegetation communities.

Significant differences ($p < 0.001$) in vegetation species composition were determined between NS and all assisted migration sites (Fig 2.1.10-A, Fig O-2 and Fig 2.1.5). This result was expected as the vegetation community at the NS is dominated by *E. codium* which does not occur naturally at any of the assisted migration sites. However, significant differences ($p < 0.001$) were also determined in vegetation functional group composition which indicates fundamental differences in the vegetation structures at these sites (Fig 2.1.10-B, Fig O-2 and Table 2.1.5). This is illustrated by NMDS ordinations of both vegetation composition and vegetation functional group composition (Fig 2.1.10-B). The clustering of NS plots in the lower left of the ordination space are spatially separated from the assisted migration sites. This separation is conserved in the upper right of the vegetation functional group composition's

ordination space. Although some overlap is present between NS and both GSP and SM3 in the ordination of vegetation composition, this small area of overlap increased slightly within the ordination of vegetation functional group composition to include SM1 and SM2 as well. However, the majority of NS extends away from the large clustering and overlap of GSP and SM 1-3 in the center of the ordination space. This observed spatial separation of NS from assisted migration sites is related to differences in subshrub, perennial forb and perennial graminoid cover, while overlaps between GSP and SM3 are related to similarities in shrub, annual forb, and annual graminoid cover (Fig 2.1.11, Fig 2.1.12, Fig 2.1.13, and Fig P-7).

When each vegetation functional group was tested independently, all functional groups showed strong significant differences between sites ($p = 0.001$) (Table 2.1.6). Pairwise comparisons determined similarities between shrub cover at NS and SM3 and both annual forb and annual graminoid cover at NS, GSP and SM3, that contrast patterns at SM 1-2 (Fig 2.1.11, Fig 2.1.12, Fig 2.1.13). ISA analysis indicated that SM1 is distinguished from all other study sites including the Native Site, by patterns in high shrub, annual forb and annual graminoid cover ($p \leq 0.02$) (Table 2.1.7). NS and SM3 had significantly lower shrub cover than both GSP and SM 1-2 (Fig 2.1.11-A and Fig P-7). SM3 had no recorded shrub cover and mean cover at NS was <1% and never exceeded 10% with low variation (sd = 1.65), while mean shrub cover at GSP and SM 1-2 was >4% with a maximum cover of 37.5%. Mean, range and standard deviation of annual forb and graminoid cover was significantly lower at NS, GSP and SM-3 than at SM 1-2 (Fig 2.1.12-B, Fig 2.1.13-B, Fig P-7). Mean annual graminoid cover was <1% at NS, GSP and SM3 and although maximum cover ranged between NS (lowest = 3%) and SM-3 (highest = 10%), it never exceeded 10%. Similarly mean cover of annual forbs at NS was <0.5% and did not exceed 10% while mean cover at GSP and SM3 was <1% and did not exceed 8%

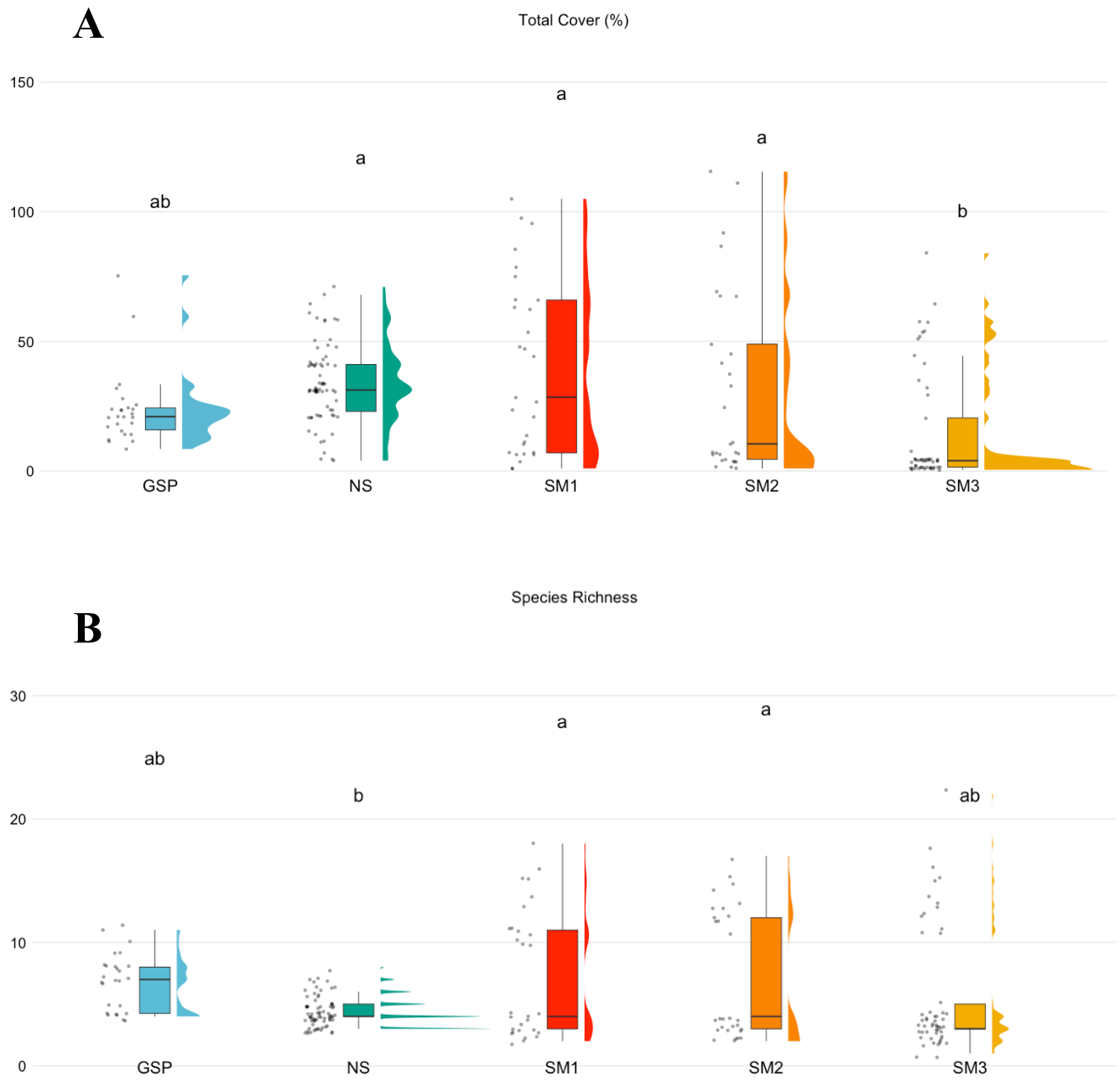


Figure 2.1.9 Raincloud Plots of Total Cover and Species Richness at the Native Site and Assisted Migration Sites
Differences in species richness (A) and total cover (B) at the native site (NS), Gingko State Park (GSP), and Snow Mountain sites 1-3 (SM1-3). Significant differences in species richness between the Native Site and Snow Mountain sites 1-2 contrast similarities in total cover. Significant differences in total cover between the Native Site and Snow Mountain 3 contrast similarities in species richness. While all assisted migration sites had similarly low total cover as the Native sites, all sites except Gingko State Park has similar higher species richness, indicating increased inter-species competition.

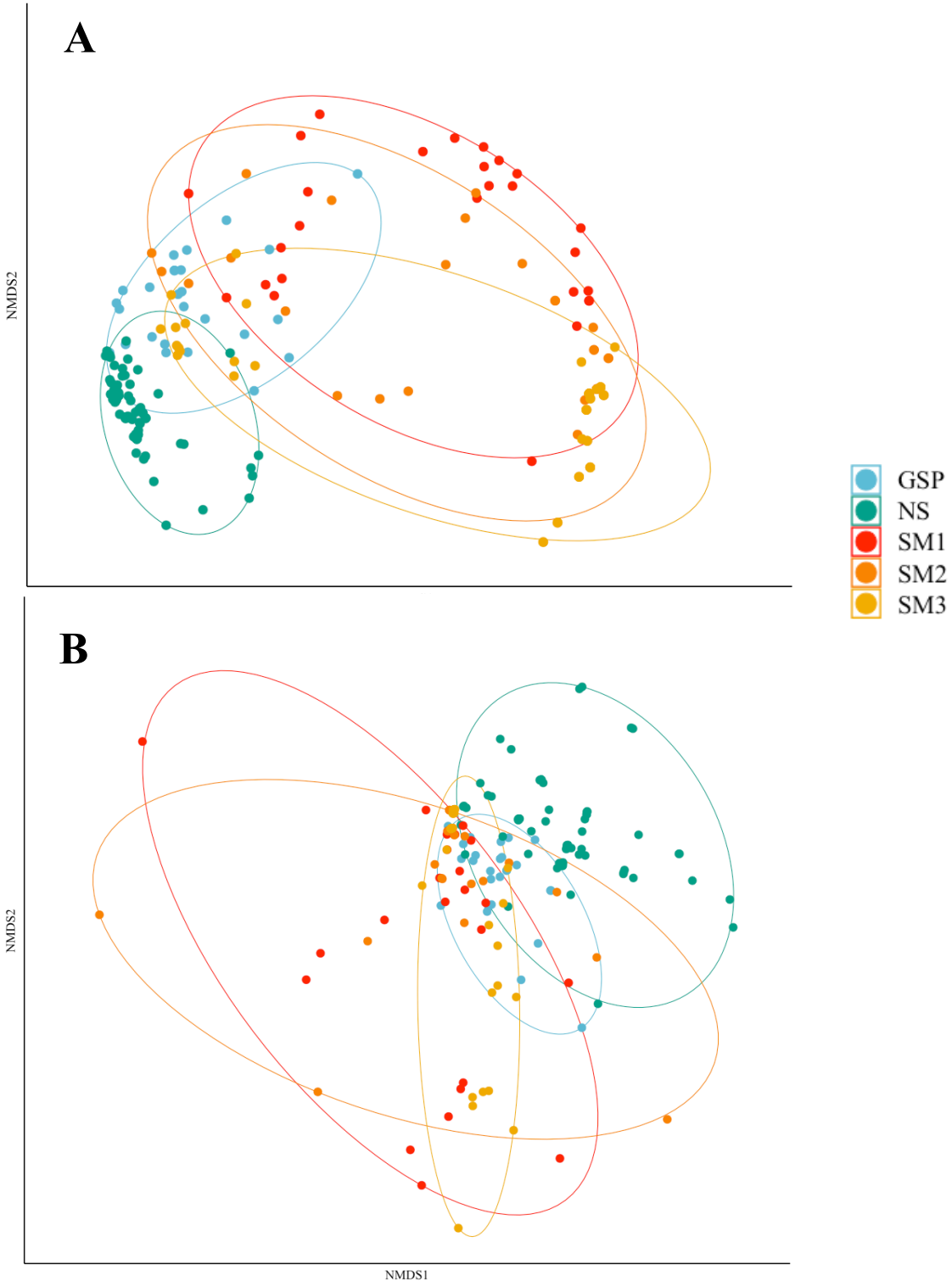


Figure 2.1.10 NMDS Ordination of Vegetation Community and Functional Group Composition at the Native Site and Assisted Migration Sites

Non-metric multidimensional scaling (NMDS) ordination of vegetation composition (k = 3 , stress = 0.119) and vegetation functional group composition (k = 3, stress = 0.68). Points and ellipses s are coded by color to correspond to site . Each point represents a $1m^2$ plot. Points closer together are more similar to than those farther apart. Clear separation of the Native Site point clouds in both vegetation composition and functional group composition indicate key differences in vegetation community structure at assisted migration sites, despite similarities in total cover and species richness.

Table 2.1.6 PERMANOVA of Differences in Vegetation Community Functional Groups Between the Native Site and Assisted Migration Sites Significant differences in all vegetation functional group components were determined between all Native and assisted migration groups, reflecting patterns illustrated in NMDS ordinations. Significant relationships are indicated by asterisks (* = significant, ** = strongly significant, ***= very strongly significant).

Site Differences of Vegetation Functional Groups

Vegetation Fuctional Group	Df	R^2	F	*Pr(>F)*	
Shrub	4	0.1283	7.51	0.001	***
Sub-Shrub	4	0.4993	50.86	0.001	***
Annual Forb	4	0.1537	9.26	0.001	***
Perennial Forb	4	0.1133	6.52	0.001	***
Annual Graminoid	4	0.1412	8.39	0.001	***
Perennial Graminoid	4	0.3221	24.23	0.001	***

cover. In contrast mean annual forb cover was >4% and annual graminoid cove was 9% at SM 1-2 including maximum cover of 40% annual forb and 100% annual graminoid cover at SM2.

Mean perennial forb cover at the NS was determined to be significantly lower than all assisted migration sites (Fig 1.1.12-A and Fig P-7). Mean cover of perennial forbs at NS was 1.3% and did not exceed 20.5%. GSP has the second lowest mean cover (5.3%) and a lower maximum (13%) than NS, while mean cover at SM 1-3 ranged from 7-10% and maximum cover ranged from ~48% in SM1 and SM3 to ~70% at SM2. Pairwise comparison indicated that although patterns in perennial forb cover at GSP were distinct from those at NS and SM 1-3, what makes it distinct is GSP's partial similarity to the other four sites (Fig 1.1.12-A). While multigroup ISA indicated all assisted migration sites were characterized by annual and perennial forb species that occurred at multiple sites, none of these species also occurred at the Native Site (Fig R-2). Classical ISA analysis indicated vegetation functional group composition at NS was distinguished from all assisted migration sites by the significantly higher cover of subshrubs and perennial graminoids (p= 0.005) species were the only species that characterized both the native

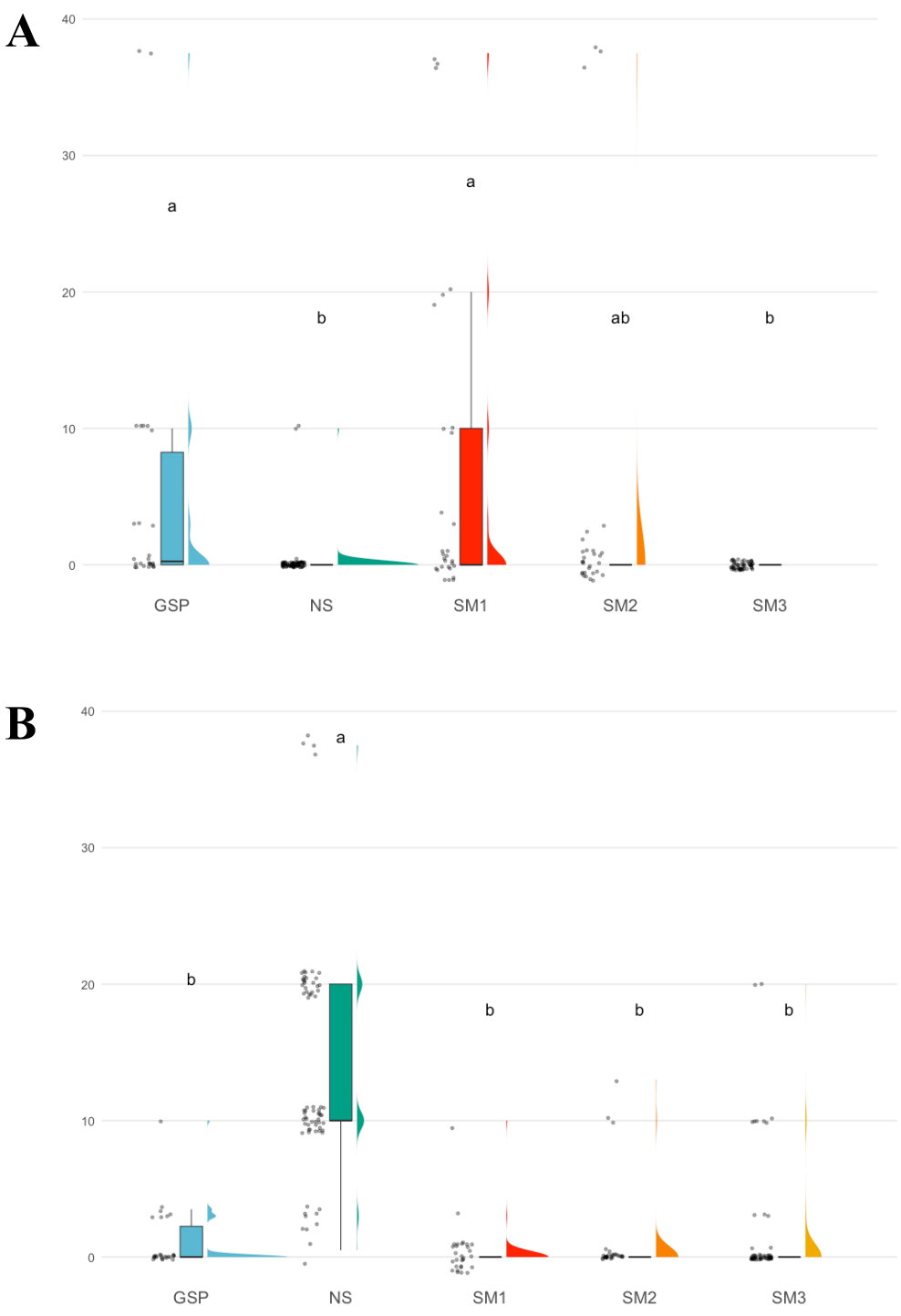


Figure 2.1.11 Raincloud Plots of Vegetation Functional Groups Shrub and Subshrub at the Native Site and Assisted Migration Sites

Differences in shrub (A) and subshrub (B) cover at the native site (NS), Gingko State Park (GSP), and Snow Mountain sites 1-3 (SM1-3). Both Gingko State Park and Snow Mountain 2 had significantly higher shrub cover than the Native Site. High shrub cover likely contributes to making these sites unsuitable for *E. codium* introduction as *E. codium* may compete with other woody shrubs for above and below ground resources. The Native Site had significantly higher subshrub cover than all assisted migration sites, indicating *E. codium* dominates its Native Site in higher abundance than other, more widely adapted *Eriogonum* species occur at assisted migration sites.

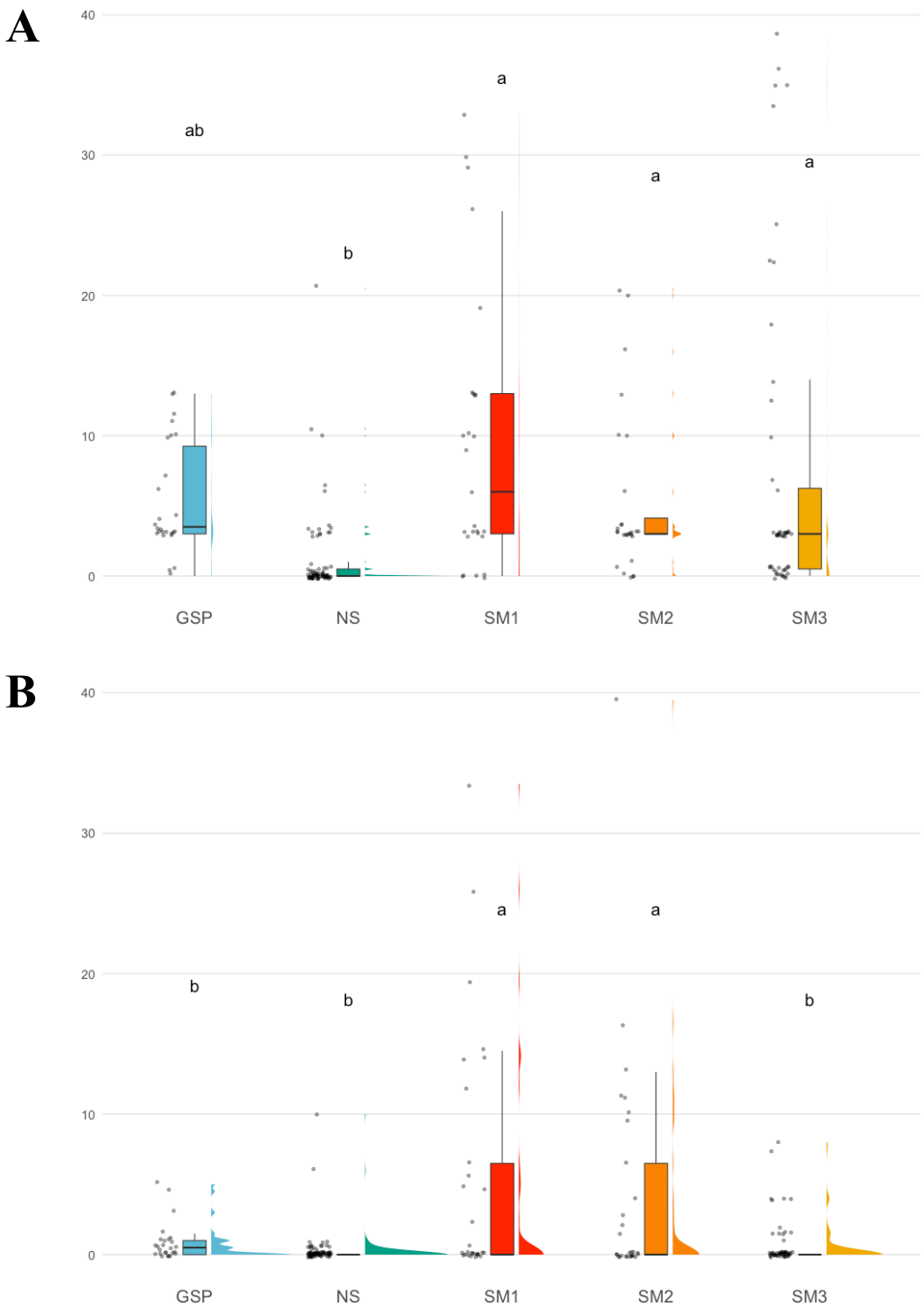


Figure 2.1.12 Raincloud Plots of Vegetation Functional Groups Perennial and Annual Forbs at the Native Site and Assisted Migration Sites

Differences in perennial (A) and annual (B) forb cover at the native site (NS), Gingko State Park (GSP), and Snow Mountain sites 1-3 (SM1-3). All sites at Snow Mountain had significantly higher perennial forb cover, while Snow Mountain 3 had similar annual forb cover to the Native Site and Gingko State Park generally had similar fob cover. High perennial forb cover at Snow Mountain sites indicate this habitat is not optimal for *E. codium* establishment due to stress from interspecies competition.

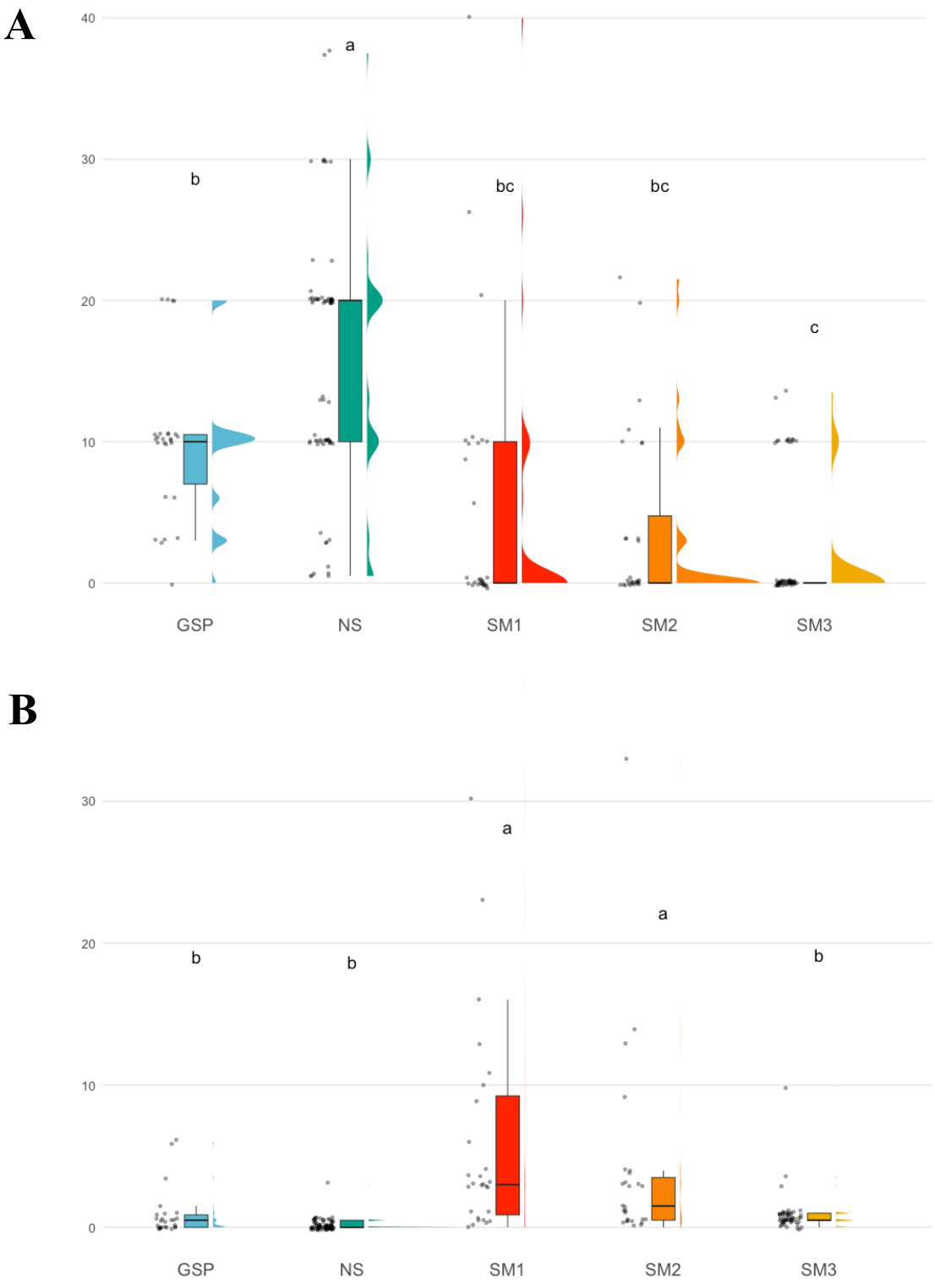


Figure 2.1.13 Raincloud Plots of Vegetation Functional Groups Perennial and Annual Graminoids at the Native Site and Assisted Migration Sites
Differences in perennial (A) and annual (B) graminoid cover at the native site (NS), Gingko State Park (GSP), and Snow Mountain sites 1-3 (SM1-3). Perennial graminoid cover was significantly higher at the Native Site than all assisted migration sites, while Snow Mountain sites 1-2 also had significantly higher annual graminoid cover.

and assisted migration sites (Fig 1.2.11-A, Fig 1.2.13-A, Table 2.1.7). Patterns in perennial forb cover ranged from significantly highest mean (17.4%), range (0.5-57.5%), and standard deviation (11.61) of cover at NS to the lowest mean (2.58%), range (0-13.5%) and standard deviation (4.6) at SM-3 (Fig P-7). GSP and SM 1-2 form distinct groups within this range. GSP has the second highest mean perennial graminoid cover (mean = 10%) but the second lowest maximum and standard deviation (max = 20%, sd = 5.4) while SM 1-2 have lower mean cover (~5%) but maximum cover and standard deviation values twice that of GSP (max = ~44%, sd = ~10) (Fig 2.1.12-A and Table P-7). Vegetation functional group composition at the NS is most strongly distinguished by the significantly higher mean, maximum and standard deviation of subshrub cover (Figure 2.1.11-B and Fig P-7). Mean subshrub cover at NS was 14% with a maximum of 37.5% cover, while mean subshrub cover was <3% at all assisted migration sites and did not exceed 13% cover at any site besides SM3 (maximum = 20%).

Two perennial graminoid species, two perennial forb species, an invasive annual forb and an invasive annual graminoid occurred in ≥10% of plots at NS (Table 2.1.9). Perennial grammoid species Sandburg's bluegrass (*Poa secunda)* occurred in 100% of plots at NS and 62% of plots across all sites surveyed in this study. Mean cover at NS was 15% and maximum cover was 37.5%. *P. secunda* occurred in 96% of plots at GSP with a mean cover of 9% and maximum cover of 20%. *P. secunda* occurred in <45% of plots at SM 1-2 and ~25% of plots at SM3 with a mean cover of ~2% and maximum of 20% (Table 2.1.9 and Fig P-8). The other perennial graminoid associated with *E. codium* at the Native Site- Bluebunch wheatgrass (*Pseudoroegneria spicata*)- occurred in ~31% of plots at NS and GSP respectively and 17% of plots across all surveyed sites. *P. spicata* occurred in 10% of plots at SM2, ~7% of plots at SM-1 and ~2% of plots at SM3. Mean cover was ~2% at both NS and SM2, ~1% at GSP and SM1, and

Table 2.1.7 ISA of Vegetation Functional Groups at the Native and Assisted Migration Sites
Vegetation functional groups that most characterized each site. NS is distinguished by the high abundance of subshrubs (i.e. *E. codium)* and associated perennial graminoid species *Poa secunda* and *Pseudoroegneria spicata*. SM-1 had significantly higher ($p<0.05$) cover of forb, annual graminoid species that distinguished it from all other sites including NS. IV_{ij} of 100 means functional group component occurs in all plots. Significant relationships are indicated by asterisks (* = significant, ** = strongly significant, ***= very strongly significant).

Site	Veg Functional Group	IVij	*P*	
NS	Perennial Graminoid	42.7	0.005	**
NS	Subshrub	74.4	0.005	**
SM1	Annual Forb	20.6	0.015	**
SM1	Annual Graminoid	41.9	0.005	**
SM1	Perennial Forb	29.2	0.010	**
SM1	Shrub	16.2	0.015	**

< 0.5% at SM3 with a maximum cover of 3%. Maximum cover was 10% at GSP, 20% at both NS and SM1 and 37.5% at SM2.

Invasive annual grass *Bromus tectorum* occurred in ~30% of plots at NS and GSP respectively and ~25% of plots across all surveyed sites (Table 2.1.8 and Table 2.1.9). *B. tectorum* occurred in 41% of plots at SM1, 38% of plots at SM2 and was not recorded at SM3. Mean cover of *B. tectorum* at NS and GSP was <1% and maximum cover was 3%, mean cover was 2% at SM1 and maximum cover was 10%, and mean cover was 3% at SM2 and maximum cover 37.5% with a high standard deviation of 9.7 indicating higher variation across the site (Table P-8). Perennial forb species *Astragalus purishii* and *A. caricinus* were recorded in 10-11% of plots at NS but did not occur at any assisted migration sites (Table 2.1.8). Similarly, invasive annual forb *Salsola tragus* occurred in 11% of plots at NS but was not recorded at any assisted migration site.

Two perennial forbs and one annual forb species occurred in >5% of plots at NS (Table 2.1.9). Perennial forbs Arrowleaf balsamroot (*Balsamorhiza sagittate*) and Canby's biscuitroot (*Lomatium canbyi*) both occurred in 8% of plots at NS and also occurred only at SM-1. Mean

Table 2.1.8 Summary of Vegetation Species at the Native Site and Assisted Migration Sites by Native Site Occurrence
Vegetation species listed include only species present at the Native Site listed in descending order of occurrence. Table shows percentage of total plots containing each species surveyed at each site (GSP, NS, SM 1-3) and accumulatively across all sites (whole site).

Species	Habit	Origin	All Sites	GSP	NS	SM1	SM2	SM3
Eriogonum codium	Perennial subshrub	Native	34.45	0.00	100.00	0.00	0.00	0.00
Poa secunda	Perennial graminoid	Native	62.68	96.15	100.00	31.03	41.38	24.53
Pseudoroegneria spicata	Perennial graminoid	Native	17.22	30.77	30.56	6.90	10.34	1.89
Bromus tectorum	Annual graminoid	Invasive	24.88	30.77	29.17	41.38	37.93	0.00
Astragalus purshii	Perennial forb	Native	3.83	0.00	11.11	0.00	0.00	0.00
Salsola tragus	Annual forb	Invasive	3.83	0.00	11.11	0.00	0.00	0.00
Astragalus caricinus	Perennial forb	Native	3.35	0.00	9.72	0.00	0.00	0.00
Balsamorhiza sagittata	Perennial forb	Native	3.35	0.00	8.33	3.45	0.00	0.00
Lomatium canbyi	Perennial forb	Native	9.57	0.00	8.33	48.28	0.00	0.00
Phacelia linearis	Annual forb	Native	3.35	7.69	6.94	0.00	0.00	0.00
Descurainia pinnata	Annual forb	Native	7.18	0.00	4.17	10.34	20.69	5.66
Balsamorhiza hookeri	Perennial forb	Native	13.88	84.62	2.78	6.90	0.00	5.66
Chaenactis douglasii	Annual forb	Native	2.39	0.00	2.78	3.45	6.90	0.00
Erigeron poliospermus	Perennial forb	Native	0.96	0.00	2.78	0.00	0.00	0.00
Phlox longifolia	Perennial forb	Native	2.39	0.00	2.78	6.90	3.45	0.00
Sphaeralcea munroana	Perennial forb	Native	0.96	0.00	2.78	0.00	0.00	0.00
Amsinckia retrorsa	Annual forb	Native	0.48	0.00	1.39	0.00	0.00	0.00
Artemisia tridentata	Perennial shrub	Native	0.96	0.00	1.39	0.00	3.45	0.00
Chrysothamnus viscidiflorus	Perennial shrub	Native	1.44	0.00	1.39	0.00	6.90	0.00
Cryptantha pterocarya	Annual forb	Native	0.48	0.00	1.39	0.00	0.00	0.00
Eriocoma hymenoides	Perennial graminoid	Native	0.48	0.00	1.39	0.00	0.00	0.00
Lomatium spp	Perennial forb	Native	0.48	0.00	1.39	0.00	0.00	0.00
Salvia dorrii	Perennial shrub	Native	0.48	0.00	1.39	0.00	0.00	0.00

cover of both species was <1% at NS with maximum *B. sagittata* cover of 20% and maximum *L. canbyi* cover of 3% (Fig P-8). *B. sagittata* occurred in fewer plots (4%) at SM1 than at NS, while *L. canbyi* occurs in more plots (48%) at SM1 (Table 2.1.9). Mean *B. sagittata* cover was <1% with a maximum of 20% and mean *L. canbyi* cover was ~2% with a maximum of 10% cover. Annual forb threadleaf phacelia (*Phacelia linearis*) occurred in 7% of plots at NS and 8% of plots at GSP and the mean cover at both NS and GSP was <1%. 53% (7 out of 13) of the species that occur in <5% of plots at NS do not occur at any assisted migration site and 30% (4 out of 13) occurred at only one or two other sites. Only the perennial forb Hooker's balsamroot (*Balsamorhiza hookeri*) and annual forb Western tanseymustard (*Descurainia pinnata*) occurred in three of the four assisted migration sites. Overall, twelve species occurred in >10% of plots across all sites surveyed in this study excluding *E. codium*, which occurred naturally only at NS (Table 2.1.9). Only four of these species occurred at NS: *P. secunda*, *B. tectorum*, *B. hookeri*, and *P. spicata*, and only *L. canbyi* and *D. pinnata* occurred in >5% of plots across all study sites and at NS.

Classical ISA of vegetation spices composition indicated each study site is characterized by at least one unique shrub or subshrub species (Table 2.1.10). 40% of indicator species at NS are native perennial forbs (n= 5), 60% of indicator species at GSP are native perennial forbs and 20% are annual forbs (n= 5), 46% of indicator species at SM1 are native perennial forbs and 23% are native annual forbs (n=13), 44% of indicator species at SM2 are native perennial forbs and 11% are native annual forbs (n=9), and 71% of indicator species at SM3 are native perennial forbs (n= 7). All sites except SM1 are uniquely characterized by a distinct subshrub species of *Eriogonum* ($p \leq 0.04$): *E. codium* at NS, *E. douglasii* at GSP, *E. ovalifolium* at SM2 and *E. thymoides* at SM3. SM 1-2 both are characterized by native shrub species ($p \leq 0.03$),

Table 2.1.9 Summary of Vegetation Species at the Native Site and Assisted Migration Sites
Vegetation species listed include only species that occur in >5% and > 10% of all surveyed sites (NS, GSP, SM 1-3) listed in descending order of occurrence. Table shows percentage of total plots containing each species surveyed at each site (GSP, NS, SM 1-3) and accumulatively across all sites (whole site).

Species	Habit	Origin	All Sites	GSP	NS	SM1	SM2	SM3
> 10%								
Poa secunda	Perennial graminoid	Native	62.68	96.15	100.00	31.03	41.38	24.53
Bromus commutatus	Annual graminoid	Invasive	41.63	0.00	0.00	86.21	82.76	71.70
Eriogonum codium	Perennial subshrub	Native	34.45	0.00	100.00	0.00	0.00	0.00
Bromus tectorum	Annual graminoid	Invasive	24.88	30.77	29.17	41.38	37.93	0.00
Sedum lanceolatum	Perennial forb	Native	23.92	0.00	0.00	0.00	48.28	67.92
Vulpia microstachys	Annual graminoid	Invasive	22.97	50.00	0.00	10.34	20.69	49.06
Draba verna	Annual forb	Naturalized	17.70	34.62	0.00	34.48	31.03	16.98
Pseudoroegneria spicata	Perennial graminoid	Native	17.22	30.77	30.56	6.90	10.34	1.89
Balsamorhiza hookeri	Perennial forb	Native	13.88	84.62	2.78	6.90	0.00	5.66
Epilobium brachycarpum	Annual forb	Native	13.88	26.92	0.00	34.48	27.59	7.55
Artemisia rigida	Perennial shrub	Native	12.92	50.00	0.00	37.93	10.34	0.00
Idahoa scapigera	Annual forb	Native	11.48	3.85	0.00	27.59	13.79	20.75
Lomatium macrocarpum	Perennial forb	Native	11.00	38.46	0.00	3.45	0.00	22.64
5-10%								
Alyssum alyssoides	Annual forb	Invasive	9.57	0.00	0.00	27.59	27.59	7.55
Lomatium canbyi	Perennial forb	Native	9.57	0.00	8.33	48.28	0.00	0.00
Poa bulbosa	Biennial graminoid	Invasive	9.09	3.85	0.00	24.14	37.93	0.00
Eriogonum thymoides	Perennial subshrub	Native	8.13	15.38	0.00	3.45	0.00	22.64
Nestotus stenophyllus	Perennial forb	Native	8.13	19.23	0.00	3.45	0.00	20.75
Descurainia pinnata	Annual forb	Native	7.18	0.00	4.17	10.34	20.69	5.66
Olsynium douglasii	Perennial forb	Native	7.18	0.00	0.00	0.00	13.79	20.75
Collinsia parviflora	Annual forb	Native	6.70	0.00	0.00	3.45	13.79	16.98
Polemonium micranthum	Annual forb	Native	6.22	3.85	0.00	17.24	17.24	3.77
Lewisia rediviva	Perennial forb	Native	5.26	0.00	0.00	0.00	3.45	18.87

Table 2.1.10 ISA of Vegetation Species at the Native Site and Assisted Migration Sites

Vegetation species that most characterize the native and assisted migration (GSP, SM 1-3) sites. All sites except SM-1 are characterized by the presence of a *Eriogonum* species filling the functional niche *E. codium* would need to fill to establish there. SM-1 is characterized by the presence of Stiff sagebrush (*Artemisia rigida*), which also similarly competes with *E. codium* for niche dominance. IV_{ij} of 100 means species occurs in all plots. Significant relationships are indicated by asterisks (* = significant, ** = strongly significant, ***= very strongly significant).

ISA of Vegetation Composition

index	Species	Habit	Origin	IVij	*P*
Gingko State Park					
GSP	*Aster spp*	Perennial forb	Native	7.7	0.025 *
GSP	*Balsamorhiza hookeri*	Perennial forb	Native	79.8	0.005 **
GSP	*Descurainia sophia*	Annual forb	Invasive	7.7	0.020 *
GSP	*Eriogonum douglasii*	Perennial subshrub	Native	10.1	0.010 **
GSP	*Lomatium macrocarpum*	Perennial forb	Native	20.4	0.005 **
Native Site					
NS	*Astragalus caricinus*	Perennial forb	Native	9.7	0.020 *
NS	*Astragalus purshii*	Perennial forb	Native	11.1	0.035 *
NS	*Eriogonum codium*	Perennial subshrub	Native	100.0	0.005 **
NS	*Poa secunda*	Perennial graminoid	Native	42.5	0.005 **
NS	*Salsola tragus*	Annual forb	Invasive	11.1	0.010 **
Snow Mt Site1					
SM1	*Allium acuminatum*	Perennial forb	Native	10.3	0.005 **
SM1	*Alyssum alyssoides*	Annual forb	Invasive	17.6	0.005 **
SM1	*Artemisia rigida*	Perennial shrub	Native	18.5	0.005 **
SM1	*Bromus commutatus*	Annual graminoid	Invasive	34.6	0.005 **
SM1	*Bromus sitchensis*	Perennial graminoid	Native	6.9	0.050 *
SM1	*Crepis intermedia*	Perennial forb	Native	10.3	0.015 **
SM1	*Epilobium brachycarpum*	Annual forb	Native	13.2	0.030 *
SM1	*Idahoa scapigera*	Annual forb	Native	21.8	0.005 **
SM1	*Lomatium canbyi*	Perennial forb	Native	47.3	0.005 **
SM1	*Lomatium nudicaule*	Perennial forb	Native	20.7	0.005 **
SM1	*Lupinus sulphureus*	Perennial forb	Native	10.3	0.010 **
SM1	*Trifolium macrocephalum*	Perennial forb	Native	13.8	0.005 **
SM1	*Viola trinervata*	Perennial forb	Native	19.0	0.005 **
Snow Mt Site2					
SM2	*Allium spp*	Perennial forb	Native	10.3	0.010 **
SM2	*Bromus tectorum*	Annual graminoid	Invasive	15.2	0.050 *
SM2	*Chrysothamnus viscidiflorus*	Perennial shrub	Native	6.2	0.030 *
SM2	*Eriogonum ovalifolium*	Perennial subshrub	Native	6.9	0.045 *
SM2	*Fritillaria pudica*	Perennial forb	Native	9.1	0.025 *
SM2	*Lomatium dissectum*	Perennial forb	Native	10.6	0.020 *
SM2	*Lupinus sericeus*	Perennial forb	Native	6.9	0.035 *
SM2	*Poa bulbosa*	Biennial graminoid	Invasive	19.1	0.005 **
SM2	*Polemonium micranthum*	Annual forb	Native	14.1	0.025 *
Snow Mt Site3					
SM3	*Antennaria flagellaris*	Perennial forb	Native	15.1	0.005 **
SM3	*Eriogonum thymoides*	Perennial subshrub	Native	12.6	0.015 **
SM3	*Lewisia columbiana*	Perennial forb	Native	15.1	0.005 **
SM3	*Lewisia rediviva*	Perennial forb	Native	15.3	0.005 **
SM3	*Olsynium douglasii*	Perennial forb	Native	16.7	0.005 **
SM3	*Sedum lanceolatum*	Perennial forb	Native	39.2	0.005 **
SM3	*Vulpia microstachys*	Annual graminoid	Invasive	28.7	0.005 **

Stiff sagebrush (*Artemisia rigida*) at SM1 and Yellow Rabbitbrush *(Chrysothamnus viscidiflorus*) at SM2.

Using classical ISA, high cover of *P. secunda* distinguished NS despite occurring at all study sites while SM2 likewise was distinguished by *B. tectorum* despite this species occurring at four out of five study sites. Multigroup ISA indicated *P. secunda* cover also characterized compositional similarities between NS and GSP ($p = 0.005$), while *P. spicata* characterized similarities between NS and all assisted migration sites except SM3 (i.e. GSP and SM 1-2) ($p= 0.01$) (Fig R-2). Despite native forb *L. canbyi* occurring at NS, classical ISA identified it as characterizing the vegetation community at SM1 ($p = 0.005$) (Fig R-2). All study sites except NS and SM3 are characterized by unique *Lomatium* species ($p \leq 0.02$) : *L. canbyi* and *L. nudicaule* at SM1, *L. dissectum* at SM2 and *L. macrocarpum* at GSP. All sites are characterized by the presence of unique invasive species ($p \leq 0.05$): annual forb *S. tragus* at NS, annual forb Tanseymustard (*Descurainia sophia*) at GSP, annual forb at Yellow alyssum (*Alyssum alyssoides*) and invasive graminoid Meadow brome *(Bromus commutatus*) at SM1, annual and biennial graminoid species *B. tectorum* and Bulbus bluegrass (*Poa bulbosa*) at SM2, and the annual graminoid Small fescue (*Vulpia microstachys).*

Part II-I: Survival of 2020 and 2021 Seedling Cohorts

Survival Outcomes of Outplanted Seedling 2022-2023

Of the 353 one-year-old seedlings planted at Badger and Snow Mountains between 2020-2021, 10 seedlings were recorded alive in May 2023 (3% survival rate) (Fig 2.2.2 and Fig T-1). In May 2023, of the 89 seedlings planted in 2020, four seedlings were still alive at Badger Mountain (BM) (14% survival rate) (Fig 2.2.2 and Fig U-1). Of the 264 seedlings planted at Snow Mountain (SM) in 2021, six seedlings were still alive (2% survival rate) in May 2023 (Fig U-2). All seedlings alive at BM occurred in out planting grouping 1 (Fig 2.10), which had an 80% survival rate (four seedlings out of five) compared all other groupings of seedlings, which had no surviving plants (Figure 2.2.2 and Fig T-1). Seedlings outplanted at Snow Mountain in 2020 are believed to have died sometime between June 2021 and July 2022 and were all recorded dead during July 2022 monitoring. The total loss of this cohort of seedlings was



Figure 2.2.1 *E. codium* Seedlings Utilized for Assisted Migration After Outplanting
Seedlings outplanted at Snow Mountain in fall of 2021 photographed alive (left) and dead (right) in July 2022.

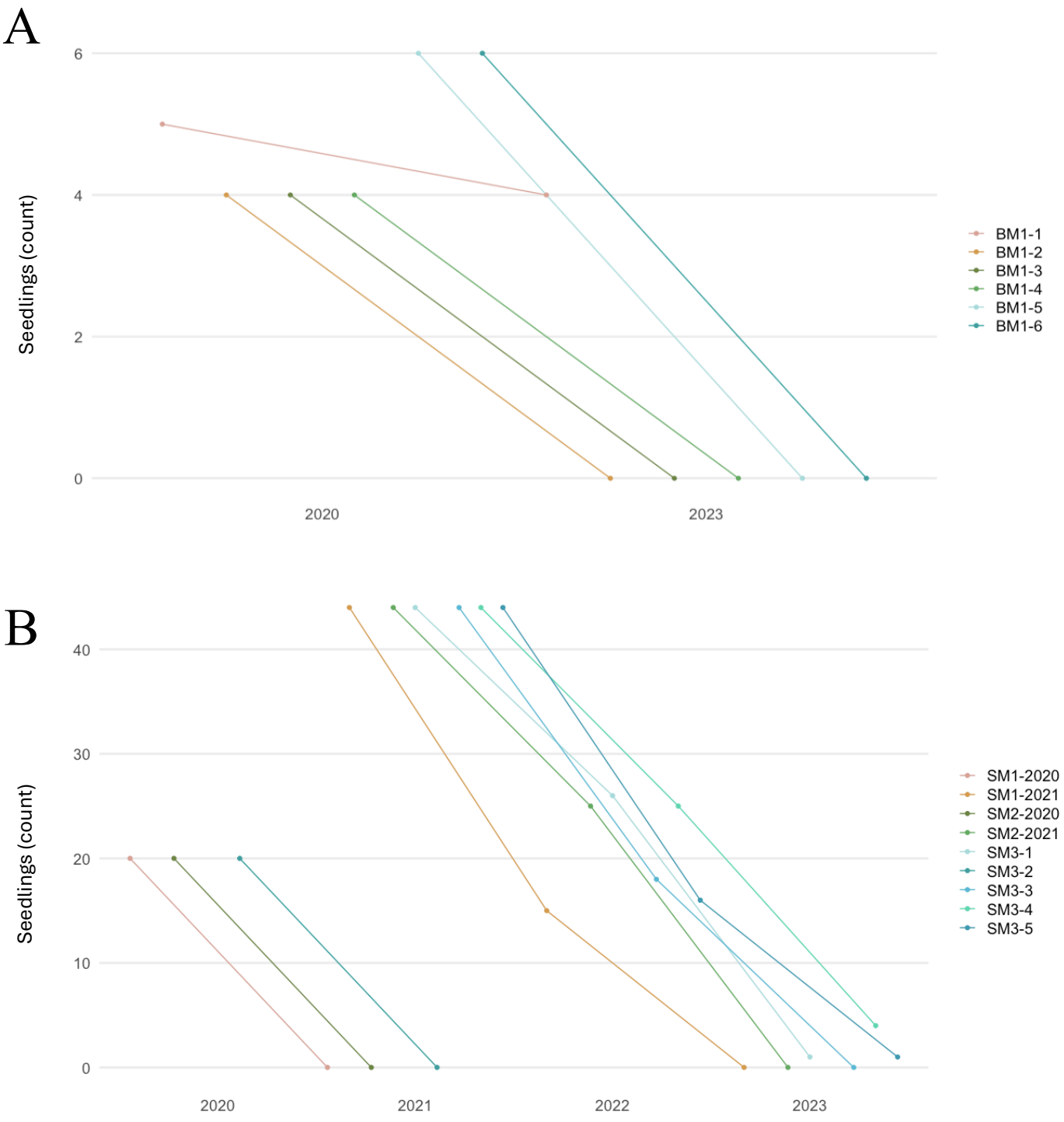


Figure 2.2.2 Survival of Outplanted E. codium Seedling at Badger and Snow Mountains 2020-2023
Graphs show decline in survival at Badger (A) and Snow (B) Mountains. Survival of seedlings outplanted at Badger Mountain in 2020 were monitored May 2023 (A). Survival of seedlings outplanted at Snow Mountain in 2020 were monitored in 2022 and are believed to have died in a heat wave Summer 2021 (B). Survival of seedlings outplanted at Snow Mountain in 2022 were monitored in July 2022 and May 2023 (B). In May 2023 alive seedlings were found only at BM1 grouping 1 and SM3 transects 1, 4, and 5 (A-B).

due to a stochastic event that wiped out the entire cohort at once- a heat wave late June/early July 2021 that pushed daytime temperatures in surrounding Yakima, WA to >110°F (>43°C) (correspondence Megan Whiteside). During monitoring in July of 2022, all the 2021 cohort showed varying levels of seedling survival (Fig 2.2.1, Fig 2.2.2, Fig T-1). In 2022, survival was highest at SM2-21, SM3-1 and SM-4 which had survival rates of 57-59%. Survival was lowest at outplanting transects at SM1-21, SM3-3 and SM3-5 which had survival rates between 34-41%. All surviving seedlings at Snow Mountain in May 2023 were located at site 3 with 60% (four out of six) of seedlings occurring in outplanting transect 4 (SM3-4), a one seedling occurring in each transects SM3-1 and SM3-5 (2.6).

Part II-II: Differences and Similarities in Site, Soil and Habitat Characteristics Between Three "Optimal" *E. codium* Habitat Groups and Seedling Outplanting Transects

Site Characteristics

Strong significant differences ($p \leq 0.003$) between optimal *E. codium* habitat groups and outplanting transects were determined in site characteristics heat load, slope, slope angle, landscape position and hillslope position (Fig 2.2.1). Weakly significant differences ($p < 0.059$) were determined between habitat groups and outplanting transects in site characteristics aspect, slope complexity and slope shape. Total rock fragment classification was similar between all optimal habitat groups and outplanting transects ($p = 0.77$). All optimal *E. codium* habitat groups and outplanting transects had the same maximum 75% cover value, and all plots in SM3-4 and SM3-5 were assigned rock fragment classification values of 75% (Figures 2.2.5-D and Fig W-2). Mean rock fragment classification of optimal *E. codium* habitat groups ranged from 54% in the optimal-low group to 64% in the optimal-high group. Mean rock fragment class cover fell within this range at transects SM1-20, SM2-20, SM2-21, SM3-1 and SM3-3. Transects BM1 and SM1-21 had mean cover values slightly below this range (BM1 = 46%, SM1-21 = 45%) while transects SM3-2, SM3-4 and SM3-5 had mean values slightly above (SM3-2 = 70%, SM3-4 and SM3-5 = 75%).

Outplanting transects BM1, SM1-20 and SM1-21 all exclusively contained plots with southern aspects (south, southeast and southwest), while SM2-20, SM2-21, and transects SM3 1-5 contained plots with exclusively either a west or northern aspect (north, northeast, northwest) (Figure 2.2.4). Mode aspect was east in the optimal-high group, west in the optimal-low group, and both east and west in the optimal-medium group (Fig W-1). Mode aspect was west at SM2-20, north at SM3-4, northwest at SM2-21, SM3-2, and SM3-5, northeast at SM3-1, north and

Table 2.2.1 PERMANOVA of Differences in Site Characteristics Between Optimal *E. codium* Habitat Groups and Outplanting Transects at Badger and Snow Mountains 1-3
Strong significant differences ($p \leq 0.003$) between optimal *E. codium* habitat groups and outplanting transects were determined in site characteristics heat load, slope, slope angle, landscape position and hillslope position. Weakly significant differences ($p < 0.059$) were determined between habitat groups and outplanting transects in site characteristics aspect, slope complexity and slope shape. Total rock fragment classification was similar between all optimal habitat groups and outplanting transects. Pairwise comparison indicates similarities in slope complexity between optimal *E. codium* habitat groups and all outplanting transects except SM-3 and SM-5. Pairwise comparisons of landscape position indicate significant differences between all habitat groups and outplanting transects. Significant pairwise differences were determined in heat load index between optimal *E. codium* habitat groups and outplanting transects. HLI in the optimal-low group was determined to be distinct from the other habitat groups and SM3-1 is the only outplanting transect that matched the patterns in HLI observed in the optimal high and medium habitat groups. Significant relationships are indicated by asterisks (* = significant, ** = strongly significant, ***= very strongly significant).

Outplanting Transect Differences in Site Characteristics

Site Characteristics (n=152)	**Df**	**R^2**	**F**	**Pr(>F)**	
Heat Load	12	0.3446	6.09	0.001	***
Slope	12	0.2195	3.26	0.003	**
Slope Angle	12	0.4235	8.51	0.001	***
Aspect	12	0.1313	1.75	0.057	
Total Rock Fragment Class	12	0.1295	1.72	0.077	
Landscape Position	12	0.8864	90.39	0.001	***
Hillslope Position	12	0.6307	19.78	0.001	***
Slope Complexity	12	0.1378	1.85	0.055	
Slope Shape	12	0.1428	1.93	0.044	*

northwest at SM3-3, and southwest at BM1, SM1-20 and SM1-2. Pairwise comparison of plot aspects indicated similarities between optimal *E. codium* habitat groups and some outplanting transects (Figure 2.2.4). Aspect in the optimal-low habitat group was similar to SM3-2. Aspect of optimal-high and optimal-medium habitat groups were similar to outplanting transects at SM2-21 and SM3-5. The range and proportion of plot aspects recorded in *E. codium* optimal habitats differed the most from BM1, SM1-20, SM1-21, and SM2-20. BM1, SM1-20 and SM1-21 had south facing plots, which was the only aspect not present in the optimal habitat groups.

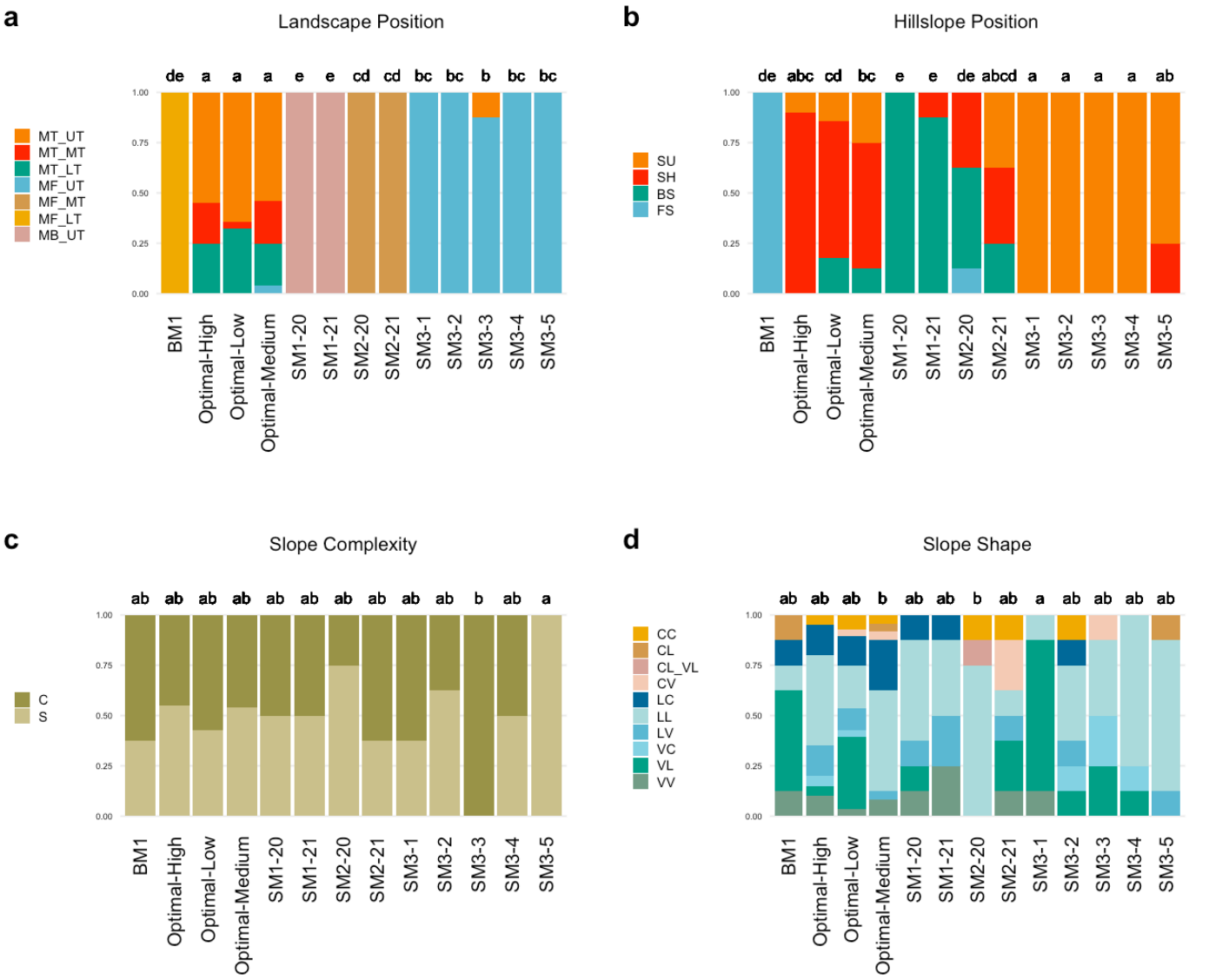


Figure 2.2.3 Bar Graphs of Categorical Site Characteristics at Optimal *E. codium* Habitat Groups and Outplanting Transects at Badger and Snow Mountains Sites 1-3

Differences in categorical site variables between optimal *E. codium* habitat groups (high, medium, low) groups and at outplanting transects at Badger Mountain (BM) and Snow Mountain (SM) sites 1, 2 and 3. Whiles strongly significant differences were determined in landscape and hillslope positions between optimal habitat groups and outplanting transects, only weakly significant differences in slope complexity and slope shape were observed. Site characteristics include landscape position (A) (MT_UT = mountaintop- upper third, MT_MT = mountaintop- middle third, MT_LT = mountaintop- lower third, MF_UT= mountain flank_ upper third, MF_MT= mountain flank_ middle third, MB_UT= mountain base_ upper third), hillslope (B) (SU= summit, SH= shoulder, BS= backslope, FS= foot-slope, TS= toe-slope), slope shape (C) (CC= concave-concave, CL= concave-linear, CV = concave-convex, LC= linear-concave, LL= linear-linear, LV= linear-convex, VC= convex-concave, VL= convex-linear, VV= convex-convex and slope complexity (D) (C= complex, S= simple).

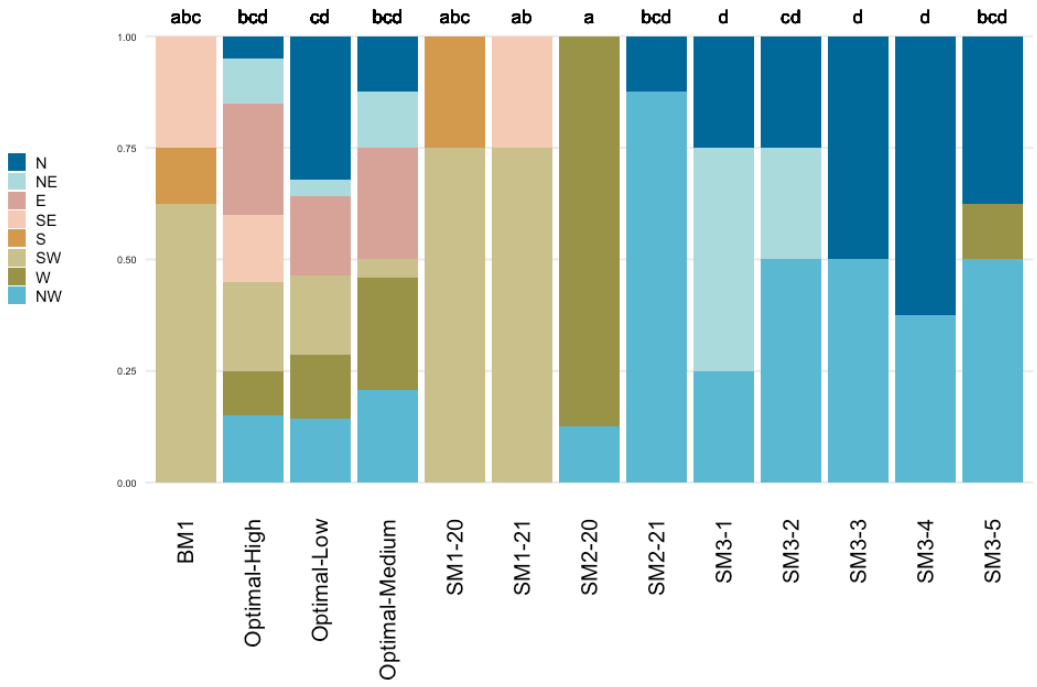


Figure 2.2.4 Bar Graph of Aspect at Optimal *E. codium* Habitat Groups and at Outplanting Transects at Badger and Snow Mountains Site 1-3
Differences in aspect between Native Site optimal *E. codium* habitat groups (high, medium, low) groups and at outplanting transects at Badger Mountain (BM) and Snow Mountain (SM) sites 1-3 (N = north, NE = northeast, E= east, SE= southeast, SW= southwest, W= west, NW= northwest).

Pairwise comparison indicates similarities in slope complexity between optimal *E. codium* habitat groups and all outplanting transects except SM-3 and SM-5 (Figure 2.2.3-C). Mode slope complexity was simple at *E. codium* habitat groups optimal-medium and optimal-high and outplanting transects SM2-20 and SM3-2, and complex for the optimal-low habitat group and transects BM1, SM2-21, SM3-1, SM3-3, and SM3-5 (Fig W-1). Transects SM1-20, SM1-21, and SM3-4 were evenly split between simple and complex plot slope, while the majority of other groups contained relatively even ratios except for SM2-20, which had a larger ratio of simple to complex plots (Figure 2.2.3-C). SM3-3 contained only complex slopes and SM3-5 contained only simple slopes. All slope shapes recorded at outplanting transects are

present at the native site and pairwise comparison indicated significant similarities between optimal *E. codium* habitat groups and outplanting transects (Figure 2.2.3-D). Slope shape in the optimal-medium habitat group was similar to SM2-20, and significantly different than SM3-1. Slope shape of optimal-high and optimal-low habitat groups were similar to outplanting transects at BM1, SM1-20, SM1-21, SM2-21, SM3-2, SM3-3, SM3-4 and SM3-5. Mode of slope shape was linear in all habitat groups and at all outplanting transects except SM2-21 which was concave-convex shape (Fig W-1). Mode of slope shape was convex-linear in the optimal-medium habitat group and at BM1 and SM3-1, and linear-linear at optimal-high and optimal-low habitat groups and at outplanting transects SM1-20, SM1-21, SM2-20, SM3-2, SM3-3, SM3-4 and SM3-5.

Optimal *E. codium* habitat groups (high, middle, low) had similar proportions of plots located in landscape positions in the upper, middle, and lower thirds of the mountain top, although the optimal-low habitat group had a lower proportion of plots in the middle third and a large proportion of plots in the lower third of the mountain-top compared to the optimal-high and optimal-medium groups (Figure 2.2.3-A). The optimal-medium group was the only group with plots that extended into the upper third of the mountain flank. In contrast, pairwise comparisons indicate significant differences between all habitat groups and outplanting transects. SM3-3 was the only transect to contain plots in the upper third of the mountain top, while the remainder of plots at SM3-3 outplanting transects where located on the upper third of the mountain-flank. BM1 and SM2-20 and SM2-21 occurred on the mountain flank, while SM1-20 and SM1-21 were

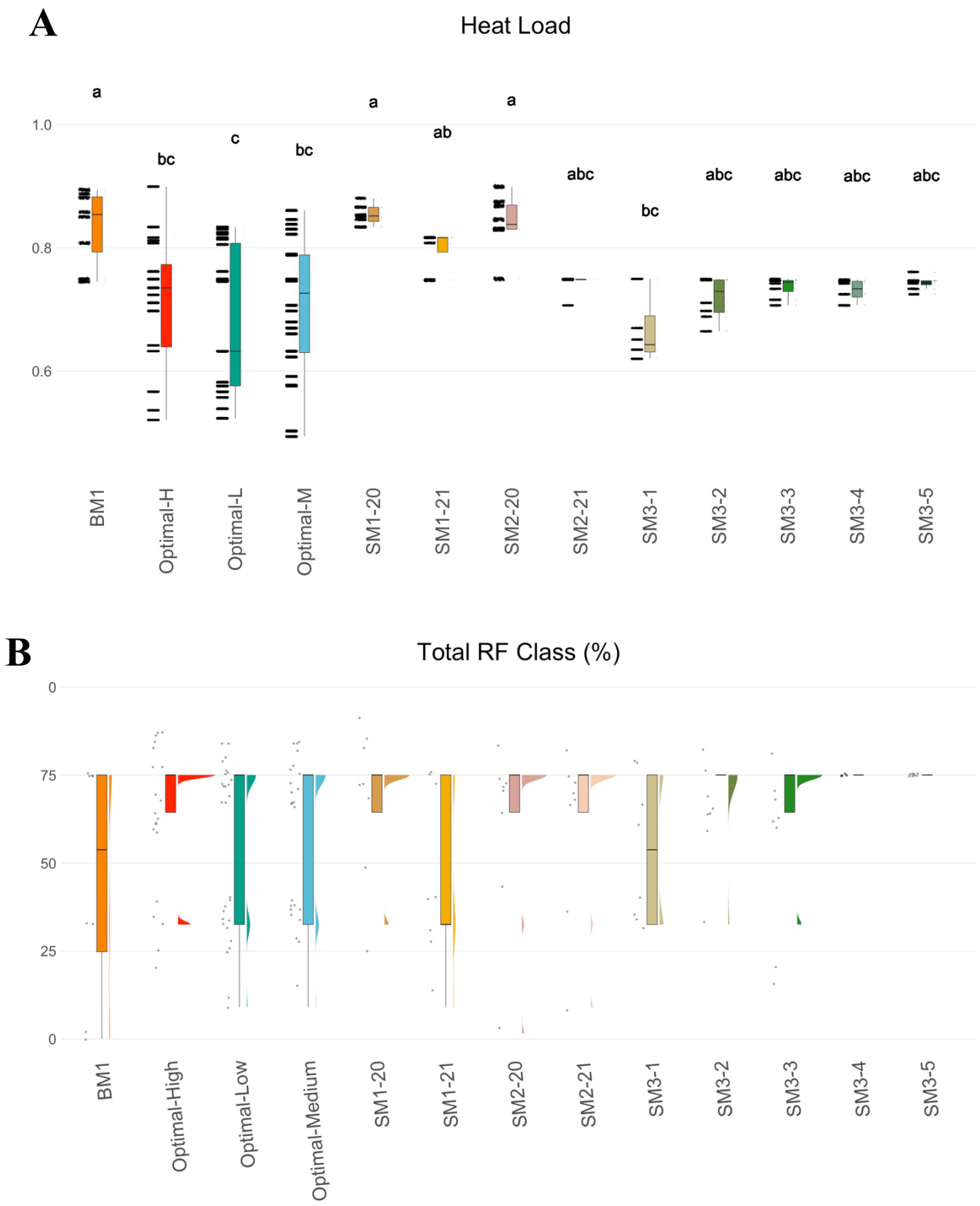


Figure 2.2.5 Raincloud Plots of Continuous Site Characteristics Heat Load Index and Total Rock Fragment Classification at Optimal *E. codium* Habitat Groups and Outplanting Transects at Badger and Snow Mountains Sites 1-3
Differences in continuous site variables heat load (A) and total percentage of rock fragment cover classification (B) between Native Site optimal *E. codium* habitat (high, medium, low) groups and at outplanting transects at Badger Mountain (BM) and Snow Mountain (SM) sites 1, 2 and 3.

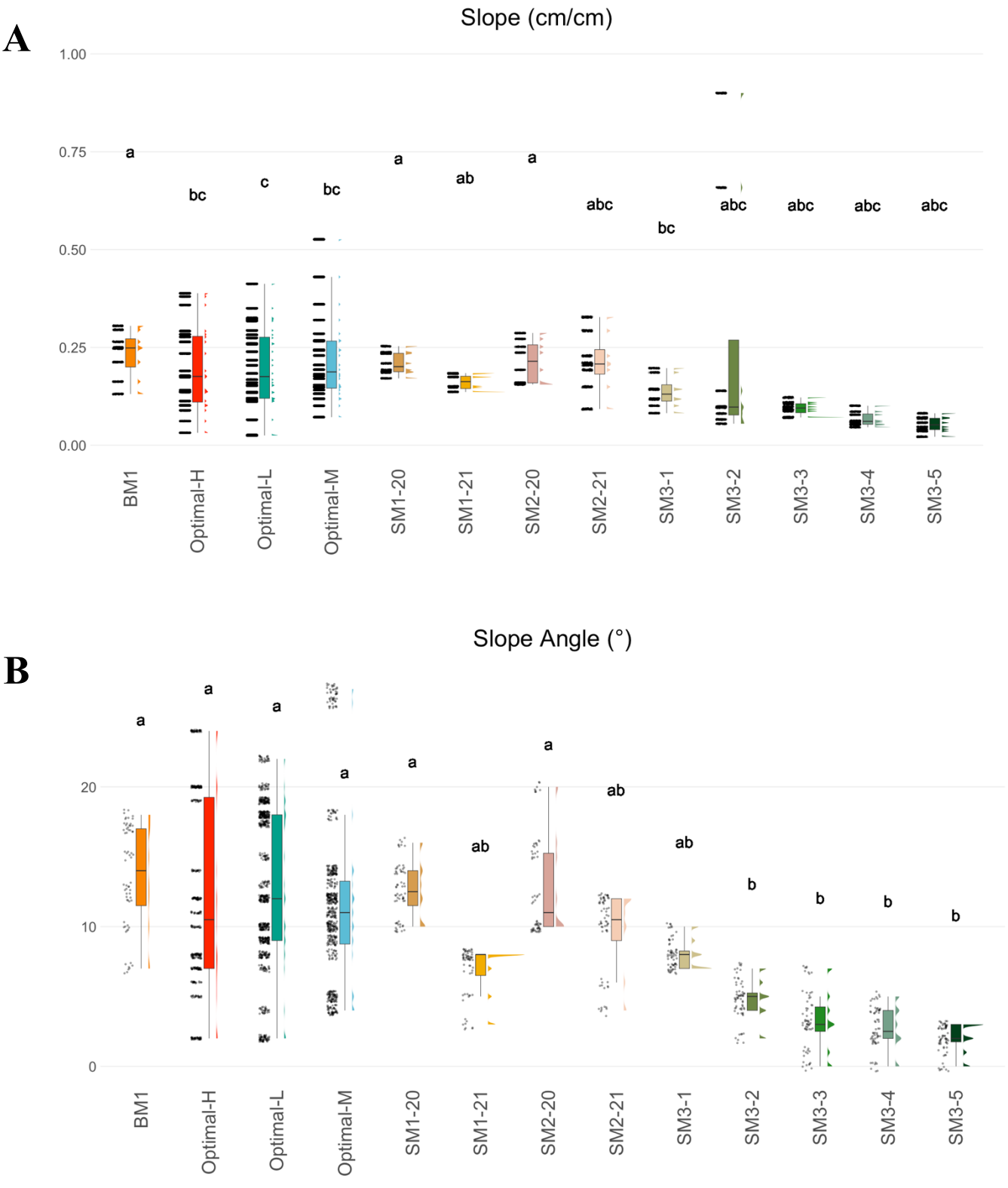


Figure 2.2.6 Raincloud Plots of Continuous Site Characteristics Slope and Slope Angle at Optimal *E. codium* Habitat Groups and Outplanting Transects at Badger and Snow Mountains Sites 1-3
Differences in continuous site variables slope (cm/cm) (A) and slope angle (°) (B) between Native Site optimal *E. codium* habitat (high, medium, low) groups and at outplanting transects at Badger Mountain (BM) and Snow Mountain (SM) sites 1, 2 and 3.

positioned on the mountain base. Pairwise comparisons indicated significant differences between all optimal *E. codium* habitat groups and outplanting transects (Figure 2.2.3-A).

Although the hillslope positions that SM1-20, SM1-21, SM2-20, SM2-21, and SM3 1-5 occupy (i.e. summit, shoulder and backslope) also occur at NS, there are differences in the proportion of these hillslope positions in optimal habitat groups and at outplanting transects. BM1 is the most different from the optimal *E. codium* habitat groups as it occurs exclusively on a foot slope, which is not a hillslope position that occurs at the native site (Fig 2.2.3-B). SM2-20 also contains plots that occur on the foot slope in addition to the shoulder and backslope. The optimal-high habitat group exclusively contains plots that occur on the summit and shoulder, while both optimal-medium and optimal-low groups also contain plots on the backslope.

Significant pairwise differences were determined in heat load index (HLI) between optimal *E. codium* habitat groups and outplanting transects (Figure 2.2.5-A). HLI in the optimal-low group was determined to be distinct from the other habitat groups, and had a lower mean value (optimal-low = 0.68, optimal-high/medium= 0.71) (Fig W-2). SM3-1 is the only outplanting transect that matched the patterns in HLI observed in the optimal high and medium habitat groups, likely due to SM3-1 having the lowest minimum HLI value (minimum = 0.62) of all outplanting transects, although it has a mean closer to the optimal-low group (mean = 0.67). Minimum HLI values in habitat groups ranged between 0.49 in the optimal-medium group to 0.52 in the optimal-high and optimal-low groups, to maximum values between 0.83 in the optimal-low group to 0.9 in the optimal-high group. All HLI values at outplanting transects fall within the range of values at the native site and have similar maximum values ranging from 0.75 at SM2-21 and SM3 1-5 to 0.9 at SM-2-20. HLI at outplanting transects had narrower ranges than optimal habitat groups, and all transects except SM2-21 and those at SM3 had higher means

(mean = 0.8 at SM1-21 to 0.85 at SM1-20) that fell within the higher range of HLI values. Despite *E. codium* habitat groups having lower minimums and larger standard deviations than at outplanting transects, mean values at SM2-21 and SM3 1-5 reflected the optimal habitat groups (0.67 at SM3-1 to 0.74 at SM3-3 and SM3-5).

Mean slope ranged between from 0.2 cm/cm in optimal-high and optimal-low *E. codium* habitat groups to 0.22 cm/cm in the optimal-medium group (Fig 2.2.6-A and Fig W-2). Mean slope at BM1, SM1-20, SM2-20, and SM2-21 ranged from 0.21-0.23 cm/cm, which was close to the range established by the optimal habitat groups, while mean slope at SM3-2 is slightly higher although still close to this range as well (mean = 0.26 cm/cm). Mean slope at SM1-21(mean = 0.16 cm/cm) and SM3-1 (mean = 0.14 cm/cm) was slightly lower than optimal habitat groups, while mean slope at SM3 3-5 was much lower (SM3-3 = 0.09 cm/cm, SM3-4 = 0.07 cm/cm, SM3-5 = 0.05 cm/cm). Significant pairwise differences in slope were determined between *E. codium* optimal-high and optimal-low habitat groups and the optimal-medium group (Figure 2.2.6-A).

Similarities in slope were observed between the optimal-medium group and SM3-2 and between the optimal-high and optimal-low habitat groups (Fig 2.2.6-A). Similarities were determined between habitat groups optimal-high and optimal-low and outplanting transects BM1, SM1-20, SM1-21, SM2-20, SM2-21, SM3-1 and SM3-3. Outplanting transects SM3-4 and SM3-5 significantly differed from all optimal habitat groups, although slope at the optimal high and low habitat groups and at transects BM1, SM1-20, SM1-21, SM2-20, SM2-21, SM3-1 and SM3-3 shared similarities, and reflected differences between these optimal habitat groups and the optimal-medium group. This is likely because the optimal-high and optimal-low groups have a lower minimum value (0.03 cm/cm) which encompasses SM3-4 and SM3-5 minimum values

(Fig W-2). In contrast, the optimal-medium group has a higher maximum value (0.53 cm/cm) which is mirrored by the extremely high maximum value and standard deviation at SM3-2 (max = 0.9 cm/cm, sd = 0.33).

Optimal *E. codium* habitat groups had similar mean slope angles which ranged from 12-13° degrees (Fig W-2). Significant similarities were also determined between all habitat groups and outplanting transects at BM1, SM1-20, and SM2-20, which had mean values close to this range (BM1= 13.62°, SM1-20= 12.62°, SM2-20 = 12.88°) (Figure 2.2.6-A). However, minimum values at these transects are higher than in the optimal habitat groups and their maximum values are lower indicating a narrower range of slope angle values (mean range habitat groups: 2.6 -22°, mean range transect groups: 9-18°). In contrast, transects SM1-21, SM2-21 and SM3 1-5 have much narrower ranges of slope angle values and lower maximum values (mean max = 7.4°), resulting in significantly lower mean values (2° at SM3-5 - 9.6° at SM2-21).

Soil Characteristics

Strong significant differences (p = 0.001) between optimal *E. codium* habitat groups and outplanting transects were determined in soil characteristics including soil texture, soil surface and soil surface rock fragment composition, but only a very weakly significant difference in hydraulic conductivity was observed (Table 2.2.2).

Post-hoc pairwise comparison of hydraulic conductivity could not determine any differences between optimal habitat groups and any of the outplanting transects, although the range of values was wider and the standard deviations larger in the optimal habitat groups than any of the outplanting transects (Fig 2.2.7). The majority of K values in the optimal-low habitat group were > 0, indicating faster and presumably deeper water infiltration (Fig 2.2.7 and Fig W-3). However, the optimal-high group had the highest maximum values observed in

Table 2.2.2 PERMANOVA of Differences in Soil Characteristics Between Optimal *E. codium* Habitat Groups and Outplanting Transects at Badger and Snow Mountains 1-3

Strong significant differences (p = 0.001) between optimal *E. codium* habitat groups and outplanting transects were determined in soil characteristics including soil texture, soil surface and soil surface rock fragment composition, but only a very weakly significant difference in hydraulic conductivity was observed. Significant relationships are indicated by asterisks (* = significant, ** = strongly significant, ***= very strongly significant).

Transect Differences in Soil Characteristics

Soil Characteristics	n	Df	R^2	F	*Pr(>F)*	
Hydraulic Conductivity (K)	141	12	0.1495	1.88	0.048	*
Soil Texture	133	12	0.3928	7.28	0.001	***
Surface Composition	152	12	0.3500	6.24	0.001	***
Surface Rock Fragment Composition	152	12	0.3595	6.50	0.001	***

this study, indicating faster infiltration rates may characterize the most optimal *E. codium* habitat to some extent. Only the optimal-high and optimal-low groups had K values > 0.05, in contrast to the optimal-medium group which was characterized by a smaller range of lower K values, suggesting slightly faster, although not significantly different, infiltration rates may be related to creating the more extreme vegetation habitat niche these two groups likely represent. Outplanting transects BM1, SM1-20 and SM1-21 had the smallest range of K values, and best reflected the slower inflation rate of the optimal-medium group. Outplanting transects SM2-20 and SM2-21 had the widest range of values of the outplanting transects, and best reflected the wide range of K values that characterize the optimal habitat groups. Outplanting transects at SM3 had the narrowest ranges of K values, indicating hydraulic conductivity was mostly consistent across this site, with the majority of plots containing K values above 0, indicating infiltration was also generally faster. Transects SM3-1 and SM3-2 had higher maximum K values and wider ranges than transects SM3 3-5, which reflected the wider range of values characterizing the optimal habitat groups. This may indicate sites closer to the top of the mountain ridge may have more variable hydraulic conductivity and better matched the wide-ranging variation of the optimal *E. codium* habitat groups.

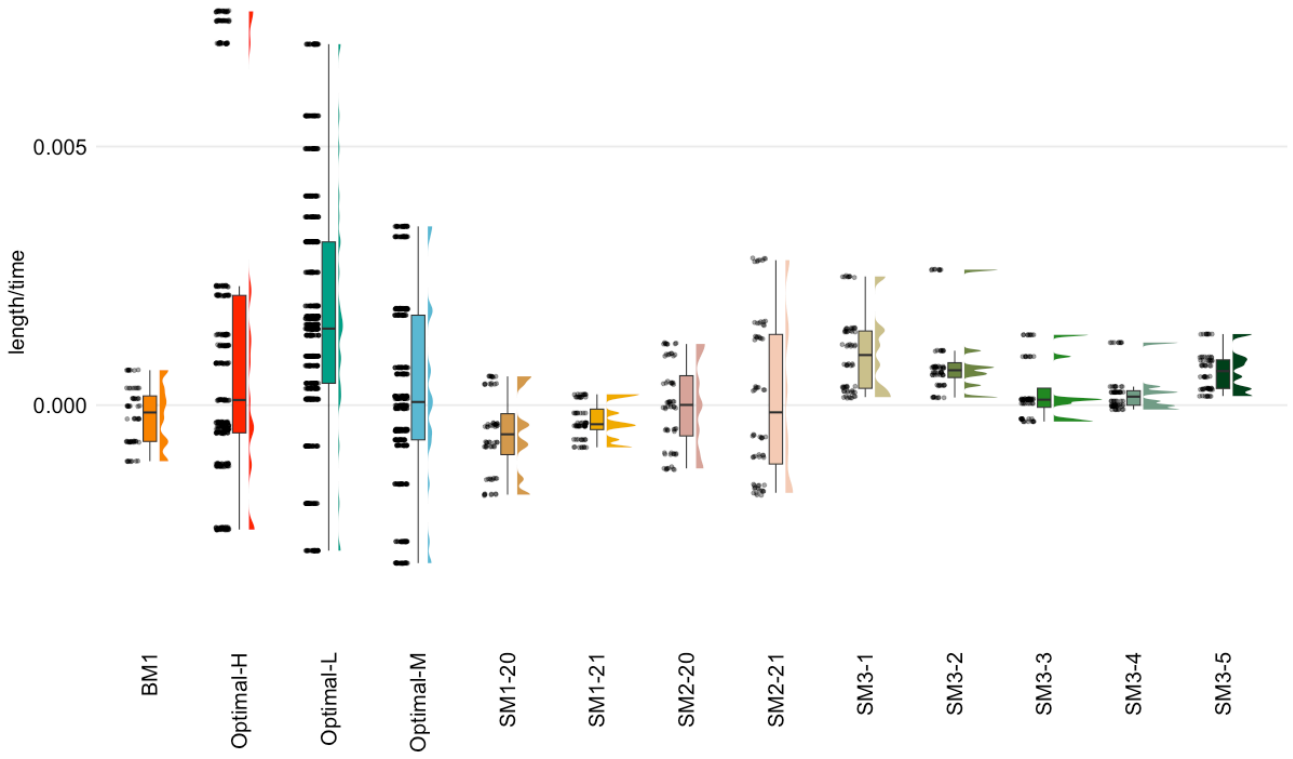


Figure 2.2.7 Raincloud Plot of Hydraulic Conductivity (K) at the Optimal *E. codium* Habitat Groups and Outplanting Transects at Badger and Snow Mountains 1-3
Differences in hydraulic conductivity between Native Site optimal *E. codium* habitat (high, medium, low) groups and outplanting transects at Badger Mountain and Snow Mountain sites 1, 2, and 3.

Pairwise comparison in soil texture indicated significant differences between optimal-high and both optimal-medium and optimal-low groups are due to the presence of one plot with loam soil and a higher proportion of plots with loamy sand soil in the optimal-high group (Figure 2.2.8). Mode soil texture in the optimal-high group was loamy sand while mode of soil texture was sandy loam in the optimal low group and split between both soil types in the optimal-medium group (Fig W-1).

All outplanting transects contained loam based soils (loam, sandy loam, silt loam), and only outplanting transects SM2-20 and SM2-21 contained any loamy sand soils (one plot in each transect) (Figure 2.2.8). In contrast, loamy sand soils were present in at least 25% of plot in all

optimal habitat groups. SM1-20, SM1-21, and SM3 1-5 all contained at least 25% of plots with loam soils and SM3-5 exclusively contained loam soil. BM1 contained only silt loam soils and SM3-2 contained one plot with silt loam soil. Mode soil texture was loam at transects SM1-21, SM3-2, SM3-3 and SM3-5, silt loam at BM1, sandy loam at transects SM2-30, SM2-21, and SM3-1, and split between loam and sandy loam at SM1-20 and SM3-4 (Fig W-1). Silt loam soil was not present in the optimal habitat groups and loam soil was only present in one plot in the optimal-high habitat group, making BM1, SM1-21, SM3-2, SM3-3 and SM3-5 the least similar to the optimal habitat groups soil types (Figure 2.2.8). SM3-1 is the most significantly similar to the optimal-high group, although all outplanting transect except BM1 shared some similarities

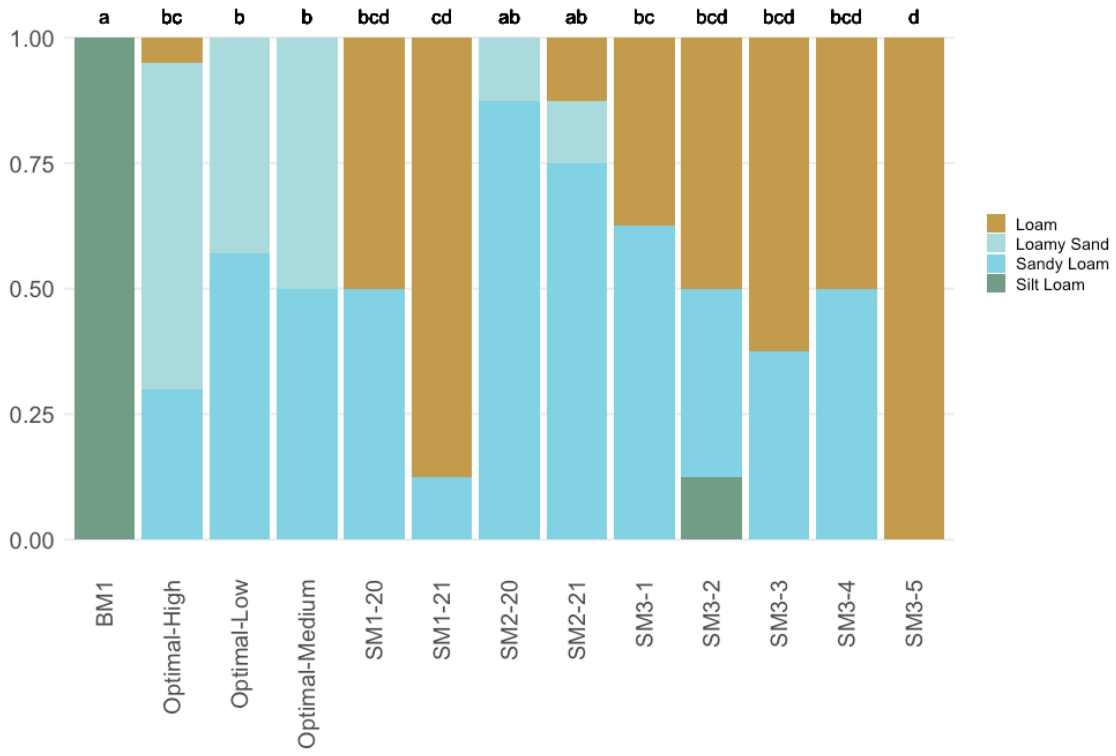


Figure 2.2.8 Bar Graph of Soil Texture at Optimal *E. codium* Habitat Groups and at Outplanting Transects at Badger and Snow Mountains 1-3

Differences in soil surface texture of optimal *E. codium* habitat (high, medium, low) groups and the soil texture in the top 15cm of the soil profile at outplanting transects at Badger Mountain and Snow Mountain sites 1-3. SM3-1 is the most significantly similar to the optimal-high group while SM2-20 and SM2-21 are the only transect with the soil types as the optimal habitat groups and the only areas where loamy sand soils were recorded. All outplanting transect except BM1 shared some similarities in soil texture to the optimal *E. codium* habitat types.

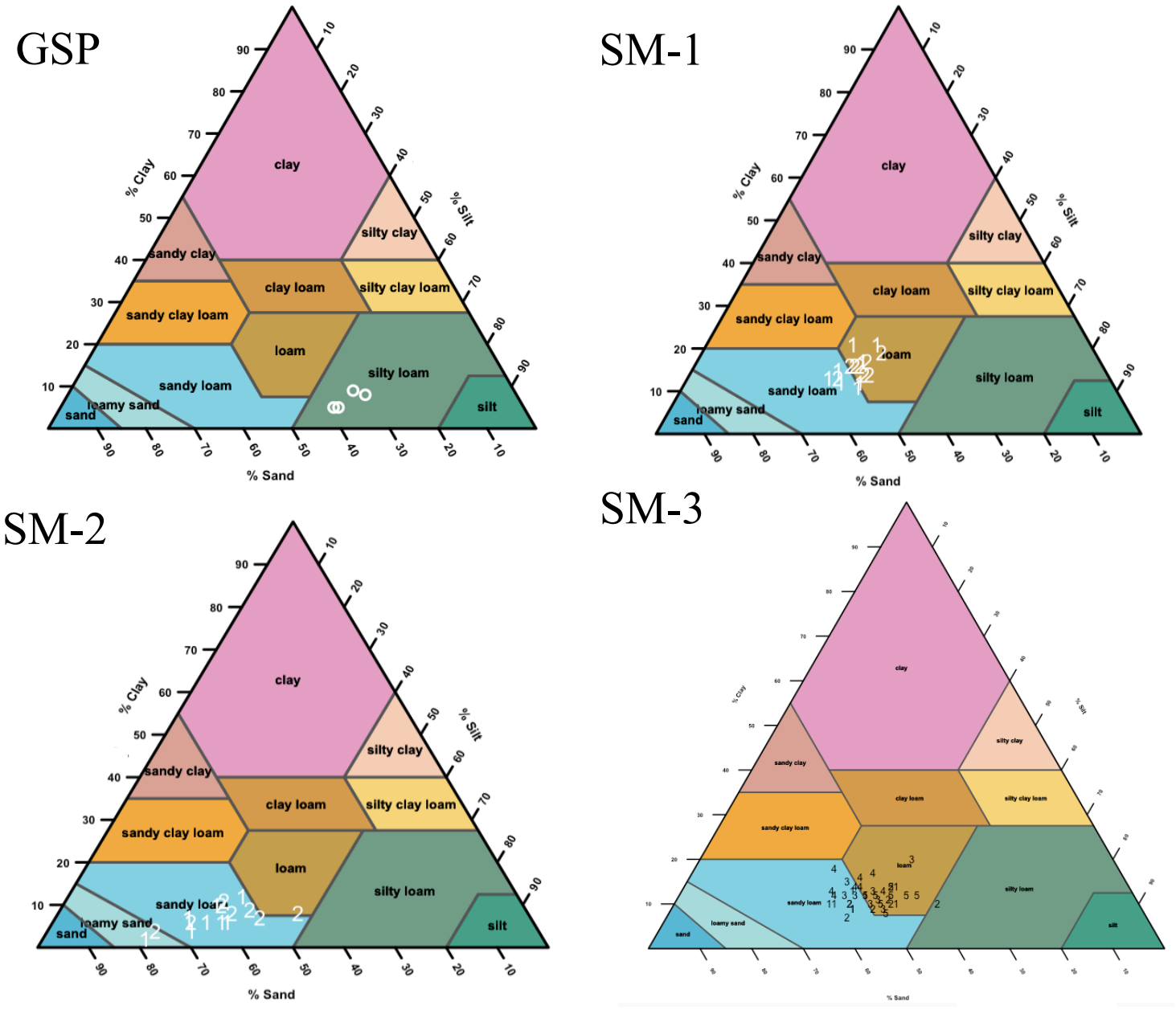


Figure 2.2.9 USDA-NCSS Soil Textural Triangles of Outplanting Transects at Badger and Snow Mountain Sites 1-3
Soil textural classification of top 15cm of soil at outplanting transects at Badger Mountain (n= 4) and Snow Mountain sites 1-3 (SM1-3) (n= 72). White circles (BM) and black and white numbers (SM 1-3) and indicate individual 1m^2 sample plots. White numbers on textural triangles at Snow Mountain sites 1-2 indicate planting year (1= 2020 and 2= 2021). Black numbers on textural triangles at Snow Mountain sites 3 indicate transect ID number (1-5). Native Site soil texture (ratio sand-silt-loam) could not be mapped onto texture triangle because soil texture was determined by hand texturing method and not quantitatively via laboratory analysis.

in soil texture to the optimal *E. codium* habitat types. SM2-21 is the only outplanting transect to have the same three soil types at the optimal-high habitat group while SM2-20 is the only transect with only the same two soil types as the optimal-medium and optimal-low groups, as SM-2 was the only site where loamy sand soils were recorded.

Pairwise comparison of soil surface composition indicated similarities between all optimal habitat groups and outplanting transect SM3-5 ($p \geq 0.4$) (Fig V-1). Similarities were also determined between the optimal-medium habitat group and SM3-4 ($p = 0.6$), although this transect was significantly different from the optimal-high and optimal-low habitat groups ($p = <0.05$). Significant differences were determined between all optimal *E. codium* habitat groups and outplanting transects BM1, SM1-20, SM1-21, SM2-20, SM2-21 and SM3 1-3. The most strongly significant differences were between the optimal-high group and outplanting transects, And these relationships are illustrated in the NMDS ordination of soil surface composition (Figure 2.2.10-A). The optimal habitat groups are clustered in the right side of the ordination space, with the optimal-high and optimal-medium points clustered furthest to the right of the ordination space, and the optimal-low points to their left, closer to the outplanting transects. As the area of overlap between all three optimal habitat groups extends into the center of the ordination space, they overlap with outplanting transects SM3-4 and SM3-5, which slightly overlap with the optimal habitat groups. The ellipses of the optimal-medium group extend the furthest into the left side of the ordination space and also overlap to a lesser extent with the upper portions of serval outplanting transect ellipses including SM3-2, SM-3 and SM1-20.

Mean rock composition in the optimal *E. codium* habitat groups ranged from 69% in the optimal-low group to 74% in optimal-high group, which also had a higher minimum rock cover (high: 38%, medium/low: 20%) (Fig W-4). All outplanting transects had mean rock cover

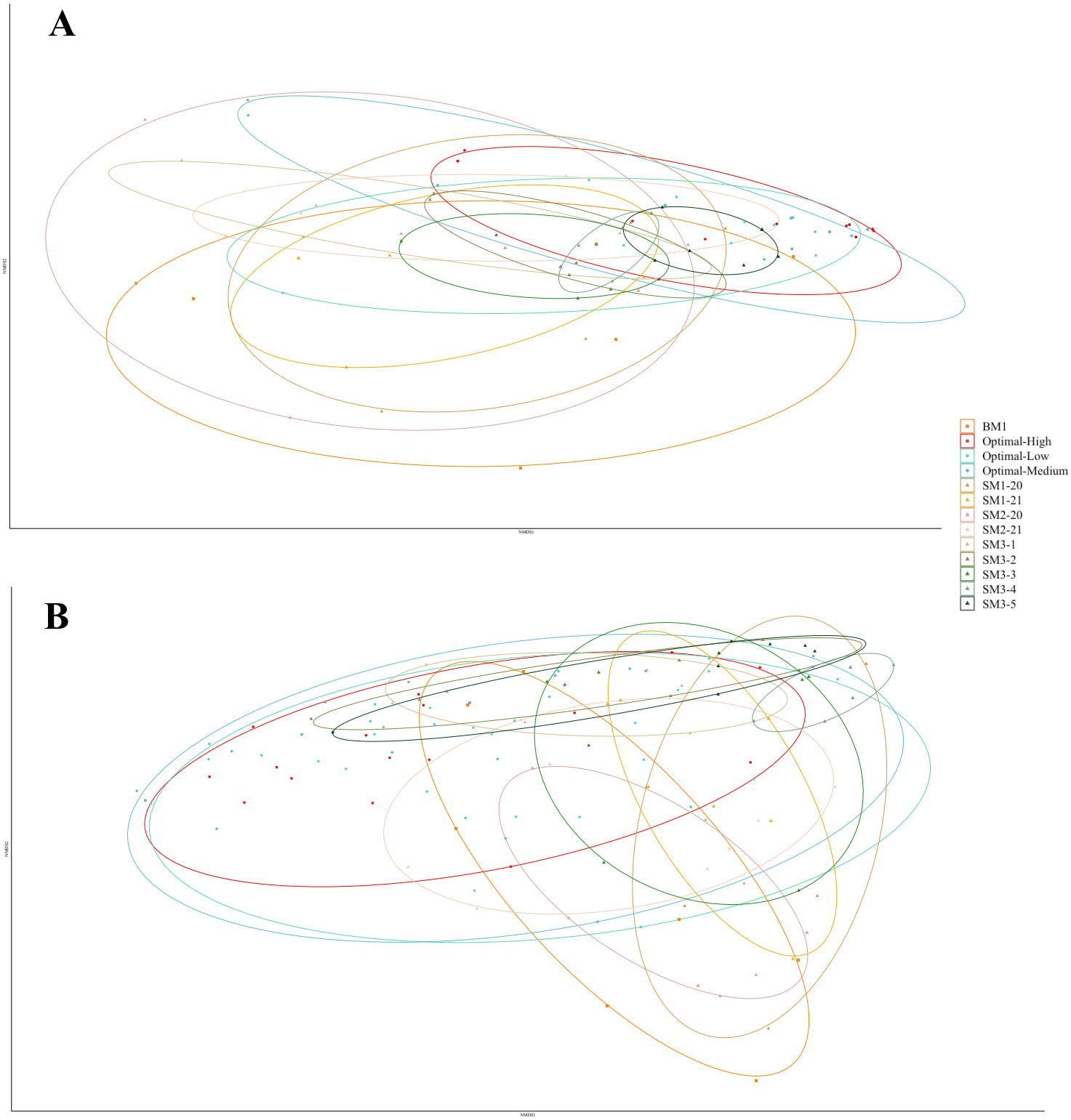


Figure 2.2.10 NMDS Ordination of Soil Surface and Soil Surface Rock Fragment Compositions of Optimal *E. codium* Habitat Groups and Outplanting Transects at Badger and Snow Mountains 1-3

Non-metric multidimensional scaling (NMDS) ordination of soil surface (k = 2 , stress = 0.051) and soil surface rock fragment (k = 3, stress = 0.0498) compositions. Points and ellipses s are coded by color to correspond to transect grouping. Point shapes correspond to site identity (Native Site, Snow and Badger Mountains). Each point represents a $1m^2$ plot. Points closer together are more similar to than those farther apart.

below this range except for SM3-5, which had mean rock cover values ranging from 35% at SM1-21 to 62% at SM3-4. SM3-5 had a mean rock cover of 78%, slightly above the mean cover value in the optimal-high group. Although maximum values at SM3-5 and SM2-21 are the same as the optimal habitat groups (88%), the minimum value at SM2-1 is lower (10%) and minimum value at SM3-5 is higher (62%). SM3-4 has the same minimum, maximum and mean rock cover value of 62%, similar to the mean cover in the optimal-low habitat group, and a standard deviation of zero as this cover was consistent across the entire transect. Mean bare ground composition in optimal *E. codium* habitat groups ranged from 11% in the optimal-high group to 15% in the optimal-medium group, which also had the highest maximum cover values (62%). Mean cover at BM1 and SM1-20 fell within this range although mean cover at SM3-5 was slightly below (10%) and mean cover at SM3-2 and SM3-4 was slightly above (SM3-2: 18%, SM3-4: 19%). Outplanting transects SM1-21, SM2-20, SM2-21, SM3-1 and SM3-3 had higher mean bareground cover than optimal habitat groups, ranging from 22 %at SM3-3 to 31% at SM2-21.

Mean and maximum litter composition was lower in optimal *E. codium* habitat groups optimal-high and optimal-medium (average mean = 3.5%, max= 20%) compared to the optimal-low habitat group (mean = 7%, max = 38%) (Fig W-4). Only SM3-2 and SM3-5 mean litter cover values fell within the range of optimal habitat groups, although BM1, SM2-21, and SM3-1 had mean values only slightly higher than the optimal-low habitat group mean value (BM1: 9%, SM2-21: 10%, SM3-1: 8%) and a similar range of values as all optimal habitat groups. Despite also having a similar range of values as all optimal habitat groups, outplanting transects SM1-20, SM1-21, SM3-3 and SM3-4 had higher mean litter cover values ranging from 12% at SM1-20 to

18% at SM1-21. SM2-20 had the highest mean and maximum litter cover and standard deviation of all habitat groups and outplanting transects (mean = 20%, maximum = 62%, sd= 20).

Mean biocrust cover in optimal-high and optimal-medium *E. codium* habitat groups was 0%, maximum cover was 3% and the standard deviation was 1 (Fig W-4). Mean biocrust cover was 1% in the optimal-low group, maximum cover was 20% and the standard deviation was 4. This extremely low cover of biocrust was unique to the optimal *E. codium* habitat groups. Mean biocrust cover of < 5% only occurred at outplanting transects SM2-20 and SM2-21 and mean cover of <10% only occurred at SM1-20, SM3-4 and SM3-5. Transects SM1-21 and SM3 1-3 had mean biocrust cover >10% and BM1 had the largest mean and maximum biocrust cover (mean= 25%, max= 62%). Despite differences in mean cover, outplanting transects SM1-20, SM1-21, SM2-20, SM2-1 and SM3 2-5 all had minimum and maximum cover values within the range of values in the optimal-low habitat group, as well as similar standard deviations. Ultimately, ISA analysis indicated outplanting transects BM1 was uniquely characterized by high biocrust cover while the optimal-high *E. codium* habitat group was uniquely characterized by higher rock cover (Table 2.2.3).

Table 2.2.3 ISA of Soil Surface Composition Characterizing Optimal *E. codium* Habitat Groups and Outplanting Transects at Badger and Snow Mountains 1-3
Soil surface components that most characterize Native Site optimal E. codium habitat (high, medium, low) groups and at outplanting transects at Badger Mountain (BM) and Snow Mountain (SM) sites 1-3. The optimal-high was distinguished by its relatively higher rock cover compared to all other habitat groups and outplanting transects, while BM1 was characterized by its comparatively higher biocrust cover. IV_{ij} of 100 means soil surface component occurs in all plots. Significant relationships are indicated by asterisks (* = significant, ** = strongly significant, ***= very strongly significant).

ISA of Soil Surface Cover

Transect	Cover Class	IVij	*P*	
BM1	Biocrust	24.0	0.015	**
Optimal-High	Rock	10.9	0.005	**

Pairwise comparison of soil surface rock fragment composition indicated significant similarities between optimal habitat groups ($p \geq 0.4$) and between the optimal-medium group and SM3-1 ($p = 0.06$), although this transect was significantly different from the optimal-high and optimal-low habitat groups ($p = <0.05$) (Fig V-2). Significant differences were determined between all optimal *E. codium* habitat groups and outplanting transects BM1, SM1-20, SM1-21, SM2-20, SM2-21 and SM3 2-5. The most strongly significant differences were between all optimal habitat groups and outplanting transects BM1, SM1-20, SM2-20, and SM3-4 and between the optimal-medium group and SM2-21. The NMDS ordination of soil surface rock fragment class illustrates the separation of optimal habitat groups to the top right of the point cloud slightly separated from the area of overlap between outplanting transects in the center of the ordination (Figure 2.2.10-B)

BM1 and SM2-21 were the only outplanting transects to have bedrock present (BM1: mean = 12%, SM1-21: mean = 6%, max at both transects= 38%), which also did not occur in any optimal *E. codium* habitat groups (Fig W-5). Boulders are only present in the optimal-high habitat group at a maximum cover of 10%, however mean boulder cover was 0% because boulders were only recorded in a few plots (sd = 2). The optimal-low habitat group and the outplanting transects at SM1-20, SM1-21, SM2-20, SM3-4 and SM3-5 had mean stone cover of 0% although SM1-20 had a few plots with low stone cover (max= 3% , sd= 1). The optimal-high and optimal-medium habitat groups had mean stone cover of 1% and maximum cover of 20% and 10% respectively. Outplanting transects at SM2-21 and SM3-2 had similar mean stone cover as the optimal-high and optimal-medium habitat groups (SM2-21: mean= 1%, SM3-2: mean= 2%), and SM3-2 had the same maximum cover (max = 20%) as the optimal-medium group while

maximum cover at SM2-21 was much lower (max = 3%). BM1, SM3-1 and SM3-3 had the highest mean and maximum stone cover (average mean = 5.5, max= 38%). The optimal-low habitat group had higher mean cobble cover than optimal-high and optimal-medium groups (high: 5%, medium: 7%, low: 14%), although the optimal-medium and optimal-low groups had the similar maximum cover and standard deviation (max= 62%, average sd= 16), which was higher than the optimal-high group (max = 20%, sd= 6). Mean cobble cover at outplanting transects SM3-1 and SM3-2 (5%) were the most similar to the optimal-high and optimal-medium habitat groups, although maximum cover (10%) was lower than in both habitat groups but closer to the maximum value in the optimal-high group. Mean and range of cobble cover at transects SM3-3 and SM3-4 were the most similar to the optimal-low habitat group, although minimum cover was higher at SM3-4 (low: 0%, SM3-4: 10%) and mean cover was slightly higher at SM3-3 (19%). Transects BM1, SM1-20, SM1-21, and SM2-20, SM2-21 had much higher mean, range, and standard deviation of cobble cover than any of the optimal habitat groups.

Coarse gravel cover was similar between optimal *E. codium* habitat groups, and ranged from 22% in the optimal-high group to 25% in the optimal-low group (Fig W-5). Range of cover (0-62%) and standard deviation (20) was the same in all habitat groups. SM2-20 was the only outplanting transect with a similar mean cover (26%) to the optimal habitat groups, although it had a smaller range and standard deviation (range = 10-38%, sd= 13). Mean, range and standard deviation of coarse gravel cover at BM1 (mean = 13%, range = 0-38%, sd= 12) was less than the mean cover in the optimal habitat groups, while mean cover at SM2-21 was lightly above the cover values at optimal habitat groups, although its maximum and standard deviation values were similar (mean = 32%, range= 10-62%, sd= 18). Mean coarse gravel cover at SM1-20, SM1-

21, and SM3 1-5 was higher than in the optimal *E. codium* habitat groups, ranging from 42% at SM1-21 to 81% at SM3-4, and maximum gravel cover was 88% at SM1-20 and SM3 2-5.

Mean medium gravel cover was similar in optimal *E. codium* groups ranging from 28% in the optimal-high and optimal-low habitat groups to 32% in the optimal-medium group (Table W-5). The optimal- low group had a higher maximum cover value than the optimal-high and optimal-medium groups (high/medium= 62%, low = 88%) and the optimal-medium group has a higher minimum cover value than the other two groups (high/low = 0%, medium= 10%). SM3-5 was the only outplanting transect with a mean, range and standard deviation of medium gravel cover similar the optimal habitat groups (mean= 26%, range = 10-62%, sd= 16). BM1, SM1-20, SM1-21, SM2-20, SM2-21, SM3-3 and SM3-4 had lower mean cover than the mean range of the optimal-habitat groups. Mean medium gravel cover at SM1-21 (23%) and SM3-3 (21%) was between 20-28%, which was slightly below the mean range of the optimal habitat groups. Similarly, their maximum cover values were lower, although standard deviations were similar to the optimal habitat groups. Mean medium gravel cover ranged from 10-19% at transects BM1 (19%), SM1-20 (12%), and SM3-4 (12%), and <10% at SM2-20 (5%) and SM2-21 (9%), which was also much lower than the mean range established in the optimal habitat groups. SM3-1 and SM3-2 had higher mean medium gravel cover than habitat groups (SM3-1: 38%, SM3-2: 42%), and SM3-2 had a higher maximum cover value while SM3-1 had a similar range of cover values as the optimal-medium group.

Optimal *E. codium* habitat groups had uniquely higher mean fine gravel cover than all outplanting transects (Fig S-7). Mean fine gravel cover ranged from 21% in the optimal-low group to 31% in the optimal-high group, and all groups had a maximum cover value of 88%.

Table 2.2.4 ISA of Soil Surface Rock Fragment Composition Characterizing Optimal *E. codium* Habitat Groups and Outplanting Transects at Badger and Snow Mountains 1-3

Soil surface rock fragment components that most characterize Native Site optimal *E. codium* habitat (high, medium, low) groups and at outplanting transects at Badger Mountain (BM) and Snow Mountain (SM) sites 1-3. The optimal-high group is distinguished by its relatively higher cover of fine and very fine gravel. Both SM3-2 and SM3-4 were characterized by cover of larger gravel grades medium and course gravel, indicating these areas may be able to provide similar, if less optimal, rock fragment composition at the optimal habitat. IV_{ij} of 100 means soil surface component occurs in all plots. Significant relationships are indicated by asterisks (* = significant, ** = strongly significant, ***= very strongly significant).

ISA of Soil RF Surface Rock Fragment Cover

Transect	Cover Class	IVij	*P*	
BM1	Bedrock	28.1	0.010	**
Optimal-High	Fine Gravel	21.2	0.005	**
Optimal-High	Very Fine Gravel	49.4	0.005	**
SM2-20	Cobble	20.4	0.015	**
SM3-2	Medium Gravel	14.3	0.010	**
SM3-3	Stone	18.8	0.025	*
SM3-4	Course Gravel	14.7	0.005	**

In contrast, outplanting transects had mean fine gravel cover ranging from 1% at BM1, SM1-20 and SM1-21 to 9% at SM3-1. SM2-21 had the highest mean gravel cover of all the outplanting transect (16%), but maximum cover of all transects was lower than in the optimal habitat groups (average maximum = 12%) (Fig W-5). SM2-21 had the highest maximum cover value (38%) of the outplanting transects, followed by SM2-20 and SM3-1 with 20% maximum cover. Very fine gravel was recorded in optimal *E. codium* habitat groups but was not recorded in outplanting transects. Mean very fine gravel ranged from 3% in the optimal-medium group to 10% in the optimal-high group. Maximum fine gravel and standard deviation was much higher in the optimal-high and optimal-low groups (max = 62%, mean sd= 13.5) compared to the optimal-medium group (max = 10%, sd= 3). Classical ISA analysis indicated the optimal-high *E. codium* group was uniquely characterized by high cover of both fine and very fine gravels (Table 2.2.10). In contrast, SM3-2 was characterized by medium gravel, and SM3-4 was characterized by coarse

gravel. SM2-20 was charactered by cobble cover, SM3-3 was characterized by stone cover, and BM1 was characterized by the presence of bedrock. Multigroup ISA analysis further indicated characteristics of high fine and very fine gravel cover are shared by all optimal *E. codum* habitat groups, and the presence of fine gravel also characterized all outplanting transects except BM1, SM1-20 and SM1-21. Furthermore, all outplanting transects except SM3-5 were characterized by high cobble cover, which also distinguished all outplanting transects from optimal habitat groups (Fig Y-1). Outplanting transects BM1, SM2-21, SM3-1 and SM3-2 were distinguished from optimal habitat groups and other transects by their stone cover.

Vegetation Characteristics

Significant differences (p = <0.001) in vegetation species composition were determined between optimal *E. codium* habitat groups and all outplanting transects, including very significant (p= <0.001) pairwise differences between all groups (Table 2.2.5 and Fig V-3). This result was expected as the vegetation community at NS is dominated by *E. codium* which does not occur naturally at any of the assisted migration sites, though it was recorded- in very low abundance due to their small size- at transects where outplanted seedlings were alive during data

Table 2.2.5 PERMANOVA of Differences in Vegetation Community Characteristics Between Optimal *E. codium* Habitat Groups and Outplanting Transects at Badger and Snow Mountains 1-3
Significant differences (p = <0.001) in vegetation species composition were determined between optimal E. codium habitat groups and all outplanting transects, including very significant (p= <0.001) pairwise differences between all groups. This result was expected as the vegetation community at NS is dominated by *E. codium* which does not occur naturally at any of the assisted migration sites. A strong significant difference in species richness and a weakly significant difference in total cover was determined between optimal E. codium habitat groups (Table 2.2.5). However, post-hoc Tukey pairwise comparison was unable to detect differences in total cover between any optimal habitat groups or outplanting transects. Significant relationships are indicated by asterisks (* = significant, ** = strongly significant, ***= very strongly significant).

Transect Differences in Vegetation Characteristics

Vegetation Characteristics (n= 152)	**Df**	**R^2**	**F**	***Pr(>F)***	
Species Richness	12	0.8498	65.55	0.001	***
Total Cover	12	0.1424	1.92	0.040	*
Vegetation Composition	12	0.6162	18.59	0.001	***
Vegetation Functional Group	12	0.7479	34.36	0.001	***

collection in 2022. This compositional difference is illustrated by the overlap of all three optimal *E. codium* habitat groups and their the separation to the left side of the NMDS ordination space (Figure 2.2.12-A). However, some areas of compositional overlap are present between the optimal-medium and optimal-low groups, and BM1, SM1-20 and SM2-20. These relationships change in the NMDS ordination of vegetation functional group composition, where clear separation between optimal-high and optimal-medium and optimal-low groups are visible, although some overlap between optimal-medium and optimal-low groups remains (Figure 2.2.12-B). The separation of optimal *E. codium* habitat groups result in increased overlap between the optimal-medium group and all outplanting transects except SM3-2 and SM3-5, and increased proximity between the optimal-low group and transects BM1 and SM1-20. In both vegetation community and functional group composition, transects SM3-2, and SM3-5 remain the transects spatially separated furthest from the optimal *E. codium* habitat groups, while SM3-4 and SM3-5 are closer to the optimal *E. codium* groups and overlap with them in the ordination of vegetation functional group composition.

A strong significant difference in species richness and a weakly significant difference in total cover was determined between optimal *E. codium* habitat groups (Table 2.2.5). However, post-hoc Tukey pairwise comparison was unable to detect differences in total cover between any optimal habitat groups or outplanting transects (Figures 2.2.11-A). Mean total cover ranged from 29% (lowest) at SM2-20 to 52% (highest) at SM3-4 (Fig W-6). Total cover at optimal *E. codium* habitat groups ranged from 28% (lowest) in that optimal-high group to 39% (highest) in the optimal-low group. Outplanting transects at BM1, SM2-20 SM3-2, and SM3-5 all had mean total cover values within this range, while transects SM1-20, SM1-21, SM2-21, SM3-1, SM3-3, and

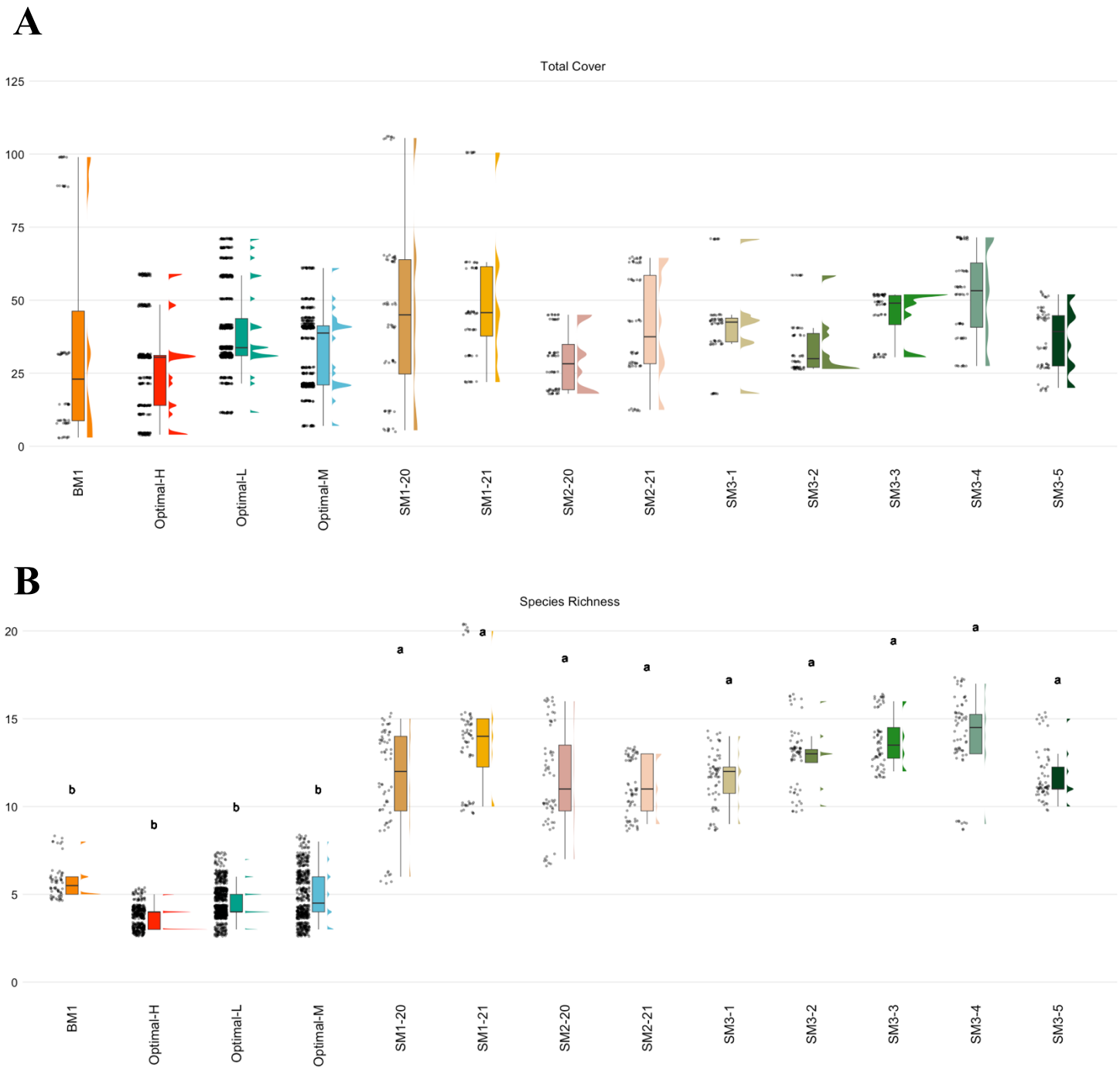


Figure 2.2.11 Raincloud Plots of Total Cover and Species Richness of Optimal *E. codium* Habitat Groups and Outplanting Transects at Badger and Snow Mountains Sites 1-3

Differences in total cover (A) and species richness (B) between Native Site optimal *E. codium* habitat (high, medium, low) groups and outplanting transects at Badger Mountain (BM), and Snow Mountain (SM) sites 1 and 2. A strong significant difference in species richness and a weakly significant difference in total cover was determined between optimal *E. codium* habitat groups. Post-hoc Tukey pairwise comparison was unable to detect differences in total cover between any optimal habitat groups or outplanting transects.

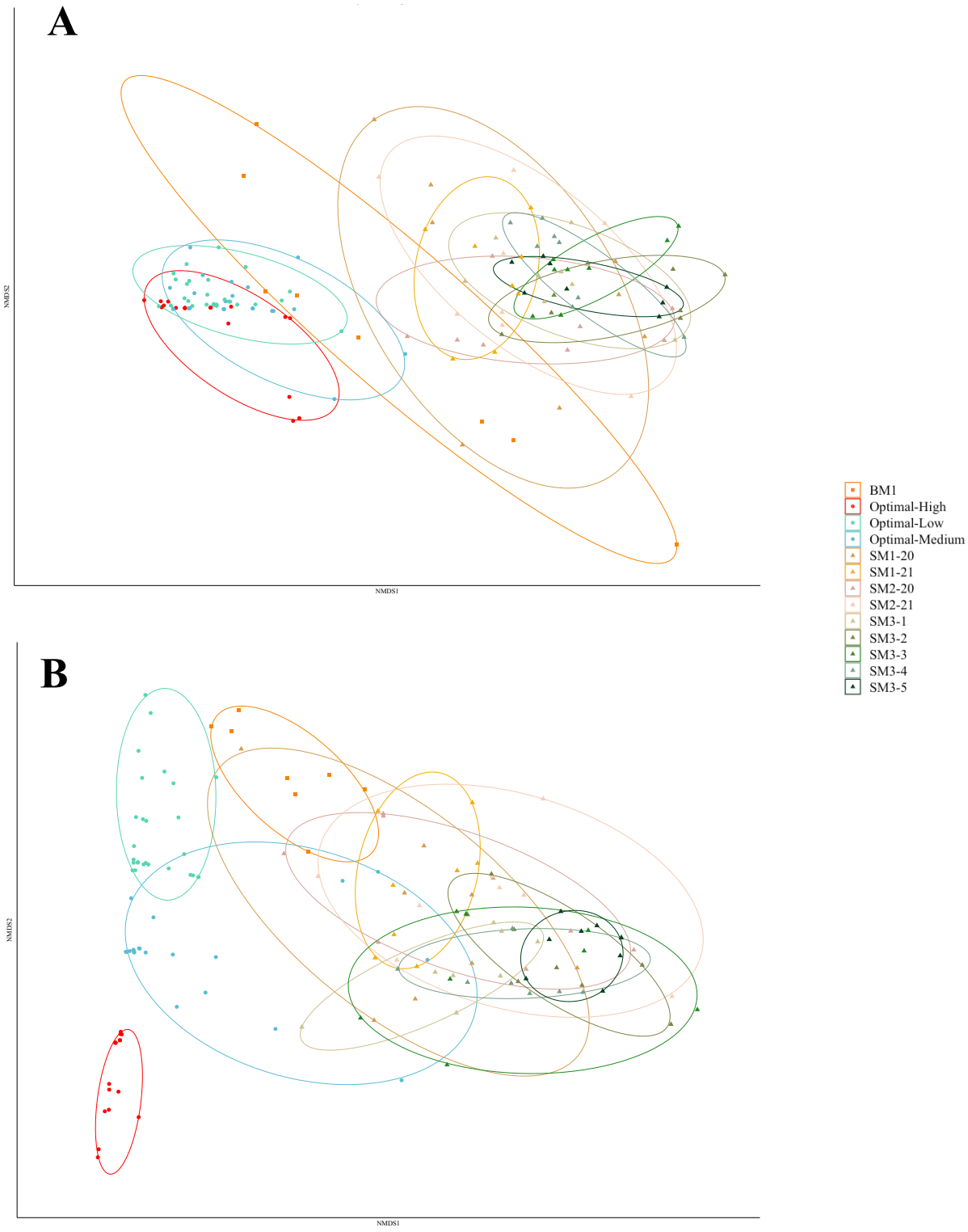


Figure 2.2.12 NMDS Ordination of Vegetation Community and Functional Group Compositions of Optimal *E. codium* Habitat Groups and Outplanting Transects at Badger and Snow Mountains 1-3
Non-metric multidimensional scaling (NMDS) ordination of vegetation community (k = 3 , stress = 0.111) and vegetation functional group (k = 3, stress = 0.046) composition. Points and ellipses s are coded by color to correspond to transect grouping. Point shapes correspond to site identity (Native Site = circle, Badger Mountains = square, Snow Mountain = triangle). Each point represents a $1m^2$ plot. Points closer together are more similar to than those farther apart.

SM3-4 all have slightly higher mean total cover values by 10-15% cover. BM1, SM1-20 and SM1-21 all have high maximum cover values around 100%, which is higher than the optimal habitat groups, which ranged from 59-71% maximum total cover. All outplanting transects had significantly higher species richness than all optimal *E. codium* habitat groups (Figures 2.2.12-B and Fig W-6). All outplanting transects had mean species richness values ranging from 6 species (lowest) at BM1 to 14 species (highest) at SM3-4, while mean species richness ranged from 4 species in the optimal-high group to 5 species in the optimal-medium and optimal-low groups.

Classical ISA of vegetation spices composition indicated the optimal-high *E. codium* habitat group is characterized by the presence of *E. codium* ($p = 0.005$), while the optimal-low group is characterized by both *E. codium* associated perennial graminoid species *P. secunda* and *P. spicata* ($p \leq 0.015$) (Table 2.2.6). BM1 is characterized solely by annual species ($p = 0.005$), including the invasive annual graminoid *B. tectorum* and invasive annual forb Common stork's-bill (*Erodium cicutarium*). SM2-21 SM3-2, and SM3-5 are only characterized by the presence of perennial forbs ($p \leq 0.01$). SM3-1 and SM3-4 are characterized by perennial forbs and woody *Eriogonum* species *E. thymoides* and *E. douglasii* respectively ($p \leq 0.025$). Similarly, SM1-21 is characterized by perennial forbs and the low growing woody shrub species *A. rigida* ($p = 0.05$). SM3-3 is characterized by two perennial forbs and an annual invasive graminoid Small fescue (*Vulpia microstachys*) ($p \leq 0.010$). SM1-20 and SM2-20 are both characterized by annual species, although SM2-20 is characterized mostly by native forbs ($p = 0.005$) and SM1-20 by both an invasive annual forb and invasive annual graminoid species ($p = 0.005$). Multigroup ISA determined *P. spicata* characterized both the optimal-low and optimal-medium *E. codium* habitat groups, distinguishing them from all outplanting transects (Fig Y-3).

Table 2.2.6 ISA of Vegetation Composition Characterizing Optimal *E. codium* Habitat Groups and Outplanting Transects at Badger and Snow Mountain 1-3

Vegetation species that most characterize Native Site optimal *E. codium* habitat (high, medium, low) groups and outplanting transects at Badger Mountain (BM) and Snow Mountain (SM) sites 1-3.

ISA of Vegetation Composition

Species	Habit	Origin	IVij	*P*	
BM1					
Bromus tectorum	Annual graminoid	Invasive	78.6	0.005	**
Descurainia pinnata	Annual forb	Native	28.1	0.005	**
Draba verna	Annual forb	Naturalized	44.6	0.005	**
Erodium cicutarium	Annual forb	Invasive	62.5	0.005	**
Optimal-High					
Eriogonum codium	Perennial subshrub	Native	49.1	0.005	**
Optimal-Low					
Poa secunda	Perennial graminoid	Native	18.9	0.005	**
Pseudoroegneria spicata	Perennial graminoid	Native	22.8	0.015	**
SM1-20					
Allium acuminatum	Perennial forb	Native	25.0	0.030	*
Alyssum alyssoides	Annual forb	Invasive	38.2	0.005	**
Bromus commutatus	Annual graminoid	Invasive	37.1	0.005	**
Poa bulbosa	Biennial graminoid	Invasive	37.3	0.005	**
Taeniatherum caput-medusae	Annual graminoid	Invasive	52.9	0.005	**
SM1-21					
Artemisia rigida	Perennial shrub	Native	37.8	0.005	**
Lomatium canbyi	Perennial forb	Native	32.1	0.005	**
Trifolium macrocephalum	Perennial forb	Native	28.7	0.005	**
Viola trinervata	Perennial forb	Native	65.4	0.005	**
SM2-20					
Collomia grandiflora	Annual forb	Native	37.5	0.005	**
Epilobium brachycarpum	Annual forb	Native	42.3	0.005	**
Lagophylla ramosissima	Perennial forb	Native	50.0	0.005	**
Lactuca serriola	Biennial forb	Invasive	20.8	0.015	**
SM2-21					
Sedum lanceolatum	Perennial forb	Native	24.7	0.010	**
SM3-1					
Eriogonum thymoides	Perennial subshrub	Native	23.3	0.015	**
Lewisia columbiana	Perennial forb	Native	27.1	0.005	**
SM3-2					
Lewisia rediviva	Perennial forb	Native	20.6	0.010	**
Nestotus stenophyllus	Perennial forb	Native	23.5	0.005	**
SM3-3					
Allium spp	Perennial forb	Native	27.8	0.005	**
Antennaria flagellaris	Perennial forb	Native	41.0	0.005	**
Vulpia microstachys	Annual graminoid	Invasive	21.0	0.010	**
SM3-4					
Balsamorhiza hookeri	Perennial forb	Native	37.8	0.005	**
Eriogonum douglasii	Perennial subshrub	Native	25.0	0.025	*
Eremogone franklinii	Perennial forb	Native	38.8	0.005	**
Phlox hoodii	Perennial forb	Native	25.2	0.015	**
SM3-5					
Lomatium macrocarpum	Perennial forb	Native	24.6	0.005	**
Olsynium douglasii	Perennial forb	Native	21.8	0.005	**

Vegetation Functional Group Composition

Significant differences in vegetation functional group composition were determined between all optimal *E. codium* habitat groups and outplanting transects at assisted migration sites BM and SM 1-3 (Table 2.2.5). Very strong significant pairwise differences in vegetation functional group composition were determined between all optimal habitat groups and outplanting transects (Fig V-4). Significant differences in vegetation functional group components were also determined between habitat groups and outplanting transects when group components were tested individually as univariate responses (Table 2.2.7). Classical ISA analysis of vegetation furcation group composition indicated the optimal-high *E. codium* habitat group is characterized by subshrub cover (p = 0.005), while the optimal-low habitat group is characterized by perennial graminoid cover (p = 0.005) (Table 2.2.8). In contrast, BM1 is characterized by annual graminoid cover (p = 0.005), while SM1-21 is less strongly characterized by shrub cover (p= 0.01) and SM3-5 by perennial forb cover (p = 0.04). Multigroup ISA further indicates all optimal *E. codium* habitat groups and SM1-20, SM1-21 and

Table 2.2.7 PERMANOVA of Differences in Vegetation Community Functional Groups Between Optimal *E. codium* Habitat Groups and Outplanting Transects at Badger and Snow Mountain 1-3
Shrub cover at transects SM1-20 and SM2-21 were significantly higher than cover in optimal E. codium habitat groups while outplanting transects BM1, SM1-20, SM1-21, and SM3 1-5 all showed similar low cover as the optimal habitat groups. Subshrub cover at transects BM1 and SM2-20 were significantly lower than the optimal *E. codium* habitat groups. Significant pairwise differences in annual forb cover indicated cover was lower in optimal *E. codium* habitat groups compared to all outplanting transects, while all transects except BM1 showed significantly higher perennial forb cover than all optimal habitat groups. Perennial graminoid cover at all outplanting transects was similar to the lower cover in both optimal-high and optimal-medium groups. Similarities in low annual graminoid cover was determined between optimal *E. codium* habitat groups and SM2-20, SM2-21, and SM3 transects 1-5. Significant relationships are indicated by asterisks (* = significant, ** = strongly significant, ***= very strongly significant).

Transect Differences of Vegetation Functional Groups

Vegetation Fuctional Group (n= 152)	**Df**	**R^2**	**F**	***Pr(>F)***	
Shrub	12	0.3241	5.55	0.001	***
Sub-Shrub	12	0.4989	11.53	0.001	***
Annual Forb	12	0.2548	3.96	0.001	***
Perennial Forb	12	0.7193	29.69	0.001	***
Annual Graminoid	12	0.3235	5.54	0.001	***
Perennial Graminoid	12	0.5665	15.14	0.001	***

SM2-21 are similarly characterized by subshrub cover ($p = 0.005$) (Fig Y-2). Shrub cover at transects SM1-20 and SM2-21 were significantly higher than cover in optimal *E. codium* habitat groups while outplanting transects BM1, SM1-20, SM1-21, and SM3 1-5 all showed similar low cover as the optimal habitat groups (Figure 2.2.13-A). Subshrub cover at transects BM1 and SM2-20 were significantly lower than the optimal *E. codium* habitat groups (Figure 2.2.13-B and Fig W-7). Transects SM1-20, SM1-21, SM2-21, SM3-2 and SM3-5 had similarity low subshrub cover as the optimal-low group, while transects SM3-1, SM3-3 and SM3-4 all shared more similarities in mean and variation of cover to the optimal-low group and to a lesser extent, the optimal-medium group.

Pairwise comparison of *E. codium* habitat groups and outplanting transects indicated similarities in low perennial forb cover between BM1 and optimal *E. codium* habitat groups (Figure 2.2.14-A). BM1 perennial forb cover was similar to the comparatively higher perennial forb cover that distinguishes the optimal-medium group from the other optimal habitat groups. All other transects showed significantly higher perennial forb cover than all optimal habitat groups (Fig 2.2.14-A and Fig W-7). Significant pairwise differences in annual forb cover indicated cover was lower in optimal *E. codium* habitat groups compared to all outplanting transects, although similarities are present with the comparatively lower annual forb cover at SM-3 and SM-4 compared to transects where annual forb cover is the highest, such as at SM1-20 (Figures 2.2.14-B). SM1-20 and SM2-20 showed the most variation in annual forb cover, and the highest maximum values, making them the least similar to the low annual forb cover in optimal habitat groups.

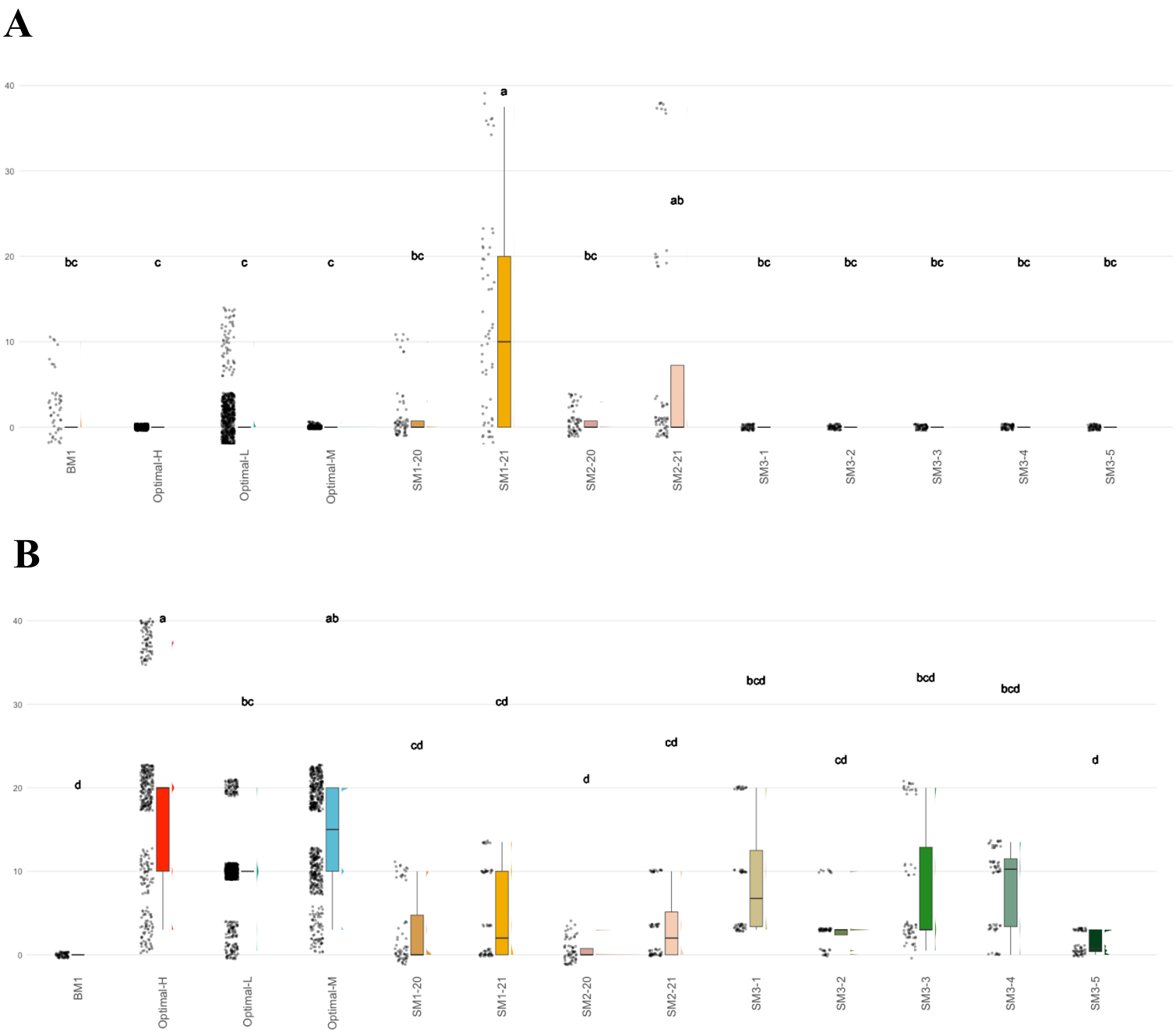


Figure 2.2.13 Differences in Shrub and Subshrub Cover Between Optimal *E. codium* Habitat Groups and Outplanting Transects at Badger and Snow Mountain 1-3

Differences in shrub (A) and subshrub (B) cover in the *E. codium* habitat groups and ten outplanting transects at two locations (Badger and Snow Mountains) and four assisted migration sites. Shrub cover at transects SM1-20 and SM2-21 were significantly higher than cover in optimal *E. codium* habitat groups while outplanting transects BM1, SM1-20, SM1-21, and SM3 1-5 all showed similar low cover as the optimal habitat groups. Subshrub cover at transects BM1 and SM2-20 were significantly lower than the optimal *E. codium* habitat groups. Transects SM1-20, SM1-21, SM2-21, SM3-2 and SM3-5 had similarity low subshrub cover as the optimal-low group, while transects SM3-1, SM3-3 and SM3-4 all shared more similarities in mean and variation of cover to the optimal-low group and to a lesser extent, the optimal-medium group.

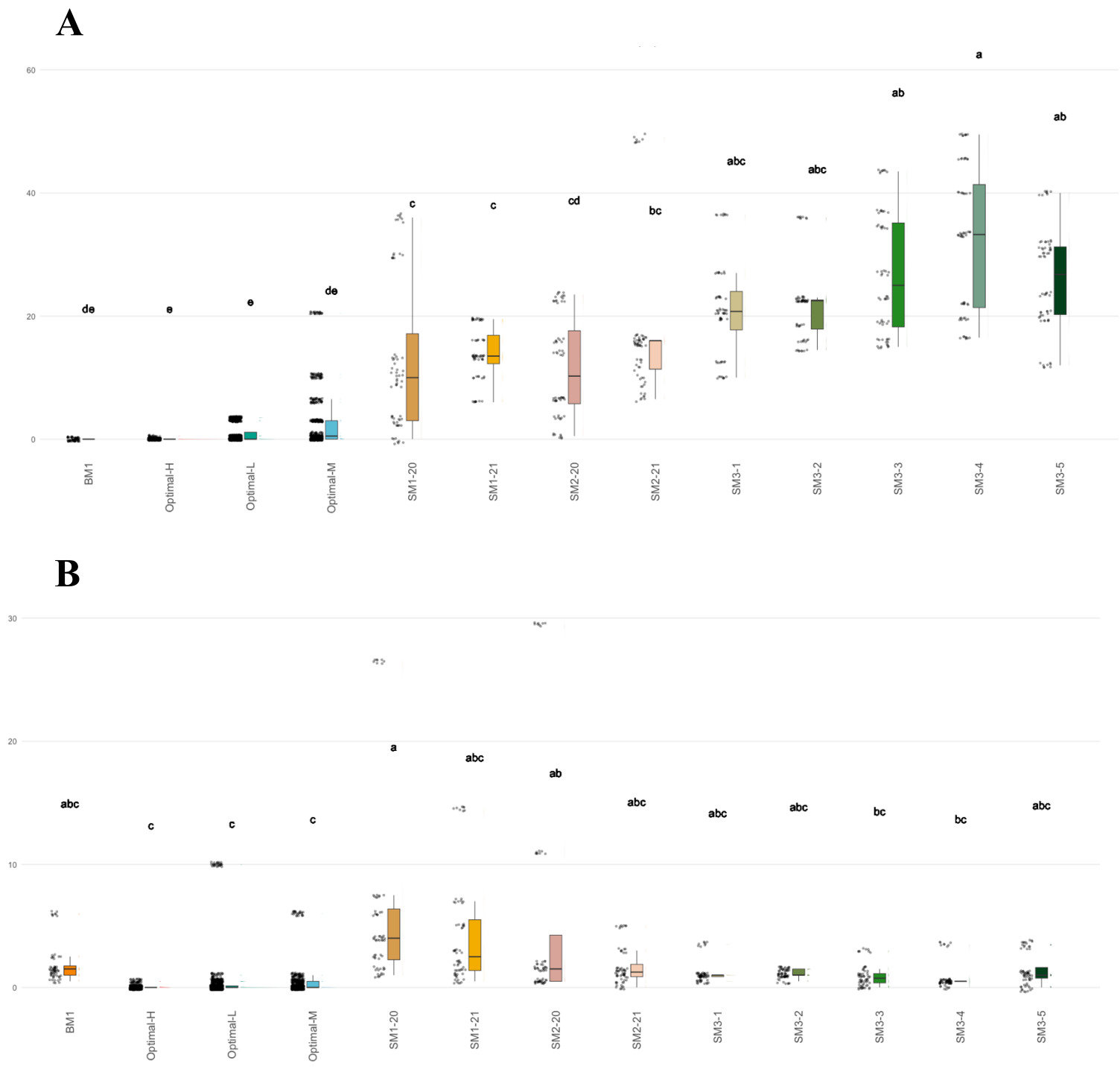


Figure 2.2.14 Differences in Perennial and Annual Forb Cover Between Optimal *E. codium* Habitat Group and Outplanting Transects at Badger and Snow Mountain 1-3

Differences in perennial (A) and annual (B) forb cover in the *E. codium* habitat groups and ten outplanting transects at two locations (Badger and Snow Mountains) and four assisted migration sites. All transects showed significantly higher perennial forb cover than all optimal habitat groups except BM1, which was similarities to the comparatively higher cover in the optimal-medium *E. codium* habitat group. Significant pairwise differences in annual forb cover indicated cover was lower in optimal E. codium habitat groups compared to all outplanting transects, although similarities are present with the comparatively lower annual forb cover at SM-3 and SM-4 compared to transects where annual forb cover is the highest, such as at SM1-20.

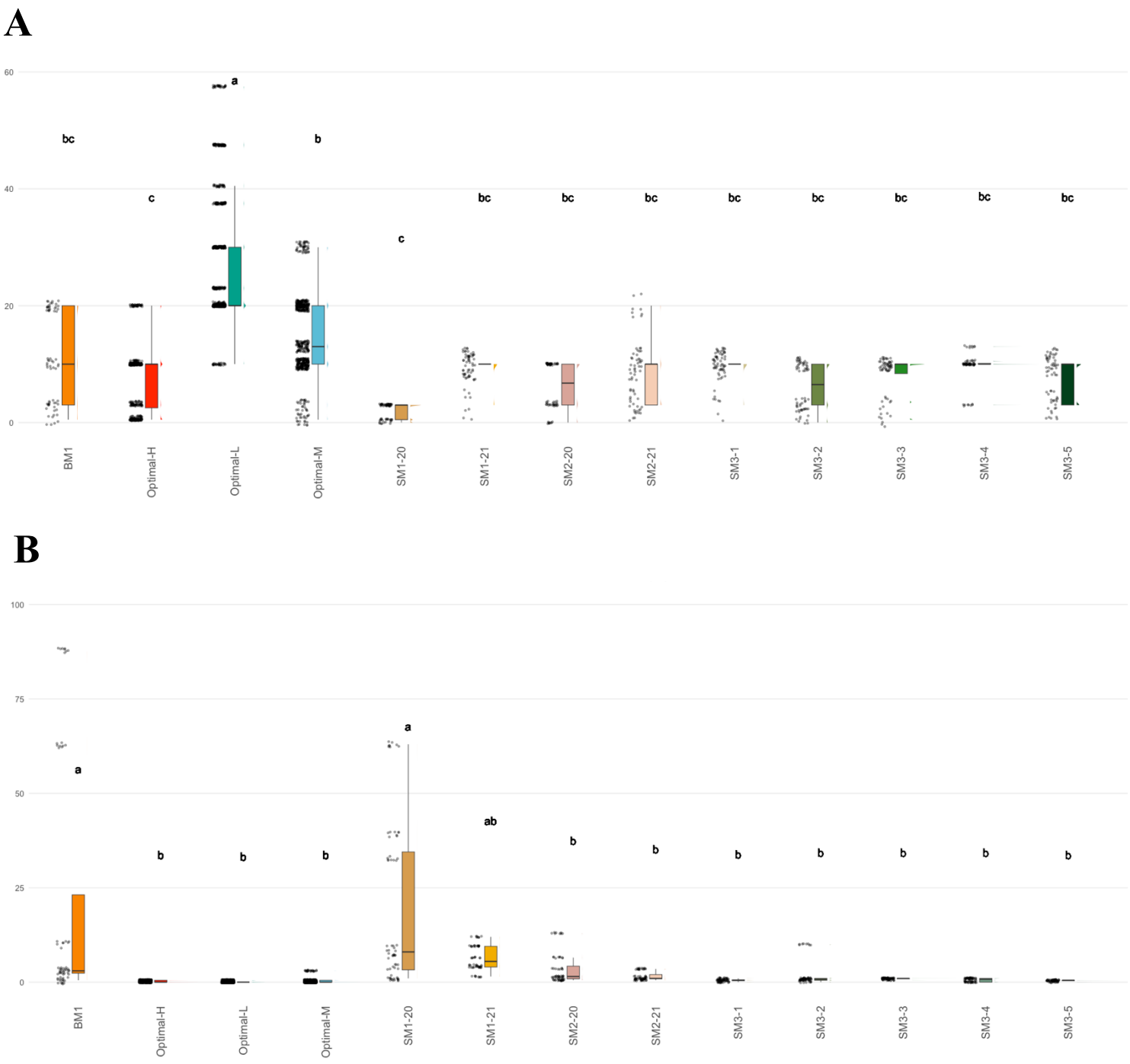


Figure 2.2.15 Differences in Perennial and Annual Graminoid Cover Between Optimal *E. codium* Habitat Groups and Outplanting Transects at Badger and Snow Mountain 1-3
Differences in perennial (A) and annual (B) forb cover in the *E. codium* habitat groups and ten outplanting transects at two locations (Badger and Snow Mountains) and four assisted migration sites. Perennial graminoid cover at all outplanting transects was similar to the lower cover in both optimal-high and optimal-medium groups, such as the low perennial graminoid cover at SM1-20 which reflects the optimal-high group. In contrast, the higher cover in the optimal-low group significantly contrasted the lower cover at outplanting transacts. Annual graminoid cover is similarly low to optimal *E. codium* habitat groups at SM2-20, SM2-21, and SM3 transects, while BM1 and SM1-20 had higher cover that distinguished them from the other sites and habitat groups.

Perennial graminoid cover was highest in the optimal-low group, and higher in the optimal-medium group than in the optimal-high group (Figure 2.2.15-A and Fig W-7). Pairwise comparison of optimal *E. codium* habitat groups and outplanting transects indicated similarities in the comparatively low perennial graminoid cover at SM1-20 and the optimal-high group, in contrast to the optimal-low and optimal-medium groups. Perennial graminoid cover at all outplanting transects was similar to the lower cover in both optimal-high and optimal-medium groups. In contrast, the higher cover in the optimal-low group that significantly distinguishes it from the other habitat groups, also contrasted with the low cover at outplanting transacts (Figure 2.2.15-A and Fig W-7). Similarities in low annual graminoid cover was determined between optimal *E. codium* habitat groups and SM2-20, SM2-21, and SM3 transects 1-5 (Figure 2.2.15-B). Although annual graminoid cover is higher at BM1, SM1-20 and SM1-21 than in the optimal habitat groups, SM1-21 has lower cover than at BM1 and SM1-20, and is more similar to the range of cover values in optimal *E. codium* habitat groups than BM1 and SM1-20. ISA indicated BM1 in particular is characterized by annual graminoid cover (i.e. *B. tectorum*), indicating this is likely a degraded vegetation habitat.

Table 2.2.8 Classical ISA of Vegetation Functional Groups Characterizing Optimal *E. codium* Habitat Groups and Outplanting Transects at Badger and Snow Mountain 1-3
Vegetation functional groups that most characterize groups of optimal *E. codium* habitat (high and low) and outplanting transects.

Transect	Veg Functional Group	IVij	*P*	
BM1	Annual Graminoid	34.8	0.005	**
Optimal-High	Subshrub	31.1	0.005	**
Optimal-Low	Perennial Graminoid	18.9	0.005	**
SM1-21	Shrub	26.3	0.010	**
SM3-5	Perennial Forb	15.3	0.040	*

Table 2.1.9 ISA of Vegetation Composition at the Native Site and Assisted Migration Sites
Vegetation species that most characterize the native and assisted migration (GSP, SM 1-3) sites.

ISA of Vegetation Composition

index	Species	Habit	Origin	IVij	*P*
Gingko State Park					
GSP	*Aster spp*	Perennial forb	Native	7.7	0.025 *
GSP	*Balsamorhiza hookeri*	Perennial forb	Native	79.8	0.005 **
GSP	*Descurainia sophia*	Annual forb	Invasive	7.7	0.020 *
GSP	*Eriogonum douglasii*	Perennial subshrub	Native	10.1	0.010 **
GSP	*Lomatium macrocarpum*	Perennial forb	Native	20.4	0.005 **
Native Site					
NS	*Astragalus caricinus*	Perennial forb	Native	9.7	0.020 *
NS	*Astragalus purshii*	Perennial forb	Native	11.1	0.035 *
NS	*Eriogonum codium*	Perennial subshrub	Native	100.0	0.005 **
NS	*Poa secunda*	Perennial graminoid	Native	42.5	0.005 **
NS	*Salsola tragus*	Annual forb	Invasive	11.1	0.010 **
Snow Mt Site1					
SM1	*Allium acuminatum*	Perennial forb	Native	10.3	0.005 **
SM1	*Alyssum alyssoides*	Annual forb	Invasive	17.6	0.005 **
SM1	*Artemisia rigida*	Perennial shrub	Native	18.5	0.005 **
SM1	*Bromus commutatus*	Annual graminoid	Invasive	34.6	0.005 **
SM1	*Bromus sitchensis*	Perennial graminoid	Native	6.9	0.050 *
SM1	*Crepis intermedia*	Perennial forb	Native	10.3	0.015 **
SM1	*Epilobium brachycarpum*	Annual forb	Native	13.2	0.030 *
SM1	*Idahoa scapigera*	Annual forb	Native	21.8	0.005 **
SM1	*Lomatium canbyi*	Perennial forb	Native	47.3	0.005 **
SM1	*Lomatium nudicaule*	Perennial forb	Native	20.7	0.005 **
SM1	*Lupinus sulphureus*	Perennial forb	Native	10.3	0.010 **
SM1	*Trifolium macrocephalum*	Perennial forb	Native	13.8	0.005 **
SM1	*Viola trinervata*	Perennial forb	Native	19.0	0.005 **
Snow Mt Site2					
SM2	*Allium spp*	Perennial forb	Native	10.3	0.010 **
SM2	*Bromus tectorum*	Annual graminoid	Invasive	15.2	0.050 *
SM2	*Chrysothamnus viscidiflorus*	Perennial shrub	Native	6.2	0.030 *
SM2	*Eriogonum ovalifolium*	Perennial subshrub	Native	6.9	0.045 *
SM2	*Fritillaria pudica*	Perennial forb	Native	9.1	0.025 *
SM2	*Lomatium dissectum*	Perennial forb	Native	10.6	0.020 *
SM2	*Lupinus sericeus*	Perennial forb	Native	6.9	0.035 *
SM2	*Poa bulbosa*	Biennial graminoid	Invasive	19.1	0.005 **
SM2	*Polemonium micranthum*	Annual forb	Native	14.1	0.025 *
Snow Mt Site3					
SM3	*Antennaria flagellaris*	Perennial forb	Native	15.1	0.005 **
SM3	*Eriogonum thymoides*	Perennial subshrub	Native	12.6	0.015 **
SM3	*Lewisia columbiana*	Perennial forb	Native	15.1	0.005 **
SM3	*Lewisia rediviva*	Perennial forb	Native	15.3	0.005 **
SM3	*Olsynium douglasii*	Perennial forb	Native	16.7	0.005 **
SM3	*Sedum lanceolatum*	Perennial forb	Native	39.2	0.005 **
SM3	*Vulpia microstachys*	Annual graminoid	Invasive	28.7	0.005 **

Discussion

This study has attempted to identify differences and similarities between the single population of *E. codium* and assisted migration sites at different scales. First, Gingko State Park and three sites at Snow Mountain (sites 1-3) were compared to conditions at the *E. codium* Native Site (NS) to determine "site-level" suitability of assisted migration locations and explore the accuracy of the habitat model developed by the Washington Natural Heritage Program (WNHP) to aid in the selection of suitable habitat. Second, ten areas (i.e. outplanting transects) at Badger and Snow Mountains where year old seedlings were planted from 2020-2021 were compared with three optimal *E. codium* habitat groups identified in Chapter 1 which represent differences in vegetation functional group composition and *E. codium* abundance at the Native Site. Differences and similarities between outplanting transects and optimal habitat groups were compared with information on outplanted seedlings survival from 2022 and 2023 to determine outplanting "transect-level" suitability of assisted migration locations. Outplanted seedling survival and the role of microhabitats, and site and transect level habitat heterogeneity on survival outcomes are considered as a means of exploring evolutionary theories postulated in Chapter 1 on what constitutes "optimal" *E. codium* habitat and which habitat variables most impact seedling establishment, growth and survival.

In this assessment woody, low growing cespitose sub-shrub species are distinguished from taller and more erect woody shrub species. This allows for other woody subshrub species in the genus *Eriogonum* to be classified and considered distinct from larger woody shrubs. In the shrub steppe ecoregion, it is common to characterize habitat types primarily by the combination of tall woody shrubs such as *Artemisia* species and their associated perennial graminoid specie(s). Subshrubs from the *Eriogonum* genus have also been utilized, usually in combination

with associated perennial graminoid species, to distinguish unique habitat types, especially in areas with shallow soils and limited species diversity (Franklin and Dryness 1973). Their presence often denotes unique variations of more commonly and widely established woody shrub- perennial graminoid habitat types. As *E. codium* likely fills a distinct ecological and spatial niche based on its slow and low growing woody habitat, and appears to dominate and characterize the habitat it thrives in, it is important to be able to distinguished analogues woody perennial subshrubs in the same genus that directly compete for that same niche, from the impacts of taller and larger shrubs that have likely overlapping but unique spatial and ecological niches. By keeping woody shrubs and subshrubs as sperate functional groups, impacts from direct completion with analogs *Eriogonum* species can be distinguished from the potentially synergetic impacts of competition with both subshrubs and shrubs.

Part I: Comparison of the *E. codium* Native Site, Three Past, and One Potential Future Assisted Migration Sites

As demonstrated in Chapter 1, the area currently occupied by the single native population of *E. codium* is not a homogenous habitat but a patchwork of varying microhabitats with important habitat characteristics differing between individual subpopulations and to some extent within subpopulations. The WNHP habitat model is a tool that was designed to help managers select locations and sites for assisted migration attempts at a landscape level. The habitat model thus considers variation of key environmental variables at this "landscape-level" of scale. Understanding the variation within and between the different microhabitats occupied by *E. codium* at the native site can help to better elucidate what conditions impact *E. codium* site occupancy and subsequent abundance. However, looking at the Native Site (NS) as a whole and considering the mean and range of habitat variables averaged across all subpopulations can better

help to characterize suitable assisted migration targets when managers are considering different sites at the landscape level. Considering the Native Site at a “site-level” characterizes the conglomeration of all the habitat patches across the five subpopulations. Similarly, by considering current and potential assisted migration locations at a “site-level”, the numerous smaller microhabitats that are heterogeneously distributed across complex landscapes, such as the Columbia Plateau, become homogenized. By comparing landscape-level designations of “high”, “moderate” and “low” habitat suitability generated by the WNHP habitat model to similarities between homogenized “site-level” variation of key habitat variables at both the Native Site and assisted migration locations, to what extent the landscape-level variation of the habitat model accurately reflects variation occurring “on the ground” can be explored. Although “ground truthing” of more locations than were assessed in this study are necessary to truly determine the accuracy of the habitat model, by comparing “site-level” differences at two assisted migration locations with the variation of the Native Site homogenized across all subpopulations, a rudimentary understanding of the accuracy of the model may be ascertained. By comparing variation across two adjacent but topographically distinct sites at Gingko State Park (GSP) and the variation of three topographically segregated sites at the top, middle and bottom of the mountain side at Snow Mountain, relationships can be determined between the extremely coarse “landscape-level” scale of the habitat model, and the smaller but still relatively coarse “site-level” scale in which individual sites at suitable locations are selected for assisted migration.

Table 2.2 Habitat Similarities Between the Native and Assisted Migration Sites at Gingko State Park and Snow Mountain 1-3
Summary table shows significantly similar site, soil and vegetation characteristics between the Native and Assisted migration sites. Significant similarities are indicated by an X and the total number of similar variables are tallied for each site and type of habitat characteristic (site, soil, vegetation) as well as the total number of similar variables across all measured habitat characteristics. Similarities are based on post hoc Tukey and pairwise ADONIS statical tests that determined significant differences between groups. Asterisks (*) are used to indicate when Tukey tests indicated enough similarity between groups to share at least one group designation (i.e. letter), but not enough similarity to be considered the same group to the extent that the entire group designation (i.e. all letters) was shared. While these similarities are important to note as they are often due to continuous site variables fitting within a wider range measured at the Native Site, these similarities are not tallied to determine the total number of site, soil and vegetation habitat similarities between the Native and assisted migration sites.

Similarities Between the Native and Assisted Migration Sites				
	GSP	**SM1**	**SM2**	**SM3**
Site Characteristics	**5**	**4**	**6**	**3**
Landscape position				
Hillslope Position	X			
Slope (rise/run)	*	X	X	
Slope (°)	X	X	X	
Slope Shape	X	X	X	X
Slope Complexity	X	X	X	X
Aspect	*		X	
Heat Load	X		X	X
Rock Fragment Class	*		*	*
Soil Characteristics	**2**	**0**	**0**	**0**
Hydraulic Conductivity (K)				*
Soil Texture	X		*	*
Soil Surface Composition	X			
Soil Surface Rock Fragment Composition				
Vegetation Characteristics	**2**	**1**	**1**	**3**
LAI	*			*
Vegetation Composition				
Total Cover	*	X	X	
Species Richness	*			*
Shrub			*	X
Subshrub				
Perennial Forb	*			
Annual Forb	X			X
Perennial Graminoid				
Annual Graminoid	X			X
Total	**9**	**5**	**7**	**6**

Similarities and Differences Between the Native Site and a "High Suitability" Location at Gingko State Park

Similarities in nine measured variables were determined between NS and GSP, including five site characteristics, two soil characteristics, and two vegetation characteristics. (Table 2.2) Significant site characteristics included hillslope position, slope angle, slope shape, slope complexity, and heat load index. GSP had a similar range of both convex, linear and concave plots as NS and although both NS and GSP had predominantly simply sloped plots, a substantial portion of plots at both sites also contained complex slopes. NS had a higher mean and range of slope (rise/run) values than GSP, however, slope values at GSP fell within the lower range of values at NS and overall, similarities in other slope characteristics indicate that GSP generally had similar microtopographic features as NS. Despite significant differences in landscape positions between the sites, GSP was comprised exclusively of plots on the shoulder of the hillslope, which is where the majority of plots at NS were also located. Furthermore, similarities in slope angle further indicate the existence of similar topographic conditions at these two sites, as the general steepness of the slope at GSP matches NS.

The site at GSP was selected because it is on a northern facing slope, which is known to have less direct solar irritation than eastern, southern, or northern slopes and is associated with cooler temperatures and higher moisture retention. As summer drought stress is thought to negatively impact the survival of *E. codium* seedlings outplanted during assisted migration attempts, focus has been put onto selecting sites on northern facing slopes to mitigate summer temperature and moisture stress. However, the dominance of north, northeast and northwestern slopes at GSP is what makes the aspect at GSP different from NS. While *E. codium* does grow in plots with northern aspects at NS, this species also occupied substantial proportions of east and western facing slopes. While GSP lacks eastern and western facing plots, HLI was still

determined to be similar between GSP and NS, indicating these sites receive analogous levels of solar irradiation. Furthermore, HLI values at GSP were on the higher end of the range of values at NS, suggesting site conditions at GSP may host some of the extreme site conditions associated with low productivity vegetation communities that *E. codium* appears to be able to dominate at NS.

GSP is the only site in this study to have significant similarities in soil characteristics to NS. Similarities in soil texture and soil surface composition indicate soil conditions at least partially reflect NS and *E. codium* may be able to tolerate the soil environment at this site. Similarities in the rock and litter components of soil surface composition suggest GPS may be rocky enough with low enough vegetation productivity for *E. codium* to become established. However, although rock composition at GSP is reflective of NS, mean and maximum cover of the bareground component is substantially smaller. As high rock: bareground ratios are likely important soil surface characteristics associated with *E. codium* occupancy, the relatively low bareground cover at GSP may not be conductive to successful *E. codium* establishment. This is especially important because, although similar cover of the rock component of soil surface composition was determined between these sites, the soil surface rock fragment composition was not similar. GSP had a smaller mean and maximum cover of fine gravel, which was significantly higher at NS, and lacked the presence of very fine gravel, which distinguished NS from the assisted migration sites. GSP also had higher mean cover of coarse and medium gravel and a high maximum medium gravel cover. However, GSP had similarly low cobble cover to NS that was significantly lower than all other assisted migration sites in this study. Although the cover of and medium gravel types are lower at NS, mean values only differed from GSP by ~10%. The overall predominance of gravel rock fragments at GSP suggest *E. codium* may be able to tolerate

these conditions, although further study of *E. codium* seedling responses to different sizes and proportions of gravel is warranted.

Although total cover at GSP and NS were significantly different, total cover at GSP was lower than at NS, indicating this is a less productive vegetation community. Although the invasive annual species *B. tectorum* is present at GSP, it is at abundance levels similar to NS. This may indicate introduced *E. codium* seedlings could tolerate this level of competition with this species or it could negatively affect the ability of *E. codium* to establish at this site. The presence of *B. tectorum* at abundance levels similar to NS further suggest GSP is experiencing a post fire invasion by annual invasive species and would likely need similar management strategies to address this as NS. In addition to the similarly low annual forb and graminoid cover at GSP and NS, GSP also had lower perennial graminoid cover. GSP was dominated by *P. secunda*, which also co-dominates *E. codium* habitat at NS. Lower perennial graminoid cover at GSP could either support *E. codium* establishment by reducing competition or inhibit *E. codium's* establishment if it requires associated perennial graminoid species to grow. Further research assessing *E. codium* seedling response to perennial graminoid cover, and especially its relationship with *P. secunda,* can help elucidate potential responses of seedlings to outplanting sites where it occurs.

GSP had the most overall similarities to NS across all three types of habitat characteristics. The similarities in site and soil characteristics suggest GSP may be a site *E. codium* could tolerate, potentially making it a possible site for successful assisted migration. GSP was deemed "highly suitable" by the WNHP habitat model, and as the model is based on climate, precipitation, geological and topographic variables, it was successful in predicting the site and soil habitat similarities between GSP and NS, which was also reflected to some extent in

similarities between vegetation communities. However, despite promising similarities is forb and graminoid cover at this site, other significant differences in both vegetation composition and vegetation functional group composition indicate *E. codium* would likely be unable to successfully compete with other vegetation species without some form of management intervention. As similarities between GSP and NS in site and soil characteristics suggest, GSP is likely an extreme environment analogous to NS. However, significantly higher perennial forb cover, LAI, and species richness indicate this site is already dominated by a productive native perennial forb community, more diverse than the community at NS, and likely better adapted to these conditions. ISA analysis further determined that GSP was characterized by the presence of a different species in the *Eriogonum* genus, *E. douglasii*, further suggesting the niche as a woody subshrub that *E. codium* would likely need to dominate in order to establish, is already being filled by more common and widespread species.

Similarities and Differences Between the Native Site and "Medium Suitability" Locations at Snow Mountain

Of the three assisted migration sites at Snow Mountain, SM2 had the most habitat similarities with NS. Similarities in seven measured variables were determined between NS and SM2, including six site characteristics and one vegetation characteristic (Table 2.2). SM1 had five overall habitat similarities to NS, while SM3 had six. This included four site characteristics and one vegetation characteristic at SM1 and three site characteristics and three vegetation characteristics at SM3. Overall, SM1 and SM2 had more site-level topographic similarities to NS, while SM3 better reflected interactions between heat load and vegetation dynamics, indicating SM2 and SM3 are better habitat analogues to NS than SM1. However, the lack of

similarities in soil characteristics between assisted migration sites at SM and NS may be related to their designation as “moderately” suitable habitat by the WNHP model.

All assisted migration sites had significantly similar slope complexity and slope shape, indicating microtopographic similarities with NS potentially impacting moisture retention from precipitation and snow melt. Mode slope shape at SM sites was linear-linear with simple slope complexity, indicating sites were fairly flat and even. A substantial proportion of plots at all sites and at NS also contained convex slope shapes, especially convex-linear and convex-concave while a few concave shaped plots occurred at SM 2 and SM3. The intermixing of convexly sloped micro topographies and flat areas at SM assisted migration sites suggest similar dynamics to the areas at NS where moisture is shed evenly down the slope instead of collecting in convex microhabitats.

Despite some similarities in soil texture between NS and SM2, including the presence of loamy sand soils which did not occur at any other assisted migration sites, hydraulic conductivity was within the low range of values observed at the native site. SM3 was the only site to have a majority of K values > 0, indicating moisture actively, though slowly, infiltrated through the soil, mirroring the large proportion of K values >0 measured at the NS. If more rapid percolation of soil moisture is important for *E. codium* root establishment, than similarities in hydraulic conductivity between SM3 and NS, in contrast to other sites, may be significant and should be the focus of future study.

Slope and slope angle were both significantly similar at both sites SM1 and SM2, indicating both sites reflect the microtopographic variability and the larger overall steepness of NS. Although the majority of plots at SM1 and SM2 were within the range of slope and slope angles values at NS, slope and slope angle mean and maximum values were slightly larger,

indicating slope was a little steeper, especially at SM2. In contrast, slope and slope angle at SM3 was significantly smaller than NS, indicating this area is less steep and generally flatter. SM2 was the only site at SM with similar aspect or HLI to NS. SM2 had a wide range of HLI values that best reflected the range of values at NS. Ranges of HLI values observed at SM1 and SM3 fell within the range of values observed at NS, with SM1 HLI values falling within the high end of this range while values at SM3 fell within the lower end. Similarly, although the majority of the aspects at SM sites occurred at NS, only SM2 has a range of aspects that reflected the full range observed at NS. SM3 was almost exclusively northern facing (north, northeast, northwest) while SM1 was predominantly southern facing and even included southeast facing plots which do not occur at NS. This indicates that SM1 receives the most direct solar irradiation and likely better reflects the stepper and more extreme HLI niches present at NS, while SM3 appears to be a flatter and less extreme habitat niche with less head load than many of the areas at NS.

SM-1 and SM-3 likely represent sites with habitat characteristics on opposite ends of *E. codium*'s range of tolerance. SM-1 appears to be a hotter, drier and steeper site than NS, while SM-3 is likely cooler, flatter, and moister. The similar range of HLI, aspects and microtopographic features at SM2 compared to NS indicates that *E. codium* is likely best adapted to the site characteristics at SM-2 of any assisted migration site at Snow Mountain. However, similarities is site characteristics are likely not enough to constitute an ideal assisted migration location. The lack of similarities in soil characteristics between NS and all Snow Mountain sites, besides some overlap in some of the soil textures present and the lower end of hydraulic conductivity values observed at NS, indicate these sites are probably not optimal.

Despite the differences at SM3 to site and soil characteristics at NS, it had the most similarities to NS vegetation characteristics of the sites at Snow Mountain, highlighted by the

similarly low shrub, annual forb and annual graminoid cover present at SM3 and NS. Both SM-1 and SM-2 had significantly higher mean and maximum total cover vales than NS, although both sites mean values fell within the range of values at NS. High mean and maximum species richness values combined with the wide range of total cover values and higher standard deviations at SM-1 and SM-2 indicate that while there are areas within these sites with low total cover and spices richness analogues to NS, there are also other areas that host significantly more productive and diverse vegetation communities than found at NS. In contrast, SM3 had a significantly smaller mean total cover and similar mean species richness as NS, including a maximum total cover value <10% greater than the maximum value at NS. This indicates SM3 had similarly sparse and simple vegetation composition as NS, although the significantly higher maximum species richness and relatively high standard deviations in total cover and species richness indicate that these conditions are somewhat heterogenous, with areas of slightly more productive and diverse communities also occurring there.

However, all sites at SM had key vegetation compositional differences that likely have important implications for the suitability of these sites for assisted migration of *E. codium.* All sites had significantly lower cover of subshrubs and perennial graminoid cover than at NS, while perennial forb cover was significantly higher. This indicates assisted migration sites at SM are perennial forb dominated communities in contrast to NS , which is a subshrub-perennial forb association characterized by *E. codium*. While SM3 contained a low and patchy cover of *Eriogonum* subshrubs similar to NS, both SM1 and SM2 contained significantly higher shrub and subshrub cover, with ISA analysis indicating SM2 was charactered by the presence of the native shrub Yellow Rabbitbrush (*Chrysothamnus viscidiflorus*). SM2 and SM3 were both characterized by different species of woody subshrubs in the *Eriogonum* genus, including

Cushion buckwheat (*E. ovalifolium*) at SM2 and Thyme leaf buckwheat (*E. thymoides*) at SM3. The presence of woody shrubs and/or subshrubs at all sites at SM, combined with the dominance of perennial forbs at all of these sites, indicates the niche as a woody subshrub that *E. codium* would likely need to dominate in order to establish is already being filled by more common and widespread species The competitive pressure from both woody shrubs and subshrubs combined with the dominance of perennial forbs and presence of invasive graminoids at SM1 likely place too much competitive pressure on young *E. codium* individuals for their success at these sites.

While sites at SM were selected due to this locations' higher elevation and increased moisture, WNHP habitat model correctly identified that these sites are substantially different from NS and thus only "moderately" optimal habitat for *E. codium* assisted migration. Although vegetation data was not included in the model, climate, participation and elevational information correctly reflected the increased moisture availability and resulting higher productivity of vegetation communities in general and native perennial forbs specifically, that makes this location less suitable. The model also seems to have been able to determine the lack of similar soil characteristics between NS and SM sites, even though the model is based on very coarse, 1000m spaced base geology data. However, this modeling of soil geology does not seem to extent to soil hydrology dynamics despite the known relationships between geology, soil texture and hydraulic conductivity (Wang et al 2023). This is likely due to soil texture, geology and other soil properties directly impacting infiltration occurring at finer spatial scales than either the landscape-level scale of model or the site-level scale of this study.

Assessing The Accuracy of the WNHP Habitat Model

Overall, the WNHP habitat model accurately discerned differences in habitat suitability between assisted migration locations at a landscape level. The habitat model designation of GSP

with a higher habitat suitability designation than SM was reflected in the site level differences and similarities observed between the assisted migration sites and NS. This indicates that the habitat model may be a useful tool for differentiating target locations at the landscape level.

Although the habitat model accurately predicting that GSP had more similarities in habitat characteristics than any one site at SM, and designated GSP as an area with the highest tier of habitat suitability, GSP shared less site, soil and vegetation similarities to NS than several of the outplanting transects, including outplanting transects at assisted migration sites at SM. This illustrates how important spatial scale is in influencing the predictive power of the habitat model. As demonstrated by the lack of suitability in key habitat variables at GSP compared to NS, there is a range of actual habitat suitability within both the "high" and "medium" designations. At both GSP and SM, assisted migration locations were selected using the habitat model, but then on the ground qualitative assessments had to be made by walking around potential locations and selecting outplanting sites based on visual assessments. The inability of the habitat model to capture fine scale differences in habitat suitability, and bridge landscape-level location selection with site-level selection of appropriate assisted migration areas, is an important gap currently limiting mangers in their selection of suitable habitat that can support successful seedling establishment.

The higher number of similarities observed at SM between outplanting areas and optimal *E. codium* habitat groups when measured at the "outplanting-transect" spatial scale, compared to the lower number of habitat similarities determined when habitat characteristics were compared to NS at the "site-level" spatial scale, highlights important microhabitat variability that is currently being lost when assisted migration locations for seedlings are considered using data collected at coarse spatial scales. This is especially illustrated by hydraulic conductivity, which

when averaged across an entire assisted migration site at the "site-level" scale, was deemed significantly different to NS at SM sites 1 and 2, and similar but not the same at SM3. However, when hydraulic conductivity at only the outplanting transects was compared to hydraulic conductivity values from optimal *E. codium* habitat groups, only a weakly significant difference was initially identified by PERMANOVA analysis, and these differences were not strong enough to be detected by a post hoc Tukey test. Ultimately, no significant differences between individual outplanting transects and optimal habitat groups were detected, highlighting how much patterns in habitat suitability can differ when observed at different spatial scales.

These results further highlight the current inability of the habitat model to accurately model suitable small-scale microhabitats that may be extremely important for assisted migration, forcing managers to make qualitative and subjective decisions about where to outplant seedlings without the guidance of quantitative habitat suitability guidelines designed for the very fine spatial scales impacting seedling survival. While the coarse scales of macro-environmental variables such as climate, elevation, and base geology can clearly make crude differentiations between suitable habitat locations, fine-scale variation within these locations that are not currently being captured by the model are likely important for determining site suitability for young *E. codium* seedlings.

Ultimately, the area of a landscape experienced by a seedling, include the topography, soil environment and competing vegetation community, is very small. Variation at extremely small scales can have life or death impacts for young plants, especially slow growing woody species such as *E. codium.* At the same time, the larger landscapes dynamics that shape the localized conditions experienced by each seedling can be connected across large areas. Assisted migration requires considering both the large, landscape level environmental changes that shape

the landscape level distribution of an entire species, with the small scale, microhabitat conditions that shape populations and even subpopulations of a species habitat. Considerations at numerous scales ultimately culminating in the suitability of where individual seedlings are planted. Until more research is done to answer key questions about *E. codium*'s life history, range of tolerance to environmental conditions, and genetic mechanisms for adapting to changing environmental conditions, the crude scale of the current WNHP habitat model likely has limited functionality in accurately differentiating locations for assisted migration. Furthermore, as shown by site-level differences between SM sites 1-3, while considering similarities and differences at the site-level is useful for defining general areas within a location to target for assisted migration, this level of scale is likely not sensitive enough to actuarily predict the microhabitat differences that impact seedlings survival.

Future habitat suitability models can incorporate fine-scale habitat information with information on *E. codium*'s range of tolerance to environmental variables, to better model micro-habitat niches *E. codium* is able to exploit. The lack of fine scale maps of habitat variables across the majority of the Columbia Plateau will likely pose a challenge to improving habitat models for *E. codium,* however, as demonstrated by this study, basic habitat suitability data on surface-level habitat variables can be collected even with a relatively low number of replicates. This baseline information can provide managers with a better idea of the range and variability of key habitat characteristics at and within potential assisted migration sites. Through even minimal data collection assessing site and transect locations before assisted migration attempts occur, managers can better discern which micro-habitat areas will be the most optimal for *E. codium* survival, allowing them to target these areas and potentially improving assisted migration outcomes.

Part II: Comparison of Three "Optimal" *E. codium* Habit Groups and 2020-2021 Seedling Outplanting Transects at Assisted Migration Sites

Patterns in Outplanted Seedling Survival Inform Transect-Level Suitability of Assisted Migration Outplanting Sites

Monitoring of seedlings outplanted at Badger and Snow Mountains between 2020-2021 did not continue after May 2023 and as of summer 2024 all seedlings are presumed dead. All outplanting attempts included in this study were ultimately not successful at accomplishing recovery action 1.2.4 to "determine the most effective methodology to establish viable individuals in the field". The overall low success rates observed in 2023 and the subsequent presumed failure of any outplanting transects to support *E. codium* seedlings over the long term, indicate these locations are likely unsuitable for this species.

Despite the complete loss of the 2020-2021 seedling cohorts, survival data collected during 2022 and 2023 monitoring is utilized to gauge an idea of location suitability based on how long a proportion of seedlings survived in each location. Differences in 2022 survival at Snow Mountain sites, including differences in seedling success at outplanting transects SM1-21, SM2-21, and SM3 1-5, are considered in terms of the differences and similarities between measured habitat variables and optimal *E. codium* habitat groups. Relationships between survival outcomes and habitat characteristics are considered for transects SM1-21, SM3-3 and SM3-5, which had the lowest survival rates between 20-41% nine months after establishment. Similarly for outplanting transects SM2-21, SM3-1 and SM3-4, where higher rates of survival between 57-59% were observed nine months after establishment, the impacts of the habitat variables that distinguish these outplanting transects on seedling survival is considered. Finally, the implications of patterns in survival observed during 2023 monitoring is considered, including the habitat characteristics that distinguish outplanting transects BM1, SM3-1, SM3-4 and SM3-5,

where seedlings survived 18 months after establishment. Finally, this study explores the potential relationships between the habitat characteristic that make these outplanting transects unique, and their impacts on patterns in *E. codium* seedling survival at each transect.

In an attempt to increase survival by aiding in the successful establishment of young seedings during the hot, dry summers when soil moisture levels drop below the range of tolerance of most species, seedlings at Snow Mountain received supplemental watering during summer 2022. However, challenges with employee availability and access to sites due to difficulties with the distance and terrain of outplanting transects, resulted in inconsistencies with watering frequency, volume, application method and duration between outplanting transects SM1-21, SM2-21, SM3-1, and SM3 3-5. Outplanting transects at SM3 only received water three times in the early summer while transects SM1-21 and SM2-21 were watered six times from June-September (Emily Orling, USFWS personnel, pers. comm.). Similarly, although it is known that seedlings at BM1 also received supplemental watering treatments, no information is available about the frequency, volume, application method, duration or for how many years and during which months watering treatments occurred.

The overall effects of watering treatments on seedling survival are unclear, and to what extent it has impacted patterns of seedling survival observed in 2023 is unknown. Transect SM3-1 and SM3 3-5, which received fewer watering treatments than SM1-21 and SM2-21, had higher overall survival rates, possibly indicating supplemental watering negatively impacted *E. codium* survival. However, as a higher number of seedlings were outplanted at SM3 in 2021 in comparison with SM1-21 and SM1-21, these differences in seedling survival could simply be more statistically probable and due to random chance. To what extent patterns in seedling survival is related to measured habitat characteristics, supplemental watering treatments,

interactions between them, or unmeasured habitat variables is ultimately unknown and not addressed in this study. Information on *E. codium's* life history using either field or greenhouse studies is necessary to test and better understand this species range of tolerance to moisture and heat gradients. Ultimately, future studies with a clear experimental design and consistently implemented protocols are necessary to better understand the impacts of habitat characteristics and supplemental watering treatments on seedlings performance.

The Role of Three "Optimal" E. codium Habitat Groups (high, medium, low) In Assessing Habitat Suitability of Outplanting Transects

In Chapter 1, hierarchical cluster analysis of vegetation functional group composition (shrub, subshrub, annual/perennial forb, annual/perennial graminoid cover) was used to identify three optimal *E. codium* habitat groups based on mean and maximum subshrub (i.e. *E. codium*) cover (high, medium and low). As discussed in Chapter 1, each group contained plots from multiple subpopulations, thus characterizing commonalities in vegetation community structure between heterogenous patches of habitat across multiple subpopulations. *E. codium* has likely evolved to exploit these heterogenous habitat patches to varying degrees of success where it occurs along the edge of Umtanum Ridge. The geological history of the Columbia Plateau region has resulted in high habitat heterogeneity at extremely variable spatial scales across the bioregion, and *E. codium's* evolutionary strategy of exploiting marginal and extreme habitats to avoid competition with less stress tolerant species has likely been driven to some extent by this spatial heterogeneity. Thus, selecting locations for seedling outplanting during assisted migration attempts require managers to make extremely fine scale decisions about where to put seedlings. Because the survival of young seedlings is so significantly impacted by the micro-habitat environment immediately surrounding them, choices about seedling placement in extremely

variable and the heterogeneity of even small areas can have enormous impacts on seedling survival rates.

Examining patterns in habitat characteristics at both the landscape-level scale of the habitat model or the site-level scale used to ground truth the accuracy of the habitat model, homogenize important patterns in habitat heterogeneity. This habitat heterogeneity has historically been qualitatively assessed by managers either shortly before or during installation of seedlings at new assisted migration sites. However, like the qualitive approaches used by mangers in selecting assisted migration sites, this approach lacks a quantitative assessment of habitat suitability at the fine spatial scales most impacting seedling survival. Assessing habitat characteristics around the 7x14m area where seedlings were planted provides a finer scale understanding of the habitat dynamics experiences by seedlings during their first year in the field. Comparing habitat characteristics at individual outplanting transects to optimal *E. codium* habitat groups provides insight into the extent these optimal habitat types were successfully targeted for assisted migration. By comparing the microhabitat characteristics directly surrounding seedlings within assisted migration sites to the distinct high, medium, and low "optimal" vegetation habitat types identified at the Native Site, the extent to which assisted migration locations successfully matched *E. codium's* required habitat can be better assessed.

Similarities and Differences Between "Optimal" E. codium Habitat Groups and the Outplanting Transact at Badger Mountain Explain Patterns in 2023 Seedling Survival Rates

Similarities in nine measured variables were determined between the optimal *E. codium* habitat groups and the outplanting transect at Badger Mountain, including four site characteristics, one soil characteristics and four vegetation characteristics (Table 2.3). Significant

Table 2.3 Habitat Similarities Between Optimal *E. codium* Habitat Groups and Outplanting Transects at Badger and Snow Mountains 1-3
Summary table of significantly similar site, soil and vegetation characteristics between the three optimal *E. codium* habitat groups (high, medium, low) and outplanting transects at assisted migration sites. Significant similarities are indicated by either "all" to indicate similarities to all optimal habitat groups, or the group name (high, medium, low) or combinations of group names are listed in bold. The total number of similar variables are tallied for each outplanting transect for each type of habitat characteristic (site, soil, vegetation) as well as the total number of similar variables across all measured habitat characteristics. Similarities are based on post hoc Tukey and pairwise ADONIS statical tests that determined significant differences between groups. Asterisks (*) are used to indicate when Tukey tests indicated enough similarity between groups to share at least one group designation (i.e. letter), but not enough similarity to be considered the same group to the extent that the entire group designation (i.e. all letters) were shared. While these similarities are important to note as they are often due to continuous site variables fitting within a wider range of measured at the Native Site, these similarities are not tallied to determine the total number of site, soil and vegetation habitat similarities between the optimal *E. codium* habitat groups and outplanting transects.

Similarities Between Optimal *E.codium* Habitat Groups and Outplanting Transects

	BM1	SM1-20	SM1-21	SM2-20	SM2-21	SM3-1	SM3-2	SM3-3	SM3-4	SM3-5
Site Characteristics	**4**	**4**	**3**	**3**	**5**	**4**	**4**	**2**	**3**	**3**
Landscape position										
Hillslope Position				*low	**all**	*high	*high	*high	*high	*high/medium
Slope (rise/run)			*high/medium		*all	**high/medium**	*all	*all	*all	*all
Slope (°)	**all**	**all**	*all	**all**	*all	*all				
Slope Shape	**high/low**	**high/low**	**high/low**	**medium**	**high/low**	*high/low	**high/low**	**high/low**	**high/low**	**high/low**
Slope Complexity	**all**	**all**	**all**	**all**	**all**	**all**	**all**	*all	**all**	*all
Aspect	*high/medium	*all	*high/medium		**high/medium**	*low	**low**	*all	*all	**high/medium**
Heat Load			*high/medium		*all	**high/medium**	*all	*all	*all	*all
Rock Fragment Class	**all**	**all**	**all**	**all**	**all**	**all**	**all**	**all**	**all**	**all**
Soil Characteristics	**1**	**1**	**1**	**1**	**1**	**3**	**1**	**1**	**2**	**2**
Hydraulic Conductivity (K)	**all**	**all**	**all**	**all**	**all**	**all**	**all**	**all**	**all**	**all**
Soil Texture		*high	*high	*all	*all	**high**	*all	*all	*all	
Soil Surface Composition									**medium**	**all**
Soil Surface Rock Fragment Composition						**medium**				
Vegetation Characteristics	**4**	**2**	**2**	**3**	**3**	**3**	**3**	**3**	**3**	**3**
Vegetation Composition										
Total Cover	**all**	**all**	**all**	**all**	**all**	**all**	**all**	**all**	**all**	**all**
Species Richness	**all**									
Shrub	*all	*all		*all		*all	*all	*all	*all	*all
Subshrub		*low	*low		*low	*low	*low	*low	*low	
Perennial Forb	**medium**			*medium						
Annual Forb	*all		*all		*all	*all	*all	*all	*all	*all
Perennial Graminoid	**high/medium**	**high**	**high/medium**	**high/medium**	**high/medium**	**high/medium**	**high/medium**	**high/medium**	**high/medium**	**high/medium**
Annual Graminoid			*all	**all**	**all**	**all**	**all**	**all**	**all**	**all**
Total	**9**	**7**	**6**	**7**	**9**	**10**	**8**	**6**	**8**	**8**

site characteristics included slope characteristics slope shape, slope complexity, slope angle (but not slope (rise/run)) and rock fragment classification. Vegetation characteristics included species richness, total cover, and perennial forb and perennial graminoid cover. The outplanting transect at BM1 reflected some of the similarities in site characteristics present between all optimal habitat groups such as simple slope complexity, a mean slope angle of ~12°, a high maximum rock fragment classification of 75% cover, and similar hydraulic conductivity, including low K values either around or below 0. This outplanting transect also had similar species richness and total cover values to all optimal habitat groups, indicating that despite the compositional and functional group differences in vegetation community structure, the community may be sparse enough to allow for *E. codium* growth with minimal competition. BM1 shared similar perennial forb and graminoid cover to the medium optimal habitat group, suggesting BM1 may reflect this slightly less extreme, forb dominated habitat type instead of the more extreme niche where *E. codium* can either reach its highest abundance (optimal-high group) or lowest abundance (optimal-low group).

Despite basic similarities in slope angle and overall rockiness, and the presence of a sparse and minimally diverse vegetation community, significant differences in important variables such as heat load, important soil variables including soil texture, soil surface and soil surface rock fragment compositions, and differences in key vegetation functional groups such as annual graminoid cover, may have impacted *E. codium's* success at this transect. ISA analysis indicated rock fragment composition was characterized by bedrock, which did not occur in any of the optimal habitat groups. Biocrust cover was significantly higher at BM1 than in the optimal habitat groups, and BM1 also had higher cover of annual invasive annual forb and graminoid species. This included cover of both the annual invasive graminoid Cheatgrass (*B. tectorum*) and

the invasive annual forb Russian thistle (*S. tragus*) whose abundance may have made the area unsuitable for seedling establishment. Mean and range of HLI at BM1 is on the high end of the range of values observed in the optimal habitat groups, and may be related to the abundance of annual species at this transect.

The high survival rate of seedings in outplanting group 1 three years after outplanting, in contrast to all other seedlings outplanted with that cohort and at that site, suggests outplanting failure at this transect may not be solely related to differences with the optimal habitat groups in key habitat characteristics such as soil, but instead may reflect observed variation in which optimal habitat groups are mirrored by which habitat variables, and the habitat differences that distinguish the optimal-high and optimal-low groups and their contrast to the optimal-medium group. Outplanted seedlings appear to be able to grow on silt loam soils not present at the Native Site, suggesting soil texture likely does not solely determine suitable habitat and *E. codium* may be able to successfully grow and become established in other soil textures not present where it currently grows in the wild. Ultimately, it is unclear to what extent soil texture impacts habitat suitability for *E. codium* and further research is necessary to better understand dynamics between seedling establishment and soil texture.

The similarities in perennial forb cover between BM1 and the optimal-medium in contrast to the optimal-high and optimal-low groups group indicates BM1 likely has site characteristics that encourage low cover of native forb and perennial graminoid growth, and could potentially host an abundance of *E. codium* under the right conditions. While BM1 may have suitable perennial forb and graminoid characteristics to support *E. codium*, under the current conditions of high annual invasive species cover, this transect is likely not optimal for *E. codium* growth and survival without rigorous and consistent management. This may be related

to differences in soil characteristics such as the dominance of silt loam and high biocrust cover, but is more likely related to the current conditions of the vegetation community, including competition with annual invasive species. *E. codium* may have been able to successfully exploit a small area within this transect where the variation of vegetation conditions and habitat characteristics create a niche suitable for its survival and growth, possibly accounting for why 80% of the seedlings in group 1 survived while all other seedlings in all other surrounding groups died. Especially as rock cover in BM1 ranged widely from 3-10%, it is possible *E. codium* was able to exploit an extreme microhabitat within the 98 m^2 outplanting area where higher rock cover and minimal annual forb and graminoid competition allowed it to survive.

Similarities and Differences Between "Optimal" E. codium Habitat Groups and Outplanting Transects at Snow Mt 1 Reflect Seedling Mortality Rates 2022-2023

Similarities in seven measured variables were determined between the optimal *E. codium* habitat groups and the 2020 outplanting transect at Snow Mountain Site 1 (SM1-20), including four site characteristics, one soil characteristic, and two vegetation characteristics (Table 2.3). Similarities in six measured variables were determined between the optimal habitat groups and the 2021 outplanting transect at Snow Mountain Site 1 (SM1-21), including three site characteristics, one soil characteristic, and two vegetation characteristics. This indicates that while both transects are similarly different from optimal *E. codium* habitat, especially in terms of vegetation community structure, the microhabitat at SM1-20 had more similarity to optimal *E. codium* habitat than SM1-21. While both transects have some similarities in site characteristics to optimal *E. codium* habitat, the lack of similarity in soil and vegetation characteristics, as well key site characteristics such as heat load, are likely related to low (34%) survival rate observed in 2022 at SM1-21 and no surviving seedlings in either the 2020 or 2021 cohorts by 2023.

Both transects had similar slope complexity, hydraulic conductivity, and soil surface rock fragment classifications as all optimal habitat groups, including simple slope complexity, a high maximum rock fragment classification of 75%, and low K values mostly <0. Higher mean and minimum rock fragment classification values and higher mean of the rock component of soil surface composition at SM1-20 indicates it was a rockier area than SM1-21. Mean and range of slope values were slightly lower in SM1-21 indicating SM1-20 had a slightly steeper slope (~5cm/cm difference), and slope angle at SM1-20 was also significantly greater and better reflected the range of values in all of the optimal habitat groups. Although patterns in variation of HLI were not the same as the optimal habitat groups, the mean and range of HLI values were on the higher end of the range of values in the optimal habitat groups, indicating outplanting transects at this site occupied a high and possibly extreme heat load niche. Overall, outplanting transects at SM1 reflected the slightly more extreme site characteristics such as high HLI and convex/ linear slope shapes that distinguish both the optimal-high groups.

The majority of the similarities in vegetation composition to the optimal habitat groups were shared by both transects, including total cover and perennial graminoid cover. Total cover at both transects reflected all optimal habitat groups while perennial graminoid cover reflected only the optimal-high group at SM1-20 and both the optimal-high and optimal-medium groups at SM1-21. While the similarity of total cover to the optimal habitat groups suggests these transects have low enough productivity to allow *E. codium* to establish, the significantly higher species richness values indicate the presence of more complex vegetation communities than in the optimal habitat groups, which likely negatively impacted *E. codium*'s ability successfully establish in these outplanting areas.

Although perennial graminoid cover may be low enough to reflect optimal habitat types, the significantly higher cover of annual graminoid species in SM1-20 and perennial and annual forb species in both transects, likely placed a competitive pressure that inhibiting long term survival and establishment of young *E. codium* seedlings. ISA analysis indicated SM1-21 is characterized by disproportionately high shrub cover as well as cover of native perennial forb species, while SM1-20 is similarly characterized by disproportionately high cover of annual forbs and graminoids. These results indicate the vegetation communities in these outplanting areas were likely too complex and species rich to provide the extreme and barren niche *E. codium* is able to exploit. This is especially true for SM1-21, where the niche *E. codium* would otherwise occupy as a woody perennial is likely already being occupied by Stiff sagebrush (*A. rigida*) and *E. thymoides*. Overall, some of the similarities between both SM1 transects and optimal *E. codium* habitat groups makes aspects of these outplanting habitats at these transects comparable, with SM1-20 likely more reflective of habitat characteristics in the optimal-high habitat group than SM1-21. However, SM1-20 also had a more productive vegetation community with forb and annual graminoid cover too high to provide the extreme and barren niche *E. codium* likely requires.

Finally, neither of these transects had key habitat characteristics similar to the optimal habitat groups such as aspect, heat load and soil characteristics beyond hydraulic conductivity. Key differences in soil characteristics included differences in soil surface composition, as outplanting transects included higher cover of bareground, litter and biocrust than optimal habitat groups. Both transects had soil surface rock fragment composition dominated by cobbles and coarse gravel, and although the soil textures at both transects also occurred in the optimal habitat groups, the proportion of loam soils was much higher at these outplanting transects compared to

the optimal habitat groups. Due to the extreme heat wave in 2021, it is not possible to compare rates of seedling decline and death between the two outplanting transects at SM1. However, seedling survival rates recorded at SM2-21 in 2022, nine months after outplanting, illustrate the impacts important habitat differences with optimal habitat groups may have had on seedlings survival. Within nine months of establishment, SM1-21 had a 66% decline in seedling survival- the lowest recorded at any of the six 2021 outplanting transects- and in 2023 no seedlings remained alive. This rapid rate of seedling decline and mortality highlights the importance of habitat and vegetation characteristics on the unsuitability of this outplanting location, even in comparison to other sites and outplanting transects at Snow Mountain.

Similarities and Differences Between "Optimal" E. codium Habitat Groups and Outplanting Transects at Snow Mt 2 Explain Seedling Survival Rates in 2022 and Mortality Rates in 2023

Outplanting transects at SM2 had more variation in their similarities to the optimal *E. codium* habitat groups than the transects at SM1. Similarities in seven measured variables were determined between the optimal *E. codium* habitat groups and the 2020 outplanting transect at Snow Mountain Site 2 (SM2-20), including three site characteristics, one soil characteristic, and three vegetation characteristics (Table 2.3). Nine measured variables were determined between the optimal habitat groups and the 2021outplating transect at Snow Mountain Site 2 (SM2-21), including five site characteristics, one soil characteristic, and three vegetation characteristics. Both transects had similar slope complexity and soil surface rock fragment classification as all optimal habitat groups, including simple slope complexity, a high maximum rock fragment classification of 75%, and similar hydraulic conductivity, including the widest range of K values after the optimal *E. codium* habitat groups.

Both SM1-20 and SM1-21 had similar slope to the optimal habitat groups, and SM2-21 was one of only two outplanting transect to also have similar slope angle to the optimal-high and medium habitat groups. SM2-21 had a lower mean and range of slope angle values and a shallower slope than SM2-20, although the range of values fell within the range of values observed in the optimal-medium group. Mean HLI at both transects was significantly higher than in the optimal habitat groups, although all values were within the range of values observed in the optimal-high habitat group. SM2-20 was particularly high, and had the only 0.9 maximum value besides the optimal-high habitat group. This indicates SM2-20 experiences a high amount of solar radiation and is likely a hotter and potentially more uniformly extreme microclimate in comparison to SM2-21 and the optimal habitat groups. Although the range of HLI values at SM2-21 was higher than in the optimal habitat groups, mean HLI was only slightly above the mean value of the optimal-high habitat group, illustrating their similarities.

In addition to significant similarities in slope complexity and soil surface rock fragment classification, SM2-21 had a similar hillslope position, slope shape, and aspect to *E. codium* optimal habitat groups. Slope shape reflected the optimal-high and optimal-low habitat groups in contrast to the optimal-medium group, while aspect reflected similarities in the optimal-high and optimal-medium groups, and hillslope position reflected all optimal habitat groups. Site characteristics at SM2-21 are likely the most similar to the optimal-high habitat group of any outplanting transect in this study. The numerous similarities between SM2-21 and the optimal-high group in measured site characteristics such as microtopography and hydraulic conductivity may indicate further similarities in important processes such as soil water retention and heat exposure. These results indicate SM2-21 likely has site characteristics that can contribute to successful establishment of *E. codium* under the right vegetation community conditions. This

general suitability at the site level is highlighted by the seedlings survival rate recorded nine months after establishment in 2022. SM2-21 had a 57% survival rate, which was the second highest survival rate at Snow Mountain at that time.

SM2-20 and SM2-21 are the only outplanting transects where loamy sand soils occurred, although the proportion of loamy sand to sandy loam was substantially lower than in the optimal *E. codium* habitat groups. SM2-21 was the only outplanting transects to have all three soil types present in the optimal-high habitat group while SM2-20 had the same two soil types as the optimal-medium and optimal-low groups. However, soil surface composition was significantly different than in the optimal habitat groups including significantly lower mean and range of the rock component and higher cover of the bareground, litter and biocrust components. Similarly, soil surface rock fragment composition differed from optimal habitat groups at both transects, although SM2-21 had more compositional similarities to the optimal habitat groups.

SM2-20 was comprised mostly of cobble and coarse gravel, and was characterized in ISA analysis by its comparatively higher cobble cover. This area contained <10% of each of the medium, fine and very fine gravel rock fragment components. While a large portion of the rock composition at SM2-21 was also comprised of cobble, coarse gravel, and to a lesser extent bedrock, ~15% was also comprised of fine gravel, which is only slightly lower than the mean fine gravel value of the optimal-low habitat group. This is significant because fine gravel was the largest compositional component of rock cover in all optimal habitat groups and SM2-21 had the highest mean and maximum cover of fine gravel of any outplanting transect, further highlighting the unique potential abiotic suitability of this outplanting area.

Total cover and annual graminoid cover at both transects reflected all habitat groups while perennial graminoid cover reflected only the optimal-high and optimal-medium groups,

indicating the high heat load combined with comparatively higher bareground cover may have resulted in a similarly low productivity graminoid community reflective of the most optimal *E. codium* habitat. However, the significantly higher species richness indicates both outplanting transects have more complex vegetation communities than all the optimal-habitat groups, likely contributed to the limited long-term seedling establishment observed in these locations. Both SM2-20 and SM2-21 had significantly higher shrub cover than optimal habitat groups, and SM2-21 in particular had significant cover of the woody shrub *A. rigida* and two woody subshrubs Rock buckwheat *(E. sphaerocephalum*) and *E. thymoides*. The abundance of these woody perennial species and the presence of two other *Eriogonum* species known to specialize on lithosol soils in the same bioregion, while likely further indicating site-level similarities to optimal *E. codium* habitats, are also placing competitive pressures on young seedlings to compete to compete with established adults for resources. It is probable that *E. codium* was unable to successfully compete with these better established and more adaptable woody perennials species because they are already established in the spatial and ecological niche *E. codium* would need to dominate in order to thrive there. Similarly, cover of the majority of native perennial and annual forbs was significantly higher in both SM2-20 and SM2-21 than in the optimal habitat groups, adding to the competitive pressures young seedlings likely experienced at these sites.

Competition with woody shrubs, other *Eriogonum* subshrubs and both annual and perennial forbs likely combined with some of the extreme site characteristics such as high heat load, placing too many environmental and biological pressures on the young *E. codium* seedlings simultaneously. The dynamics between site, soil and vegetation habitat characteristics underlaying the similarities between the high and low optimal habitat groups in contrast the

optimal medium group likely influenced observed patterns of seedling survival at SM2-21. While low vegetation productivity, high bare ground cover, and site characteristics that reflected the optimal-high *E. codium* habitat may have contributed to the existence of the low productivity vegetation community favored by *E. codium*, these same extreme site characteristics and resulting habitat conditions, when combined with high niche competition with established and more widely adapted vegetation communities, likely pushed seedlings beyond their range of stress tolerance. The lack of any surviving seedlings 18 months after establishment and the seeming crash of seedling populations at SM2-21 after the first year despite relatively high survival rates nine months after outplanting, is likely due to these combined pressures and their accumulative impacts over time as stressed seedlings were continuously pushed beyond their survivable range of tolerance by multiple factors over an extended period of time.

Similarities and Differences Between "Optimal" E. codium Habitat Groups and Outplanting Transects at Snow Mountain 3 Reflect the Spatial Heterogeneity of Key Site and Soil Habitat Characteristics

At Snow Mountain 3, similarities in ten measured habitat variables were determined between optimal *E. codium* habitat groups and the 2021 outplanting transect SM3-1, while eight similarities were determined between the adjacent 2020 outplanting transect SM3-2 and optimal habitat groups (Table 2.3). Similarly, both transect SM3-4 and adjacent transect SM3-5 each had eight observed similarities in measured habitat variables to optimal habitat groups. The patterns of variation in habitat similarities to optimal habitat groups observed between outplanting transects reflect the spatial arrangement of transects at SM3, and their unique topographic positions in relationship to the hillslope. As twice as many outplanting attempts were made at SM3 compared to SM1 or SM2, outplanting transects were spaced wider apart and covered a larger total area across this site. Overall, outplanting transects at SM3 had the most inter-site

variation compared to the other sites at Snow Mountain, and this inter-site variation at fine spatial scales was likely an important factor impacting differences in observed rates of seedling survival between outplanting transects in 2022 and 2023.

Outplanting transect SM3-3 was determined to have the lowest number (six) significantly similar habitat variables as the optimal *E. codium* habitat groups, and showed the most variation in habitat similarities compared to the other transects (Table 2.3). SM3-3 was spatially separated from SM3 1-2 and SM3 4-5, which were grouped closer together within the sampling area, at the top and bottom of the slope respectively. This slight spatial separation of SM3-3 likely resulted in the differences in site similarities observed between SM3-3 and the other outplanting transects, which all had greater numbers of similar habitat variables to the optimal habitat groups than SM3-3. Only two similar habitat variables at SM3-3 were site characteristics (slope shape and rock fragment class), and both of these variables were similar to optimal habitat groups at all outplanting transects assessed in this study, indicating that of all the outplanting transects established at Snow Mountain, SM3-3 was uniquely placed in a microhabitat area that least reflected the optimal *E. codium* habitat groups. The unfortunate placement of this outplanting transect within the heterogenous landscape of this assisted migration site, and the unique localized conditions that made this area the most different from the optimal *E. codium* habitat groups, likely played important roles in the comparatively low rates of seedlings survival observed at this transect in both 2022 and 2023. The wide range of variation in habitat suitability between outplanting transects at SM3 contrast with the relatively small and seemingly topographically homogenous area targeted for assisted migration, highlighting how important the fine-scale selection of outplanting areas within assisted migration sites can be for determining seedling survival. Even within a selected assisted migration site, small scale variations between

outplanting locations can have important impacts on the suitability of these locations for both short term survival and long-term seedling establishment.

SM3 was the only assisted migration site in this study to show significant similarities in soil characteristics between optimal habitat groups and outplanting transects beyond hydraulic conductivity (Table 2.3). Similarities in soil surface and rock fragment compositions were only determined at outplanting transects SM3-1, SM3-4, and SM3-5, which corresponded to the only transects at SM where seedlings were observed alive in 2023, 18 months after outplanting. These results suggest similarities in soil characteristics may be impacting the long-term survival of seedlings at assisted migration locations, although variation did occur in which soil composition characteristics were similar between the different transects and optimal habitat groups. Similarities at SM3-4 and SM3-5 in soil surface composition contrasted with similarities in both soil texture and soil surface rock fragment composition at SM3-1. The areas between SM3-1 and SM3-4 where SM3-2 and SM3-3 both occurred did not share any similarities in soil characteristics to the optimal habitat groups beyond hydraulic conductivity, further highlighting how spatially variable these habitat characteristics can be. While SM3-2 had the greatest number of site similarities at SM3 to the optimal habitat groups-with four similar site characteristics- the lack of similarities in soil characteristics could have negatively impacted seedling establishment in this area. As seedlings at SM3-2 were likely wiped out during an extreme stochastic event (i.e. heat wave) nine months after outplanting, to what extent the uniquely high number of similarities in site characteristics, and lack of similarities in soil characteristics, might have impacted seedling survival outcomes remains unclear.

SM3-1 had similarities in four site characteristics and three soil characteristics while SM3-4 and SM3-5 each had similarities in three site characteristic and two soil characteristics

(Table 2.3). SM3-1 had the most similarities in soil characteristics to the optimal habitat groups of any outplanting transect assessed in this study, and likewise shared the most overall habitat similarities to the optimal habitat groups of any of the transects assessed in this study. Two site characteristic (slope and heat load) and two soil characteristics (soil texture and surface composition) were uniquely similar to the optimal habitat groups, as the level of similarity of these variables at SM3-1 and optimal habitat groups were not observed at any other sampling transects. Despite the failure of the methods used in this study to detect significant differences in landscape and hillslope positions between outplanting transects at SM3, unique patterns in site and soil characteristics illustrate the impact even subtle topographic heterogeneity likely has on determining habitat suitability.

SM3-1 likely had the most overall similarities to the optimal habitat groups because it was the outplanting transect observed in this study spatially located closest to the summit and shoulder of the mountain top- the area where the majority of plants occur at Umtanum Ridge. While the spatial proximity of SM3-1 and SM3-2 resulted in some similarities in the site characteristics that reflected the optimal habitat groups, SM3-1 was the only outplanting transect assessed to have significantly similar heat load. While SM3-4 and SM3-5 were the only other transects besides SM3-1 with similar soil variables other than hydraulic conductivity, the soil characteristics these transects had in common were not the same. These patterns highlight how key similarities in habitat characteristics between outplanting transects and the optimal *E. codium* groups are spatially heterogenous across assisted migration sites, and that landscape heterogeneity at fine spatial scales impacts microhabitat suitability for young seedlings and resulting patterns of establishment and survival.

Similarities and Differences in Site and Soil Characteristics Between "Optimal" E. codium Habitat Groups and Outplanting Transects at Snow Mountain 3 Explain Varying Spatial and Temporal Patterns in Seedling Survival Rates 2022-2023

The site characteristic slope shape was determined to match the optimal-high and optimal-low *E. codium* habitat groups at all outplanting transects at SM3 except SM3-1. Transects SM3 2-5 were dominated by a prevalence of linear-linear slopes followed by convex slopes. In contrast SM3-1 was dominated by convex-linear slope shapes, suggesting the microtopography of this transect may trap less precipitation and snowmelt, potentially resulting in slightly drier microhabitat conditions in this area. Transects SM3-1, SM3-2 and SM3-4 had significantly similar ratios of simple and complex slope microtopography as all optimal habitat groups, while SM3-3 had exclusively complex microtopography and SM3-5 had exclusively simple microtopography. Transects SM3-1 had similar slope to the optimal-high and optimal-medium groups, although optimal habitat groups had a wider range of values.

SM3 1-3 are stepper and more micro topographically variable areas, while SM3-4 and SM3-5 are flatter and topographically simpler, although there is variability between transects in these two groupings. SM3-1 was the only outplanting transect with a range of slope angles high enough to be significantly similar to the optimal habitat groups. Although the slope angle values at SM3-1 were on the low end of the optimal habitat groups slope angle range, all other outplanting transects had significantly lower slope angles.

Slope complexity was the only habitat characteristic that was similar between SM3-4 and the optimal habitat groups that was not similar at SM3-5 and may have determined the observed differences in seedling survival at each transect. Similar slope complexity to optimal habitat groups also occurred at SM3-1, which had low seedlings survival in 2023. These significant similarities in slope complexity between optimal habitat groups and both SM3-1 and SM3-4

indicate this microtopographic feature may play an important role in impacting seedling establishment, likely through its dynamic interactions with other habitat characteristics. However, as similarities in slope complexity was also shared with other outplanting transects where no seedling survival occurred in 2023, it is unlikely this variable is directly or uniquely dictating survival outcomes.

Significant similarities in aspect were determined between outplanting transect SM3-2 the optimal-low habitat group and SM3-5 and the optimal-high and optimal-medium habitat groups. Both groups had the largest proportion of northwest facing plots (n=4), while the remaining plots in SM3-2 were evenly split between north (n=2) and northwest (n=2) facing plots. The remaining plots in SM3-5 were split between mostly northwest facing (n= 3) and west facing (n=1) plots. Although site SM3 was selected for assisted migration because of its northern facing hillslope, it is actually the prevalence of north and northwestern facing aspects at SM3-3 and SM3-4 combined with the northeast facing aspect at SM3-1 that makes the aspect at these transects different from the optimal *E. codium* habitat groups. Although plots with north, northeast and northwest aspects occur in all optimal habitat groups, these groups are dominated by the larger number of eastern and western facing aspects. Outplanting transects dominated by north facing aspects could potentially have made the majority of outplanting transects at SM3 less suitable, as the increased shading, moisture retention, and productivity of vegetation associated with these areas increased the competitive pressure on young seedlings.

Significant similarities in the soil characteristic soil surface composition were determined between both outplanting transects SM3-4 and SM3-5 and optimal *E. codium* habitat groups. While SM3-5 was similar to all optimal habitat groups, SM3-4 only showed significant similarities to the optimal-medium group. SM3-5 has the highest mean cover value of the rock

component of soil surface composition compared to all outplanting transects in this study and all optimal *E. codium* habitat groups, as well as the same maximum value as the optimal habitat groups. SM3-5 also had low mean and range of bareground and litter cover values, which were slightly lower, but still analogous, to the cover in the optimal habitat groups. Although SM3-5 had higher biocrust cover than optimal habitat groups, mean cover was still low and the maximum cover value was only 10%.

While SM3-4 had a lower mean rock cover value than the optimal-habitat groups and SM3-5, this value was the second highest mean cover value of any of the outplanting transects in this study and the only transect with a standard deviation of zero. This indicated SM3-4 had a high rock cover that was consistently rocky across the outplanting area, in contrast to the high variability of surface composition observed within other outplanting transect areas. SM3-4 had a mean bareground cover value twice the mean of SM3-5, but only slightly higher than the mean in the optimal-medium group, indicating it had the most similar rock and bareground cover of all the outplanting transects. The narrow range and low standard deviation of bareground cover values (range = 10-20%, sd= 4) indicate this was consistent across the outplanting area, in contrast to the high variability observed at all other outplanting transects and optimal-habitat groups in this study. The highest variation in soil surface composition that occurred at SM3-4 was in the litter and biocrust components, which has similar standard deviations below 10 and maximum cover values of 20%. This further indicates soil surface composition as a whole, and particularly the rock: bareground ratios important to determining *E. codium* habitat, was uniquely consistent across this outplanting transect. Although mean litter and biocrust cover was slightly above the mean values of the optimal habitat groups, these patterns in soil surface composition, including higher cover of bareground and biocrust components, was consistent with the optimal-

medium group and the patterns in soil surface composition that distinguished this group from the optimal-high group.

As seedlings surviving eighteen months after establishment was recorded at both SM3-4 and SM3-5 in 2023, and these transects were uniquely distinguished from all other outplanting transects by their significant similarities in soil surface rock fragment composition to the optimal habitat groups, it is likely that soil surface composition is a key component impacting long term seedling survival at these transects. Results suggest that the high rock cover and rock: bareground ratios identified as potentially important to optimal *E. codium* habitat in general, are likely important to determining the suitability of assisted migration locations as well. In 2023 four seedlings were recorded as alive in transect SM3-4 (9% survival rate) in contrast to a single seedling found at SM3-5 (2% survival rate), despite both outplanting transects sharing soil surface composition with the optimal habitat groups. This may be related to the uniquely low standard deviation of rock composition at SM3-4 transect, which may have provided a consistency in soil surface rock composition across the outplanting area that enabled more individual seedlings to survive there. Furthermore, it is likely that the similarities between SM3-4 and the optimal-medium habitat group as opposed to the optimal-high or optimal-low groups, is important.

Although outplanting transect SM3-1 was uniquely characterized by its similarities to the optimal *E. codium* habitat groups in three key habitat variables- heat load, soil texture and soil surface rock fragment composition- only one seedling survived eighteen months after establishment. While heat load index at SM3-1 was significantly similar to the range and distribution of the optimal-high and optimal-medium groups in contrast to the optimal-low group, SM3-1 had the lowest mean and minimum HLI values of all the outplanting transects in

this study. HLI values SM3-1 fell into the lower end of the range of values in the optimal-high and optimal-medium groups, and best reflected the r distribution of lower HLI values that characterizes the optimal-medium habitat group. However, as higher mean and minimum HLI values were observed in SM3-4 and SM3-5, which collectively had higher rates of seedling survival than observed in SM3-1, similarities in HLI alone may not be as important as similarities in soil characteristics such as soil surface composition, or the interaction between these variables. The interaction between solar irritation and soil surface composition, and their combined impacts on determining soil surface temperatures, are likely more important for young seedling survival than either surface composition or heat load alone, and warrants further study.

SM3-1 soil texture was comprised predominantly of sandy loam with a smaller proportion of loams soil similar to the optimal-high habitat group. In contrast, all other outplanting transects at SM-3 had significantly higher proportions of loam, especially SM3-5 which contained only loam textured soils and SM3-2 which also contained a small proportion of silt loam soil. Composition of soil texture was the most similar between SM-1 and SM-4, which was also comprised of loam and sandy loam soils, although with a higher proportion of loam than SM3-1 and the optimal habitat groups. This could indicate that soil texture generally, and possibly the sand composition in loam soils more specifically, may play a role in habitat suitability and seedlings survival. However, as significant similarities in soil texture were not determined between SM3-4 and the optimal habitat groups despite similarities in soil surface composition to SM3-1, soil texture may be less important to ensuring seedlings establishment than surface composition components such as rock, bareground, or biocrust cover.

SM3-1 is the only transect with significantly similar soil surface rock fragment composition to the optimal-medium group, despite not sharing similarities in soil surface

composition. Similarities to the optimal-medium group are related to similarities in low mean and range of cobble cover combined with a similar proportions of medium gravel cover. Although ISA analysis indicated SM2-3 is the transect most distinguished by its high proportion of medium gravel, the mean value at this transect is 10% higher than at the optimal-medium group and does not reflect the compositional similarities in mean gravel cover that SM3-1 and the optimal-medium groups share. Furthermore, although soil surface rock fragment composition at SM3-4 was not the same as the optimal habitat groups, ISA analysis indicated this transect was distinguished by the significantly high cover of coarse gravel. These results may indicate that the substantial presence of gravel, even if fine and very fine grades are not extensively present, may be tolerable to young *E. codium* seedlings. However, it is also possible that the extremely low overall survival rates observed at this site could be directly related to lack of fine and very fine gravel grades at transects SM3-1, and SM3-4 and SM3-5, despite the many other habitat similarities these transects share with the optimal habitat groups. Ultimately, the fact that SM3-1, SM3-4 and SM3-5 were the only outplanting transects at Snow Mountain where seedlings survived eighteen months after establishment, and that these transects where also the only transects where significant similarities in either soil surface or soil surface rock fragment composition where determined, suggest that these variables are important. Both the composition of these soil variables and their dynamic interactions with site characteristics are likely determining the vegetation community and overall suitability of an outplanting area and subsequent rates of seedling survival. Future studies both evaluating the response of seedlings to differences in soil surface and rock fragment compositions, and determining what larger habitat dynamics these compositional differences are indicative of, is important for better understanding

the role soil surface and rock fragment compositions play in determining seedlings survival outcomes.

Similarities and Differences in Vegetation Characteristics Between "Optimal" E. codium Habitat Groups and Outplanting Transects at Snow Mountain 3 Explain Varying Spatial and Temporal Patterns in Seedling Survival Rates 2022-2023

Although outplanting transects at SM3 showed numerous similarities in site characteristics to the optimal habitat groups and 60% of the transects also showed similarities in soil characteristics, vegetation community and functional group compositions were different to optimal habitat groups at all outplanting transects. While significant differences in vegetation community and functional group compositions mirrored the variation and spatial heterogeneity between transects observed in site and soil characteristics, species richness and total cover were surprisingly homogenous. Although all transects had three vegetation characteristics similar to the optimal habitat groups- total cover and both perennial and annual graminoid cover- like all other outplanting transects in this study, key differences in vegetation characteristics- and perennial forb abundance in particular- resulted in competitive pressures on *E. codium* seedlings that likely inhibited the long-term establishment of the majority seedlings introduced in 2021. Generally, both annual forb and graminoid cover was low, with maximum annual forb cover values at outplanting transects lower than then those observed in optimal habitat groups, although the mean values of both annual forb and graminoid cover were higher. Likewise, perennial graminoid cover at all SM3 transects was low compared to both the optimal-medium and optimal-low habitat groups and other outplanting transects at other assisted migration sites in this study. Mean and range of perennial graminoid cover was low enough to reflect the optimal-high habitat group, which is characterized by relatively low cover of all other functional groups except subshrubs. This low cover, when combined with other suitable site and soil

characteristics, likely contributed to the survival of seedlings at SM1-3, SM1-4 and SM1-5 eighteen months after outplanting.

Unlike all other assisted migration locations, woody shrubs were not present at any outplanting transect at SM3, which may have positively decreased the level of niche competition *E. codium* seedlings experienced at this site. However, perennial forb cover was significantly higher at all outplanting transects than in the optimal habitat groups. Mean perennial forb cover ranged from 20-30% which was 10-15x higher than the mean cover values recorded in the optimal-medium group, which was characterized from the other habitat groups by its comparatively higher maximum perennial forb cover.

Similarly, the woody *Eriogonum* subshrub species *E. thymoides* was present to some extent in all outplanting transects, although its distribution and resulting abundance was inconsistent. Mean subshrub cover at transects SM3-1, SM3-3 and SM3-4 was <10%, which only reflected the optimal-low group as both the optimal-high and optimal-medium groups had significantly higher subshrub cover. Similarities in cover between the optimal-low habitat group and transects SM3-1 and SM3-4 may indicate habitat characteristics at these outplanting transects are suitable for occupancy by woody subshrubs and *Eriogonum* species in particular. However, strong niche competition between *E. codium* seedlings and established adult *E. thymoides* plants in the areas where were both species were present likely resulted in competitive pressure on *E. codium* seedlings that inhibited successful establish of seedlings in high abundance at this site. In contrast, SM3-5 had mean subshrub cover values <5% and the lowest mean and range of subshrub cover values of any outplanting transects at SM3. The relatively lower cover of *E. thymoides* at transect SM3-5 may be why one seedling survived for eighteen months despite this transect initially having lower rates of seedling survival in 2022

than SM3-1 and SM3-4. Ultimately, despite similarities in key site and soil characteristics to the optimal habitat groups at transects SM3-1, SM3-4, and SM3-5, *E. codium* was unable to successfully compete enough to become established in areas already dominated by a native and productive *E. thymoides*- perennial forb community.

It is likely that similarities between outplanting transects and the optimal-high and optimal-low habitat groups, indicate a habitat type where *E. codium* can either reach maximum abundance or its productivity is inhibited. In contrast, the optimal-medium group likely characterizes a less optimal but more generally common and tolerable environment where *E. codium* can consistently grow but does not reach maximum abundance. Differences between outplanting transects and the extent to which habitat characteristics reflect either the optimal-high/low groups or the optimal-medium group, could have important implications for seedlings survival. It is possible that the variables that made SM3-4 similar to the optimal-medium group may indicate that SM3-4 matched this "tolerable" habitat type, enabling it to better support long term seedlings establishment. It may be that unless an outplanting location is extremely close to the habitat characteristics in the optimal-high group, the habitat similarities between the optimal-high and low groups that differentiate them from the optimal-medium group may actually indicate an extreme habitat niche where *E. codium* seedlings are pushed beyond their range of tolerance to abiotic and biotic habitat conditions. These areas may ultimately be less suitable for long term seedling establishment than areas that more closely match the optimal-medium group, but are less able to foster maximum *E. codium* abundance. This is likely especially true for sites like SM-3 which are dominated by perennial forbs, and thus have the most potential to match the vegetation characteristics of the optimal-medium habitat group.

Ultimately, it is probable that the highest survival rates observed at Snow Mountain that is unique to transect SM3-4 is related to microhabitat similarities between this transect and the optimal-medium habitat group occurring at extremely fine spatial scales. Although no significant differences were determined in total cover between SM3 outplanting transects and optimal habitat groups, minimum total cover values were generally higher at SM3 outplanting transects. Mean total cover was lower in the optimal-high and optimal-medium habitat groups than at any of the outplanting transects, while SM3-3 and SM3-4 had lower mean total cover values than the optimal-low habitat group. SM3-2 had the lowest mean total cover of the outplanting transects, and best reflected the mean cover value of the optimal-medium group, while transect SM3-1 has a similar mean and range as the optimal-low group. Although all transects had significantly higher species richness than the optimal habitat groups, SM3-1 had the lowest mean and maximum values. Despite SM3-4 having the highest mean species richness, it shared the lowest minimum species richness value (9 species) with SM3-1, which was similar to the maximum species richness values of the optimal-medium habitat group (8 species). Likewise, both transects SM3-2 and SM3-5 had minimum species richness values (10 species), closer to the optimal-medium group minimum than SM3-3 which had the highest minimum species richness value (12 species). Similar to patterns observed at Badger Mountain, the range of variability in species richness and total cover observed at transects SM3-1, SM3-4 and SM3-5 suggest that patterns in seedlings survival are directly related to patterns of spatial heterogeneity of vegetation communities within these areas.

Significant similarities in total cover, the perennial and annual graminoid components of vegetation functional group composition, and the site characteristic soil surface rock fragment classification were determined between all outplanting transects at SM3 and all optimal habitat

groups. This indicates at the most basic site level, all transects were located in rocky areas with relatively low vegetation and graminoid cover that reflected the optimal *E. codium* habits. However, the comparison of patterns in seedling survival across numerous outplanting transects at SM3 highlighted similar patterns observed at other outplanting transects at BM1, SM1 and SM2, indicating finer scale variation even within small areas of seedling introduction, are likely acting as major drivers of seedling success.

Ultimately the areas at SM3-1, SM3-4 and SM3-5 where minimum values of both species richness and total cover overlapped with the maximum values observed in optimal habitat groups likely constituted fine scale heterogeneous habitat patches of low competition *E. codium* seedlings were able to exploit. The seeming relationships between the presence of these fine scale habitat niches within even the 5-7 meter scale assed in this study, highlight the importance of targeting these micro-habitats during assisted migration attempts. By comparing fine scale inter-site spatial heterogeneity at assisted migration sites, to the fine scale habitat heterogeneity of key habitat characteristics represented by differences in the three optimal habitat groups, managers may be able to more successfully targeted key habitat niches to improve seedling survival and assisted migration outcomes.

Conclusion

Validation of the WNHP Habitat Suitability Model

To "ground-truth" and validate the Washington Natural Heritage Program suitable habitat model, this study explored to what extent the habitat model was able to predict the similarity of habitat characteristics between assisted migration sites and the native site when measured at a 30m site-level spatial scale. While all assisted migration sites shared some site and soil habitat similarity to the range of habitat variation observed at the Native Site, the similarities were highly variable between sites. Varying levels of overlap between site and soil characteristics indicate no one assisted migration site matched the Native Site, although the habitat model was able to successfully determine that Gingko State Park (deemed "highly suitable potential habitat") shares more similarities in site and soil characteristics to the Native Site than any site at Snow Mountain (deemed "moderately suitable potential habitat").

Significantly, the model's prediction of habitat suitability at each assisted migration location is reflected in the greater similarities between Gingko State Park and the Native Site in key habitat variables shaping suitable *E. codium* habitat: the site characteristic heat load and two soil characteristic soil texture and surface composition. However, similarities in heat load at Snow Mountain 2 were not indicated by the model. This indicates that while the habitat model is based on coarse scales of habitat characteristics such as base geology at 100,000m, this base geology does in fact accurately reflect finer scale similarities in soil surface characteristics between the Native and assisted migration sites, while the coarse scale of other variables such as elevation and relief are not fine enough to capture important similarities in heat load, or these similarities are not reflected in the final suitability classification designated by the model.

To what extent Gingko State Park constitutes a "highly suitable" habitat is debatable. Few similarities in vegetation composition or vegetation functional group composition were determined between the Native Site and any assisted migration sites in this study, although the most compositional overlap was observed in some of the habitat areas surveyed at both Gingko State Park and Snow Mountain 3. Overall, while Snow Mountain 3 had the most similarities in vegetation composition to the Native Site, only Snow Mountain sites 1 and 2 had similarities in one of the key vegetation characteristics defining *E. codium* habitat, total cover.

Ultimately, all assisted migration sites had more productive vegetation communities than the native site with higher shrub cover observed at all sites except Snow Mountain 3, and significantly higher perennial forb cover at all assisted migration sites. Perennial graminoid cover was significantly higher at the Native Site than assisted migration sites, indicating that while *E. codium* is associated with mainly a perennial graminoid community type, vegetation communities at assisted migration sites were forb dominated. As *E. codium* is likely only able to withstand moderate to low competition with perennial forbs, the high cover of perennial forbs at these sites makes them unsuitable. Similarly, all assisted migration sites also had either woody shrubs and/or woody subshrubs in the *Eriogonum* genus already occupying the site. Gingko State Park and Snow Mountain sites were all characterized by more widespread and abundant *Eriogonum* species growing in association with perennial graminoids and forbs, indicating the niche *E. codium* occupies at the Native Site is already being taken, likely making these sites unsuitable for *E. codium* occupancy despite other habitat similarities, as it is unlikely to successfully compete for niche occupancy with more widely adapted and established species. While the inclusion of physical and biological criteria is important to ensuring a reintroduced species be able to survive and grow initially, it is essential for ensuring a species continued

persistence, that assisted migration occurs at sites that also allow the species to become embedded in a larger ecological community in which it has a functional role (Fiedler and Laven 1996).

Both broad- and fine-scale environmental qualities are important to consider when selecting an assisted migration site (Maschinski et al 2012). While the habitat model accurately reflected the over-all higher suitability of Gingko State Park compared to sites at Snow Mountain, it failed both to distinguish significant differences in habitat suitability within different sites at Snow Mountain, and failed to identify key differences in vegetation characteristics likely impacting the suitability of sites for *E. codium* establishment. While sites at Snow Mountain lacked similarities in soil characteristics to the Native Site, Snow Mountain site 2 had the highest number of similar site characteristics to the Native Site, including similarities in slope and aspect not observed at Gingko State Park. Snow Mountain 3 also had more and very different similarities in vegetation characteristics than observed at Snow Mountain sites 1 and 2, while having significantly fewer similarities in site characteristics. These differences between sites at Snow Mountain are significant and have important implications for the suitability of the habitat there and impacts on how *E. codium* seedlings will respond to habitat conditions. The failure of the habitat model to differentiate habitat differences between these sites, and to classify the entire Snow Mountain region equally as "moderate" habitat, highlights issues with the model's accuracy and ability to predict suitable habitat at scales finer than "landscape-level".

Assessments of potential assisted migration sites should focus on matching vegetation characteristics and dynamics relationships between vegetation and site and soil characteristics such as heat load, soil surface and rock fragment cover. Because *E. codium* characterizes its own sparse vegetation type, it may be challenging to find sites that match the vegetation

characteristics at the Native Site. The current coarse spatial scale of habitat variation within the model is not adequate to assess the variation of habitat similarities between assisted migration sites with a location such as Snow Mountain, or to distinguish on the ground variation in vegetation composition that will likely impact successful *E. codium* site occupancy. Finally, comparing habitat suitability of the Native Site averaged across the known habitat variation between subpopulations and "optimal" habitat groups described in chapter 1, loses important variation within the population indicative of *E. codium* evolutionary ecology that likely also impacts successful *E. codium* site occupancy. Tools are needed that better distinguish habitat suitability at finer spatial scales, and that quantitatively link location selection across the Columbia Plateau bioregion to assisted migration site selection within a target location.

Importance of Microhabitat Variation on Umtanum Desert Buckwheat Seedlings Survival

While significant differences in key habitat variables were determined between the Native Site and assisted migration sites, some overlap in the variation and range within each habitat variable was observed. This suggests microhabitat similarities are occurring between sites at smaller spatial scales than captured at the site-level scale used in this study, or the landscape level scale used by the habitat model. Observations of fine scale microhabitat variation at the Native Site observed in chapter one indicate that variation within assisted migration sites and outplanting areas may provide small-scale habitat heterogeneity that *E. codium* can exploit and likely requires for establishment. It is likely that *E. codium* is able to exploit fine scale niches of low competition when introduced at sites where competitive pressure from other species limits establishment. Thus capturing fine scale microhabitat variation is an important part of determining potential habitat suitability.

Germination, establishment, and early growth are critical phases that are greatly influenced by microenvironment and the preexisting established species occupying these microenvironments (Grubb 1977, Veblen 1992, Tilman 2004,Wendelberger and Maschinski 2009, Maschinski et al 2012). Heterogeneity in environmental variables such as light and heat load, soil surface composition, and soil moisture can influence seedling survival on scales less than $1m^2$ (Molofsky and Augspurger 1992, Wendelberger and Maschinski 2009). Spatial pattern of soil surface properties in particular, are quite complex and critical for seedling establishment in semiarid ecosystems with low vegetation cover (Bromley et al 1997, Seguieri et al 1997, Maestre and Cortina 2002, Maestre et al 2003).

Through the assessment of outplanting transects, this study was able to capture important micro-habitat similarities between the three "optimal" *E. codium* habitat types established in chapter one, and the areas within assisted migration sites directly surrounding outplanted seedling locations. Currently these similarities are challenging to predict at the coarser spatial scales of the habitat model and site level assessments used to qualitatively select areas for seedling establishment. While managers have used qualitative "impressions" of species target habitat requirements to select outplanting location, actual quantitative assessment of key abiotic and biotic niche attributes at a potential assisted migration site is an important step (Maschinski et al 2012). Quantitative assessments of micro-habitat heterogeneity at assisted migration sites and proposed outplanting areas to identify suitable recipient patches at a fine scale will allow mangers to better target "optimal" habitat characteristics in heterogenous landscapes.

Short-term studies (2-3 years) have found significant correlations between microhabitat parameters and seedling survival, with several studies showing reintroduced plant performance and population growth depend on microhabitat conditions (Baraloto and Goldberg 2004,

Akasaka and Tsuyuzaki 2005, Maschinski et al 2006, Maschinski et al 2012, Possley et al 2009). However, suitable habitat for rare species is not randomly distributed, and is thus unlikely to be randomly present in any given location (Maschinski et al 2012). Consequently, despite the ubiquitous use of a random experimental design in which seedlings are planted along a regular grid, this method is known to be an ineffective establishment method doomed to low success, especially with woody species such as *E. codium* (Noble et al 2001, Maestre et al 2003, Maschinksi 2012). Instead of uniform plantings, success has been found with arranging seedlings utilizing a stratified random sampling design, so that they follow the natural vegetation and microhabitat patterns at the site (Maestre et al 2003 and Maschinski et al 2012).

Understanding the unique threats faced by edaphic endemic species, and adequately developing management strategies to ensure their resiliency to climatic change, will require both protocols adapted to the fine scale and often abrupt variations that characterize edaphic island environments, and focus on understanding the limits of a species' tolerances to changing in situ conditions and assisted migration to new locations. As a relatively young geologic region, better understanding how *E. codium* has adapted to the heterogeneity of soil environments found in the Columbia Plateau is an essential step to addressing ongoing threats to ecosystem integrity by increasing fire intervals and anthropogenic threats. As climate change and resulting loss of habitat places *E. codium* at risk of severe population loss and even extinction, understanding the relationships between the extremely limited distribution of *E. codium* and the conditions in which it grows, is essential to developing management plans aimed at expanding its distribution. Understanding the relationships between landscape level distributions and the fine-scale heterogeneity of habitat characteristics is an essential step in this species' conservation and management.

Potential Effects of Low Genetic Variability and Nursery Stock Production on Outplanted Seedling Mortality

The ultimate goal of rare species assisted migration is to enhance a species' survival prospects in the wild through the establishment of resilient, self-sustaining populations (Guerrent and Kaye 2007). For an introduced population to be both resilient and self-sustaining, it is imperative that it have sufficient genetic resources to undergo adaptive evolutionary change (Guerrant 1996*a,* Guerrent and Kaye 2007). The genetic diversity of plant materials used in assisted migration are of the utmost importance, as they provide the entire genetic basis of the new population and will define the population's capacity for adaptation to changing environmental conditions (Neale 2012). Ensuring adequate genetic diversity of plant materials can help to lessen or even prevent the eventual effects of inbreeding depression, or other genetic consequences, on introduced populations of small size **(**Ellstrand and Elam 1993, Newman and Pilson 1997, Reed and Frankham 2003, Neale 2012).

The selection the "founding" individuals that will be used to establishing a new population is an important step in determining the new population's evolutionary potential and ability to adapt (Neale 2012). The selection of plant materials for assisted migration should aim to avoid inbred progeny while maximizing the retention of genetic diversity (Kettle 2008). Managers should exercise caution when deciding strategies for capturing genetic diversity of wild populations, as small and isolated populations experiencing inbreeding depression are generally not suitable sources for reintroductions (Armbruster and Reed 2005, Maschinski and Albrecht 2017). As discussed in chapter one, determining the current genetic variation remaining within the *E. codium* population, and establishing to what extent this species may be undergoing a genetic bottleneck, are critical steps in its conversation and recovery (Ramp et al 2006, Ayers et al 2007, Neale 2012).

Attempts at the assisted migration of *E. codium* have historically utilized seed stock from a few individuals grow in a nursery from a single cohort of wild seed. The need for genetically diverse plant materials for use in restoration and assisted migration is well established, and is especially acute for rare species of high conservation concern with limited distributions such as *E. codium* (Barrett and Kohn 1991, Falk and Holsinger 1991, Ellstrand and Elam 1993, Fenster and Dudash 1994, Knapp and Rice 1994, Center for Plant Conservation 1996, Hamrick and Godt 1996, McKay et al 2005, Broadhurst et al 2008, Jacquemyn et al 2009, Bischoff et al 2010**,** Bouzat 2010, Albrecht and Maschinski 2012, Neale 2012, Maschinski et al 2013, Basey et al 2015, Rieseberg and Swensen 1996, Maschinski and Albrecht 2017). Numerous studies have demonstrated the importance of incorporating both genetic data and evolutionary theory in reintroduction of rare species, with particular emphasis made on the importance of provenance and diversity of the "founder" populations (Fenster and Dudash 1994, Mistretta 1994, Havens 1998, Falk et al 2001, Hamilton 2001, Wilkinson 2001, Hufford and Mazer 2003, Falk et al 2006, Bischoff et al 2010).

Ideally, the genetic composition of an introduced population should be as diverse as possible while representing existing local gene pools of the species, and information on the genetic structure of a species' populations should guide decisions on the best ways to collect appropriate seed materials (Ennos 2003, Burgarella et al 2007, Kettle 2008, Maschinski and Albrecht 2017). Much work has been done both establishing theoretical and empirical evidence for maximizing the number of founding individuals and equalizing their contributions in the gene pool (Pilson 1997, Guerrent and Kaye 2007). Genetic diversity is essential to ensuring introduced populations mirror the adaptive potential of natural populations in their capacity to respond to environmental change and survive yearly variation in weather, disease, competition,

and soil conditions and to ensure resiliency to stressful conditions such as drought or wildfire (Kettle 2008, Basey et al 2015, Colas et al 2008, Falk et al 1996, Guerrant et al 2004, Neale 2012, Maschinski and Albrecht 2017). Establishing additional populations of rare and at-risk species with a low genetic base will fail to ensure that introduced populations have the functionality and resilience necessary to become self-sustaining in the face of environmental change (Broadhurst et al 2008).

Limited sampling from spatially restricted populations, such as collecting seed from only a few individuals and/or in collection years, limit the range of ecological conditions captured within the genetic capacity of the seed, and lead to a narrow genetic base in any new populations that might be established from that seed (Lengkeek et al 2005, Kettle 2008). High variance in fertility can often occur between reproductively active individuals within the same population, resulting in a few individuals contributing disproportionately to creating offspring within any given year or population. Similarly, utilizing collections made over only a few years limits the genetic diversity present in the adult population that is actually captured by seed collections (Kettle 2008). These reductions in the genetic diversity captured from "founder" populations contribute to the rapid accumulation of relatedness and inbreeding in subsequent generations, ultimately resulting in a "cryptic"[19] genetic bottleneck occurring within introduced populations (Luikart et al 1998, Kettle 2008).

The use of genetically diverse plant materials is known to be tied to lower seedling mortality rates and the successful establishment of new populations, with research showing genetically diversity can improve establishment success under a range of conditions and support

[19] A "cryptic" genetic bottleneck refers to a hidden or subtle reduction in genetic diversity within a population, where the effects of the bottleneck are not immediately apparent but can manifest under specific environmental or genetic conditions

faster recovery after disturbances or climatic extremes when compared to material with low diversity (Hughes and Stachowicz 2004, Reusch and others 2005, Crawford and Whitney 2011, Neale 2012, Basey et al 2015, Koko et al 2017, Maschinski and Albrecht 2017).

The more founders, the greater the chance that offspring will become established and survive, as genetically diverse plant materials are more likely to adapt and persist into the future than those with limited diversity (Falk et al 1996, Guerrant 1996, Jump 2009, Guerrent and Kaye 2007, Basey et al 2015). Ultimately, a range of genetic factors including maternal effects, phenotypic plasticity and population specific environmental effects can all have important influences on the successful establishment, survival and reproduction of introduced plant materials (Dudash et al 2005, Broadhurst et al 2008).

It has been well established that the nursery production of wild collected seed acts as a bottle neck filtering the genetic diversity inherent in wild populations to genomes with traits better conductive to successful growth and establishment in nursery conditions (Barrett 1981, Menges et al 2004, Rogers 2004, McKay et al 2005, Neale 2012, Basey et al 2015). Addressing genetic loss within nursery production is an essential step in successful rare species reintroduction, as the resulting genetic diversity of nursery stock, regardless of how diverse initial seed collections are, ultimately provide the baseline genetic diversity of newly established populations (Neale 2012). Because wild type genetic diversity can translate to nonuniformity in characteristics important to nursery production such as seed germination requirements, plant size and structure, timing of flowering and seed development, genetic diversity can be lost at every stage of the plant production process (Kitzmiller 1990, Smith 2007, Pedrini et al 2020) If loss of genetic diversity is not mitigated for at every step between collecting seeds from wild populations to the introduction of seedlings at assisted migration locations, resulting introduced

populations will not be representative of natural ones (Broadhurst et al. 2008, Erickson and Halford 2020, Pedrini et al 2020).

Seed increase breeding from a low number of individuals combined with the genetic bottlenecks wild-adapted traits undergo during nursery production, means the development of plant materials for assisted migration of *E. codium* may be exacerbating already existing issues around the lack of genetic diversity and conservation of adaptable traits within the *E. codium* genome. For many native species introduced into the field from nursery stock, including *E. codium* seedlings utilized in reintroduction efforts over the past fifteen years, plants have been known to grow well in a greenhouse setting, but haven't been able withstand natural conditions in the field (Primack 1996, Raabová et al 2007, Fant et al 2008, Neale 2012). Recent studies show potential risks associated with a lack of genotypic diversity in source populations, and have demonstrated the inability of introduced populations to functionally mimic natural populations when genetic diversity is lost (DeMauro 1993, Keller et al 2000, Williams 2001, Honjo et al 2008, Dolan et al 2008, Fant et al 2008, McKay et al 2005, Bischoff 2010).

Currently, processes of genetic stochasticity and genetic drift could be having powerful effects on individual *E. codium* seedling's fitness, significantly impacting this species' ability to become established at assisted migration locations and adapt and persist in a changing climate. While it is true that no amount of additional genetic diversity can improve outplanting success if the plant material is not adapted to conditions at the assisted migration site, it is possible that the high rates of seedling mortality observed at numerous assisted migration locations over the past fifteen years, may be more related to genetic bottlenecks and low diversity within either the single population of *E. codium* or the plant materials utilized in assisted migration attempts (Johnson et al 2010, Basey et al 2015). Work aimed at establishing the genetic diversity of plants

currently used for seed increase, and understanding both the genetic and functional trait diversity of current nursery stock used in assisted migration attempts, are important steps in assessing to what extent significant genetic bottlenecks may already be having powerful consequences on the successfully establishment of new *E. codium* populations.

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Chapter 3

Recommendations for the Recovery of Umtanum Desert Buckwheat

(*Eriogonum codium*)

Part I: Important Habitat Characteristics for Selection of Assisted Migration Sites

Site Characteristics

Slope: impacts site suitability for other vegetation. *E. codium* likely prefers marginal habitats afforded by stepper slopes to avoid competition, but slope steepness may also be limiting growth in areas that are too steep, especially on rocky substrates prone to erosion.

Aspect: Eastern and western facing sites are likely more optimal than southern or norther facing sites. Southern facing areas likely results in sites too hot to support seedling establishment, while northern facing slopes may result in moister and shadier sites with more productive vegetation communities and increased competition.

Landscape position: upper portions of mountain slope (summit, shoulder) likely have rockier, more barren well-draining soils resulting in marginal habitats afforded with more limited competition.

Heat Load: similar to slope, higher HLI values likely result in marginal habitats that allow avoidance of competition, but highest HLI values (>0.75) may be limiting growth.

Soil Characteristics

Surface composition: high rock or bareground cover, may be able to grow with up to 15-20% biocrust cover)

Rock fragment composition: gravel components may be important, especially fine and very fine gravel components although may also be able to grow in course and medium gravel grades

Possibly soil texture: loam to loamy sand soils may be optimal *but more work needs to be done.*

Vegetation Characteristics

***P. secunda* or *P. secunda/ P. spicata* habitat**: perennial graminoid cover around 20-30% but not exceeding 60%.

Low species richness: 10 species or less. 5 or less species most ideal.

Low total cover: 30% or less cover of other species is likely most optimal.

Low cover of woody species (shrub and subshrub): avoid niche competition (<5% cover).

Low cover of forbs (especially perennial forbs): 10% cover or less.

Low cover of annual forbs and graminoids: <5% cover

Note: If perennial graminoid cover is >25%, then perennial forb cover likely needs to be less than 5%. If perennial graminoid cover is lower (<25%), than perennial forb cover likely can be 20% or less.

Part II: Additional Research Recommended to Support the Recovery of Umtanum Desert Buckwheat (*E. codium)*

Native Site

Additional research at the single native population of *E. codium* is necessary to better understand the ecology and life history of *E. codium* and what factors are impacting its current confinement to the edge of Umtanum Ridge.

i. Priority 1: Assess relationship of habitat characteristics to *E. codium* occupancy

Goal: Determine what habitat characteristics distinguish current *E. codium* subpopulations from the surrounding areas where *E. codium* does not currently grow.

- While measuring habitat characteristics within the existing subpopulations allowed some indications of which variables are likely impacting where *E. codium* grows, it did not adequacy assess what distinguishes the *E. codium* subpopulations from the surrounding inhospitable habitat.

- Exploring differences between site, soil and vegetation characteristics along transect lines running from outside the boundaries of the existing subpopulations to inside where plants occur can provide a more robust and reliable indication of what distinguishes *E. codium's* current habitat.

- This is especially important in areas such as subpopulations II, III and IV where the number of *E. codium* plants has significantly declined and plants no longer occupy the surrounding areas that formerly hosted *E. codium*. Particular attention should be paid to understanding changes in habitat characteristic in the areas between current

subpopulations IV and V that used to host contiguous plants, and potential ecological gradients that may be occurring perpendicular to the ridge edge.

ii. Priority 2: Analysis of soil physical and chemical properties

Goal: Describe the physical and chemical properties of the soil environment surrounding *E. codium* subpopulations to determine soil habitat.

- Exploring relationships between *E. codium* abundance and soil's physical and chemical characteristics can help to further elucidate which soil variables may be impacting *E. codium's* occurrence and determining it's suitable habitat.

- Comparing soil physical and chemical properties in the areas within the subpopulations where *E. codium* grows, to the soils in the surrounding areas where it does not grow, can help to elucidate if this species is an edaphic specialist adapted to significantly different soil properties that distinguish the area within its subpopulations from the surrounding soil substates.

- Variables warranting further exploration include soil profile textural composition and horizonation patterns, soil chemistry (macro/micronutrients and trace elements), soil organic content, and rock fragment composition within the soil profile.

iii. Priority 2: Conduct a demographic study of all remaining subpopulations

Goal: Determine the range of age classes present within the remaining subpopulations and explore the relationship between plant size and age.

- This study assumes increased cover of *E. codium* indicates increased abundance of the species, thus indicating the presence of favorable or "optimal" habitat. However, increased size of plants may be more reflective of an individual's age than their "abundance" or ability to thrive in a particular location. Conversely, the presence of small plants may result in low cover values, but may be better reflective of the presence of young individuals more than unfavorable or "less-optimal" habitat conditions. Better understanding the range of age classes and relationships between size and age can help mangers better determine which areas within the existing population constitute "optimal" habitat, and if plant size and *E. codium* cover are related to "abundance".

- Identifying which areas within the existing population have the most young plants can help mangers identify what habitat characteristics and vegetation communities are most conducive to seedling germination and long-term survival. Better understanding populations demographics can elucidate time intervals between successful recruitment events that can provide important insights into this species reproductive strategy.

Native Site and Assisted Migration Locations

Additional information collected at both the single native population of *E. codium* and assisted migration locations where *E. codium* is currently being outplanted is important for better understanding similarities and differences in key habitat variables impacting seedling survival. Comparing the response of established individuals to habitat conditions at the Native Site, with seedling response and survival at assisted migration sites, can help mangers better understand this species range of tolerance to environmental conditions.

iv. Priority 2: Assess seasonal and annual fluctuation in soil moisture and temperature

Goal: Determine spatial patterns of variation, and monitor seasonal and temporal changes, in soil moisture and temperature.

- Soil moisture and temperature are likely key environmental variables impacting both the existing *E. codium* population and any additional populations established at assisted migration locations. While these variables were not explored in this study, they likely have important impacts on both seedling and adult survival and should not be overlooked. Results indicating heat load is impacting *E. codium* abundance indicate impacts of solar radiation on fluctuations of soil moisture and temperature are likely significant. Spatial heterogeneity of these variables may be an important in creating micro-habitats that *E. codium* is able to exploit.

- As both soil moisture and temperature are highly dynamic variables that fluctuate both seasonally and annually, it is important that future work attempts to capture this variation. By quantifying the range of soil moisture and temperature conditions *E. codium*

experiences under field conditions, managers can better understand this species range of tolerance of environmental variation and predict how this species might respond to changing conditions and climate scenarios.

v. <u>Priority 3</u>: Assess the role of disturbance as a potential site preparation method for successful assisted migration

Goal: Determine if *E. codium* is able to exploit less competitive conditions following ecological disturbance and colonize barren or partially barren recently disturbed areas.

- Both the site of the existing population, and many potential future assisted migration locations, have undergone disturbances due to ecological and anthropogenic processes such as wildfire or development. As *E. codium* likely dominates its own vegetation community, and may rely on marginal habitat conditions that decrease competition with other more abundant and widely adapted species to become established, targeting recently disturbed areas may be a useful stagey to establish new plants in the field.

- Future work should look at the role of disturbance as a site preparation method, as well as the combined use of disturbance and herbicide to help control competition with other species during initial establishment.

Greenhouse Studies

Experimentally testing *E. codium*'s growth response to a range of important habitat variables is essential for determining this specie's basic life history information. By conducting these experiments under controlled greenhouse conditions, confounding variables such as aspect, slope, microtopography and climate are avoided. Furthermore, the greenhouse setting is more cost-effective and logistically feasible compared to conducting field trials at multiple locations. Better understanding *E. codium*'s response to isolated habitat variables under controlled conditions can help elucidate important evolutionary strategies impacting this species distribution.

vi. <u>Priority 1</u>: Assess plant trait and functional response diversity of *E. codium* to environmental variables

Goal: Experimentally determine the range of tolerance and response diversity of *E. codium* to key environmental variables such as soil moisture, drought/humidity, heat, and cold under controlled conditions.

- Understanding *E. codium*'s range of tolerance to environmental variables are important steps in being able to assess potential habitat for assisted migration. Without accurate information on how this species responds to a range of environmental variables and what variable ranges exceed this species tolerance, accurately assessing habitat conditions on current and potential site occupancy is difficult.

- Experimentally assessing the functional response diversity of *E. codium* to a range of key environmental variables can help to better elucidate to what extent *E. codium* is phenotypically plastic and adaptable to a range of habitat conditions. Better

understanding this species phenotypic adaptability to environmental conditions, and the range of physiological responses it is capable of, can help managers predict this species' response to changes occurring in its existing habitat as well as potential responses to new habitat conditions.

vii. <u>Priority 1</u>: Assess *E. codium's* response diversity to different soil textures and chemical properties

Goal: Experimentally determine if *E. codium* growth is significantly impacted by differences in soil texture and chemical properties.

- Soil preference experiments using plant growth and stress as indicators of habitat suitability provide insight into the effects of soil variation on various plant life stages as means of ground truthing assumptions about species relationship to base geology and soil series.

- To what extent *E. codium* is only able to grow on the soil textures found at the Native Site is unclear. Experimentally growing seedlings in soils varying in ratios of sand/loam similar to the Native Site, and comparing seedling growth response to a range of soil textures such as silt or clay soils, can help establish to what extent soil texture is impacting *E. codium* growth and optimal habitat.

- Varying ranges of rock fragment components in soil is likely an important variable impacting *E. codium* growth and abundance. Assessing the impacts of varying ratios of rock fragment components on seedling growth is important for better understanding the role the rock component is have on seedling survival. Particular focus should be made on

understanding seedling growth responses to ratios of cobbles vs gravel rock fragment components, and especially the fine and very fine gravel grades.

- Better understanding *E. codium's* response diversity to soil chemical properties such as macronutrients and organic carbon, can provide insights into this species ability to occupy marginal, nutrient poor and less productive habitats. Understanding this species range of tolerance to soil chemical properties can help managers determine which evolutionary strategies may be impacting *E. codium*'s habitat preferences and if a specialized soil type need to be target for assisted migration.

viii. <u>Priority 1:</u> Assess *E. codium's* response diversity to vegetation competition

Goal: Experimentally assess *E. codium's* response to competition with key vegetation functional groups and associated species.

- Species interactions and their impacts on *E. codium* growth should be experimentally assessed to determine how strongly inter species competition limits growth and what abundance of other species is most tolerable for *E. codium* growth and seedling survival.

- Observations made in this study suggest *E. codium's* relationship with primarily *P. secunda* may be benign if not mutualistic at lower abundance, but may become competitive when *P. secunda* abundance is high or when *P. spicata* is present. Relationships between *E. codium* and associated perennial graminoid species *P. secunda* and *P. spicata* should be assessed to determine if relationships are competitive, mutualistic or benign.

- Assess relationships between *E. codium* growth and survival and the species present at the Native Site, including native perennial forbs in the *Astragalus* genus and invasive annual species Cheatgrass (*Bromus tectorum*) and Russian thistle (*Salsola tragus*).

- Understanding *E. codium's* response diversity to perennial forbs and combinations of perennial forbs and graminoid species can help elucidate to what extent *E. codium* is able to successfully grow in associations with other native species. Better understanding of *E. codium's* relationships to native flora is important for assessing the impacts of established native plant communities on seedling survival, and if establishing *E. codium* seedlings with other associated species such would improve or harm survival outcomes.

- Conversely, understanding impacts of competition with known invasive species present within the single native population can help mangers better understand the competitive pressure these species may pose to existing and future *E. codium* populations.

Other Studies

ix. <u>Priority 1</u>: Conduct genetic analyses to assess remaining polyploidy within the existing populations, if this population has gone through a genetic bottleneck, and the genetic diversity of seed stock used to grow seedlings for assisted migration.

Goal: Better understand current levels of genetic diversity and identify if a genetic bottle neck is impacting current recovery efforts.

- Due to *E. codium's* small population and highly restricted range, it is likely that this species is either currently experiencing or is at high risk of genetic stochasticity. It is possible that observed low rates of reproductive success are indicators of inbreeding depression, in which the limited number of reproducing individuals may have extremely low genotypic variability, resulting in low fecundity and seedling survival. The genetic variability between individuals and subpopulations, and any potential relationships between observed rates of high seedling mortality and low genetic variability, are currently unknown as no population wide genetic work has been done on this species. For a more detailed discussion of stochasticity within the single *E. codium* population, see Appendix AD.
- As current assisted migration and out planting attempts are utilizing seed stock from only three individuals grow in a nursery from wild seed, significant genetic bottlenecks could have powerful consequences for the adaptability of future populations to successfully established at other locations. Seed increase breeding from a low number of individuals combined with the genetic bottleneck wild-adapted traits undergo during nursery production, means genetic stochasticity and genetic drift could have powerful effects on individual fitness and this species' ability to adapt and persist in a changing climate.

- It is essential that the existing genetic diversity within the remaining population, as well as the diversity within the seed stock utilized for assisted migration, is assessed. Low rates of seedling survival both at the native population and assisted migration locations may be *more indicative of inbreeding depression and low genetic variability than habitat preference or range of species tolerance*. Understanding the remaining genetic variation within the species, and the extent to which polyploidy and haplotype diversity have been conserved within individual genomes, are important to determining if observed rates of seedling survival, and any experimentally determined trait and response diversity, is actually indicative of this species' adaptive potential or only reflective of a limited gene pool.

x. <u>Priority 2</u>: Collect fine-scale environment and habitat data from both the Native Site and other areas of the Columbia Plateau to better model finer scale habitat heterogeneity.

Goal: Develop a suitable habitat model that is able to predict the existence of microhabitats at finer-spatial scales more appropriate for selection of sites and areas of seedling establishment.

- While the current habitat model is able to identify locations of potential suitable habitat at a landscape level, it is unable to distinguish habitat differences at potential assisted migration sites within locations or pick up on the fine-scale microhabitat differences within sites impacting *E. codium* seedling establishment.

- Finer-scale habitat suitability models could be developed for locations of interest to hep mangers quantitively select sites within a location for assisted migration.

- By conducting pre-outplanting surveys and collecting baseline habitat data at selected assisted migration sites, microhabitat suitability models could be developed to help managers target the best microhabitat niches within assisted migration sites.

- Mapping microhabitat niches within sites selected for assisted migration can help managers outplant seedlings along existing habitat gradients within the sites, instead of using randomized grid layouts that have been shown to result in low establishment and success when introducing even more common and widely adapted species.

Appendix A:
Summary of Thesis Conclusions

Summary of Study Goals

Utilizing the non-destructive assessment of site, soil, and vegetation community characteristics, chapter 1 aims to identify what habitat characteristics are empirically associated with the occurrence and abundance of *E. codium* within the areas where it currently grows. Through the identification of *E. codium*'s ecological niche, this study endeavors to provide insight into the evolutionary drivers resulting in *E. codium*'s current confinement to Umtanum Ridge. Finally, an exploration of habitat characteristics across spatial scales is used to characterize "optimal" and less-optimal" vegetation habitat characteristics.

The aim of chapter two is to compare habitat characteristics measured at the single native population of *E. codium* with those present at sites identified by the WNHP habitat model as suitable habitat for assisted migration. This includes comparing areas where experimental assisted migration attempts have already occurred (Badger Mountain) or ongoing (Snow Mountain) at the time of this study, and sites deemed highly suitable where assisted migration attempts have not yet occurred (Gingko Petrified Forest State Park) (Fig 2.1). Site- level habitat characteristics at the Native Site are compared to potential habitat at Gingko State Park and three assisted migration sites at Snow Mountain. "High", "medium", and "low" "optimal" habitat groups derived from Native Site vegetation functional group data are compared to fine scale variation in habitat characteristics where outplanting of seedlings occurred at Badger and Mountain Mountains from 2020-2021.

Table A-1 **Relationship Between USFWS Recovery Actions for Umtanum Desert Buckwheat, Project Goals and Thesis Sections**
Top table indicates priority 1 and 2 recovery actions stipulated by USFWS and indicates which project goals address each recovery action. Bottom table describes the project goals and indicates in which thesis section each project goal is addressed.

Recovery Actions	Priority	Description	Project Goal
1.2.4	1	Determine the most effective methodology to establish viable individuals in the field	1,2,3,4
1.3.3	1	Ground truth model of suitable habitat for introduced efforts	1,2,3
1.4.1	1	Determine the best augmentation and reintroduction methods in suitable habitat	2,4
2.6.1	2	Investigate the species ecology	1,4

Project Goal	Description	Thesis Section
1	Determine habitat characteristics of the native site	**Chapter 1**: Habitat Assessment of the Single Native Population
2	Determine habitat differences and similarities between the native site and assisted migration sites	**Chapter 2**: Assessment of Habitat Differences Between the Native Population and Assisted Migration Locations
3	Ground truth habitat model and explore what spatial scales variation occurs	**Chapter 2 Part I**: Site Differences Between the Native and Assisted Migration Sites
4	Monitor 2020 & 2021 outplanted seedling survival and identify habitat characteristics related to seedling success	**Chapter 2 Part II**: Differences Between "Optimal" *E. codium* Vegetation Habitat Groups and Outplanting Transects

Chapter 1: Habitat Assessment of the Single Native Population

Part I: Relationship of Habitat Characteristics to *E. codium* Occurrence (presence/absence) and Abundance

Goal: Assesses importance of habitat variables on *E. codium* habitat occupancy.

Site Characteristics
Heat Load

- Heat load index is the only site variable significantly associated with *E. codium* abundance.
- *E. codium* is able to grow to highest abundance when HLI >0.75.
- The relationship between lowest *E. codium* abundance and only the highest and lowest HLI values may indicate *E. codium* is exploiting an extreme heat load niche that may begin to exceed its range of tolerance under certain habitat conditions while allowing for maximum abundance under other conditions. This may be indicative of this species evolutionary ecology

Soil Characteristics
Soil Texture

- Soil texture is the only soil variable significantly associated with *E. codium* occurrence
- *E. codium* currently grows on a range of loam derived soils with varying sand content.
- *E. codium* may be unable to tolerate clay content in soils.

Vegetation Characteristics
Total Cover

- Total cover is significantly associated with *E. codium* abundance.
- Total cover, and more specifically high cover of other species, is likely impacting where *E. codium* grows.
- Because *E. codium* cover is used to calculate total cover, this may represent a circular logical argument. Further study is necessary to better understand the relationship between cover of other species and *E. codium* abundance.

Vegetation Composition

- Vegetation composition is significantly associated both with *E. codium* occurrence and abundance.
- Vegetation composition is likely impacting both where *E. codium* can grow and how abundant it is in the areas where it occurs.
- ISA analysis indicates *E. codium* is the unique "indicator" of its own habitat, suggesting it characterizes its own "optimal" vegetation habitat type.
- Perennial bunchgrass Sandburg Bluegrass (*Poa secunda*) occurred in 100% of surveyed plots. Bluebunch wheatgrass (*Pseudoroegneria spicata*) occurred in 30% of plots. These are the only native (i.e. non-invasive) species that were recorded in 10% or more of surveyed plots. *E. codium* likely forms a primary association with *P. secunda* and a secondary association with *P. spicata*.

Vegetation Functional Group Composition

- Vegetation functional group composition is significantly associated with *E. codium* occurrence. Shrub cover is significantly associated with *E. codium* absence.
- The significant relationship between shrub cover and *E. codium* occupancy may indicate niche competition with other woody, long lived perennials.
- Avoidance of competition may be important to "optimal" *E. codium* habitat.

Part II: Variation of Habitat Characteristics Between Five *E. codium* Subpopulations
Goal: Assess differences to explore evolutionary drivers of *E. codium*'s distribution.

Despite variation in site and soil characteristics between all subpopulations, similarities in vegetation composition between the subpopulations with the largest number and/or highest abundance *E. codium* in contrast to the subpopulations with lower occurrence and abundance of *E. codium* indicate vegetation community is likely important to determining "optimal" habitat.

Subpopulation I
Largest and most abundant existing subpopulation.

→ Highest mean and range of heat load values suggests high/extreme heat load niche (upper range of specie's tolerance).
→ Low variation of soil surface composition.
→ High rock cover and high rock: bareground ratio.
→ High variation of rock fragment composition.
→ Characterized by cobble, medium and fine gravel components of rock fragment composition.
→ Significantly similar vegetation composition to subpopulations II and V despite differences in site and soil characteristics.
→ Low species richness (<5) and mean total cover (<30%).
→ Likely represents "optimal" vegetation habitat.

Subpopulation II
Remnant of formerly larger subpopulation.

→ Most variation of site and soil characteristics over the smallest areas.
→ Abundance of *E. codium* is similar to subpopulation I and consistent despite high variability of other site and soil characteristics.
→ Shares site and soil characteristics with I, III and V making it a habitat transition zone.
→ Characterized by fine and very fine gravel components of rock fragment composition.
→ Significantly similar vegetation composition to subpopulations II and V despite unique patterns in site and soil characteristics.
→ Low species richness (<5) and mean total cover (<25%).
→ Likely represents "optimal" vegetation habitat.

Subpopulation III
Remnant of formerly larger subpopulation.

→ Subpopulation crosses two distinct “habitat types”.
→ *E. codium* abundance is similar to subpopulation V.
→ Shares site and soil characteristics with all other subpopulations making it a habitat transition. zone.
→ Significantly different vegetation composition to all other subpopulations.
→ Characterized by the medium gravel component of rock fragment composition.
→ Highest perennial forb cover and high *P. spicata* cover.
→ Highest mean species richness (5) and second highest mean total cover (~35%).
→ Vegetation community is likely “less-optimal”.

Subpopulation IV
Remnant of formerly larger subpopulation.

→ Unique site, soil and vegetation characteristics.
→ Lowest abundance of *E. codium*.
→ Characterized by high biocrust component of surface composition.
→ Characterized by the cobble component of rock fragment composition.
→ Significantly different vegetation composition to all other subpopulations.
→ Highest perennial graminoid cover and highest *P. spicata* cover.
→ Similar mean species richness to subpopulations I, II and V (<5).
→ Highest mean total cover (~35%) indicates most productive vegetation community.
→ Vegetation community is likely “least-optimal”.

Subpopulation V
Second largest and most abundant existing subpopulation.

→ Lower mean and range of heat load values than subpopulation I indicates *E. codium* has the ability to grow in areas with more moderate heat loads.
→ High variation of soil surface composition.
→ High bareground cover and high bareground: rock ratio.
→ Low variation of rock fragment composition.
→ Characterized by coarse gravel component of rock fragment composition.
→ Significantly similar vegetation composition to subpopulations I and II despite differences in site and soil characteristics.
→ Low species richness (<5) and mean total cover (<25%).
→ Likely represents “optimal” vegetation habitat.

Part III: Defining "Optimal" and "Less-Optimal" *E. codium* Habitat
Goal: Assesses similarities to explore what distinguished "optimal" habitat

Six vegetation habitat groups with significant differences in *E. codium* abundance were created based on vegetation functional group composition data across all five subpopulations. These groups significantly reflect vegetation differences between subpopulations I, II and V and subpopulations III and IV.

The groups characterize high "optimal" habitat associated with the highest abundance of *E. codium* (mean cover = 23%, maximum cover = 37.5%), medium "optimal" habitat associated with moderate abundance of *E. codium* (mean cover = 10-15%), and the low "optimal" habitat associated with the lowest abundance of *E. codium* (mean cover = 4%).

High *E. codium* abundance group:

High mean *E. codium* cover- 23.5% (14% plots):
"Optimal" *P. secunda/P. spicata* vegetation association. Low perennial graminoid cover <20%.

Medium *E. codium* abundance groups:

Medium mean *E. codium* cover- 16% (30% plots):
Moderate *P. secunda/P. spicata* - moderate perennial forb (<10%) vegetation association. Moderate perennial graminoid cover <30%

Medium *E. codium* cover- 15.4% (14% plots):
Low *P. secunda/P. spicata* vegetation association. Barren/*E. codium* dominates with very low perennial graminoid cover <10%.

Medium mean *E. codium* cover- 11.36% (30% plots):
High *P. secunda/P. spicata* - low perennial forb (<3.5%) vegetation association. High perennial graminoid cover <50% and moderate annual forb cover (<10%).

Low *E. codium* abundance groups:

Low mean *E. codium* cover- 4.5% (8% plots):
High *P. secunda/P. spicata* - low perennial forb (<3.5%) vegetation association. High perennial graminoid cover up to 60%.

Low mean *E. codium* cover- 4.75% (4% plots):
Moderate *P. secunda/P. spicata* - high perennial forb (<20%) vegetation association. Moderate perennial graminoid cover <30%.

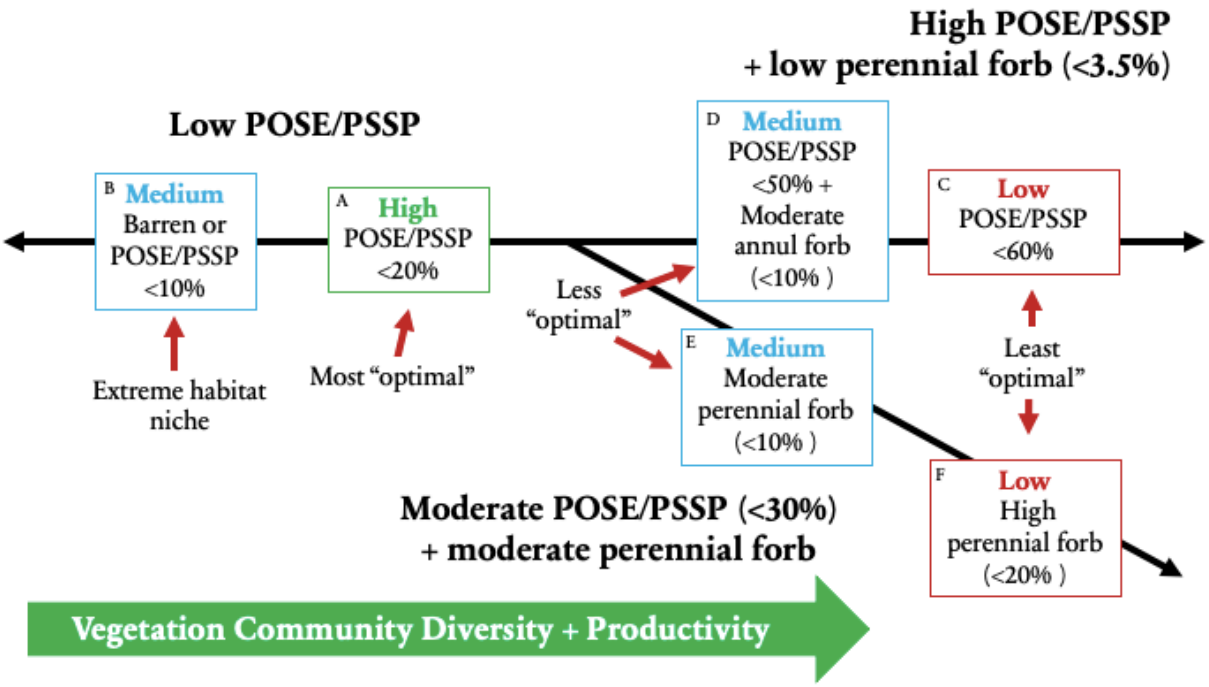


Figure A-1 **Six *E codium* Abundance Groups Illustrate a Range of "Optimal" and "Less -Optimal" *E. codium* Vegetation Habitats** Compositional similarities in vegetation functional groups between six *E. codium* abundance groups indicate *E. codium* is adapted to three distinct vegetation community types: low *P. secunda/P. spicata*, moderate *P. secunda/P. spicata*, and *P. secunda/P. spicata* + low perennial. forb cover (<3.55). These vegetation habitats exist on a continuum of lowest to highest vegetation productivity and community diversity, reflecting the continuum of high, medium and low *E. codium* abundance.

- Six habitat groups are grouped into three vegetation habitat types based on compositional similarities. Vegetation habitat types do not reflect spatial differences between subpopulations and instead reflects similarities between different microhabitats occurring in a heterogenous spatial arrangements across the five subpopulations.

- Highest *E. codium* abundance (high "optimal" habitat) is associated with low *P. secunda/P. spicata* cover. Medium *E. codium* abundance (medium "optimal" habitat) is associated with moderate *P. secunda/P. spicata* cover and moderate to high perennial forb cover. Low *E. codium* abundance (low "optimal" habitat) is associated with high *P. secunda/P. spicata* cover and low perennial forb cover (<3.5%).

- The majority of measured site, soil and vegetation characteristics were similar between the three "optimal" *E. codium* habitat groups: high, medium and low.

- Despite this, more key habitat characteristics differed between the high/low and medium groups than between the high and low groups:

Hillslope Position- High group distinct
Soil Texture- High group distinct
Heat Load- Medium group distinct
Slope Shape- Medium group distinct
Slope (rise/run)- Medium group distinct

Perennial Forb Cover- Medium group distinct
Aspect- Low group distinct

- This likely indicates high and low "optimal" vegetation habitat groups occupy similar marginal habitats areas. Variation in localized conditions likely at fine spatial scales results in either successful *E. codium* occupancy and high abundance when perennial graminoid competition is low or less successful *E. codium* occupancy and low abundance when perennial graminoid competition is high.

- The medium group likely represents a distinct habitat type that is more conducive to perennial forb cover. While *E. codium* is able to occupy these areas and survive, these areas do not provide the most optimal conditions required to reach highest abundance.

- Differences in mean variables strength between high, medium, and low "optimal" *E. codium* habitat groups indicate which site, soil and vegetation characteristics are positively or negatively associated with *E. codium* abundance:

Likely *Positively* Associated with *E. codium* Abundance:
Total Cover
Heat Load
Total Rock Fragment Class
Rock component of surface composition
Stone and fine gravel components of surface rock fragment composition

Likely *Negatively* Associated with *E. codium* Abundance:
Shrub, annual forb, and perennial graminoid components of vegetation functional group composition
Litter and biocrust component of surface composition
Cobble and coarse gravel components of surface rock fragment composition

Chapter 2: Assessment of Habitat Differences Between the Native Population and Assisted Migration Location

Part I: Site Differences Between the Native and Assisted Migration Sites

Significant differences were determined between the Native Site and Assisted Migration Sites at Gingko State Park and Snow Mountain for all site, soil and vegetation characteristics *except* slope shape and slope complexity.

Table A-2 **Habitat Similarities Between the Native and Assisted Migration Sites**
Summary table of significantly similar site, soil and vegetation characteristics between the Native and Assisted migration sites.

Similarities Between the Native and Assisted Migration Sites				
	GSP	**SM1**	**SM2**	**SM3**
Site Characteristics	**5**	**4**	**6**	**3**
Landscape position				
Hillslope Position	X			
Slope (rise/run)	*	X	X	
Slope (°)	X	X	X	
Slope Shape	X	X	X	X
Slope Complexity	X	X	X	X
Aspect	*		X	
Heat Load	X		X	X
Rock Fragment Class	*		*	*
Soil Characteristics	**2**	**0**	**0**	**0**
Hydraulic Conductivity (K)				*
Soil Texture	X		*	*
Soil Surface Composition	X			
Soil Surface Rock Fragment Composition				
Vegetation Characteristics	**2**	**1**	**1**	**3**
LAI	*			*
Vegetation Composition				
Total Cover	*	X	X	
Species Richness	*			*
Shrub			*	X
Subshrub				
Perennial Forb	*			
Annual Forb	X			X
Perennial Graminoid				
Annual Graminoid	X			X
Total	**9**	**5**	**7**	**6**

Site and Soil Characteristics

- Assisted migration sites showed variable similarity to the Native Site across site and soil characteristics. All sites share some site and soil habitat similarity to the range of habitat variation observed at the Native Site.

- ISA analysis indicates the Native Site is uniquely characterized by the rock component of surface composition and the fine and very fine gravel components of rock fragment composition.

- Varying levels of overlap between site and soil characteristics indicate no one site matches the Native Site. Gingko State Park shares the most similarities in site and soil characteristics to the Native Site while Snow Mt 2 and Snow Mt 3 have more similarities than Snow Mt 1.

- Significant differences in key site variables such as heat load and soil texture were determined between the Native and assisted migration sites. Some overlap in soil texture classification and the range of heat load index values were observed between sits despite significant differences in site-level variation. This suggests microhabitat similarities occur between sites at smaller scales than captured at the 30m scale or the scale used by the habitat model.

Vegetation Characteristics

- Little to no similarities in vegetation composition or vegetation functional group composition was determined between the Native Site and assisted migration site. The most compositional overlap with the native sites was observed with some areas of Gingko State Park and Snow Mountain 3.

- Assisted migration sites have more productive vegetation communities than the native site. Gingko State Park and Snow Mountain 3 have the significantly lower productivity vegetation communities than Snow Mountains 1 and 2.

- ISA analysis indicates the Native Site is uniquely characterized by subshrub and perennial graminoid cover.

- Shrub cover and perennial forb cover was significantly higher at assisted migration sites than at the Native Site, while subshrub and perennial graminoid cover was significantly higher at the Native Site than assisted migration sites.

- All assisted migration sites had either woody shrubs and/or woody subshrubs in the *Eriogonum* genus already occupying the site. Gingko State Park and Snow Mountain sites 2 and 3 are all characterized by more widespread and abundant *Eriogonum* species growing in association with perennial graminoids and forbs. This suggests the niche *E. codium* occupies at the Native Site is already being filled by other woody perennial

species and subshrubs in the *Eriogonum* genus, likely making these sites unsuitable for *E. codium* occupancy if it is unable to successfully compete for niche occupancy with more widely adapted and established species.

Assessment of WNHP Habitat Model

- Washington Natural Heritage Program habitat model reflets overall similarities and differences between Gingko State Park and Snow Mountain at a landscape-scale, but did not accurately reflect variation between assisted migration sites within locations.

- The scale of habitat variation within the model is not adequate to assess the variation of microhabitat similarities between assisted migration sites and the Native Site likely impacting successful *E. codium* site occupancy

- A more accurate tool is needed to quantitatively link location selection across the Columbia Plateau bioregion to assisted migration site selection within a target location.

- Comparing habitat suitability of the Native Site averaged across subpopulations losses important variation within the population indicative of *E. codium* evolutionary ecology that likely impact successful *E. codium* site occupancy

Part II: Differences Between "Optimal" *E. codium* Vegetation Habitat Groups and Outplanting Transects, and Their Relationships to Seedling Survival

Monitoring 2020 and 2021 Seedling Survival at Badger and Snow Mountains 2022-2023

Badger Mountain

- 14% (4/29) of seedlings planted in 2020 survived at Badger Mountain in 2023. All seedlings belonged to the same spatial cluster of seedlings (group 1). In group 1 80% (4/5) seedlings survived, suggesting the microhabitat niche occupied by this cluster was more suitable for *E. codium* than the surrounding area.

Snow Mountain

- No seedlings planted in 2020 survived at Snow Mountain in 2022. This is likely due to the heat wave and extreme temperatures experience by young seedlings during the heat wave in June-July 2021.

- >50% of seedlings planted in 2021 were alive at Snow Mountain outplanting transects SM2-21, SM3-1 and SM3-4 in 2022. <50% of seedlings were alive at the 2021 outplanting transect at Snow Mountain Site 1 and at SM3-2. SM3-3, and SM3-5.

- In 2023, 3% of seedlings planted in 2021 were alive at Snow Mountain. One seedlings was alive at both outplanting transects SM-1 and SM-5, while four seedlings were alive at SM-4.

- Highest survival at SM-4 suggests this outplanting transects provides a microhabitat niche more suitable for *E. codium* than the surrounding outplanting transects. Low survival at SM-1 and SM-5 suggest seedlings are able to take advantages in small-scale differences in habitat suitability across an assisted migration site.

- SM-5 has low survival in 2022 but one seedlings remaining in 2023, while SM2-21 initially had higher survival rates recorded in 2022 but no seedlings surviving in 2023. These contrasting patterns in survival suggest *E. codium* may respond differently to differences in habitat similarity to the Native Site.

Three "Optimal" E. codium Vegetation Habitat Groups

High: mean *E. codium* cover- 20%
E. codium – P. secunda/P. spicata association with low perennial graminoid cover <20%

Medium: mean *E. codium* cover- 14%
E. codium – P. secunda/P. spicata - perennial forb association cover <20%

Low: mean *E. codium* cover- 10%
E. codium – P. secunda/P. spicata association with high perennial graminoid cover <60%

Comparison of "Optimal" E. codium Vegetation Habitat Groups and Outplanting Transects

- Significant differences were determined between the "Optimal" *E. codium* habitat groups and outplanting transects for all site, soil and vegetation characteristics *except* total rock fragment class.

- Slope shape, slope complexity and total cover were close to being statically similar between the "optimal" habitat groups and outplanting transects.

Table A-3 **Outplanted Seedling Survival at Badger and Snow Mountains 2020-2023**
Summary table of seedling survival for 2020 and 2021 cohorts. Survival was monitored in 2022 and 2023. Survival rates are shown for six distinct planting clusters with a 7x14m area at Badger Mountain, and for individual outplanting transects at Snow Mountain sites 1, 2 and 3.

Seedling Outplanting Survival

Outplanting Grouping	2020	2021	2022	% Surivival	% Decline	2023	% Surivival	% Decline
Badger Mt (14%)								
BM1-1	5	-	-	-	-	4	80	-20
BM1-2	4	-	-	-	-	0	0	-100
BM1-3	4	-	-	-	-	0	0	-100
BM1-4	4	-	-	-	-	0	0	-100
BM1-5	6	-	-	-	-	0	0	-100
BM1-6	6	-	-	-	-	0	0	-100
Snow Mt 1 (0%)								
SM1-2020	20	20	0	0	-100	0	0	0
SM1-2021	-	44	15	34	-66	0	0	-34
Snow Mt 2 (0%)								
SM2-2020	20	20	0	0	-100	0	0	0
SM2-2021	-	44	25	57	-43	0	0	-57
Snow Mt 3 (3%)								
SM3-1	-	44	26	59	-41	1	2	-57
SM3-2	20	20	0	0	-100	0	0	0
SM3-3	-	44	18	41	-59	0	0	-41
SM3-4	-	44	25	57	-43	4	9	-48
SM3-5	-	44	16	36	-64	1	2	-34

Table A-4 **Habitat Similarities Between the three "Optimal" *E. codium* Habitat Groups (high, medium, low) and Outplanting Transects at Badger and Snow Mountain Sites 1-3**
Summary table of significantly similar site, soil and vegetation characteristics between Optimal" *E. codium* Habitat Groups and outplanting Transects.

Similarities Between Optimal *E.codium* Habitat Groups and Outplanting Transects

	BM1	SM1-20	SM1-21	SM2-20	SM2-21	SM3-1	SM3-2	SM3-3	SM3-4	SM3-5
Site Characteristics	**4**	**4**	**3**	**3**	**5**	**4**	**4**	**2**	**3**	**3**
Landscape position										
Hillslope Position				*low	**all**	*high	*high	*high	*high	*high/medium
Slope (rise/run)			*high/medium		*all	**high/medium**	*all	*all	*all	*all
Slope (°)	**all**	**all**	*all	**all**	*all	*all				
Slope Shape	**high/low**	**high/low**	**high/low**	**medium**	**high/low**	*high/low	**high/low**	**high/low**	**high/low**	**high/low**
Slope Complexity	**all**	**all**	**all**	**all**	**all**	**all**	**all**	*all	**all**	*all
Aspect	*high/medium	*all	*high/medium		**high/medium**	*low	**low**	*all	*all	**high/medium**
Heat Load			*high/medium		*all	**high/medium**	*all	*all	*all	*all
Rock Fragment Class	**all**	**all**	**all**	**all**	**all**	**all**	**all**	**all**	**all**	**all**
Soil Characteristics	**1**	**1**	**1**	**1**	**1**	**3**	**1**	**1**	**2**	**2**
Hydraulic Conductivity (K)	**all**	**all**	**all**	**all**	**all**	**all**	**all**	**all**	**all**	**all**
Soil Texture		*high	*high	*all	*all	**high**	*all	*all	*all	
Soil Surface Composition									**medium**	**all**
Soil Surface Rock Fragment Composition						**medium**				
Vegetation Characteristics	**4**	**2**	**2**	**3**	**3**	**3**	**3**	**3**	**3**	**3**
Vegetation Composition										
Total Cover	**all**	**all**	**all**	**all**	**all**	**all**	**all**	**all**	**all**	**all**
Species Richness	**all**									
Shrub	*all	*all		*all		*all	*all	*all	*all	*all
Subshrub		*low	*low		*low	*low	*low	*low	*low	
Perennial Forb	**medium**			*medium						
Annual Forb	*all		*all		*all	*all	*all	*all	*all	*all
Perennial Graminoid	**high/medium**	**high**	**high/medium**	**high/medium**	**high/medium**	**high/medium**	**high/medium**	**high/medium**	**high/medium**	**high/medium**
Annual Graminoid			*all	**all**	**all**	**all**	**all**	**all**	**all**	**all**
Total	**9**	**7**	**6**	**7**	**9**	**10**	**8**	**6**	**8**	**8**

Badger Mountain

Site Characteristics

- Badger Mountain occupies a high HLI niche that *E. codium* may be able to exploit under certain habitat conditions but was likely at the edge of its range of tolerance and was intolerable under stressful conditions

Soil Characteristics

- Outplanted seedlings appear to be able to grow on silt loam soils not present at the Native Site. It is unclear to what extent soil texture impacts *E.* codium habitat suitability.

Vegetation Characteristics

- Outplanting transect at Badger Mountain was the only one to have both similar species richness and total cover to all optimal habitat groups. This suggests important similarities in vegetation productivity that likely impacted seeding survival there.

- While perennial graminoid and perennial forb cover was similarly low at Badger Mountain and in the optimal habitat groups, annual graminoid cover was significantly higher and likely negatively impacted habitat suitability for young seedlings.

- Vegetation compositional similarity at Badger Mountain to “medium” and “low” optimal habitat groups suggest existence of a micro-habitat niche seedlings may have been able to exploit.

Snow Mountain

Site Characteristics

- All outplanting transects had varying similarity in site characteristics to the optimal habitat groups. SM2-21 had the most site similarities which may have resulted in early rates of high seedling survival observed in 2022.

- Outplanting transects at Snow Mt 1 and Snow Mt 2-20 occupy a high HLI niche that reflected the extreme conditions of the optimal low habitat group and likely contributed to seedlings loss in these areas. Outplanting transects at SM-3 occupied a mid- range of heat loads that reflected the high and medium optimal habitat groups and may have contributed to higher overall survival rates at this outplanting site.

Soil Characteristics

- Only outplanting transects where seedlings were alive in 2023-SM3-1, SM3-4 ,and SM3-5- had soil similarities to the optimal habitat groups. This suggests these similarities may be important in determining seedlings survival.

- Outplanting transects SM3-4 and SM3-5 both showed significant similarities in soil surface composition to the optimal medium group, while SM3-1 showed significant similarity in rock fragment composition to the optimal medium group. This suggests both soil surface composition and rock fragment composition are important habitat characteristics impacting seedling survival. Targeting habitat conditions in the optimal medium group, while likely not optimal for maximum *E. codium* growth, may be tolerable enough for seedling survival and successful assisted migration.

Vegetation Characteristics

- While all outplanting transects has similarly low total cover as the optimal habitat groups, species richness was significantly higher. This indicates outplanting occurred in more diverse and spices rich communities than *E. codium* associates with in its optimal vegetation habitat.

- Low total cover and wide variation of species richness at outplanting transects SM3-1, SM3-4 and SM-5 suggesting seedlings that survived were able to exploit microhabitat areas that had both low total cover and species richness, minimizing competition.

- While outplanting transects SM3-1, SM3-4 and SM-5 had low graminoid cover similar to optimal habitat groups, forb cover was significantly higher and likely contributed to the overall low seedling survival observed. Wide variation in forb cover within these outplanting areas suggests the areas where minimum forb cover values overlapped with the maximum forb cover values of the optimal medium group comprise low competition microhabitats surviving seedlings may have been able to exploit.

- Vegetation functional group similarity within outplanting transects SM2-21, SM3-1, SM3-4, and SM-5 and the “medium” optimal habitat group likely constitutes the best micro-habitat areas to “target” for assisted migration.

Importance of Microhabitat Variation in E. codium Seedlings Survival

- Fine scale micro-habitat variation within outplanting areas may provide the small-scale habitat heterogeneity that *E. codium* can exploit and thus requires for establishment.

- *E. codium* may be able to exploit niches of low competition when introduced at sites where competitive pressure from other species limits establishment.

- Outplanting transects may be able to capture important micro-habitat similarities at assisted migration sites challenging to predict at the coarser spatial scales of the habitat model and site level assessment.

- Quantitative assessments of micro-habitat heterogeneity at assisted migration sites and proposed outplanting areas may allow mangers to better target "optimal" habitat characteristics in heterogenous landscapes.

Final Conclusions

- While this research has attempted to established a range of key habitat characteristics *E. codium* is known to grow within and identify which of these habitat characteristics might determine suitable habitat for assisted migration, future research is necessary to establish this species range of tolerance to key environmental and ecological conditions such as heat, moisture, soil characteristics and inter-species competition.

- Evolutionary models of rarity and speciation within the genus *Eriogonum* rely on species adaptability to a range of marginal and possibly extreme habitat conditions that restrict the growth of other more widely adapted species

- Better understanding both genetic and functional trait diversity of the seed used for assisted migration can help to better understand and model the response of *E. codium* to habitat variation in the field

Appendix B: Chapter 1 Part I
ERCO Occurrence/ Abundance Data Summary Tables

Table B-1 **Summary of Site Characteristics by *E. codium* Occurrence**
Mode of categorical site characteristics (top) and mean, maximum/minimum (range), and standard deviation (sd) of continuous site characteristics (bottom) where *E. codium* is present and absent (n=90). Mode of soil suface texture is included with catagorical varaiables (top). Catagorical site characteristics include landscape position (BS_UT = backslope- upper third, SH_LT= shoulder-lower third, SH_MT = shoulder-middle third, SH_UT= shoulder- upper third, SU_LT = summit-lower third, SU_UT = summit-lower third), slope shape (CC= concave-concave, CL= concave-linear, CV = concave-convex, LC= linear-concave, LL= linear-linear, LV= linear-convex, VC= convex-concave, VL= convex-linear, VV= convex-convex), slope complexity (C= complex, S= simple), and aspect (N = north, NE = northeast, E= east, SE= southeast, SW= southwest, W= west, NW= northwest).

Occurance of of *E. codium*		
Site Characteristics	**Absent** (n=26)	**Present** (n=64)
Landfrom	MT	MT
Hillslope Position	SH	SH
Slope Position	UT	UT
Slope Complex	S	S
Slope Shape	LL	LL
Aspect	W	E
Soil Surface Texture	Loamy Sand	Sandy Loam

	Absent (n=26)			**Present** (n=64)		
Site Characteristics	Mean	Range	sd	Mean	Range	sd
Heat Load	0.73	0.47-0.92	0.11	0.70	0.49-0.9	0.11
Slope (cm/cm)	0.18	0-0.51	0.11	0.20	0.03-0.53	0.11
Slope Angle (°)	10.85	2-30	7.11	11.74	2-27	6.25
Total Rock Fragment Class (%)	59.21	9-75	24.99	58.62	9-75	22.55

Table B-2 **Summary of Soil Characteristics by *E. codium* Occurrence**
Mode of categorical site characteristics (top) and mean, maximum/minimum (range), and standard deviation (sd) of continuous site characteristics (bottom) where *E. codium* is present and absent (n=90).

	Occurance of *E. codium*					
	Absent			**Present**		
Soil Characteristics	Mean	Range	sd	Mean	Range	sd
Soil Hydrology (n= 71)						
Hydraulic Conductivity (k)	9.20×10^{-4}	-0.00267-0.00621	2.27×10^{-3}	1.53×10^{-3}	-0.00264-0.01548	3.09×10^{-3}
Soil Surface Cover (n=90)						
Bareground	13	0-38	14	11	0-62	14
Biocrust	0.00	0-3	1.00	1.00	0-20	3.00
Litter	4	0-20	5	5	0-38	7
Rock	72	38-88	20	73	20-88	20
Soil Surface Rock Fragment Cover (n=90)						
Boulder	2	0-20	5	0	0-10	1
Cobble	10	0-62	18	10	0-62	15
Course Gravel	19	0-62	17	23	0-62	21
Fine Gravel	26	3-62	16	26	0-88	25
Medium Gravel	29	0-88	20	27	0-88	17
Stone	1	0-20	4	0	0-20	3
Very Fine Gravel	11	0-88	20	6	0-62	12

Table B-3 **Summary of Vegetation Characteristics by *E. codium* Occurrence**
Mean, maximum/minimum (range), and standard deviation (sd) of vegetation characteristics where *E. codium* is present and absent (n= 90).

	Occurance of *E. codium*							
	Absent (n=26)				**Present** (n=64)			
Vegetation Characteristics	n	Mean	Range	sd	n	Mean	Range	sd
ERCO	26	0.00	0-0	0.00	64	14.09	0.5-37.5	8.62
Leaf Area Index	21	0.02	0-0.08	0.02	50	0.03	0-0.78	0.11
Species Richness	26	3.00	0-9	1.81	64	3.00	2-7	1.09
Total Cover	26	26.48	0-98	27.99	64	33.02	3.5-70.5	15.92
Total Cover Adjusted	26	26.48	0-98	27.99	64	18.92	0.5-60.5	13.30

Appendix C: Chapter 1 Part I

Stress Plots of NMDS ordinations of Soil Surface, Soil Surface Rock Fragment, and Vegetation Composition Data for Visualizing *E. codium* Occurrence and Abundance

Table C-1 **NMDS Stress Plot for Soil Surface Composition for *E. codium* Occurrence (n= 90)**
Shepard plot of soil surface composition showing the Euclidean distances between plots in the 2-dimensional ordination space (Ordination Distance).

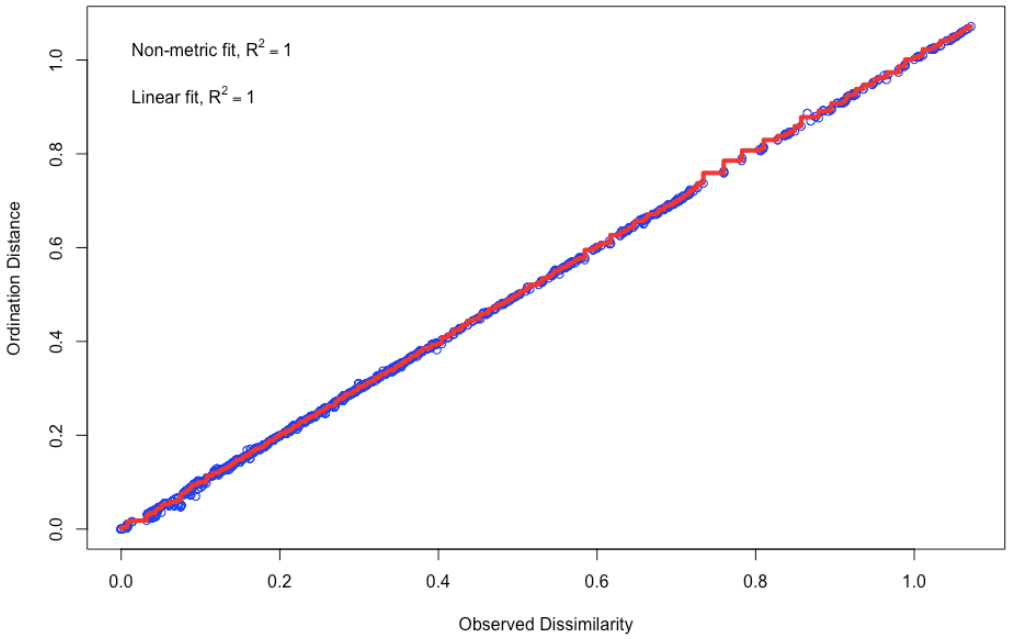


Table C-2 **NMDS Stress Plot of Soil Surface Rock Fragment Composition for *E. codium* Occurrence (n= 90)**
Shepard plot of soil surface rock fragment composition showing the Euclidean distances between plots in the 3-dimensional ordination space (Ordination Distance).

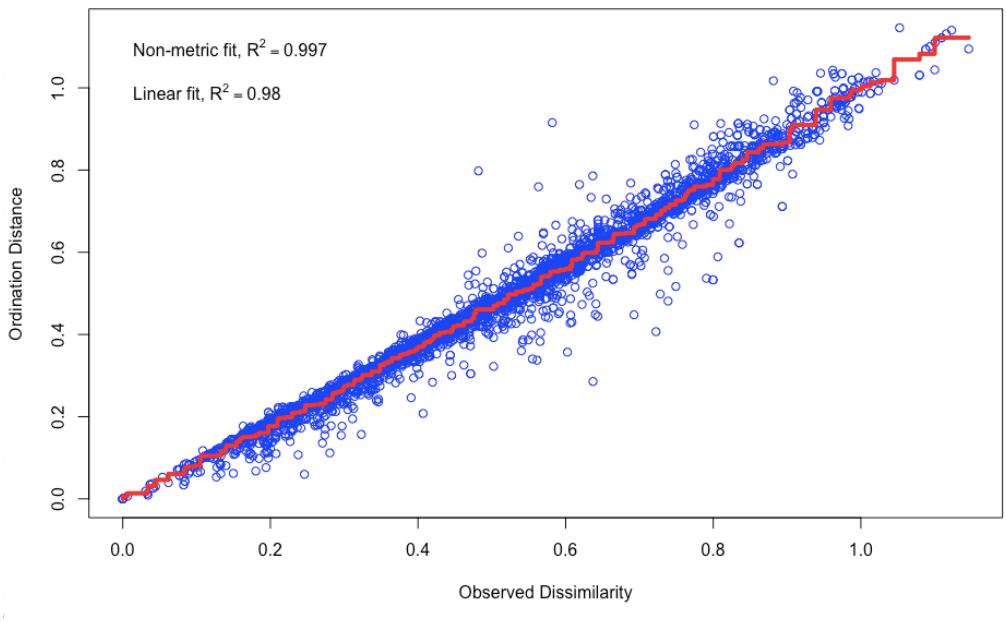


Table C-3 **NMDS Stress Plot of Vegetation Composition for *E. codium* Occurrence (n= 90)**
Shepard plot of vegetation composition showing the Bray-Curtis distances between plots in the 3-dimensional ordination space (Ordination Distance).

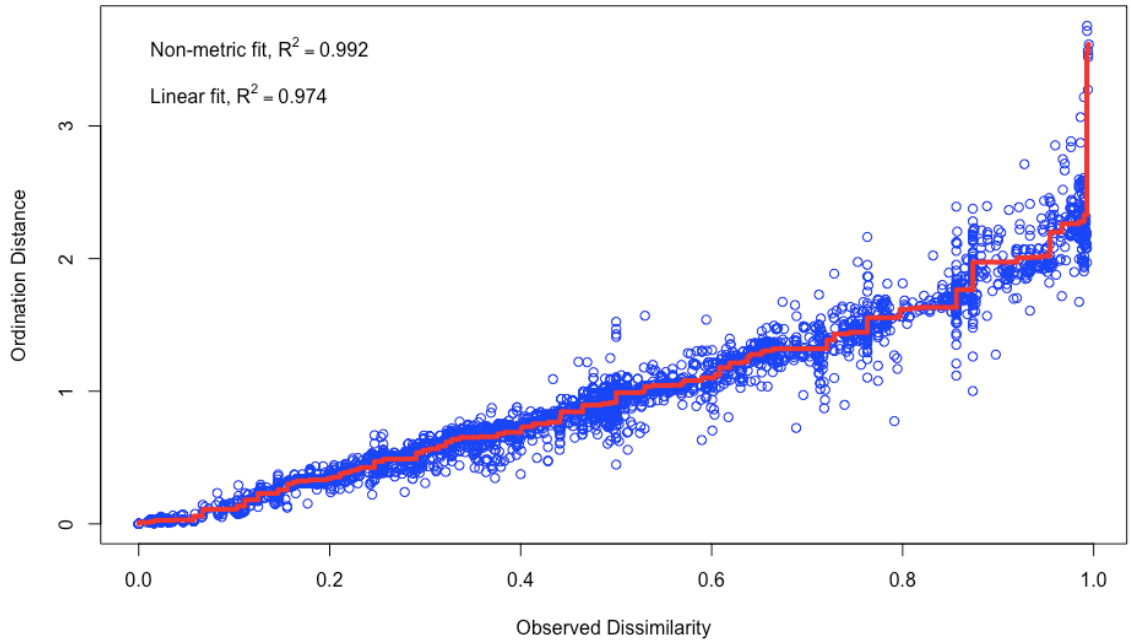


Table C-4 **NMDS Stress Plot for Soil Surface Composition for *E. codium* Abundance (n= 98)**
Shepard plot of soil surface composition showing the Euclidean distances between plots in the 2-dimensional ordination space (Ordination Distance).

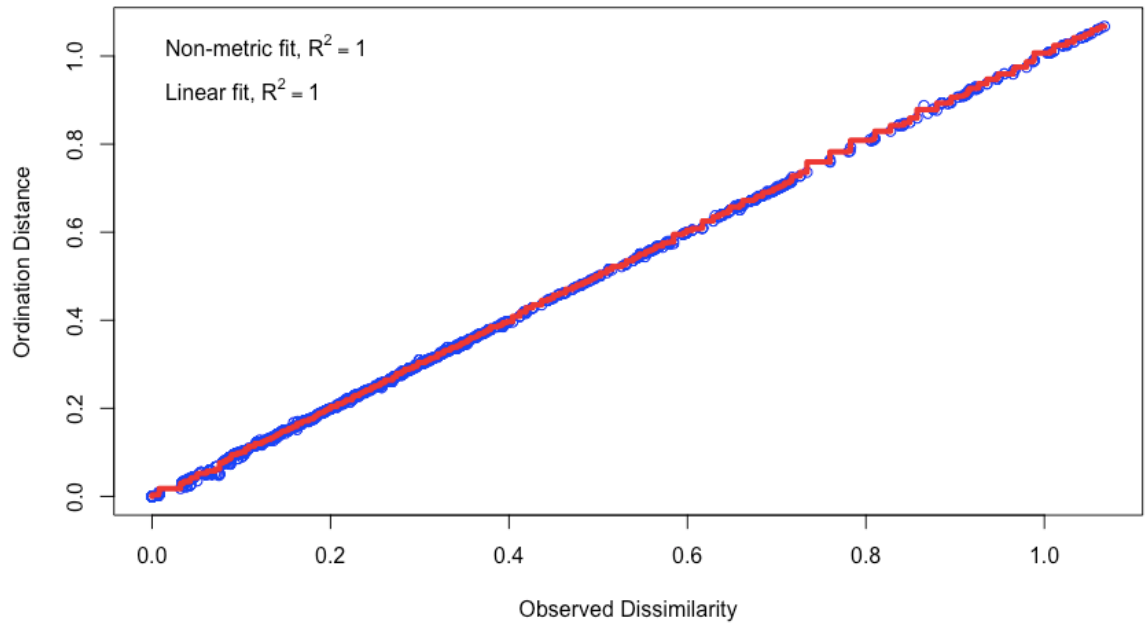


Table C-5 **NMDS Stress Plot of Soil Surface Rock Fragment Composition for *E. codium* Abundance (n= 72)**
Shepard plot of soil surface rock fragment composition showing the Euclidean distances between plots in the 3-dimensional ordination space (Ordination Distance).

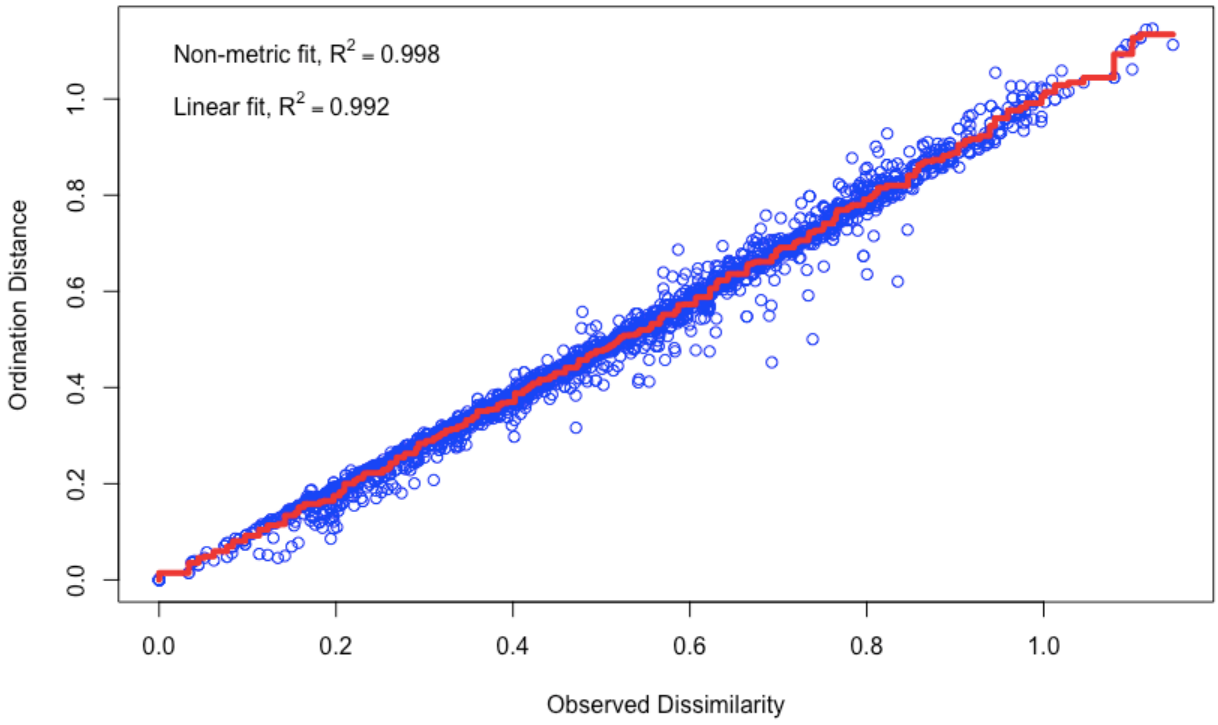
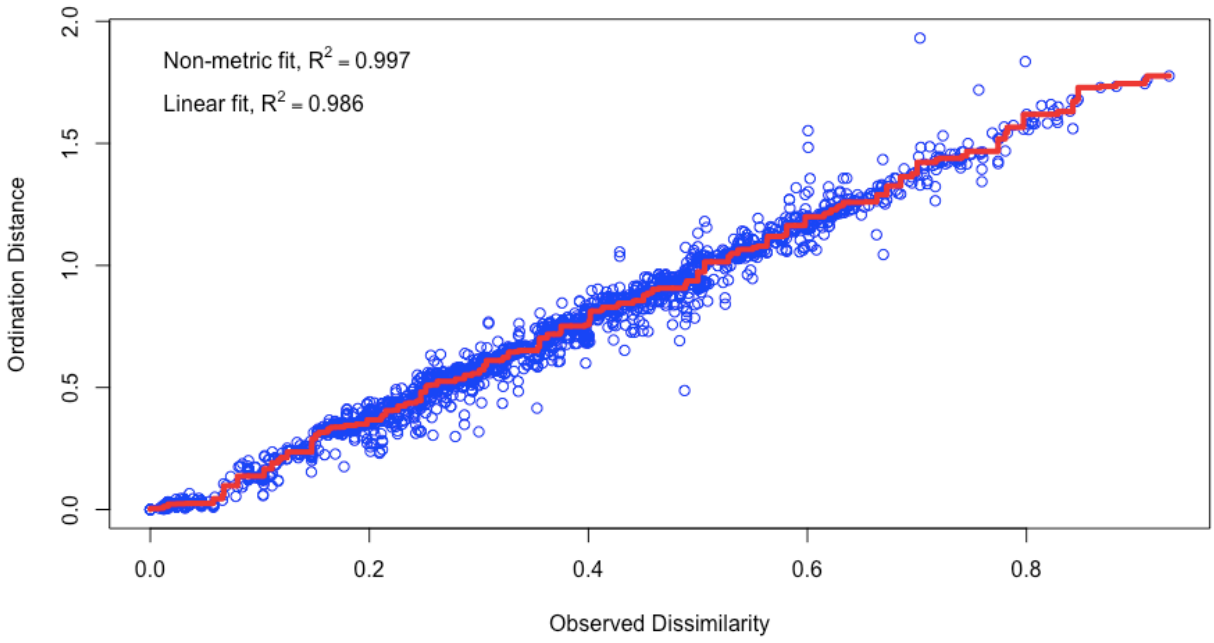


Table C-6 **NMDS Stress Plot of Vegetation Composition for *E. codium* abundance (n= 72)**
Shepard plot of vegetation composition showing the Bray-Curtis distances between plots in the 3-dimensional ordination space (Ordination Distance).



Appendix D: Chapter 1 Part I
Subpopulation/Transect Pairwise ADONIS Tables

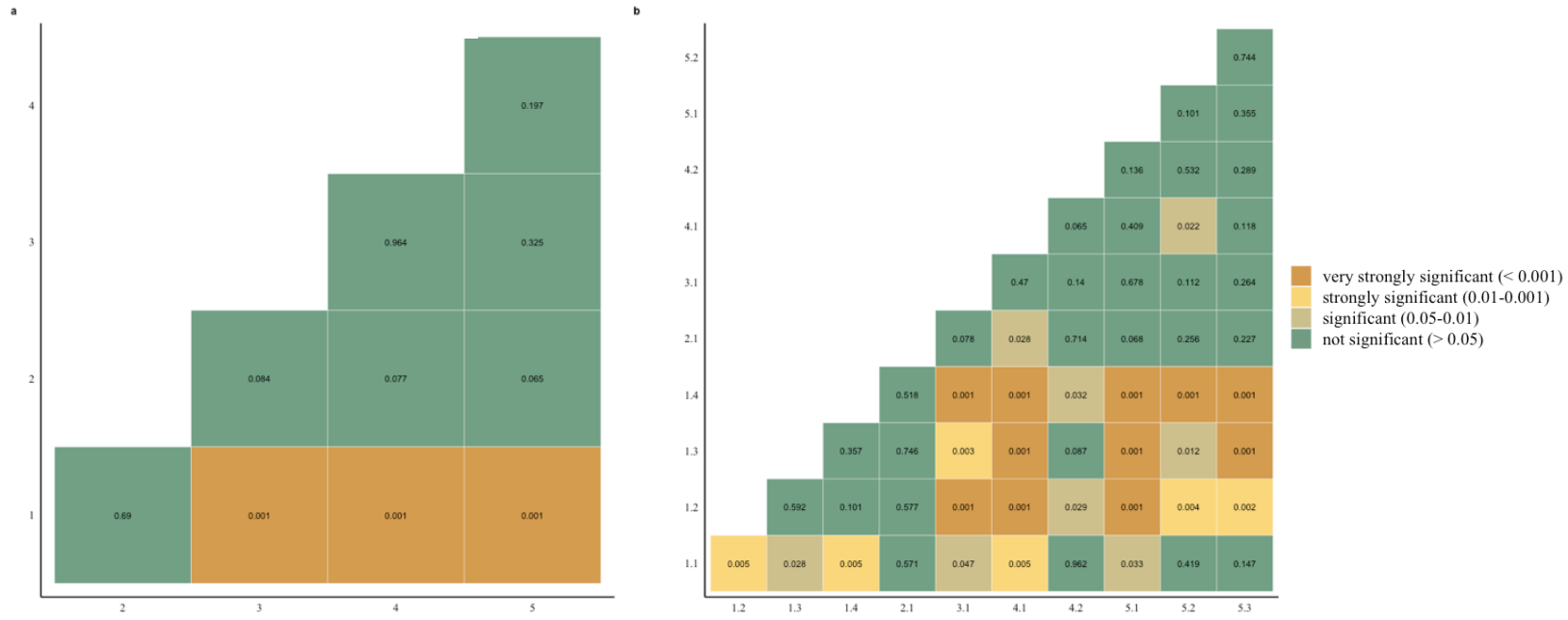


Figure D-1 **Pairwise Comparison of Soil Surface Composition by Subpopulation and Transects** Heatmap of p-values resulting from ADONIS pairwise comparison of differences in soi surface composition by subpopulation (A) and transect (B) (n= 98). Tile colors correspond to strength of significance: brown = ≤ 0.001 (very strong significant difference), yellow = 0.01-.001 (strong significant difference), beige = 0.05-0.01 (significant difference), green = no significant difference (p = > 0.05) .

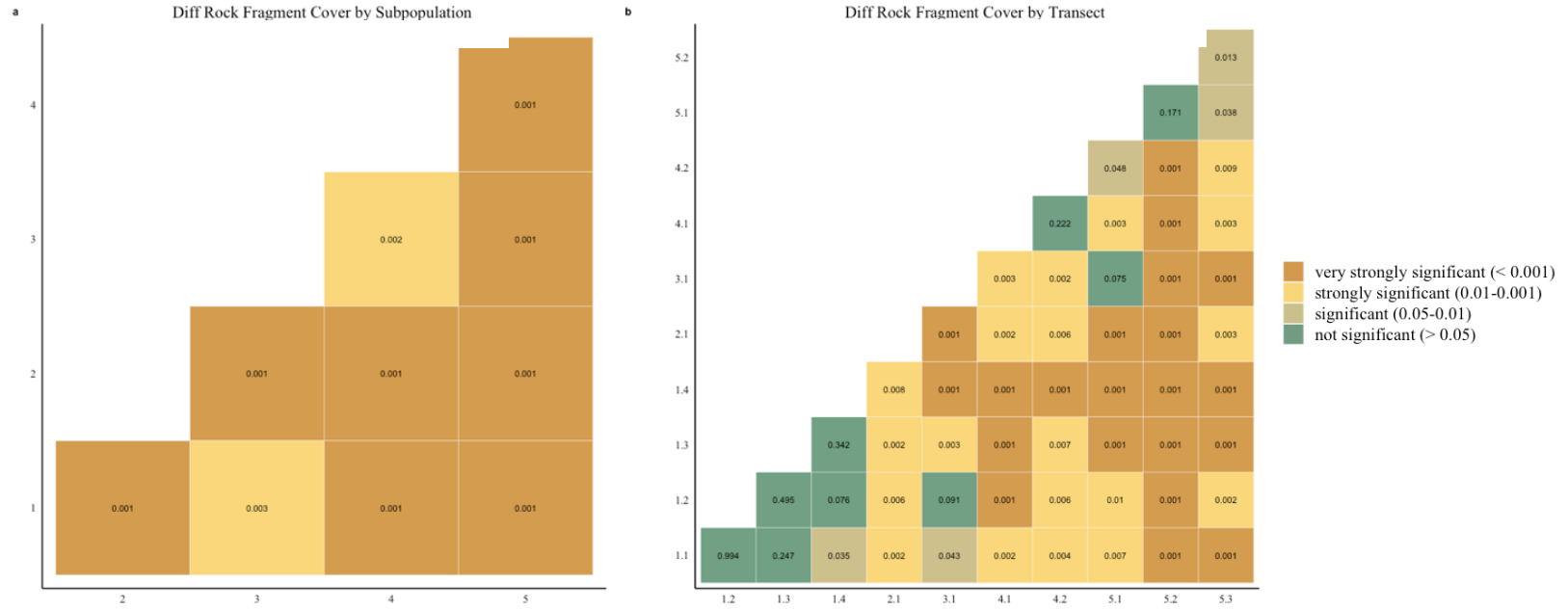


Figure D-2 **Pairwise Comparison of Soil Surface Rock Fragment Composition by Subpopulation and Transects** Heatmap of p-values resulting from ADONIS pairwise comparison of differences in soi surface rock fragment composition by subpopulation (A) and transect (B) (n= 98). Tile colors correspond to strength of significance: brown = ≤ 0.001 (very strong significant difference), yellow = 0.01-.001 (strong significant difference), beige = 0.05-0.01 (significant difference), green = no

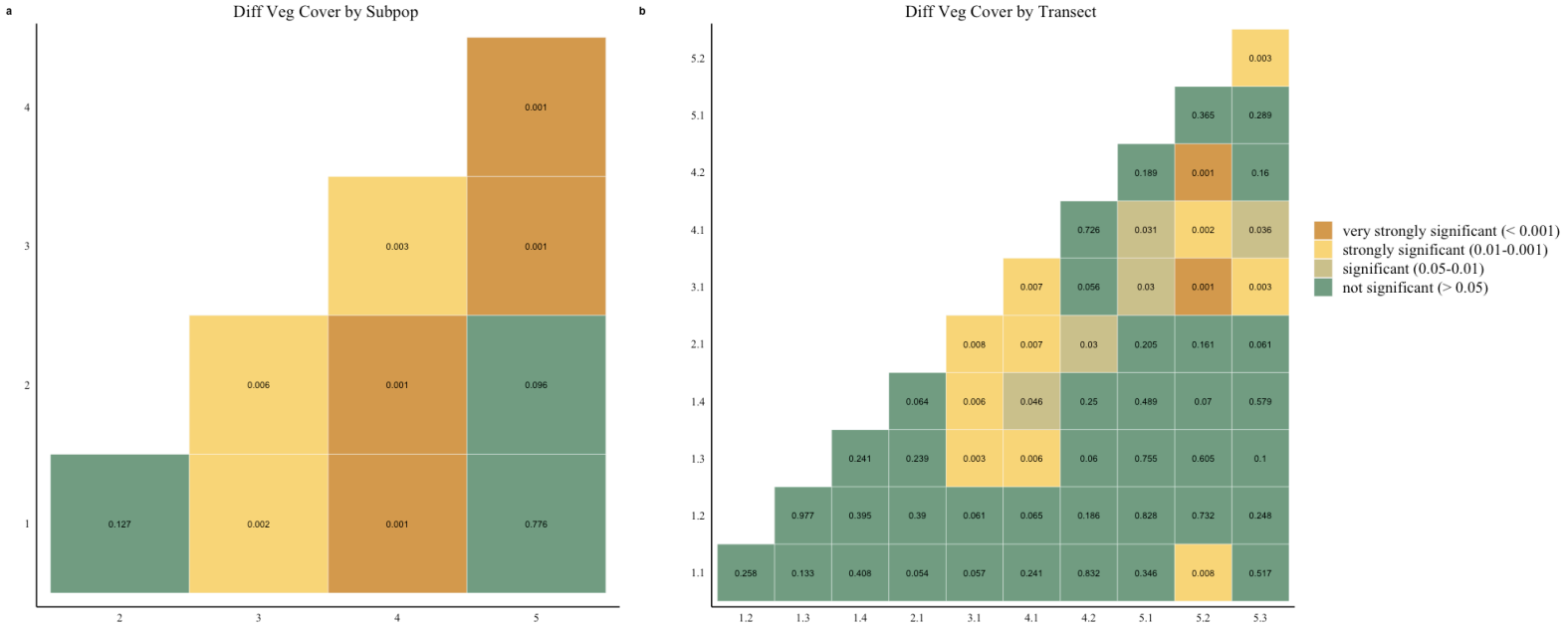


Figure D-3 **Pairwise Comparison of Vegetation Composition by Subpopulation and Transects**
Heatmap of p-values resulting from ADONIS pairwise comparison of differences in vegetation composition by subpopulation (A) and transect (B) where *E. codium* is present (n=72). Tile colors correspond to strength of significance: brown = $\leq$ 0.001 (very strong significant difference), yellow = 0.01-.001 (strong significant difference), beige = 0.05-0.01 (significant difference), green = no significant difference (p = > 0.05) .

Appendix E: Chapter 1 Part II
Subpopulation/Transect Summary Tables

Table E-1 **Summary of Categorical Site Characteristics by Subpopulation and Transect**
Mode of categorical site characteristics by subpopulation and transect (n= 98). Multilpe levels are included when frequencies are the same. Site characteristics include landscape position (BS_UT = backslope- upper third, SH_LT= shoulder-lower third, SH_MT = shoulder-middle third, SH_UT= shoulder- upper third, SU_LT = summit-lower third, SU_UT = summit-lower third) (A), slope shape (CC= concave-concave, CL= concave-linear, CV = concave-convex, LC= linear-concave, LL= linear-linear, LV= linear-convex, VC= convex-concave, VL= convex-linear, VV= convex-convex (B), slope complexity (C= complex, S= simple) (C), and aspect (N = north, NE = northeast, E= east, SE= southeast, SW= southwest, W= west, NW= northwest). Mode of soil suface texture where *E. codium* is present is included with catagorical varaiables (n= 72).

Spatial Grouping	n	Landform	Hillslope Position	Slope Position	Slope Complex	Slope Shape	Aspect	Soil Surface Texture
Subpopulation								
1	44	MT	SH	UT	S	LL	W	Loamy Sand
2	6	MT	SH	UT	LC + VL	LC	N	Loamy Sand
3	8	MT	SU	LT	C	LC	NW	Loamy Sand
4	13	MT	BS	UT	LC + VV	LC	N	Sandy Loam
5	27	MT	SH	MT	S	LL	E	Sandy Loam
Transect								
1.1	8	MT	SH	UT	S	LL	W	Loamy Sand
1.2	10	MT	SH	UT	S	LL	SW	Loamy Sand
1.3	11	MT	SH	UT	S	LL	SW + W	Loamy Sand
1.4	15	MT	SH	UT	S	LL	NW	Loamy Sand + Sandy Loam
2.1	6	MT	SH	UT	S	VV	N	Loamy Sand
3.1	8	MT	SU	LT	C	CC + LL + VL	NW	Loamy Sand
4.1	9	MT	BS	LT + UT	C	VL	N	Sandy Loam
4.2	4	MT	SH	UT	C	LC	N	Sandy Loam
5.1	10	MT	SH	UT	C + S	LL	E	Sandy Loam
5.2	12	MT	SH	MT	S	LL	E	Sandy Loam
5.3	5	MT	SH	LT	C	LV	E	Loamy Sand + Sandy Loam

Table E-2 **Summary of Continuous Site Characteristics by Subpopulation and Transect**
Mean, minimum/maximum (range), and standard deviation (sd) of site characteristics by subpopulation and transect (n= 98).

		Heat Load Index			Slope (cm/cm)			Slope Angle (°)			Total RF Fragment Class		
Spatial Grouping	**n**	Mean	Range	sd	Mean	Range	sd	Mean	Range	sd	Mean	Range	sd
Subpopulation													
1	44	0.80	0.71-0.86	0.04	0.13	0.03-0.28	0.06	7.79	2-24	4.44	64.17	9-75	22.25
2	6	0.75	0.66-0.9	0.11	0.23	0.1-0.38	0.10	14.33	5-20	6.59	56.92	9-75	28.98
3	8	0.68	0.57-0.75	0.09	0.26	0.2-0.32	0.03	15.00	12-19	2.88	48.44	32-75	22.00
4	13	0.56	0.5-0.62	0.03	0.30	0.12-0.43	0.09	17.36	11-26	4.09	40.50	9-75	20.69
5	27	0.63	0.49-0.75	0.07	0.23	0-0.53	0.12	14.04	4-30	6.81	59.26	32-75	20.91
Transect													
1.1	8	0.83	0.78-0.92	0.04	0.15	0.11-0.22	0.04	10.50	4-24	5.83	50.25	9-75	34.16
1.2	10	0.80	0.71-0.84	0.05	0.14	0.07-0.24	0.05	7.60	4-11	2.80	70.75	32-75	13.44
1.3	11	0.79	0.71-0.83	0.04	0.11	0.03-0.19	0.05	7.34	2-10	3.07	63.41	32-75	19.85
1.4	15	0.78	0.74-0.86	0.04	0.12	0.03-0.28	0.07	6.80	2-18	5.13	67.77	9-75	19.60
2.1	6	0.73	0.56-0.9	0.12	0.23	0.1-0.38	0.10	14.33	5-20	6.59	56.92	9-75	28.98
3.1	8	0.68	0.57-0.75	0.09	0.26	0.2-0.32	0.03	15.00	12-19	2.88	48.44	32-75	22.00
4.1	9	0.58	0.5-0.64	0.04	0.32	0.24-0.43	0.06	18.11	11-26	4.62	34.61	9-75	17.02
4.2	4	0.58	0.52-0.62	0.04	0.25	0.12-0.36	0.12	15.68	13-17	2.11	53.75	32-75	24.54
5.1	10	0.60	0.47-0.73	0.09	0.30	0.12-0.53	0.14	16.80	4-30	8.48	49.50	32-75	21.95
5.2	12	0.64	0.57-0.75	0.06	0.20	0-0.36	0.09	12.75	4-24	5.48	67.92	32-75	16.54
5.3	5	0.64	0.57-0.7	0.05	0.20	0.12-0.32	0.08	11.60	5-19	5.03	58.00	32-75	23.28

Table E-3 **Summary of Hydraulic Conductivity Characteristics by Subpopulation and Transect**
Mean, minimum/maximum (range), and standard deviation (sd) of hydraulic conductivity by subpopulation and transect (n= 80).

Spatial Relationship of Hydraulic Conductivity (K) (n=80)

Spatial Groupings	Mean	Minimum	Maximum	sd
Subpopulation				
1	5.80×10^{-4}	-2.67×10^{-3}	7.61×10^{-3}	2.33×10^{-3}
2	4.33×10^{-3}	2.30×10^{-3}	7.43×10^{-3}	2.73×10^{-3}
3	2.00×10^{-5}	-3.05×10^{-3}	3.16×10^{-3}	2.57×10^{-3}
4	1.92×10^{-3}	1.20×10^{-4}	3.64×10^{-3}	1.21×10^{-3}
5	2.04×10^{-3}	-1.53×10^{-3}	1.55×10^{-2}	3.61×10^{-3}
Transect				
1.1	1.80×10^{-4}	-2.64×10^{-3}	3.52×10^{-3}	2.01×10^{-3}
1.2	-5.40×10^{-4}	-2.41×10^{-3}	1.27×10^{-3}	1.13×10^{-3}
1.3	1.73×10^{-3}	-2.37×10^{-3}	7.61×10^{-3}	2.67×10^{-3}
1.4	7.60×10^{-4}	-2.67×10^{-3}	6.98×10^{-3}	2.74×10^{-3}
2.1	4.33×10^{-3}	2.30×10^{-3}	7.43×10^{-3}	2.73×10^{-3}
3.1	2.00×10^{-5}	-3.05×10^{-3}	3.16×10^{-3}	2.57×10^{-3}
4.1	2.47×10^{-3}	1.67×10^{-3}	3.64×10^{-3}	8.80×10^{-4}
4.2	5.30×10^{-4}	1.20×10^{-4}	9.50×10^{-4}	5.90×10^{-4}
5.1	3.35×10^{-3}	-1.53×10^{-3}	1.55×10^{-2}	5.41×10^{-3}
5.2	4.70×10^{-4}	-1.13×10^{-3}	2.93×10^{-3}	1.26×10^{-3}
5.3	3.43×10^{-3}	-1.00×10^{-5}	5.59×10^{-3}	2.23×10^{-3}

Table E-4 **Summary of Soil Surface Composition by Subpopulation and Transect**
Mean, minimum/maximum (range), and standard deviation (sd) of soil surface compositional components by subpopulation and transect (n= 98).

Spatial Relationship of Soil Surface Cover (n=98)

	Rock			Bareground			Litter			Biocrust		
Spatial Groupings	Mean	Range	sd	Mean	Range	sd	Mean	Range	sd	Mean	Range	sd
Subpopulation												
1	81	38-88	12	4	0-20	5	4	0-20	6	0.00	0-0	0.00
2	79	38-88	20	7	0-38	15	4	0-10	4	0.00	0-0	0.00
3	59	38-88	21	22	3-38	14	8	0-20	6	0.25	0-0.5	0.27
4	54	20-88	24	22	3-62	19	8	0-38	10	2.42	0-20	5.42
5	66	20-88	19	20	3-62	13	3	0-20	4	0.35	0-3	0.96
Transect												
1.1	75	38-88	19	11	10-20	4	2	0-10	3	0.00	0-0	0.00
1.2	85	62-88	8	4	0-10	4	2	0-10	3	0.00	0-0	0.00
1.3	81	62-88	12	4	0-20	6	4	0-10	3	0.00	0-0	0.00
1.4	82	62-88	10	2	0-3	1	8	0-20	7	0.00	0-0	0.00
2.1	79	38-88	20	7	0-38	15	4	0-10	4	0.00	0-0	0.00
3.1	59	38-88	21	22	3-38	14	8	0-20	6	0.00	0-0	0.00
4.1	48	20-88	26	27	3-62	20	10	3-38	12	3.00	0-20	6.00
4.2	69	62-88	12	12	3-20	10	2	0-3	2	1.00	0-3	1.00
5.1	58	20-88	24	26	10-62	18	4	0-20	6	0.00	0-0	0.00
5.2	71	38-88	16	16	3-38	10	3	0-10	3	0.00	0-3	1.00
5.3	68	62-88	11	18	10-20	4	2	0-3	1	1.00	0-3	2.00

Table E-5 **Summary of Soil Surface Rock Fragment Composition by Subpopulation and Transect**
Mean, minimum/maximum (range), and standard deviation (sd) of soil surface rock fragment compositional components by subpopulation and transect (n= 98).

Spatial Relationship of Soil Surface Rock Fragment Cover (n=98)

Spatial	Boulder			Stone			Cobble			Course Gravel			Medium Gravel			Fine Gravel			Very Fine Gravel		
Groupings	Mean	Range	sd	Mean	Range	sd	Mean	Range	sd	Mean	Range	sd	Mean	Range	sd	Mean	Range	sd	Mean	Range	sd
Subpopulation																					
1	1	0-20	4	1	0-20	3	6	0-62	11	11	0-62	10	29	0-88	19	39	0-88	24	6	0-20	4
2	0	0-0	0	4	0-20	8	5	0-20	8	6	0-20	7	20	0-88	34	34	10-62	18	45	0-88	32
3	0	0-0	0	1	0-10	4	2	0-10	4	25	10-38	11	47	38-62	13	19	10-38	12	4	0-10	4
4	0	0-0	0	0	0-0	0	37	10-62	19	21	3-38	13	29	3-62	15	9	0-20	6	7	0-62	17
5	0	0-0	0	0	0-3	1	5	0-20	7	44	20-62	17	27	0-62	14	10	0-20	5	2	0-10	2
Transect																					
1.1	0	0-0	0	0	0-0	0	8	0-62	22	11	0-20	8	36	10-62	19	28	10-38	11	5	0-10	4
1.2	0	0-0	0	0	0-3	1	7	0-20	7	16	3-62	17	35	10-88	22	34	0-88	25	6	0-20	6
1.3	1	0-10	3	2	0-20	6	8	0-20	8	10	3-20	7	27	0-62	18	42	10-88	24	5	0-10	4
1.4	3	0-20	6	0	0-0	0	2	0-10	3	8	0-20	6	23	3-62	15	47	10-88	26	9	3-10	3
2.1	0	0-0	0	4	0-20	8	5	0-20	8	6	0-20	7	20	0-88	34	34	10-62	18	45	0-88	32
3.1	0	0-0	0	1	0-10	4	2	0-10	4	25	10-38	11	47	38-62	13	19	10-38	12	4	0-10	4
4.1	0	0-0	0	0	0-0	0	37	10-62	19	17	3-38	10	33	3-62	17	10	0-20	6	9	0-62	20
4.2	0	0-0	0	0	0-0	0	37	10-62	21	31	10-38	14	20	20-20	0	6	3-10	4	3	3-3	0
5.1	0	0-0	0	0	0-3	1	8	0-20	9	31	20-62	14	29	0-62	19	10	3-20	5	2	0-3	1
5.2	0	0-0	0	0	0-0	0	4	0-20	6	48	38-62	13	29	10-38	12	10	3-20	5	2	0-10	3
5.3	0	0-0	0	0	0-0	0	3	0-10	4	62	62-62	0	18	10-20	4	8	0-10	4	2	0-3	1

Table E-6 **Summary of Vegetation Characteristics by Subpopulation and Transect**
Mean, minimum/maximum (range), and standard deviation (sd) of site characteristics by subpopulation and transect. LAI was only collected in subpopulations I and V (n=71). Species abundance, total cover and *E. codium* cover where it occurs (present) (n=72).

		LAI				Species Abundance			Total Cover			*E.codium*		
Spatial Groupings	**n**	Mean	Min	Max	sd	Mean	Range	sd	Mean	Range	sd	Mean	Range	sd
Subpopulation														
1	28	0.042	0	0.78	0.117	3.36	2-7	1.37	33.79	3.5-64	16.78	15.55	0.5-37.5	11.22
2	4	-	-	-	-	3.50	3-4	0.58	21.62	13.5-31	7.18	15.00	10-20	5.77
3	8	-	-	-	-	5.12	4-6	0.64	37.12	24.5-50	8.67	12.88	3-20	6.36
4	10	-	-	-	-	3.50	2-5	0.85	50.80	30.5-70.5	14.18	12.00	10-20	4.22
5	22	0.001	0	0.01	0.004	2.86	2-5	0.77	26.02	4-40.5	8.79	13.02	0.5-20	6.50
Transect														
1.1	4	0.043	0	0.16	0.053	4.50	3-6	1.29	33.50	6.5-64	23.60	9.00	3-20	8.04
1.2	7	0.091	0	0.78	0.242	3.14	2-5	1.07	23.71	4-48	16.57	13.00	0.5-37.5	12.47
1.3	9	0.034	0.02	0.08	0.018	3.67	2-7	1.73	45.00	23-58.5	12.53	23.61	10-37.5	11.19
1.4	8	0.015	0	0.05	0.017	2.62	2-4	0.74	30.12	3.5-40.5	12.43	12.00	3-20	7.23
2.1	4	-	-	-	-	3.50	3-4	0.58	21.62	13.5-31	7.18	15.00	10-20	5.77
3.1	8	-	-	-	-	5.12	4-6	0.64	37.12	24.5-50	8.67	12.88	3-20	6.36
4.1	6	-	-	-	-	3.67	3-4	0.52	52.83	30.5-70.5	15.57	11.67	10-20	4.08
4.2	4	-	-	-	-	3.25	2-5	1.26	47.75	33-60.5	13.36	12.50	10-20	5.00
5.1	9	0.002	0	0.01	0.004	3.11	2-5	0.78	20.61	4-30.5	9.03	9.61	0.5-20	6.95
5.2	9	0	0	0	0	2.33	2-3	0.50	27.94	20-40.5	6.73	16.67	10-20	5.00
5.3	4	0.004	0	0.01	0.005	3.50	3-4	0.58	33.88	30.5-40.5	4.61	12.50	10-20	5.00

Appendix F: Chapter 1 Part II

Stress Plots of NMDS Ordinations Visualizing Soil Surface, Soil Surface Rock Fragment, and Vegetation Composition Data

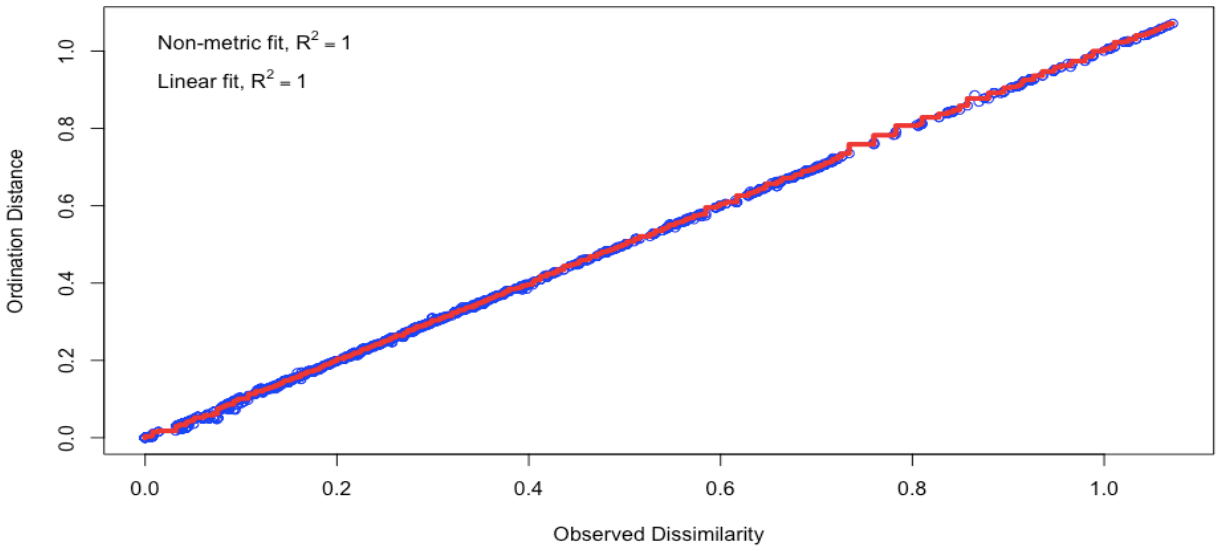


Figure F-1 **NMDS Stress Plot for Soil Surface Composition (n= 98)**
Shepard plot of soil surface composition showing the Euclidean distances between plots in the 2-dimensional ordination space (Ordination Distance).

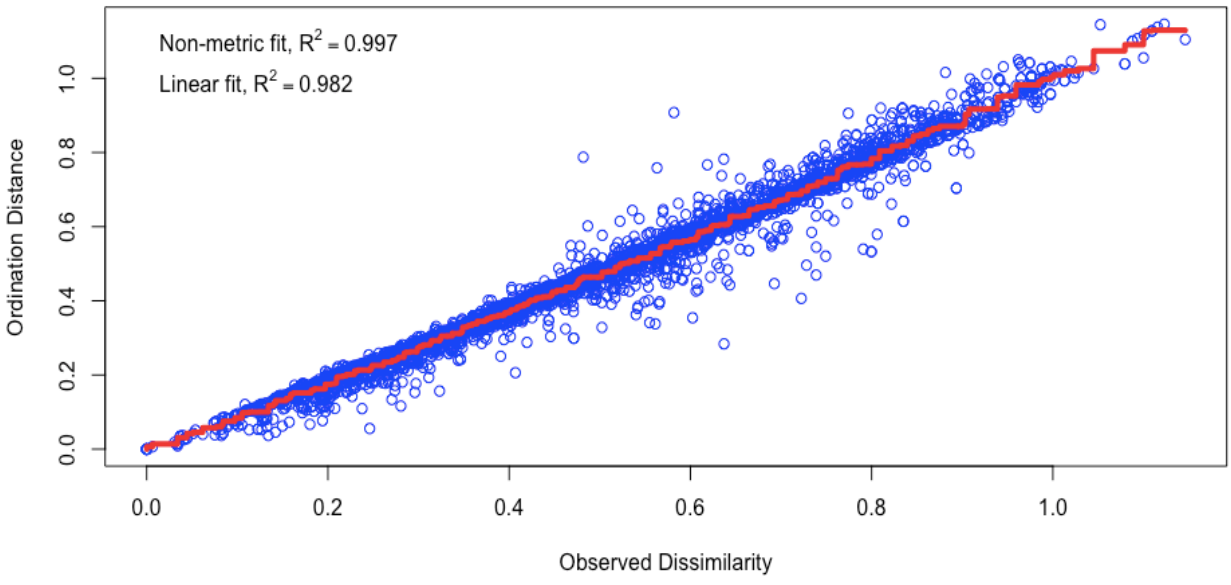


Figure F-2 **NMDS Stress Plot for Soil Surface Rock Fragment Composition (n= 98)**
Shepard plot of soil surface composition showing the Euclidean distances between plots in the 3-dimensional ordination space (Ordination Distance).

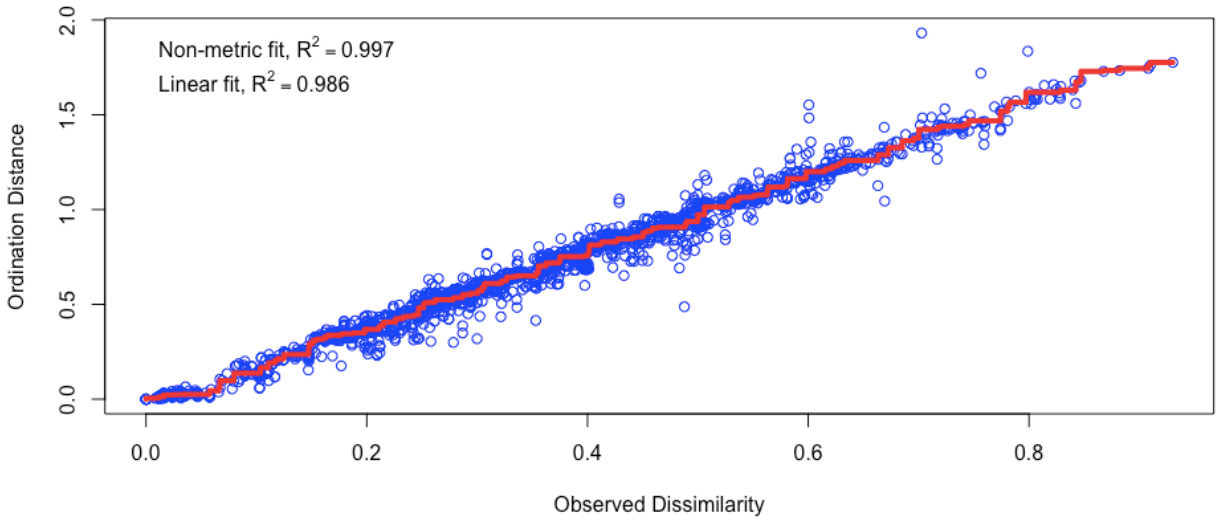


Figure F-3 **NMDS Stress Plot for Vegetation Composition (n= 72)** Shepard plot of soil surface composition showing the Bray-Curtis between plots in the 3-dimensional ordination space (Ordination Distance).

Appendix G: Chapter 1 Part II
Vegetation Species ISA Table (Simplified and Multigroup)

Table G-1 **ISA of Vegetation Composition by Subpopulation and Transect**
Vegetation species that most characterize subpopulations and individual transects within subpopulations where *E. codium* is present (n= 72). IV_{ij} value of 100 means species occurs in all plots. Significant relationships are indicated by asterisks (* = significant, ** = strongly . significant, ***= very strongly significant)

ISA of Vegetation Composition (n=90)

Species	ISA	Group	IVij	*P*	
Subpopulation					
Amsinckia retrorsa	Classical	2	25.0	0.045	*
Astragalus caricinus	Simplified	3	26.7	0.045	*
Bromus tectorum	Multiple Group	2+5	46.6	0.015	**
Bromus tectorum	Simplified	2+3+5	41.4	0.005	**
Poa secunda	Classical	4	27.0	0.035	*
Pseudoegneria spicata	Classical	3	55.4	0.015	**
Pseudoegneria spicata	Multiple Group	3+4	89.5	0.005	**
Pseudoegneria spicata	Simplified	2+3+4	82.7	0.005	**
Transect					
Astragalus caricinus	Multiple Group	1.1+ 3.1+ 5.3	33.5	0.025	*
Bromus tectorum	Classical	5.1	53.3	0.005	**
Bromus tectorum	Multiple Group	2.1+ 5.1+ 5.3	57.9	0.005	**
Pseudoegneria spicata	Classical	3.1	37.9	0.005	**
Pseudoegneria spicata	Multiple Group	3.1+ 4.1+ 4.2	85.1	0.005	**
Pseudoegneria spicata	Simplified	1.1+ 2.1+ 3.1+ 4.1+ 4.2	78.4	0.005	**

Appendix H: Chapter 1 Part II
Vegetation Species Summary Tables

Table H-1 **Summary of Vegetation Species Occurrence by Transect**
Vegetation species in plots where *E. codium* is present (n = 72). Table includes number of times species presence was recorded (plot counts) and percentage of total plots surveyed in all transects and across the whole site.

Species	Code	Class	Habit	Origin	Site (count)	plots (%)	1.1	1.2	1.3	1.4	2.1	3.1	4.1	4.2	5.1	5.2	5.3
Eriogonum codium	ERCO	subshrub	Perennial	Native	72	100.00	4	7	9	8	4	8	6	4	9	9	4
Poa secunda	POSE	graminoid	Perennial	Native	72	100.00	4	7	9	8	4	8	6	4	9	9	4
Pseudoegneria spicata	PSSP	graminoid	Perennial	Native	22	30.56	2	0	1	0	2	8	6	3	0	0	0
Bromus tectorum	BRTE	graminoid	Annual	Invasive	21	29.17	0	2	3	0	2	2	0	0	8	2	2
Astragalus purshii	ASPU	forb	Perennial	Native	8	11.11	1	0	2	2	0	2	0	0	0	0	1
Salsola tragus	SATR	forb	Annual	Invasive	8	11.11	1	2	2	0	1	2	0	0	0	0	0
Astragalus caricinus	ASCA	forb	Perennial	Native	7	9.72	2	0	1	0	0	3	0	0	0	0	1
Balsamorhiza sagittata	BASA	forb	Perennial	Native	6	8.33	2	0	0	0	0	2	0	1	1	0	0
Lomatium canbyi	LOCA	forb	Perennial	Native	6	8.33	0	0	0	0	0	1	2	0	1	1	1
Phacelia linearis	PHLI	forb	Annual	Native	5	6.94	0	1	1	2	0	1	0	0	0	0	0
Descurainia pinnata	DEPI	forb	Annual	Native	3	4.17	0	2	1	0	0	0	0	0	0	0	0
Balsamorhiza hookeri	BAHO	forb	Perennial	Native	2	2.78	0	0	1	1	0	0	0	0	0	0	0
Chaenactis douglasii	CHDO	forb	Annual	Native	2	2.78	0	0	0	0	0	1	1	0	0	0	0
Erigeron poliospermus	ERPO	forb	Perennial	Native	2	2.78	0	0	0	0	0	0	0	1	0	0	1
Phlox longifolia	PHLO	forb	Perennial	Native	2	2.78	0	0	0	0	0	1	1	0	0	0	0
Sphaeralcea munroana	SPMO	forb	Perennial	Native	2	2.78	1	0	1	0	0	0	0	0	0	0	0
Amsinckia retrorsa	AMRE	forb	Annual	Native	1	1.39	0	0	0	0	1	0	0	0	0	0	0
Artemisia tridentata	ARTR	shrub	Perennial	Native	1	1.39	0	0	1	0	0	0	0	0	0	0	0
Chrysothamnus viscidiflorus	CHVI	shrub	Perennial	Native	1	1.39	0	0	1	0	0	0	0	0	0	0	0
Cryptantha pterocarya	CRPT	forb	Annual	Native	1	1.39	0	0	0	0	0	1	0	0	0	0	0
Eriocoma hymenoides	ERHY	graminoid	Perennial	Native	1	1.39	0	1	0	0	0	0	0	0	0	0	0
Lomatium species	Lomatium.spp	forb	Perennial	Native	1	1.39	1	0	0	0	0	0	0	0	0	0	0
Salvia dorii	SADO	shrub	Perennial	Native	1	1.39	0	0	0	0	0	1	0	0	0	0	0

Table H-2 **Summary of Vegetation Species by Subpopulation and Transect**
Mean, minimum/maximum (range), and standard deviation (sd) of site characteristics by subpopulation and transect where *E. codium* occurs (n=72).

	Poa secunda			*Pseudoroegneria spicata*			*Astragalus purshii*			*Astragalus caricinus*			*Bromus tectorum*			*Salsola tragus*			*Amsinckia retrorsa*		
Spatial Groupings	Mean	Range	sd	Mean	Range	sd	Mean	Range	sd	Mean	Range	sd	Mean	Range	sd	Mean	Range	sd	Mean	Range	sd
Subpopulation																					
1	15.71	0.5-37.5	9.64	0.32	0-3	0.94	0.61	0-10	2.00	0.23	0-3	0.79	0.09	0-0.5	0.20	0.18	0-3	0.58	0.00	0-0	0.00
2	5.88	0.5-10	4.87	0.25	0-0.5	0.29	0.00	0-0	0.00	0.00	0-0	0.00	0.25	0-0.5	0.29	0.12	0-0.5	0.25	0.12	0-0.5	0.25
3	11.25	10-20	3.54	8.62	3-20	5.76	0.44	0-3	1.05	0.50	0-3	1.04	0.12	0-0.5	0.23	0.12	0-0.5	0.23	0.00	0-0	0.00
4	27.00	20-37.5	9.04	8.35	0-20	5.89	0.00	0-0	0.00	0.00	0-0	0.00	0.00	0-0	0.00	0.00	0-0	0.00	0.00	0-0	0.00
5	12.11	0.5-20	6.13	0.00	0-0	0.00	0.02	0-0.5	0.11	0.14	0-3	0.64	0.39	0-3	0.63	0.00	0-0	0.00	0.00	0-0	0.00
Transect																					
1.1	19.50	0.5-37.5	15.12	1.50	0-3	1.73	0.12	0-0.5	0.25	0.88	0-3	1.44	0.00	0-0	0.00	0.12	0-0.5	0.25	0.00	0-0	0.00
1.2	10.14	0.5-20	7.96	0.00	0-0	0.00	0.00	0-0	0.00	0.00	0-0	0.00	0.14	0-0.5	0.24	0.14	0-0.5	0.24	0.00	0-0	0.00
1.3	17.83	3-37.5	9.70	0.33	0-3	1.00	0.39	0-3	0.99	0.33	0-3	1.00	0.17	0-0.5	0.25	0.39	0-3	0.99	0.00	0-0	0.00
1.4	16.31	0.5-20	7.28	0.00	0-0	0.00	1.62	0-10	3.54	0.00	0-0	0.00	0.00	0-0	0.00	0.00	0-0	0.00	0.00	0-0	0.00
2.1	5.88	0.5-10	4.87	0.25	0-0.5	0.29	0.00	0-0	0.00	0.00	0-0	0.00	0.25	0-0.5	0.29	0.12	0-0.5	0.25	0.12	0-0.5	0.25
3.1	11.25	10-20	3.54	8.62	3-20	5.76	0.44	0-3	1.05	0.50	0-3	1.04	0.12	0-0.5	0.23	0.12	0-0.5	0.23	0.00	0-0	0.00
4.1	28.75	20-37.5	9.59	10.08	0.5-20	6.17	0.00	0-0	0.00	0.00	0-0	0.00	0.00	0-0	0.00	0.00	0-0	0.00	0.00	0-0	0.00
4.2	24.38	20-37.5	8.75	5.75	0-10	5.06	0.00	0-0	0.00	0.00	0-0	0.00	0.00	0-0	0.00	0.00	0-0	0.00	0.00	0-0	0.00
5.1	9.61	0.5-20	6.95	0.00	0-0	0.00	0.00	0-0	0.00	0.00	0-0	0.00	0.72	0-3	0.87	0.00	0-0	0.00	0.00	0-0	0.00
5.2	11.11	10-20	3.33	0.00	0-0	0.00	0.00	0-0	0.00	0.00	0-0	0.00	0.11	0-0.5	0.22	0.00	0-0	0.00	0.00	0-0	0.00
5.3	20.00	20-20	0.00	0.00	0-0	0.00	0.12	0-0.5	0.25	0.75	0-3	1.50	0.25	0-0.5	0.29	0.00	0-0	0.00	0.00	0-0	0.00

Appendix I: Chapter 1 Part II
NMDS of Vegetation Composition Coded by Vegetation Species Cover

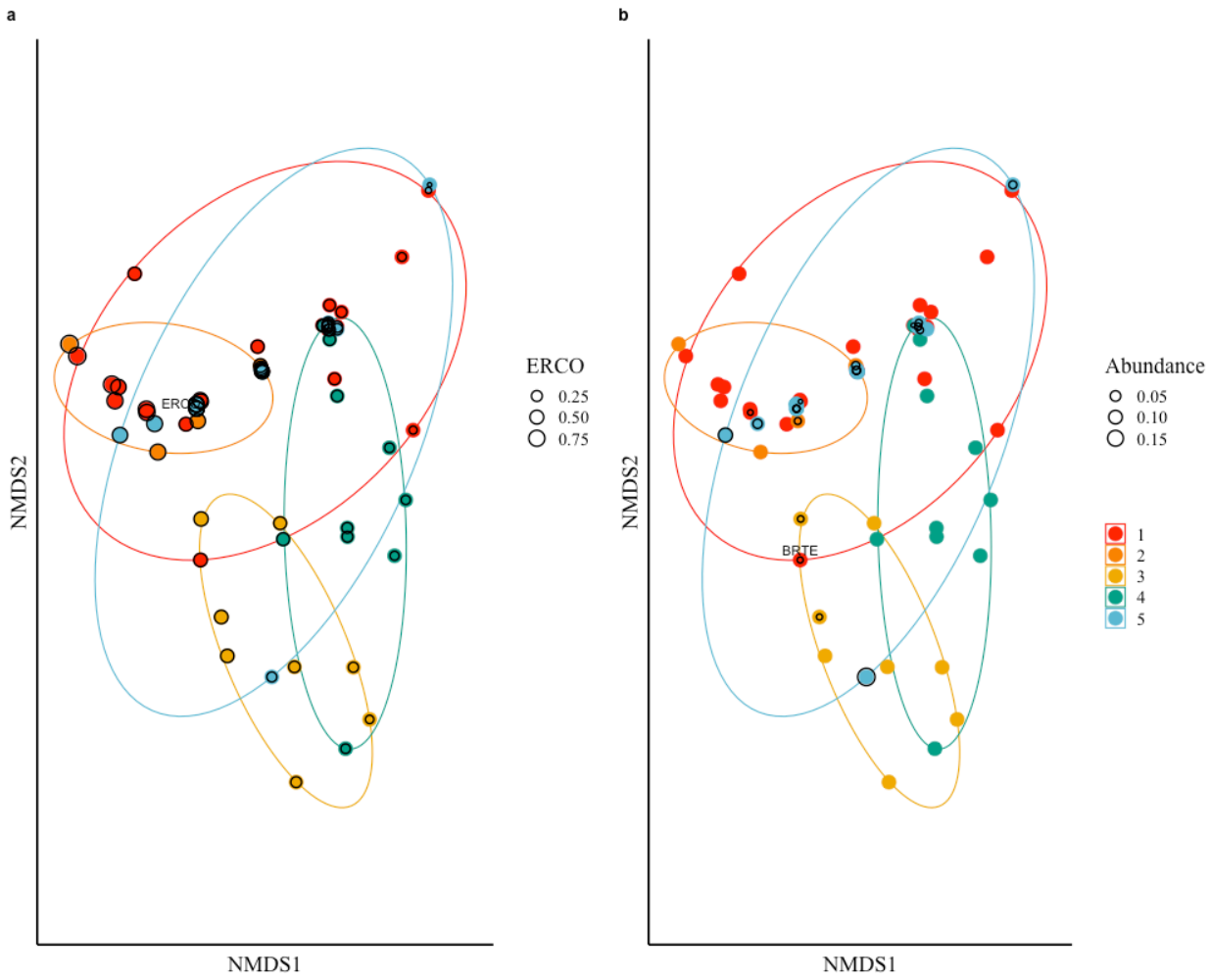


Figure I-1 **NMDS Ordination of Vegetation Composition by Subpopulation and Species Abundance of *E. codium* and *Bromus tectorum***
Non-metric multidimensional scaling (NMDS) ordination of vegetation composition (k =3, stress = 0.057) (n= 72). Points and ellipses are coded by color to correspond to subpopulation. Each point represents a $1m^2$ plot and abundance of *E. codium* (A) and *Bromus tectorum* (B) is depicted. Points closer together are more similar to than those farther apart.

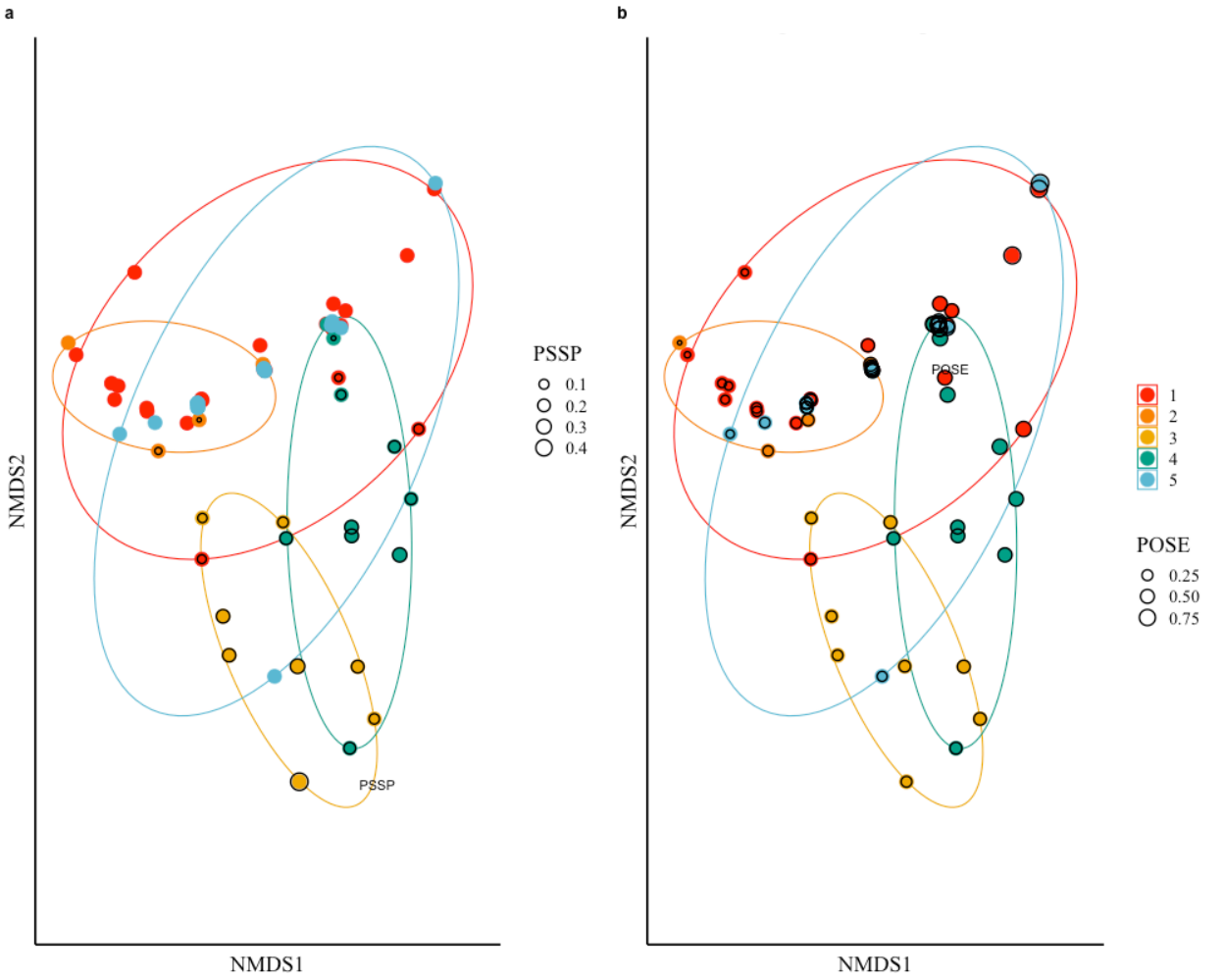


Figure I-2 **NMDS Ordination of Vegetation Composition by Subpopulation and Species Abundance of *Poa secunda* and *Pseudoroegneria spicata***

Non-metric multidimensional scaling (NMDS) ordination of vegetation composition (k =3, stress = 0.057) (n= 72). Points and ellipses are coded by color to correspond to subpopulation. Each point represents a $1m^2$ plot and abundance of *Poa secunda* (A) and *Pseudoroegneria spicata* (B) is depicted. Points closer together are more similar to than those farther apart.

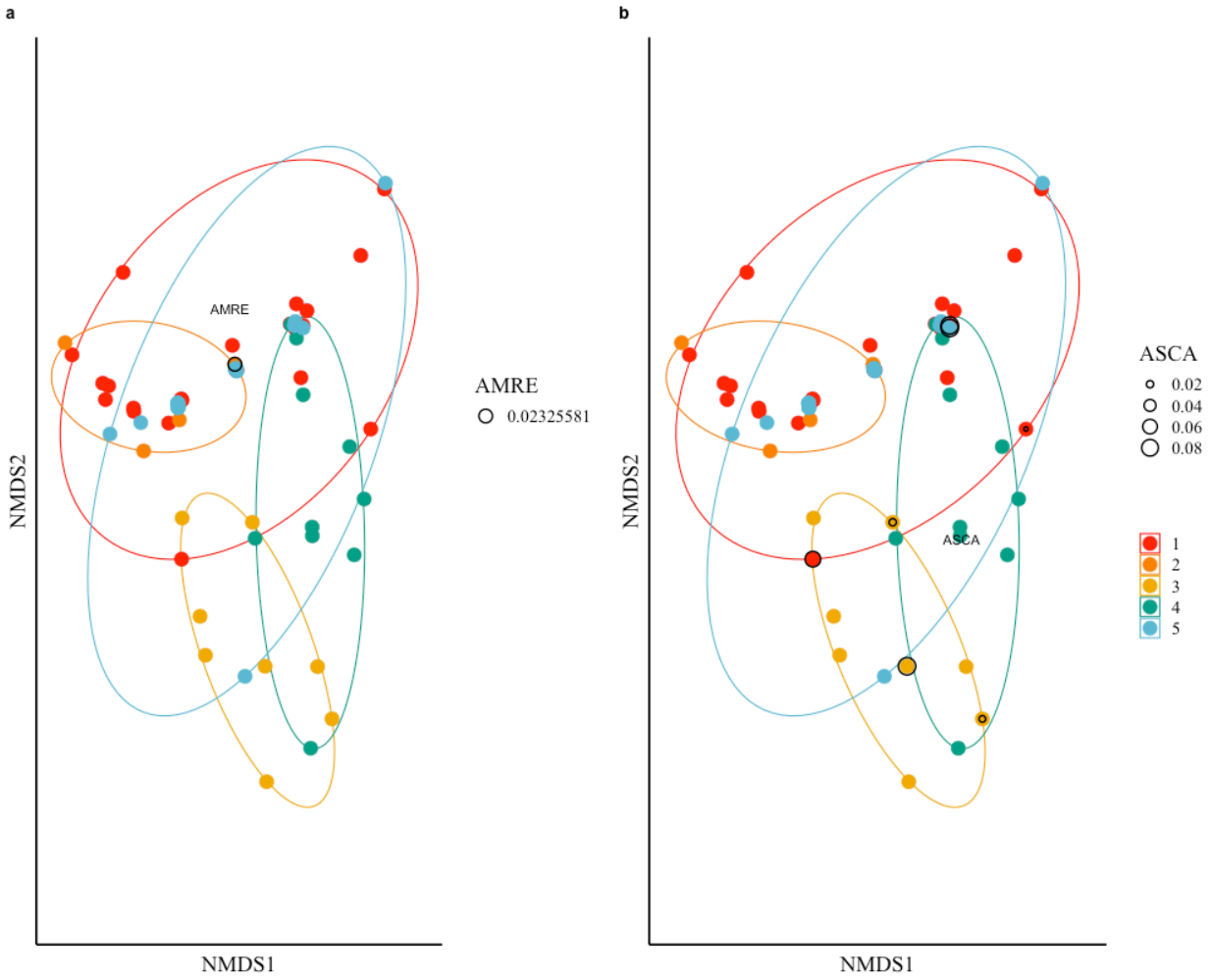


Figure I-3 **NMDS Ordination of Vegetation Composition by Subpopulation and Species Abundance of *Astragalus carcinus* and *Astragalus purshii***
Non-metric multidimensional scaling (NMDS) ordination of vegetation composition (k =3, stress = 0.057) (n= 72). Points and ellipses are coded by color to correspond to subpopulation. Each point represents a $1m^2$ plot and abundance of *Astragalus carcinus* (A) and *Astragalus purshii* (B) is depicted. Points closer together are more similar to than those farther apart.

Appendix J: Chapter 1 Part II
Site, Soil and Vegetation Habitat Characteristics that Significantly Differ by Sampling Transect

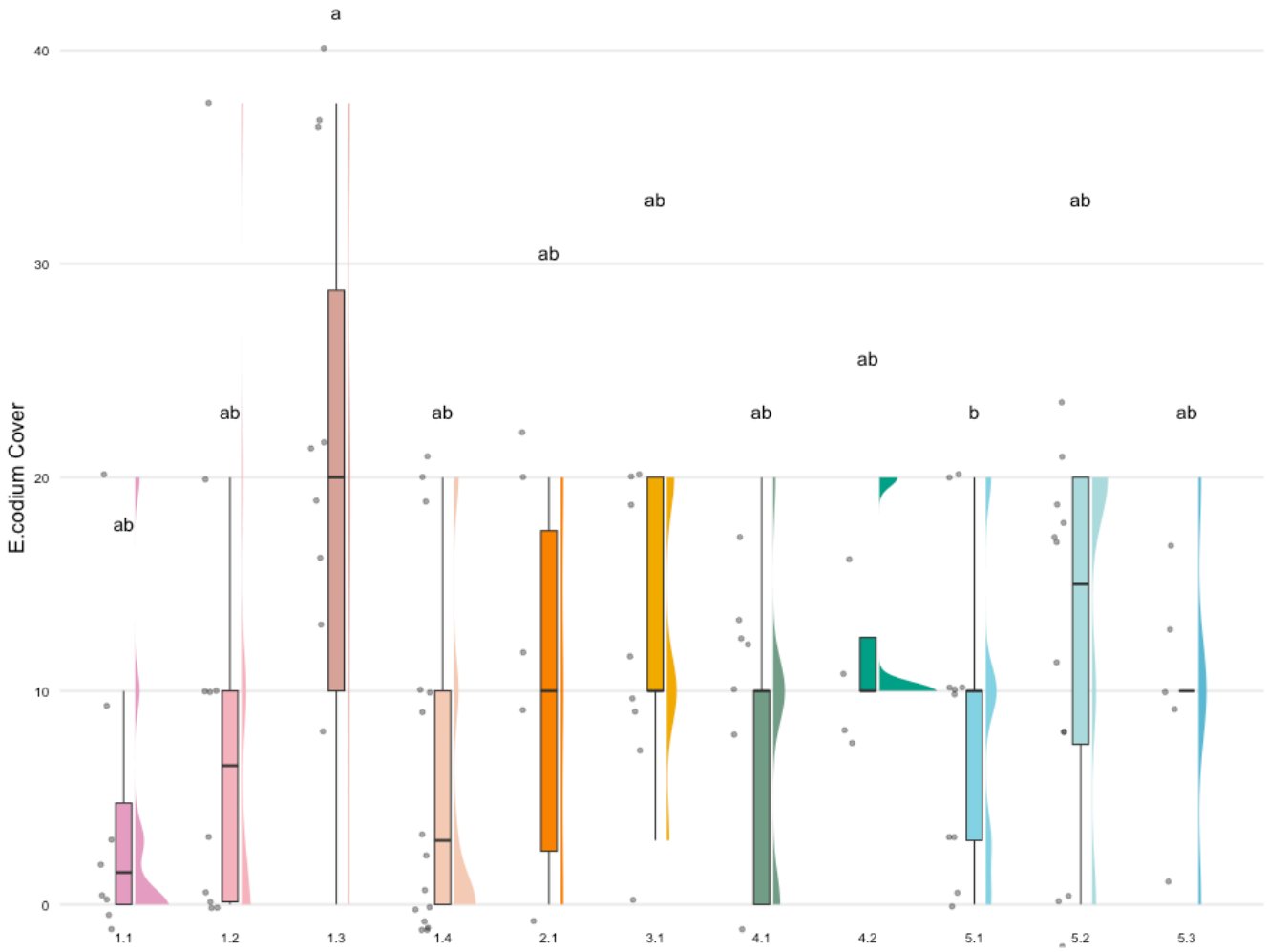


Figure J-1 **Raincloud Plot of *E. codium* Cover by Sampling Transect**
Similarities in *E. codium* cover between sampling transects where it is present (n= 72). Sampling transects 1.3 had significantly higher *E. codium* abundance than all other sampling transects, in contrast to 5.1 which had significantly lower *E. codium* abundance than all other transects. Sampling transect 1.3 is likely the most optimal *E. codium* habitat and should be the focus of continued monitoring and study of habitat characteristics. Transect 5.1 likely represents an area of degraded habitat and should be the focus on management concerns focused on identifying habitat variables inhibiting *E. codium* abundance in this area.

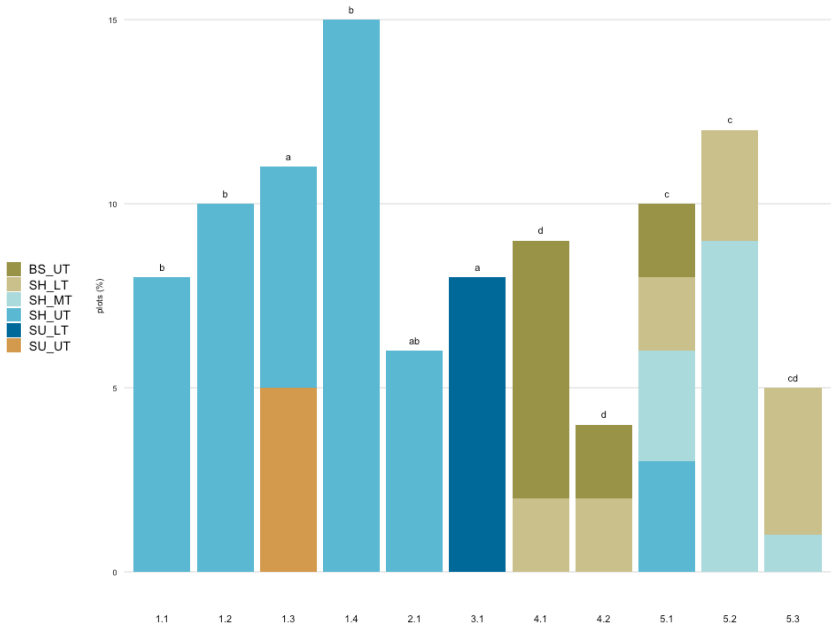


Figure J-2 **Bar Graph of Landscape Position by Sampling Transect**
Differences in categorical landscape position (BS_UT = backslope- upper third, SH_LT= shoulder-lower third, SH_MT = shoulder-middle third, SH_UT= shoulder- upper third, SU_LT = summit-lower third, SU_UT = summit-lower third) between sampling transects (n= 98).

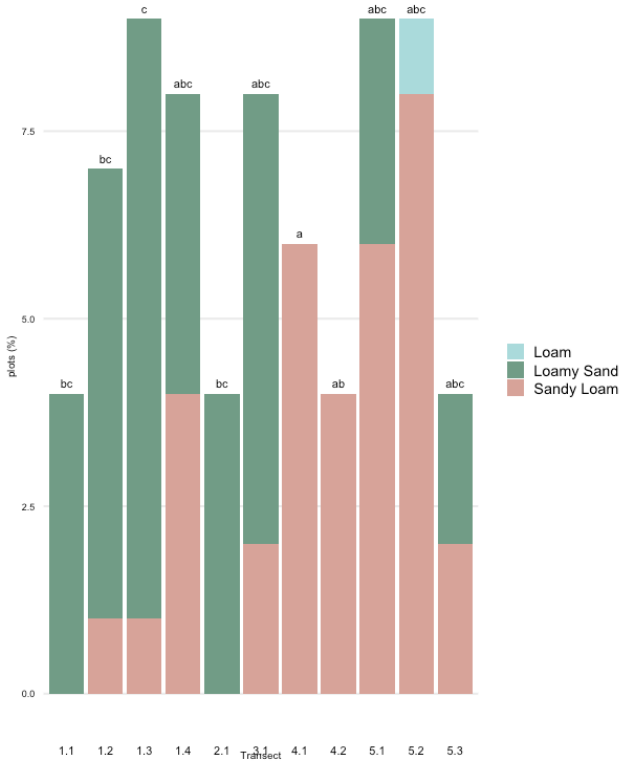


Figure J-3 **Bar Graph of Soil Surface Texture by Sampling Transect**
Significant ($p < 0.05$) differences in surface soil texture where *E. codium* is present (n= 72) by subpopulation.

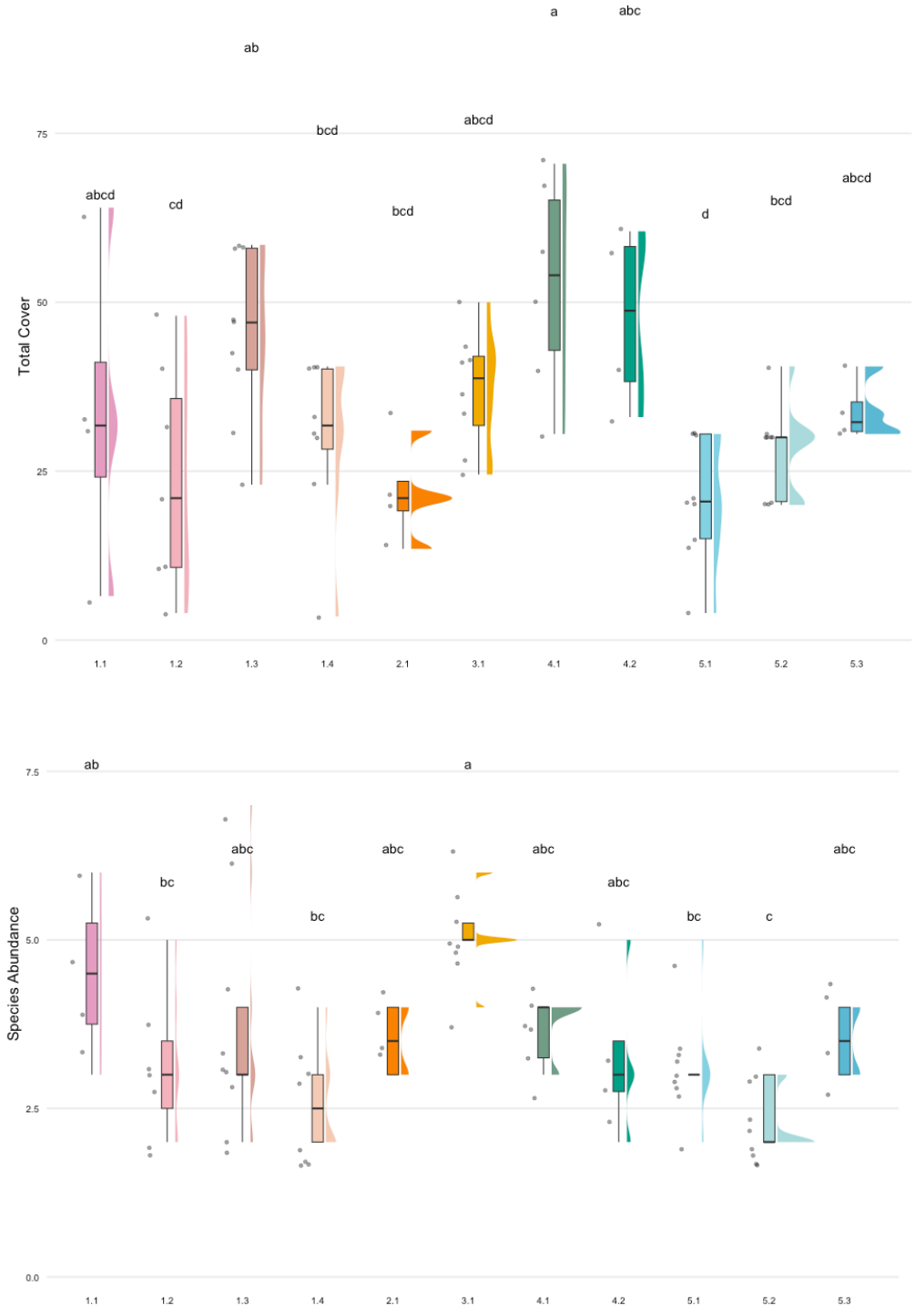


Figure J-4 **Raincloud Plots of Species Richness and Total Cover by Sampling Transect**
Differences in total cover (top) and species richness (bottom) by subpopulation where *E. codium* is present (n= 72).

Appendix K: Chapter 1 Part III
Cluster Analysis Groups Based on Differences in Functional Group Composition at the Native Site

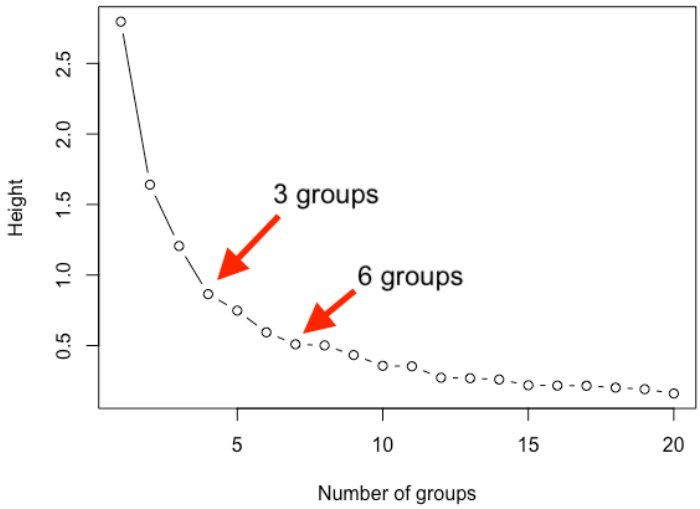


Figure K-1 **Scree Plot of Groups via Agglomerative Cluster Analysis**
Height indicates level of dissimilarity between groups. Dissimilarity between groups diminishes at three and six groups indicating these are most optimal.

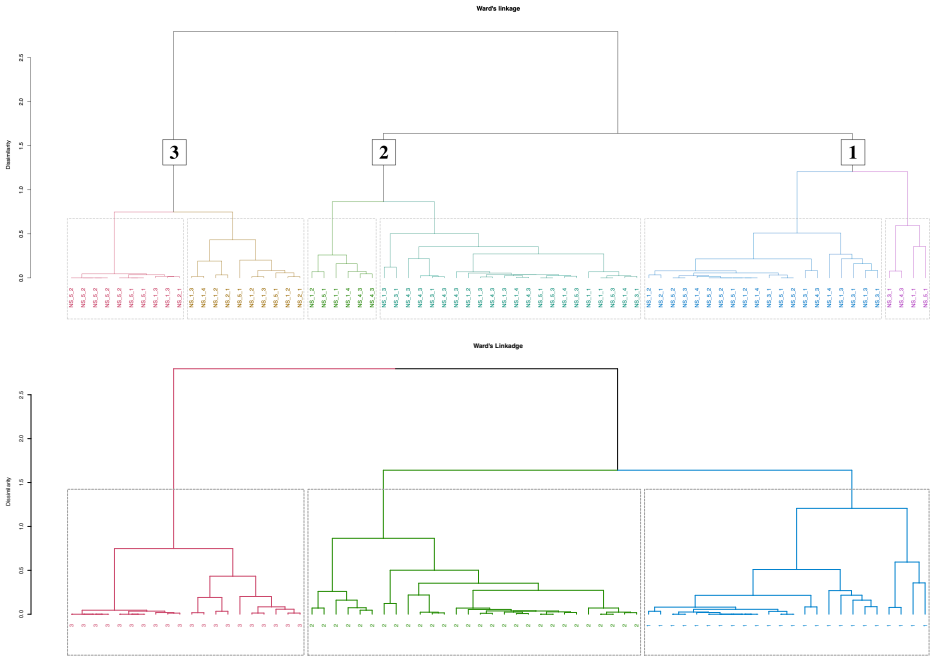


Figure K-2 **Dendrogram of Native Site Cluster Analysis Groups Based on Vegetation Functional Group Composition**
Three cluster analysis groups based on vegetational functional group composition were created by agglomerating the six cluster analysis groups of optimal *E. codium* vegetation habitat. Dendrogram shows the transect number of each plot (top) and its assigned group number (bottom). Dendrogram structure shows how dissimilarity is minimized at three or six groupings.

Appendix L: Chapter 1
TITAN Analysis of Heat Load Index and Compositional Data

Table L-1 **TITAN of Soil Surface, Soil Surface Rock Fragment and Vegetation Composition Relationship to Heat Load Index**
Taxa Indicator Threshold Analysis (TITAN) was used to assess the compositional components relationship to threshold changes in heat load index. Two soil surface components (bareground/biocrust), soil surface rock fragment components (cobble/coarse gravel), and vegetation species (*Lomatium canbyi* and *Pseudoregineria spicata*) indicate higher HLI values. Rock (soil surface composition) and fine gravel (soul surface rock fragment composition) indicate lower HLI values.

Relationship of Heat Load Index to Soil and Vegetation Composition

Composition	Group	Change Point	Frequency	IndVal	Purity	Reliability
Soil Surface (n= 98)						
Bareground	increaser	0.66	89	77.56	1.000	1.000
Biocrust	increaser	0.63	17	45.81	1.000	1.000
Rock	decreaser	0.58	98	59.16	1.000	1.000
Soil Surface Rock Fragment (n= 98)						
Cobble	increaser	0.66	59	52.30	1.000	0.998
Course gravel	increaser	0.75	97	70.21	0.998	0.998
Fine gravel	decreaser	0.65	97	72.50	1.000	1.000
Vegetation (n= 98)						
Lomatium canbyi	increaser	0.58	6	28.97	0.986	0.954
Pseudoroegneria spacta	increaser	0.63	22	45.41	0.996	0.998

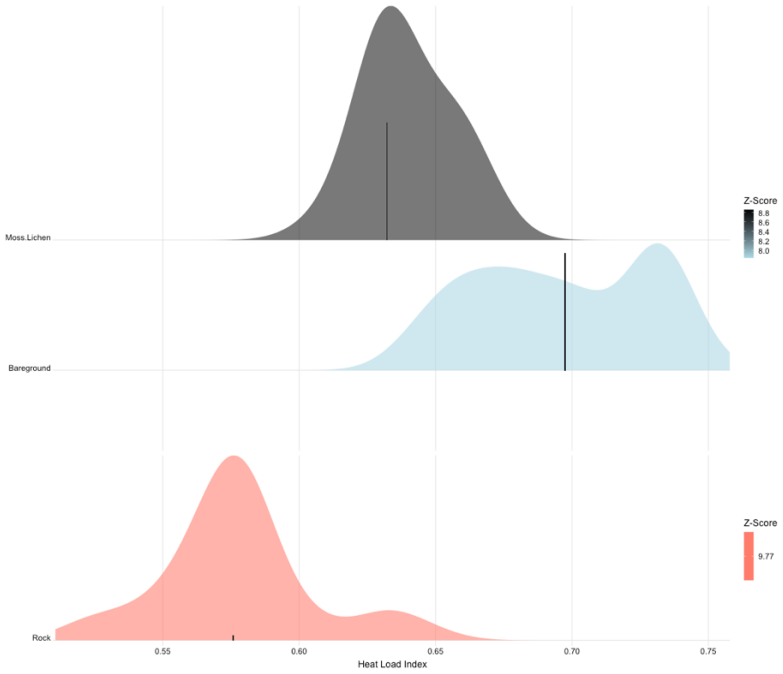


Figure L-2 **TITAN of Soil Surface Composition Relationship to Heat Load Index**
Ridge plot of soil surface components as strong and consistent indicators of high heat load index (blue) or low heat load index (red). Moss/lichen = biocrust

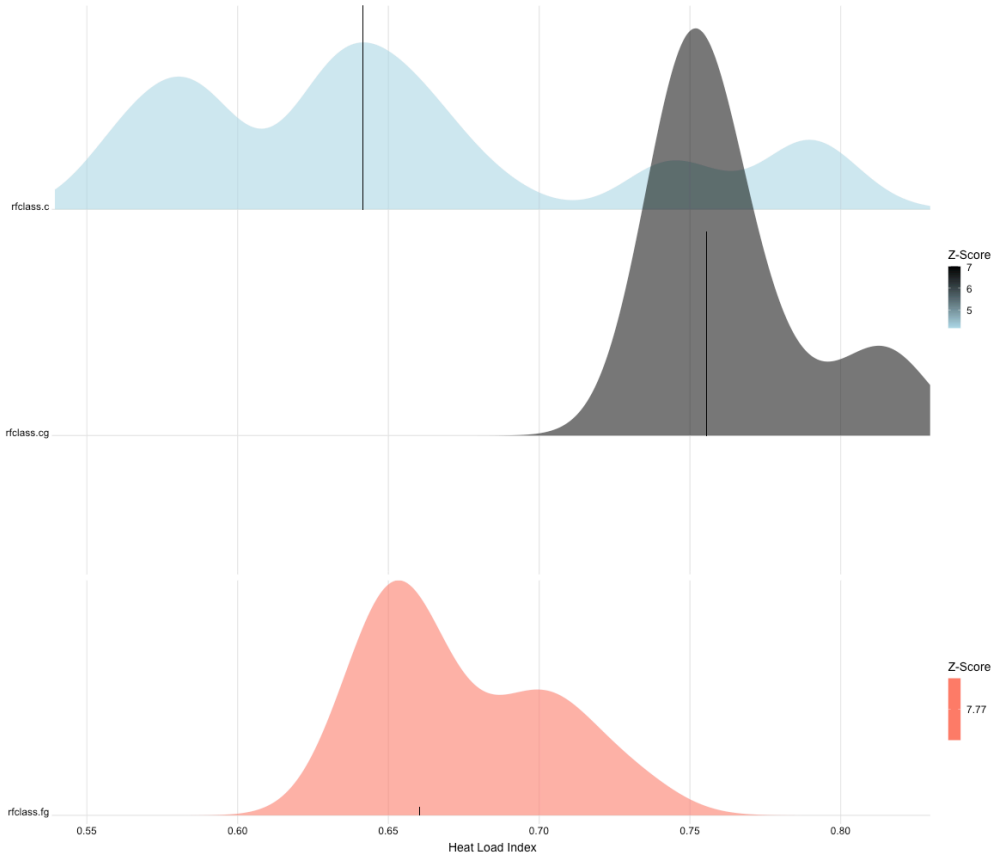


Figure L-3 **TITAN of Soil Surface Rock Fragment Composition Relationship to Heat Load Index**
Ridge plot of soil surface rock fragment components as strong and consistent indicators of high heat load index (blue) or low heat load index (red). C= cobble, CG= course gravel, FG= fine gravel

Appendix M: Chapter 2
Mapped Soil Series of *E. codium* Native and Assisted Migration Sites

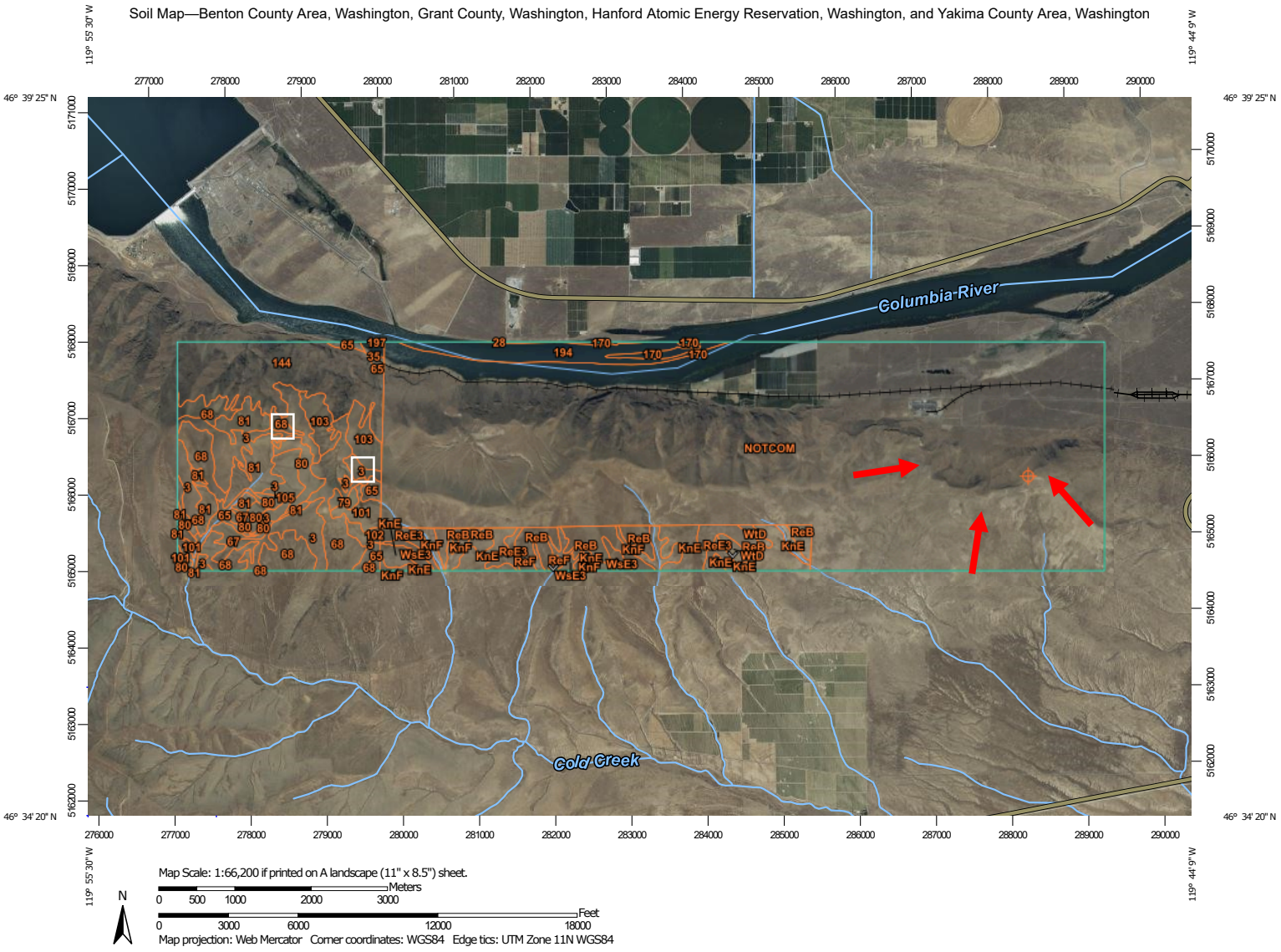


Figure M-1 USDA Mapped Soil Series of Umtanum Ridge at Hanford Nuclear Facility

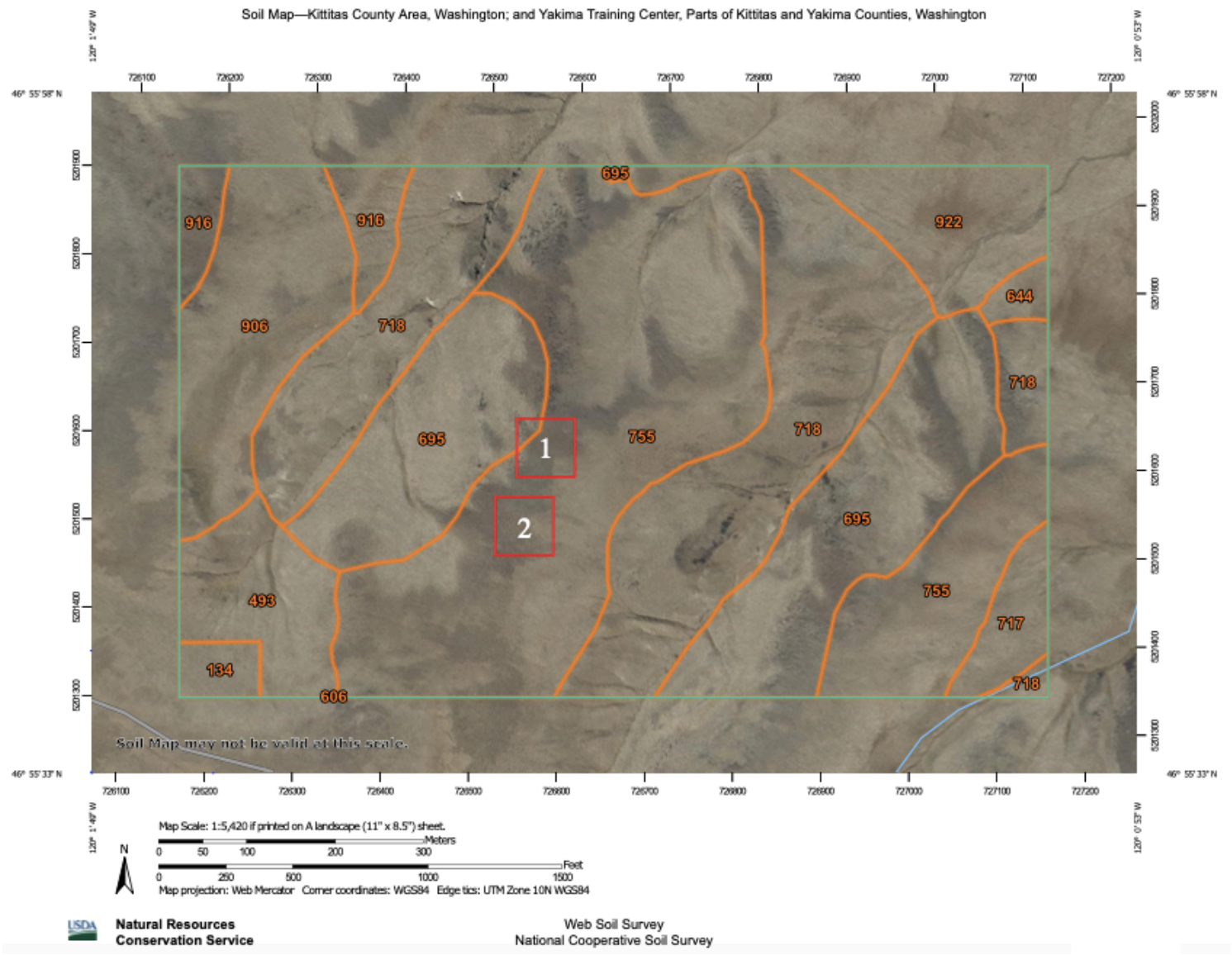


Figure M-2 USDA Mapped Soil Series of Potential Assisted Migration Sites at Gingko Petrified Forest State Park

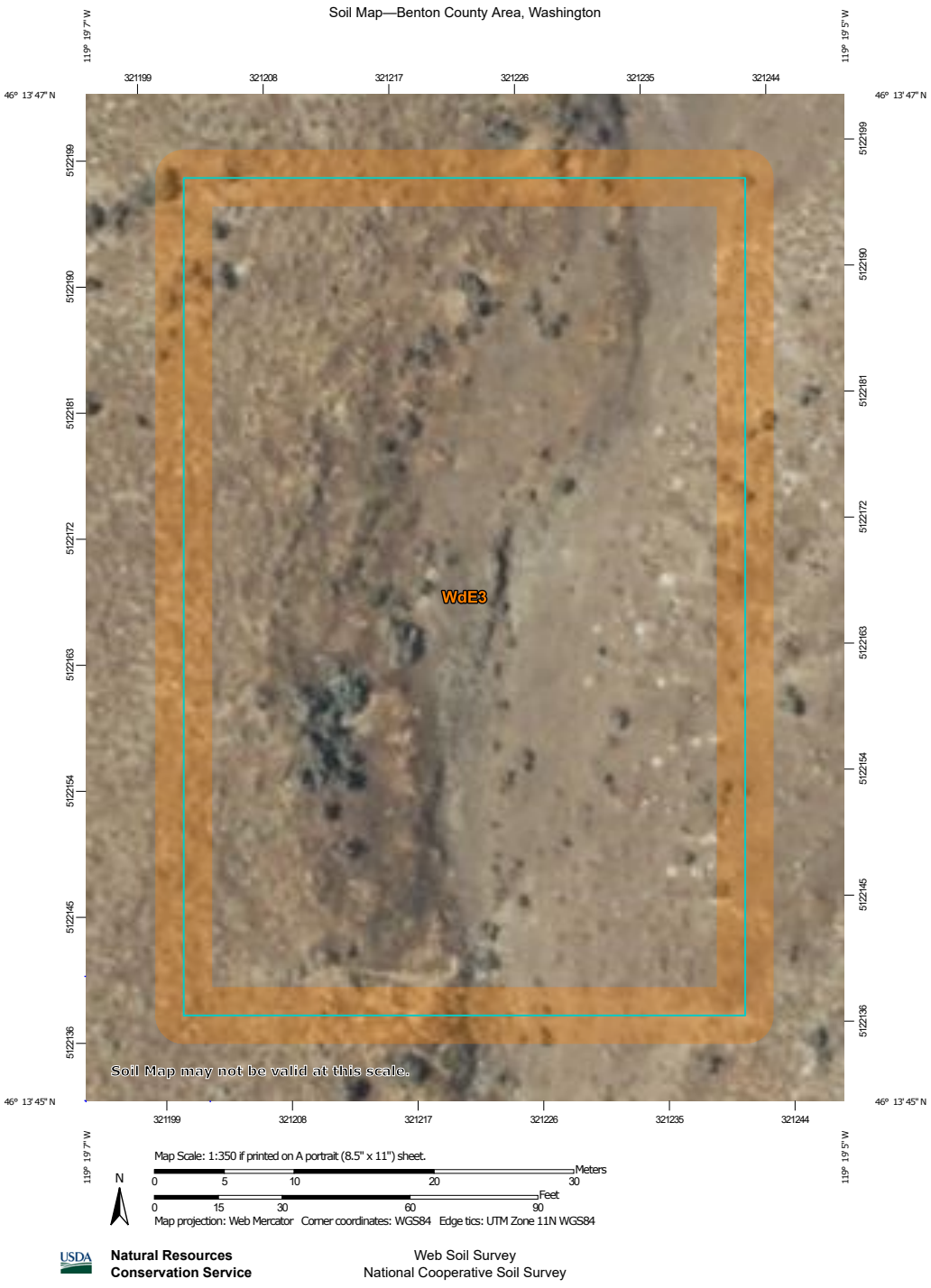


Figure M-3 USDA Mapped Soil Series of the Assisted Migration Site at Badger Mountain



Figure M-4 USDA Mapped Soil Series of Assisted Migration Site at Snow Mountain Site 1

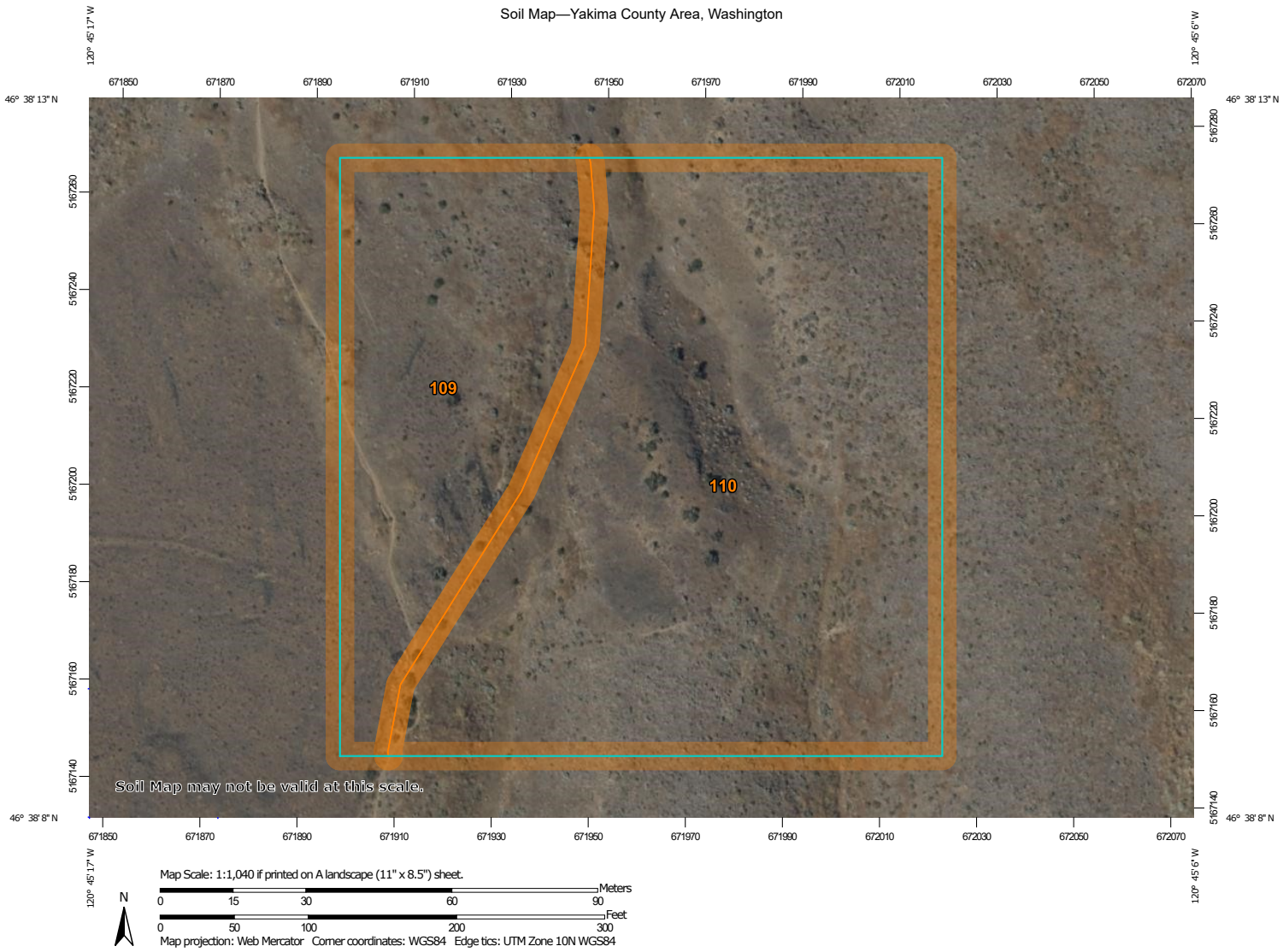


Figure M-5 USDA Mapped Soil Series of Assisted Migration Site at Snow Mountain Site 2



Figure M-6 USDA Mapped Soil Series of Assisted Migration Site at Snow Mountain Site 3

Appendix N: Chapter 2

USDA-NCSS Soil Textural Triangle of Assisted Migration Sites Soil Texture Classifications

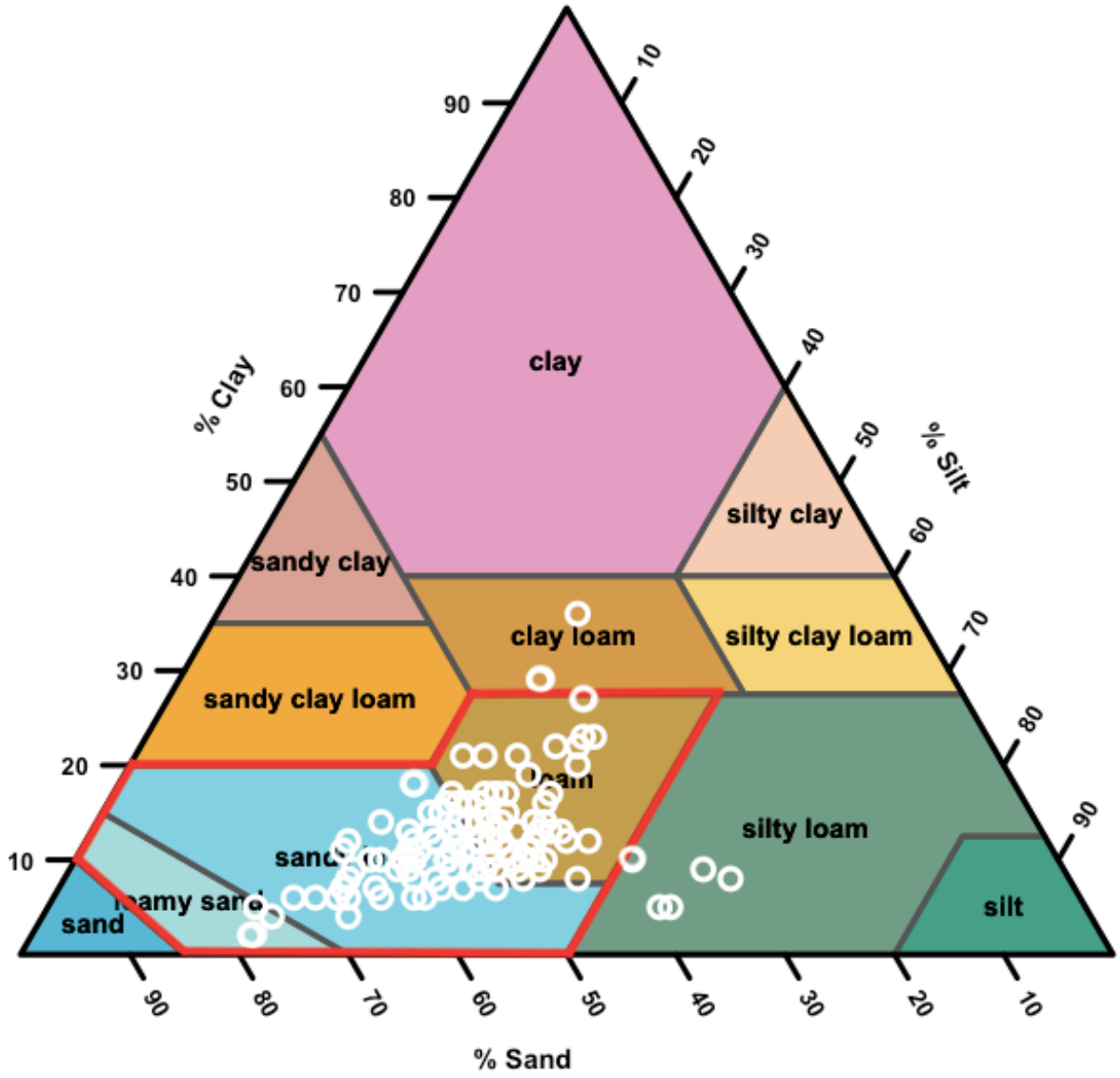


Figure N-1 **USDA-NCSS Soil Textural Triangle of Assisted Migration Sites**
Soil textural classification of top 15cm of soil at all assisted migration sites: Gingko State Park (GSP) (n= 18), Snow Mountain sites 1-3 (SM1-3*)* (n= 111) and Badger Mountain (BM) (n=4). White circles indicate individual $1m^2$ sample plots. Red lines outline soil textural classifications (loamy sand, sandy loam, loam) determined by hand texture method where *E. codium* occurs at the Native Site.

Appendix O: Chapter 2 Part I
Pairwise ADONIS Tables of Native and Assisted Migration Sites

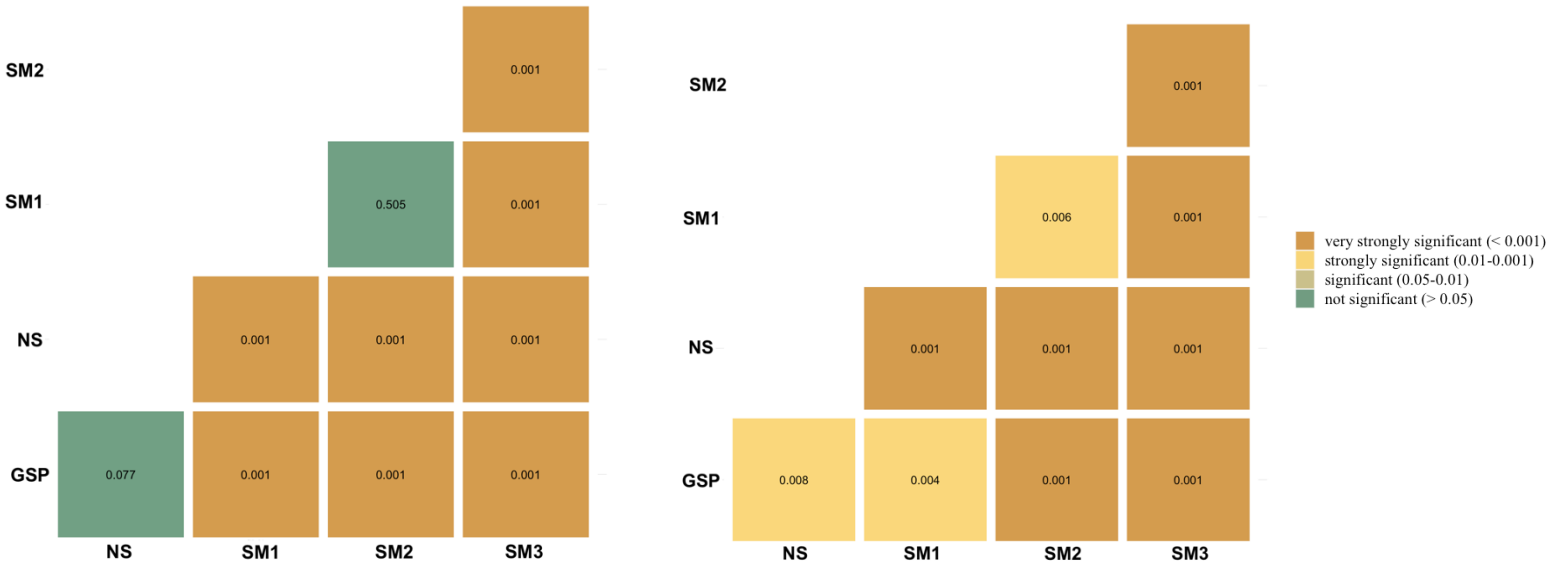


Figure O-1 **Pairwise Comparison of Differences in Soil Surface and Soil Surface Rock Fragment Composition Between the Native and Assisted Migration Sites**
Heatmap of p-values resulting from ADONIS pairwise comparison of differences in soil surface composition (left) and soil surface rock fragment composition (right) between the native site (NS), Gingko State Park (GSP) and Snow Mountain sites 1-3 (SM1-3). Tile colors correspond to strength of significance: brown = $\leq$ 0.001 (very strong significant difference), yellow = 0.01-.001 (strong significant difference), beige = 0.05-0.01 (significant difference), green = no significant difference (p = > 0.05) .

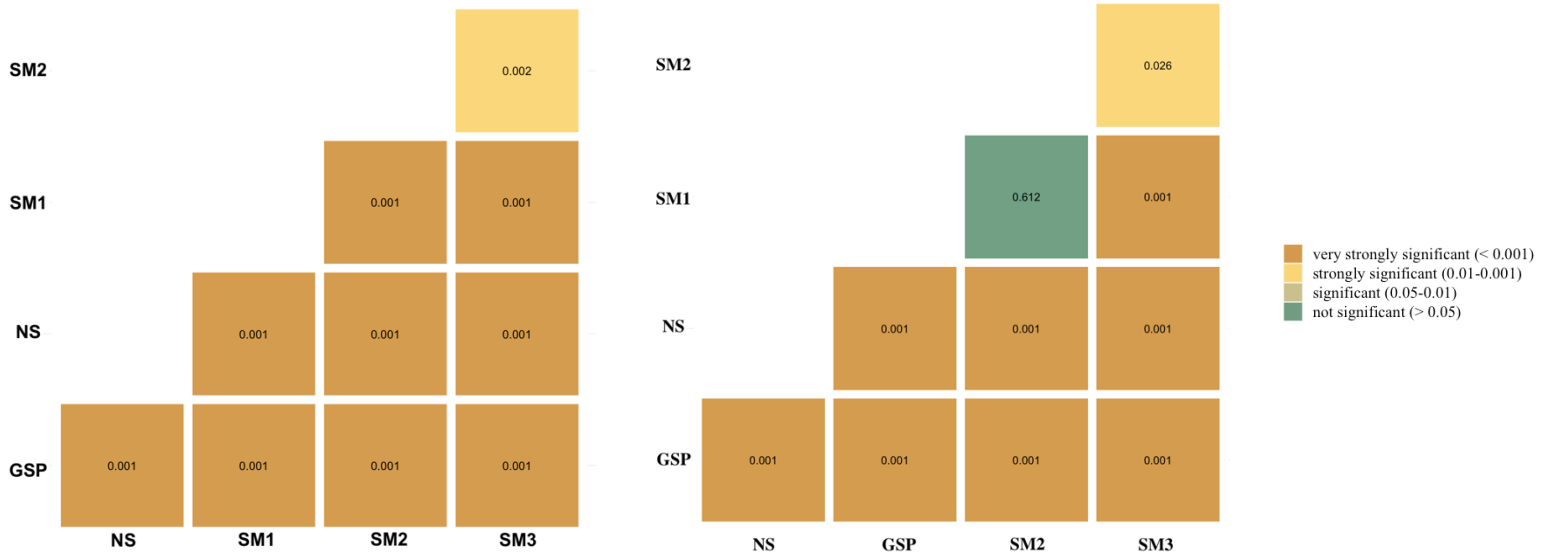


Figure O-2 **Pairwise Comparison of Differences in Vegetation Community and Functional Group Composition Between the Native and Assisted Migration Sites**
Heatmap of p-values resulting from ADONIS pairwise comparison of differences in vegetation community composition (A) and vegetation functional group composition (B) between the native site (NS), Gingko State Park (GSP) and Snow Mountain sites 1-3 (SM1-3). Tile colors correspond to strength of significance: brown = $\leq$ 0.001 (very strong significant difference), yellow = 0.01-.001 (strong significant difference), beige = 0.05-0.01 (significant difference), green = no significant difference (p = > 0.05) .

Appendix P: Chapter 2 Part I
Summary Tables of Differences in the Native and Assisted Migration Sites

Table P-1 **Summary of Differences in Categorical Site Characteristics Between the Native and Assisted Migration Sites**
Mode of categorical site characteristics at the native site (NS), Gingko State Park (GSP) and Snow Mountain sites 1-3 (SM1-3*).* Multilpe levels are included when frequencies are the same. Site characteristics include landscape position, hillslope position (SU= summit, SH= shoulder, BS= backslope), slope shape (CC= concave-concave, CL= concave-linear, CV = concave-convex, LC= linear-concave, LL= linear-linear, LV= linear-convex, VC= convex-concave, VL= convex-linear, VV= convex-convex (B), slope complexity (C= complex, S= simple), and aspect (N = north, NE = northeast, E= east, SE= southeast, SW= southwest, W= west, NW= northwest). Mode of soil suface texture is included with catagorical varaiables .

Site	n	Landscape Position	Hillslope Position	Slope Complex	Slope Shape	Aspect	Soil Texture
Gingko State Park	26	Mountainflank-Middle/Upperthird	SH	S	LL	NW	Sandy Loam
Native Site	98	Mountaintop-Upperthird	SH	S	LL	E	Loamy Sand
Snow Mountain Site 1	29	Mountainbase-Upperthird	BS	S	LL	SW	Loam
Snow Mountain Site 2	29	Mountainflank-Middlethird	BS	C	LL	NW	Sandy Loam
Snow Mounatin Site 3	53	Mountainflank-Upperthird	SU	C	LL	N	Loam

Table P-2 **Summary of Differences in Continuous Site Characteristics Between the Native and Assisted Migration Sites**
Differences in mean, minimum/maximum (range), and standard deviation (sd) of heat load index (HLI), slope (cm/cm), slope angle (°) and total rock fragment classification between the native site (NS), Gingko State Park (GSP) and Snow Mountain sites 1-3 (SM1-3*).*

		Heat Load Index			Slope (cm/cm)			Slope Angle (°)			Total RF Fragment Class		
Site	n	Mean	Range	sd	Mean	Range	sd	Mean	Range	sd	Mean	Range	sd
Gingko State Park	26	0.71	0.55-0.89	0.08	0.15	0.02-0.35	0.09	9.27	1-21	5.32	71.73	32-75	11.55
Native Site	98	0.71	0.47-0.92	0.11	0.20	0-0.53	0.10	11.77	2-30	6.34	57.95	9-75	23.12
Snow Mountain Site 1	29	0.82	0.5-0.94	0.08	0.22	0.13-0.58	0.10	11.90	3-30	5.98	42.22	0-75	30.22
Snow Mountain Site 2	29	0.72	0.33-0.9	0.15	0.24	0.09-0.57	0.11	12.62	4-33	6.65	45.07	0-75	33.22
Snow Mounatin Site 3	53	0.71	0.56-0.76	0.05	0.13	0.02-0.9	0.14	4.85	0-12	2.88	66.18	32-75	17.40

Table P-3 **Summary of Differences in Hydraulic Conductivity Between the Native and Assisted Migration Sites**
Differences between mean, minimum/maximum (range), and standard deviation (sd) of soil surface compositional components between the native site (NS), Gingko State Park (GSP) and Snow Mountain sites 1-3 (SM1-3*).*

Site Differences in Hydraulic Conductivity (K)

Site	n	Mean	Minimum	Maximum	sd
GSP	26	-8.12×10^{-4}	-1.63×10^{-3}	6.59×10^{-4}	6.48×10^{-4}
NS	80	1.27×10^{-3}	-3.05×10^{-3}	1.55×10^{-2}	2.88×10^{-3}
SM1	29	-2.29×10^{-4}	-1.73×10^{-3}	1.21×10^{-3}	6.45×10^{-4}
SM2	29	-2.98×10^{-4}	-3.42×10^{-3}	2.80×10^{-3}	1.31×10^{-3}
SM3	53	5.91×10^{-4}	-3.73×10^{-4}	2.62×10^{-3}	6.30×10^{-4}

Table P-4 **Summary of Differences in Soil Surface Composition Between the Native and Assisted Migration Sites** Differences between mean, minimum/maximum (range), and standard deviation (sd) of soil surface compositional components between the native site (NS), Gingko State Park (GSP) and Snow Mountain sites 1-3 (SM1-3*).*

Site Differences in Soil Surface Cover

		Rock			Bareground			Litter			Biocrust		
Site	**n**	Mean	Range	sd	Mean	Range	sd	Mean	Range	sd	Mean	Range	sd
GSP	26	74	0-88	22	8	0-38	10	7	0-38	8	6	0-62	12
NS	98	71	20-88	20	13	0-62	14	5	0-38	6	0	0-20	2
SM1	29	33	0-62	22	23	0-62	15	20	3-62	14	8	0-20	8
SM2	29	30	0-88	26	30	3-88	21	24	0-88	26	6	0-38	8
SM3	53	56	10-88	19	21	3-62	14	9	3-20	5	10	0-20	6

Table P-5 **Summary of Differences in Soil Surface Rock Fragment Composition Between the Native and Assisted Migration Sites** Differences between mean, minimum/maximum (range), and standard deviation (sd) of soil surface compositional components between the native site (NS), Gingko State Park (GSP) and Snow Mountain sites 1-3 (SM1-3*).*

Site Differences Soil Surface Rock Fragment Composition

		Bedrock			Boulder			Stone			Cobble			Course Gravel			Medium Gravel			Fine Gravel			Very Fine Gravel		
Site	**n**	Mean	Range	sd	Mean	Range	sd	Mean	Range	sd	Mean	Range	sd	Mean	Range	sd	Mean	Range	sd	Mean	Range	sd	Mean	Range	sd
GSP	26	0	0-0	0	0	0-0	0	3	0-20	6	9	0-38	10	34	0-88	26	35	3-88	24	15	0-38	15	0	0-0	0
NS	98	0	0-0	0	1	0-20	3	1	0-20	3	9	0-62	15	22	0-62	19	29	0-88	18	25	0-88	22	8	0-88	14
SM1	29	0	0-0	0	0	0-0	0	0	0-10	2	33	0-88	27	39	0-88	26	23	0-88	24	2	0-10	3	0	0-0	0
SM2	29	5	0-62	15	0	0-10	2	1	0-10	2	38	0-88	33	22	0-62	17	7	0-38	11	9	0-38	13	0	0-0	0
SM3	53	0	0-0	0	0	0-0	0	2	0-38	8	12	0-88	16	61	3-88	27	25	3-88	19	5	0-20	4	0	0-0	0

Table P-6 **Summary of Vegetation Characteristics at the Native and Assisted Migration Sites**
Differences between mean, minimum/maximum (range), and standard deviation (sd) of vegetation characteristics between the native site (NS), Gingko State Park (GSP) and Snow Mountain sites 1-3 (SM1-3*).*

	POSE			PSSP			BRTE			BASA			LOCA4			PHLI		
Site	Mean	Range	sd	Mean	Range	sd	Mean	Range	sd	Mean	Range	sd	Mean	Range	sd	Mean	Range	sd
GSP	9.15	0-20	5.20	0.71	0-10	2.06	0.44	0-3	0.96	0.00	0-0	0.00	0.00	0-0	0.00	0.04	0-0.5	0.14
NS	15.14	0.5-37.5	9.40	2.26	0-20	4.59	0.18	0-3	0.41	0.55	0-20	2.67	0.08	0-3	0.37	0.07	0-3	0.37
SM1	2.97	0-20	5.22	1.38	0-20	5.16	1.69	0-10	3.47	0.69	0-20	3.71	2.17	0-10	3.06	0.00	0-0	0.00
SM2	2.19	0-10	3.77	2.33	0-37.5	7.90	3.24	0-37.5	9.69	0.00	0-0	0.00	0.00	0-0	0.00	0.00	0-0	0.00
SM3	2.45	0-10	4.34	0.06	0-3	0.41	0.00	0-0	0.00	0.00	0-0	0.00	0.00	0-0	0.00	0.00	0-0	0.00

Table P-7 **Summary of Vegetation Functional Group Cover at the Native and Assisted Migration Sites**
Differences between mean, minimum/maximum (range), and standard deviation (sd) of vegetation characteristics between the native site (NS), Gingko State Park (GSP) and Snow Mountain sites 1-3 (SM1-3*)*.

		Shrub			Subspecies			Perennial Forb			Annual Forb			Perennial Graminoid			Annual Graminoid		
Site	**n**	Mean	Range	sd	Mean	Range	sd	Mean	Range	sd	Mean	Range	sd	Mean	Range	sd	Mean	Range	sd
GSP	26	5.21	0-37.5	10.26	1.12	0-10	2.26	5.33	0-13	3.96	0.85	0-5	1.33	9.90	0-20	5.40	0.90	0-6	1.67
NS	72	0.28	0-10	1.65	13.96	0.5-37.5	8.37	1.31	0-20.5	3.14	0.34	0-10	1.37	17.40	0.5-57.5	11.61	0.18	0-3	0.41
SM1	29	7.19	0-37.5	12.30	2.28	0-10	4.09	10.19	0-47	12.21	5.45	0-33.5	8.84	5.55	0-40	9.45	8.86	0-62.5	14.05
SM2	29	4.19	0-37.5	11.55	1.17	0-13	3.43	7.38	0-70.5	13.39	4.41	0-39.5	8.35	5.36	0-47.5	10.20	8.86	0-100.5	20.71
SM3	53	0.00	0-0	0.00	2.08	0-20	4.80	7.99	0-48.5	12.39	0.79	0-8	1.79	2.58	0-13.5	4.60	0.88	0-10	1.42

Table P-8 **Summary of Cover for Vegetation Species Occurring > 5% of Plots at the Native Site**
Differences between mean, minimum/maximum (range), and standard deviation (sd) of vegetation characteristics between the native site (NS), Gingko State Park (GSP) and Snow Mountain sites 1-3 (SM1-3*)*.

		LAI			Species Abundance			Total Cover		
Site	**n**	Mean	Range	sd	Mean	Range	sd	Mean	Range	sd
GSP	26	0.104	0.01-0.53	0.119	6.85	4-11	2.24	23.81	8.5-75.5	14.44
NS	72	0.026	0-0.78	0.094	4.43	3-8	1.21	33.97	4-71	15.30
SM1	29	0.232	0.01-0.76	0.225	7.38	2-18	5.21	40.02	1-105	33.47
SM2	29	0.385	0.02-1.35	0.408	7.24	2-17	5.28	31.88	1-115.5	35.78
SM3	53	0.115	0-0.71	0.185	5.70	1-22	5.12	14.81	0.5-84	21.90

Appendix Q: Chapter 2 Part I

Stress Plots of NMDS Ordinations Visualizing Soil Surface, Soil Surface Rock Fragment, and Vegetation Composition Data of Native and Assisted Migration Sites

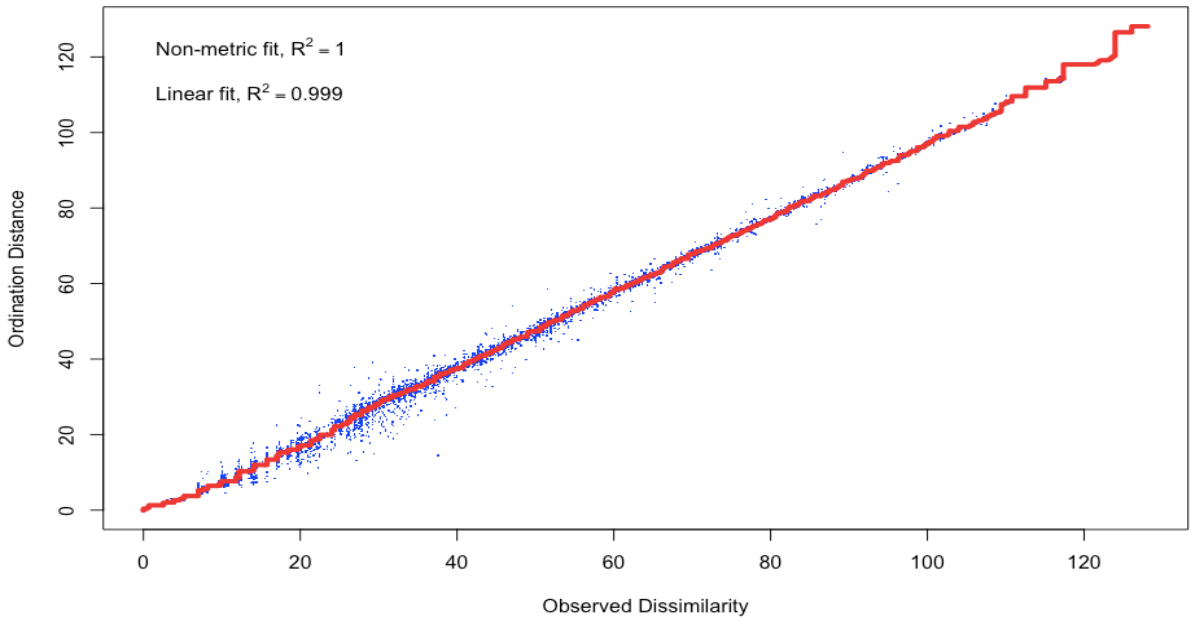


Figure Q-1 **NMDS Stress Plot of Soil Surface Composition**
Shepard plot of soil surface composition showing the Euclidean distance between plots in the 3-dimensional ordination space (Ordination Distance).

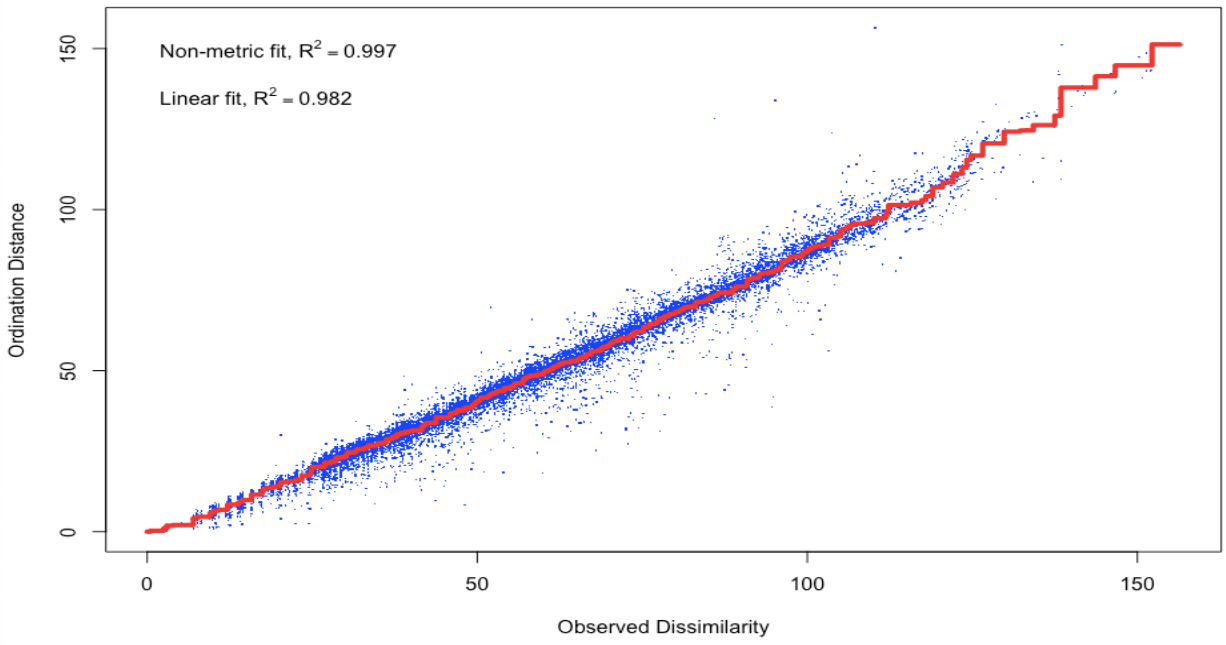


Figure Q-2 **NMDS Stress Plot of Soil Surface Rock Fragment Composition**
Shepard plot of soil surface composition showing the Euclidean distance between plots in the 3-dimensional ordination space (Ordination Distance).

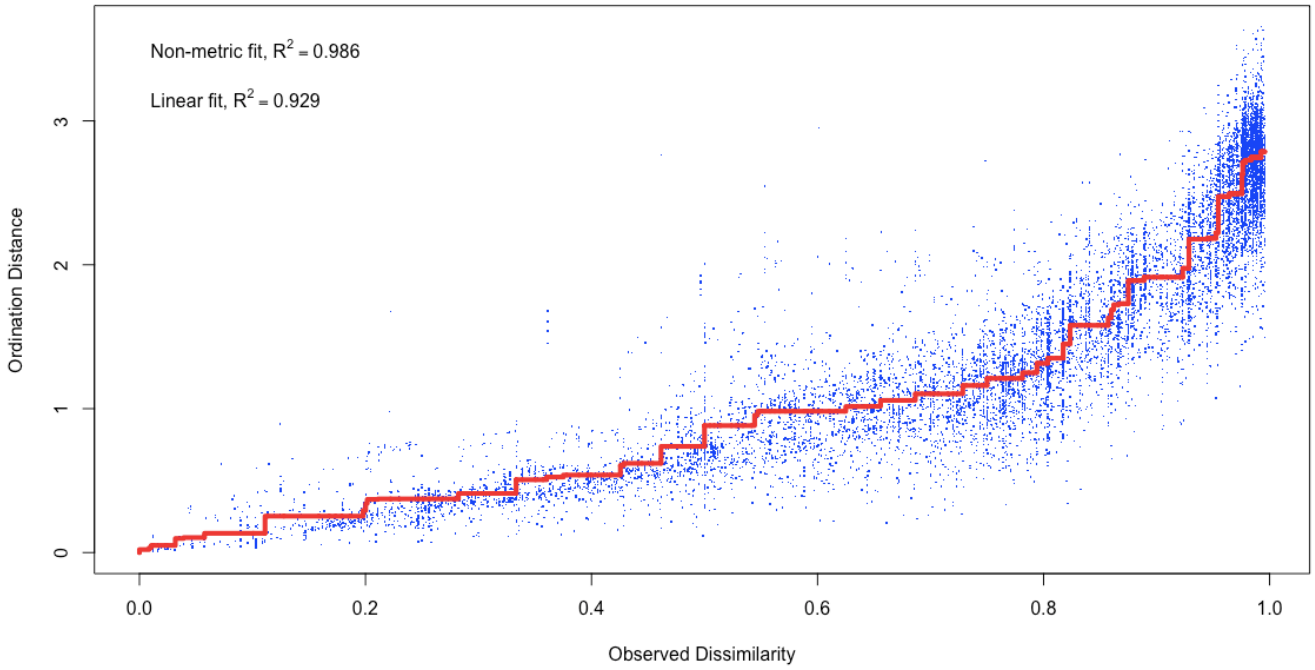


Figure Q-3 **NMDS Stress Plot of Vegetation Composition**
Shepard plot of vegetation composition showing the Bray-Curtis distance between plots in the 3-dimensional ordination space (Ordination Distance).

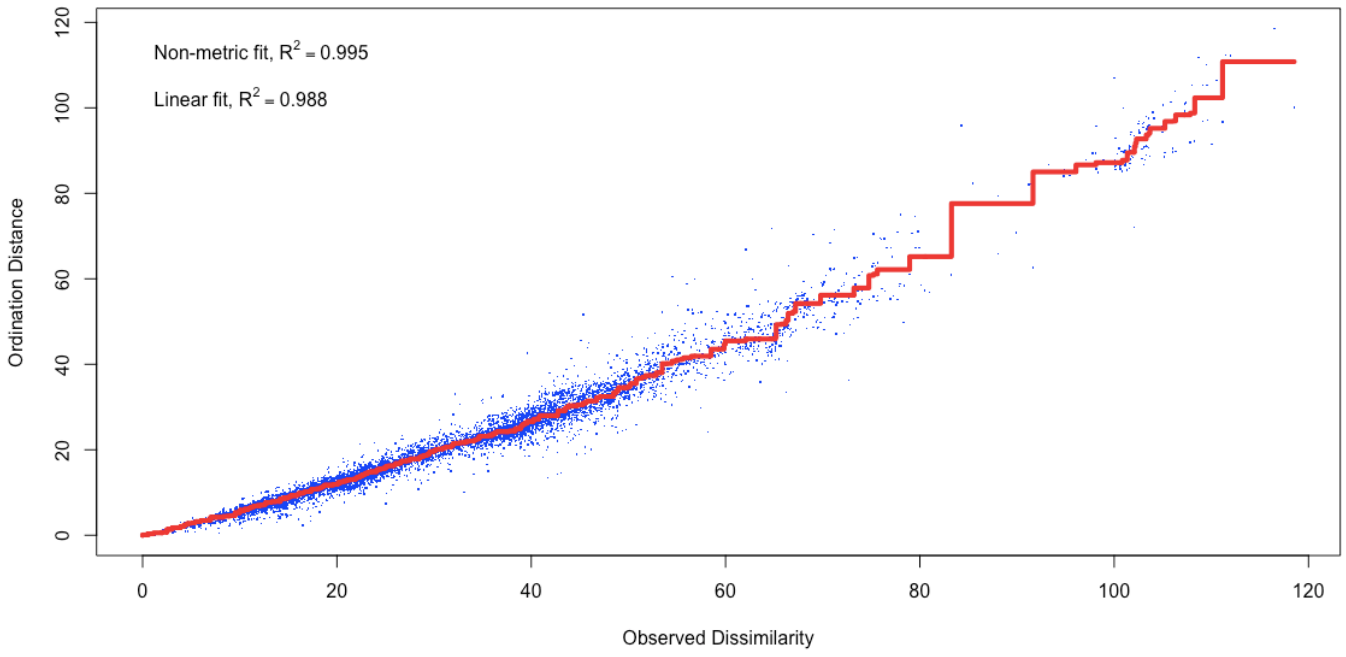


Figure Q-4 **NMDS Stress Plot of Vegetation Functional Group Composition**
Shepard plot of vegetation composition functional groups showing the Euclidean distance between plots in the 3-dimensional ordination space (Ordination Distance).

Appendix R: Chapter 2 Part I
Multigroup Indicator Species Analysis (ISA) Table by Native and Assisted Migration Sites

Table R-1 **Multigroup ISA of Soil Surface Rock Fragment Composition by Native and Assisted Migration Sites**
Vegetation species that most characterize the native site (NS), Gingko State Park (GSP) and Snow Mountain sites 1-3 (SM1-3*)*. IV_{ij} of 100 means species occurs in all plots. Significant relationships are indicated by asterisks (* = significant, ** = strongly significant, ***= very strongly significant).

ISA of Soil Surface Rock Fragment Composition- Multigroup

Cover Class	GSP	NS	SM1	SM2	SM3	IVij	*P*	
Bedrock				X		13.7	0.005	**
Cobble	X		X	X	X	79.2	0.005	**
Fine Gravel	X	X		X	X	92.2	0.005	**
Very Fine Gravel		X				96.0	0.005	**
Stone	X				X	17.6	0.015	**

Table R-2 **Multigroup ISA of Vegetation Composition by Native and Assisted Migration Sites**
Vegetation species that most characterize the native site (NS), Gingko State Park (GSP) and Snow Mountain sites 1-3 (SM1-3*)*. IV_{ij} of 100 means species occurs in all plots. Significant relationships are indicated by asterisks (* = significant, ** = strongly significant, ***= very strongly significant).

ISA of Vegetation Composition (multigroup)

Species	Habit	Origin	GSP	NS	SM1	SM2	SM3	IVij	*P*	
Poa secunda	Perennial graminoid	Native	X	X				83.1	0.005	**
Artemisia rigida	Perennial shrub	Native	X		X			37.0	0.005	**
Eriogonum thymoides	Perennial subshrub	Native	X				X	18.5	0.005	**
Lomatium macrocarpum	Perennial forb	Native	X				X	27.4	0.005	**
Nestotus stenophyllus	Perennial forb	Native	X				X	17.3	0.010	**
Achnatherum thurberianum	Perennial graminoid	Native			X	X		6.9	0.035	*
Alyssum alyssoides	Annual forb	Invasive			X	X		25.6	0.005	**
Lomatium dissectum	Perennial forb	Native			X	X		12.1	0.005	**
Microsteris gracilis	Annual forb	Native			X	X		8.2	0.040	*
Poa bulbosa	Biennial graminoid	Invasive			X	X		30.5	0.005	**
Polemonium micranthum	Annual forb	Native			X	X		16.6	0.005	**
Collinsia parviflora	Annual forb	Native				X	X	15.3	0.010	**
Olsynium douglasii	Perennial forb	Native				X	X	18.3	0.005	**
Sedum lanceolatum	Perennial forb	Native				X	X	61.0	0.005	**
Bromus tectorum	Annual graminoid	Invasive	X		X	X		33.4	0.005	**
Collomia grandiflora	Annual forb	Native	X		X	X		10.7	0.010	**
Draba verna	Annual forb	Naturalized	X		X	X		28.8	0.005	**
Epilobium brachycarpum	Annual forb	Native	X		X	X		29.2	0.005	**
Lactuca serriola	Biennial forb	Invasive	X		X	X		10.7	0.020	*
Vulpia microstachys	Annual graminoid	Invasive	X			X	X	39.9	0.005	**
Bromus commutatus	Annual graminoid	Invasive			X	X	X	78.4	0.005	**
Pseudoroegneria spicata	Perennial graminoid	Native	X	X	X	X		22.3	0.010	**

Appendix S: Chapter 2 Part I
Vegetation Species Summary Tables of Native and Assisted Migration Sites

Table S-1 **Summary of Vegetation Species with <5% Occurrence by Native and Assisted Migration Sites**
Percentage of plots occurrence of vegetation species with <5% occurrence across all sites by Native Site (NS), Gingko State Park (GSP), Snow Mountain (SM) sites 1-3). Table shows percentage of total plots surveyed across the whole site and by site.

Species	Habit	Origin	All Sites	GSP	NS	SM1	SM2	SM3
Collomia grandiflora	Annual forb	Native	4.31	15.38	0.00	3.45	13.79	0.00
Lactuca serriola	Biennial forb	Invasive	4.31	11.54	0.00	10.34	10.34	0.00
Phlox hoodii	Perennial forb	Native	4.31	7.69	0.00	3.45	3.45	9.43
Antennaria flagellaris	Perennial forb	Native	3.83	0.00	0.00	0.00	0.00	15.09
Astragalus purshii	Perennial forb	Native	3.83	0.00	11.11	0.00	0.00	0.00
Lewisia columbiana	Perennial forb	Native	3.83	0.00	0.00	0.00	0.00	15.09
Salsola tragus	Annual forb	Invasive	3.83	0.00	11.11	0.00	0.00	0.00
Viola trinervata	Perennial forb	Native	3.83	0.00	0.00	20.69	0.00	3.77
Astragalus caricinus	Perennial forb	Native	3.35	0.00	9.72	0.00	0.00	0.00
Balsamorhiza sagittata	Perennial forb	Native	3.35	0.00	8.33	3.45	0.00	0.00
Lomatium dissectum	Perennial forb	Native	3.35	0.00	0.00	10.34	13.79	0.00
Phacelia linearis	Annual forb	Native	3.35	7.69	6.94	0.00	0.00	0.00
Elymus elymoides	Perennial graminoid	Native	2.87	7.69	0.00	6.90	0.00	3.77
Lomatium nudicaule	Perennial forb	Native	2.87	0.00	0.00	20.69	0.00	0.00
Microsteris gracilis	Annual forb	Native	2.87	0.00	0.00	6.90	10.34	1.89
Chaenactis douglasii	Annual forb	Native	2.39	0.00	2.78	3.45	6.90	0.00
Phlox longifolia	Perennial forb	Native	2.39	0.00	2.78	6.90	3.45	0.00
Achnatherum thurberianum	Perennial graminoid	Native	1.91	0.00	0.00	6.90	6.90	0.00
Eriogonum douglasii	Perennial subshrub	Native	1.91	11.54	0.00	0.00	0.00	1.89
Eriogonum sphaerocephalum	Perennial subshrub	Native	1.91	7.69	0.00	3.45	3.45	0.00
Fritillaria pudica	Perennial forb	Native	1.91	0.00	0.00	3.45	10.34	0.00
Trifolium macrocephalum	Perennial forb	Native	1.91	0.00	0.00	13.79	0.00	0.00
Allium acuminatum	Perennial forb	Native	1.44	0.00	0.00	10.34	0.00	0.00
Allium spp	Perennial forb	Native	1.44	0.00	0.00	0.00	10.34	0.00
Chrysothamnus viscidiflorus	Perennial shrub	Native	1.44	0.00	1.39	0.00	6.90	0.00
Crepis intermedia	Perennial forb	Native	1.44	0.00	0.00	10.34	0.00	0.00
Lupinus sulphureus	Perennial forb	Native	1.44	0.00	0.00	10.34	0.00	0.00
Antennaria stenophylla	Perennial forb	Native	0.96	0.00	0.00	0.00	3.45	1.89
Artemisia tridentata	Perennial shrub	Native	0.96	0.00	1.39	0.00	3.45	0.00
Aster spp	Perennial forb	Native	0.96	7.69	0.00	0.00	0.00	0.00
Bromus sitchensis	Perennial graminoid	Native	0.96	0.00	0.00	6.90	0.00	0.00
Crepis spp	Perennial forb	Native	0.96	0.00	0.00	0.00	0.00	3.77
Dactylis glomerata	Perennial graminoid	Invasive	0.96	0.00	0.00	0.00	6.90	0.00
Descurainia sophia	Annual forb	Invasive	0.96	7.69	0.00	0.00	0.00	0.00
Erodium cicutarium	Annual forb	Invasive	0.96	0.00	0.00	6.90	0.00	0.00
Eriogonum compositum	Perennial subshrub	Native	0.96	0.00	0.00	0.00	6.90	0.00
Eriogonum ovalifolium	Perennial subshrub	Native	0.96	0.00	0.00	0.00	6.90	0.00
Erigeron poliospermus	Perennial forb	Native	0.96	0.00	2.78	0.00	0.00	0.00
Lupinus spp	Perennial forb	Native	0.96	3.85	0.00	3.45	0.00	0.00
Lupinus sericeus	Perennial forb	Native	0.96	0.00	0.00	0.00	6.90	0.00
Sisymbrium altissimum	Annual forb	Invasive	0.96	0.00	0.00	0.00	6.90	0.00
Sphaeralcea munroana	Perennial forb	Native	0.96	0.00	2.78	0.00	0.00	0.00
Achillea millefolium	Perennial forb	Naturalized	0.48	3.85	0.00	0.00	0.00	0.00
Amsinckia retrorsa	Annual forb	Native	0.48	0.00	1.39	0.00	0.00	0.00
Amsinckia spp	Annual forb	Native	0.48	0.00	0.00	3.45	0.00	0.00
Antennaria dimorpha	Perennial forb	Native	0.48	0.00	0.00	0.00	0.00	1.89
Ceratocephala testiculata	Annual forb	Invasive	0.48	0.00	0.00	0.00	0.00	1.89
Cryptantha pterocarya	Annual forb	Native	0.48	0.00	1.39	0.00	0.00	0.00
Eremogone franklinii	Perennial forb	Native	0.48	0.00	0.00	0.00	0.00	1.89
Eriocoma hymenoides	Perennial graminoid	Native	0.48	0.00	1.39	0.00	0.00	0.00
Erigeron linearis	Perennial forb	Native	0.48	0.00	0.00	0.00	3.45	0.00
Eriogonum niveum	Perennial subshrub	Native	0.48	0.00	0.00	0.00	3.45	0.00
Festuca idahoensis	Perennial graminoid	Native	0.48	0.00	0.00	0.00	3.45	0.00
Lagophylla ramosissima	Perennial forb	Native	0.48	0.00	0.00	0.00	3.45	0.00
Lomatium spp	Perennial forb	Native	0.48	0.00	1.39	0.00	0.00	0.00
Lomatium triternatum	Perennial forb	Native	0.48	0.00	0.00	3.45	0.00	0.00
Lupinus saxosus	Perennial forb	Native	0.48	0.00	0.00	0.00	0.00	1.89
Physaria geyeri	Perennial forb	Native	0.48	3.85	0.00	0.00	0.00	0.00
Poa cusickii	Perennial graminoid	Native	0.48	0.00	0.00	0.00	3.45	0.00
Ranunculus glaberrimus	Perennial forb	Native	0.48	0.00	0.00	0.00	3.45	0.00
Salvia dorrii	Perennial shrub	Native	0.48	0.00	1.39	0.00	0.00	0.00
Zigadenus paniculatum	Perennial forb	Native	0.48	0.00	0.00	0.00	3.45	0.00

Table S-2 **Summary of Vegetation Species Present at Gingko State Park**
Occurrence of vegetation species present at the native site across all sites (Native Site (NS), Gingko State Park (GSP), Snow Mountain (SM) sites 1-3). Table shows percentage of total plots surveyed across the whole site and by site.

Species	Habit	Origin	All Sites	GSP	NS	SM1	SM2	SM3
Poa secunda	Perennial graminoid	Native	62.68	96.15	100.00	31.03	41.38	24.53
Balsamorhiza hookeri	Perennial forb	Native	13.88	84.62	2.78	6.90	0.00	5.66
Artemisia rigida	Perennial shrub	Native	12.92	50.00	0.00	37.93	10.34	0.00
Vulpia microstachys	Annual graminoid	Invasive	22.97	50.00	0.00	10.34	20.69	49.06
Lomatium macrocarpum	Perennial forb	Native	11.00	38.46	0.00	3.45	0.00	22.64
Draba verna	Annual forb	Naturalized	17.70	34.62	0.00	34.48	31.03	16.98
Bromus tectorum	Annual graminoid	Invasive	24.88	30.77	29.17	41.38	37.93	0.00
Pseudoroegneria spicata	Perennial graminoid	Native	17.22	30.77	30.56	6.90	10.34	1.89
Epilobium brachycarpum	Annual forb	Native	13.88	26.92	0.00	34.48	27.59	7.55
Nestotus stenophyllus	Perennial forb	Native	8.13	19.23	0.00	3.45	0.00	20.75
Collomia grandiflora	Annual forb	Native	4.31	15.38	0.00	3.45	13.79	0.00
Eriogonum thymoides	Perennial subshrub	Native	8.13	15.38	0.00	3.45	0.00	22.64
Eriogonum douglasii	Perennial subshrub	Native	1.91	11.54	0.00	0.00	0.00	1.89
Lactuca serriola	Biennial forb	Invasive	4.31	11.54	0.00	10.34	10.34	0.00
Aster spp	Perennial forb	Native	0.96	7.69	0.00	0.00	0.00	0.00
Descurainia sophia	Annual forb	Invasive	0.96	7.69	0.00	0.00	0.00	0.00
Elymus elymoides	Perennial graminoid	Native	2.87	7.69	0.00	6.90	0.00	3.77
Eriogonum sphaerocephalum	Perennial subshrub	Native	1.91	7.69	0.00	3.45	3.45	0.00
Phlox hoodii	Perennial forb	Native	4.31	7.69	0.00	3.45	3.45	9.43
Phacelia linearis	Annual forb	Native	3.35	7.69	6.94	0.00	0.00	0.00
Achillea millefolium	Perennial forb	Naturalized	0.48	3.85	0.00	0.00	0.00	0.00
Idahoa scapigera	Annual forb	Native	11.48	3.85	0.00	27.59	13.79	20.75
Lupinus spp	Perennial forb	Native	0.96	3.85	0.00	3.45	0.00	0.00
Physaria geyeri	Perennial forb	Native	0.48	3.85	0.00	0.00	0.00	0.00
Poa bulbosa	Biennial graminoid	Invasive	9.09	3.85	0.00	24.14	37.93	0.00
Polemonium micranthum	Annual forb	Native	6.22	3.85	0.00	17.24	17.24	3.77

Table S-3 **Summary of Vegetation Species Present at Snow Mountain Site 1**
Occurrence of vegetation species present at the native site across all sites (Native Site (NS), Gingko State Park (GSP), Snow Mountain (SM) sites 1-3). Table shows percentage of total plots surveyed across the whole site and by site.

Species	Habit	Origin	All Sites	GSP	NS	SM1	SM2	SM3
Bromus commutatus	Annual graminoid	Invasive	41.63	0.00	0.00	86.21	82.76	71.70
Lomatium canbyi	Perennial forb	Native	9.57	0.00	8.33	48.28	0.00	0.00
Bromus tectorum	Annual graminoid	Invasive	24.88	30.77	29.17	41.38	37.93	0.00
Artemisia rigida	Perennial shrub	Native	12.92	50.00	0.00	37.93	10.34	0.00
Draba verna	Annual forb	Naturalized	17.70	34.62	0.00	34.48	31.03	16.98
Epilobium brachycarpum	Annual forb	Native	13.88	26.92	0.00	34.48	27.59	7.55
Poa secunda	Perennial graminoid	Native	62.68	96.15	100.00	31.03	41.38	24.53
Alyssum alyssoides	Annual forb	Invasive	9.57	0.00	0.00	27.59	27.59	7.55
Idahoa scapigera	Annual forb	Native	11.48	3.85	0.00	27.59	13.79	20.75
Poa bulbosa	Biennial graminoid	Invasive	9.09	3.85	0.00	24.14	37.93	0.00
Lomatium nudicaule	Perennial forb	Native	2.87	0.00	0.00	20.69	0.00	0.00
Viola trinervata	Perennial forb	Native	3.83	0.00	0.00	20.69	0.00	3.77
Polemonium micranthum	Annual forb	Native	6.22	3.85	0.00	17.24	17.24	3.77
Trifolium macrocephalum	Perennial forb	Native	1.91	0.00	0.00	13.79	0.00	0.00
Allium acuminatum	Perennial forb	Native	1.44	0.00	0.00	10.34	0.00	0.00
Crepis intermedia	Perennial forb	Native	1.44	0.00	0.00	10.34	0.00	0.00
Descurainia pinnata	Annual forb	Native	7.18	0.00	4.17	10.34	20.69	5.66
Lactuca serriola	Biennial forb	Invasive	4.31	11.54	0.00	10.34	10.34	0.00
Lomatium dissectum	Perennial forb	Native	3.35	0.00	0.00	10.34	13.79	0.00
Lupinus sulphureus	Perennial forb	Native	1.44	0.00	0.00	10.34	0.00	0.00
Vulpia microstachys	Annual graminoid	Invasive	22.97	50.00	0.00	10.34	20.69	49.06
Achnatherum thurberianum	Perennial graminoid	Native	1.91	0.00	0.00	6.90	6.90	0.00
Balsamorhiza hookeri	Perennial forb	Native	13.88	84.62	2.78	6.90	0.00	5.66
Bromus sitchensis	Perennial graminoid	Native	0.96	0.00	0.00	6.90	0.00	0.00
Elymus elymoides	Perennial graminoid	Native	2.87	7.69	0.00	6.90	0.00	3.77
Erodium cicutarium	Annual forb	Invasive	0.96	0.00	0.00	6.90	0.00	0.00
Microsteris gracilis	Annual forb	Native	2.87	0.00	0.00	6.90	10.34	1.89
Phlox longifolia	Perennial forb	Native	2.39	0.00	2.78	6.90	3.45	0.00
Pseudoroegneria spicata	Perennial graminoid	Native	17.22	30.77	30.56	6.90	10.34	1.89
Amsinckia spp	Annual forb	Native	0.48	0.00	0.00	3.45	0.00	0.00
Balsamorhiza sagittata	Perennial forb	Native	3.35	0.00	8.33	3.45	0.00	0.00
Chaenactis douglasii	Annual forb	Native	2.39	0.00	2.78	3.45	6.90	0.00
Collomia grandiflora	Annual forb	Native	4.31	15.38	0.00	3.45	13.79	0.00
Collinsia parviflora	Annual forb	Native	6.70	0.00	0.00	3.45	13.79	16.98
Eriogonum sphaerocephalum	Perennial subshrub	Native	1.91	7.69	0.00	3.45	3.45	0.00
Eriogonum thymoides	Perennial subshrub	Native	8.13	15.38	0.00	3.45	0.00	22.64
Fritillaria pudica	Perennial forb	Native	1.91	0.00	0.00	3.45	10.34	0.00
Lomatium macrocarpum	Perennial forb	Native	11.00	38.46	0.00	3.45	0.00	22.64
Lomatium triternatum	Perennial forb	Native	0.48	0.00	0.00	3.45	0.00	0.00
Lupinus spp	Perennial forb	Native	0.96	3.85	0.00	3.45	0.00	0.00
Nestotus stenophyllus	Perennial forb	Native	8.13	19.23	0.00	3.45	0.00	20.75
Phlox hoodii	Perennial forb	Native	4.31	7.69	0.00	3.45	3.45	9.43

Table S-4 **Summary of Vegetation Species Present at Snow Mountain Site 2**
Occurrence of vegetation species present at the native site across all sites (Native Site (NS), Gingko State Park (GSP), Snow Mountain (SM) sites 1-3). Table shows percentage of total plots surveyed across the whole site and by site.

Species	Habit	Origin	All Sites	GSP	NS	SM1	SM2	SM3
Bromus commutatus	Annual graminoid	Invasive	41.63	0.00	0.00	86.21	82.76	71.70
Sedum lanceolatum	Perennial forb	Native	23.92	0.00	0.00	0.00	48.28	67.92
Poa secunda	Perennial graminoid	Native	62.68	96.15	100.00	31.03	41.38	24.53
Bromus tectorum	Annual graminoid	Invasive	24.88	30.77	29.17	41.38	37.93	0.00
Poa bulbosa	Biennial graminoid	Invasive	9.09	3.85	0.00	24.14	37.93	0.00
Draba verna	Annual forb	Naturalized	17.70	34.62	0.00	34.48	31.03	16.98
Alyssum alyssoides	Annual forb	Invasive	9.57	0.00	0.00	27.59	27.59	7.55
Epilobium brachycarpum	Annual forb	Native	13.88	26.92	0.00	34.48	27.59	7.55
Descurainia pinnata	Annual forb	Native	7.18	0.00	4.17	10.34	20.69	5.66
Vulpia microstachys	Annual graminoid	Invasive	22.97	50.00	0.00	10.34	20.69	49.06
Polemonium micranthum	Annual forb	Native	6.22	3.85	0.00	17.24	17.24	3.77
Collomia grandiflora	Annual forb	Native	4.31	15.38	0.00	3.45	13.79	0.00
Collinsia parviflora	Annual forb	Native	6.70	0.00	0.00	3.45	13.79	16.98
Idahoa scapigera	Annual forb	Native	11.48	3.85	0.00	27.59	13.79	20.75
Lomatium dissectum	Perennial forb	Native	3.35	0.00	0.00	10.34	13.79	0.00
Olsynium douglasii	Perennial forb	Native	7.18	0.00	0.00	0.00	13.79	20.75
Allium spp	Perennial forb	Native	1.44	0.00	0.00	0.00	10.34	0.00
Artemisia rigida	Perennial shrub	Native	12.92	50.00	0.00	37.93	10.34	0.00
Fritillaria pudica	Perennial forb	Native	1.91	0.00	0.00	3.45	10.34	0.00
Lactuca serriola	Biennial forb	Invasive	4.31	11.54	0.00	10.34	10.34	0.00
Microsteris gracilis	Annual forb	Native	2.87	0.00	0.00	6.90	10.34	1.89
Pseudoroegneria spicata	Perennial graminoid	Native	17.22	30.77	30.56	6.90	10.34	1.89
Achnatherum thurberianum	Perennial graminoid	Native	1.91	0.00	0.00	6.90	6.90	0.00
Chaenactis douglasii	Annual forb	Native	2.39	0.00	2.78	3.45	6.90	0.00
Chrysothamnus viscidiflorus	Perennial shrub	Native	1.44	0.00	1.39	0.00	6.90	0.00
Dactylis glomerata	Perennial graminoid	Invasive	0.96	0.00	0.00	0.00	6.90	0.00
Eriogonum compositum	Perennial subshrub	Native	0.96	0.00	0.00	0.00	6.90	0.00
Eriogonum ovalifolium	Perennial subshrub	Native	0.96	0.00	0.00	0.00	6.90	0.00
Lupinus sericeus	Perennial forb	Native	0.96	0.00	0.00	0.00	6.90	0.00
Sisymbrium altissimum	Annual forb	Invasive	0.96	0.00	0.00	0.00	6.90	0.00
Antennaria stenophylla	Perennial forb	Native	0.96	0.00	0.00	0.00	3.45	1.89
Artemisia tridentata	Perennial shrub	Native	0.96	0.00	1.39	0.00	3.45	0.00
Erigeron linearis	Perennial forb	Native	0.48	0.00	0.00	0.00	3.45	0.00
Eriogonum niveum	Perennial subshrub	Native	0.48	0.00	0.00	0.00	3.45	0.00
Eriogonum sphaerocephalum	Perennial subshrub	Native	1.91	7.69	0.00	3.45	3.45	0.00
Festuca idahoensis	Perennial graminoid	Native	0.48	0.00	0.00	0.00	3.45	0.00
Lagophylla ramosissima	Perennial forb	Native	0.48	0.00	0.00	0.00	3.45	0.00
Lewisia rediviva	Perennial forb	Native	5.26	0.00	0.00	0.00	3.45	18.87
Phlox hoodii	Perennial forb	Native	4.31	7.69	0.00	3.45	3.45	9.43
Phlox longifolia	Perennial forb	Native	2.39	0.00	2.78	6.90	3.45	0.00
Poa cusickii	Perennial graminoid	Native	0.48	0.00	0.00	0.00	3.45	0.00
Ranunculus glaberrimus	Perennial forb	Native	0.48	0.00	0.00	0.00	3.45	0.00
Zigadenus paniculatum	Perennial forb	Native	0.48	0.00	0.00	0.00	3.45	0.00

Table S-5 **Summary of Vegetation Species Present at Snow Mountain Site 3**
Occurrence of vegetation species present at the native site across all sites (Native Site (NS), Gingko State Park (GSP), Snow Mountain (SM) sites 1-3). Table shows percentage of total plots surveyed across the whole site and by site.

Species	Habit	Origin	All Sites	GSP	NS	SM1	SM2	SM3
Bromus commutatus	Annual graminoid	Invasive	41.63	0.00	0.00	86.21	82.76	71.70
Sedum lanceolatum	Perennial forb	Native	23.92	0.00	0.00	0.00	48.28	67.92
Vulpia microstachys	Annual graminoid	Invasive	22.97	50.00	0.00	10.34	20.69	49.06
Poa secunda	Perennial graminoid	Native	62.68	96.15	100.00	31.03	41.38	24.53
Eriogonum thymoides	Perennial subshrub	Native	8.13	15.38	0.00	3.45	0.00	22.64
Lomatium macrocarpum	Perennial forb	Native	11.00	38.46	0.00	3.45	0.00	22.64
Idahoa scapigera	Annual forb	Native	11.48	3.85	0.00	27.59	13.79	20.75
Nestotus stenophyllus	Perennial forb	Native	8.13	19.23	0.00	3.45	0.00	20.75
Olsynium douglasii	Perennial forb	Native	7.18	0.00	0.00	0.00	13.79	20.75
Lewisia rediviva	Perennial forb	Native	5.26	0.00	0.00	0.00	3.45	18.87
Collinsia parviflora	Annual forb	Native	6.70	0.00	0.00	3.45	13.79	16.98
Draba verna	Annual forb	Naturalized	17.70	34.62	0.00	34.48	31.03	16.98
Antennaria flagellaris	Perennial forb	Native	3.83	0.00	0.00	0.00	0.00	15.09
Lewisia columbiana	Perennial forb	Native	3.83	0.00	0.00	0.00	0.00	15.09
Phlox hoodii	Perennial forb	Native	4.31	7.69	0.00	3.45	3.45	9.43
Alyssum alyssoides	Annual forb	Invasive	9.57	0.00	0.00	27.59	27.59	7.55
Epilobium brachycarpum	Annual forb	Native	13.88	26.92	0.00	34.48	27.59	7.55
Balsamorhiza hookeri	Perennial forb	Native	13.88	84.62	2.78	6.90	0.00	5.66
Descurainia pinnata	Annual forb	Native	7.18	0.00	4.17	10.34	20.69	5.66
Crepis spp	Perennial forb	Native	0.96	0.00	0.00	0.00	0.00	3.77
Elymus elymoides	Perennial graminoid	Native	2.87	7.69	0.00	6.90	0.00	3.77
Polemonium micranthum	Annual forb	Native	6.22	3.85	0.00	17.24	17.24	3.77
Viola trinervata	Perennial forb	Native	3.83	0.00	0.00	20.69	0.00	3.77
Antennaria dimorpha	Perennial forb	Native	0.48	0.00	0.00	0.00	0.00	1.89
Antennaria stenophylla	Perennial forb	Native	0.96	0.00	0.00	0.00	3.45	1.89
Ceratocephala testiculata	Annual forb	Invasive	0.48	0.00	0.00	0.00	0.00	1.89
Eriogonum douglasii	Perennial subshrub	Native	1.91	11.54	0.00	0.00	0.00	1.89
Eremogone franklinii	Perennial forb	Native	0.48	0.00	0.00	0.00	0.00	1.89
Lupinus saxosus	Perennial forb	Native	0.48	0.00	0.00	0.00	0.00	1.89
Microsteris gracilis	Annual forb	Native	2.87	0.00	0.00	6.90	10.34	1.89
Pseudoroegneria spicata	Perennial graminoid	Native	17.22	30.77	30.56	6.90	10.34	1.89

Appendix T: Chapter 2 Part II
Seedling Survival at Badger and Snow Mountain Outplanting Transects 2020-2023

Table T-1 Outplanted *E. codium* Seedling Survival at Badger and Snow Mountains 2020-2023
Number of seedlings initially outplanted in 2020 at Badger and Snow Mountains and 2021 at Snow Mountain and the number of surviving seedlings in 2021-2023. Percentage of survival (alive seedlings) and decline (dead seedlings) in July 2022 and May 2023 at each outplanting groupings, and the overall survival in May 2023 at each site, is included. Survival of seedlings outplanted at Badger Mountain in 2020 were monitored May 2023. Survival of seedlings outplanted at Snow Mountain in 2020 were monitored in 2022 and are believed to have died in a heat wave Summer 2021. Survival of seedlings outplanted at Snow Mountain in 2022 were monitored in July 2022 and May 2023. In May 2023 alive seedlings were found only at BM1 grouping 1 and SM3 transects 1, 4, and 5.

Outplanting Grouping	2020	2021	2022	% Surivival	% Decline	2023	% Surivival	% Decline
Badger Mt (14%)								
BM1-1	5	-	-	-	-	4	80	-20
BM1-2	4	-	-	-	-	0	0	-100
BM1-3	4	-	-	-	-	0	0	-100
BM1-4	4	-	-	-	-	0	0	-100
BM1-5	6	-	-	-	-	0	0	-100
BM1-6	6	-	-	-	-	0	0	-100
Snow Mt 1 (0%)								
SM1-2020	20	20	0	0	-100	0	0	0
SM1-2021	-	44	15	34	-66	0	0	-34
Snow Mt 2 (0%)								
SM2-2020	20	20	0	0	-100	0	0	0
SM2-2021	-	44	25	57	-43	0	0	-57
Snow Mt 3 (3%)								
SM3-1	-	44	26	59	-41	1	2	-57
SM3-2	20	20	0	0	-100	0	0	0
SM3-3	-	44	18	41	-59	0	0	-41
SM3-4	-	44	25	57	-43	4	9	-48
SM3-5	-	44	16	36	-64	1	2	-34

Appendix U: Chapter 2 Part II
Photographs of Alive and Dead *E. codium* Seedlings Outplanted at Badger and Snow Mountains 2020-2021

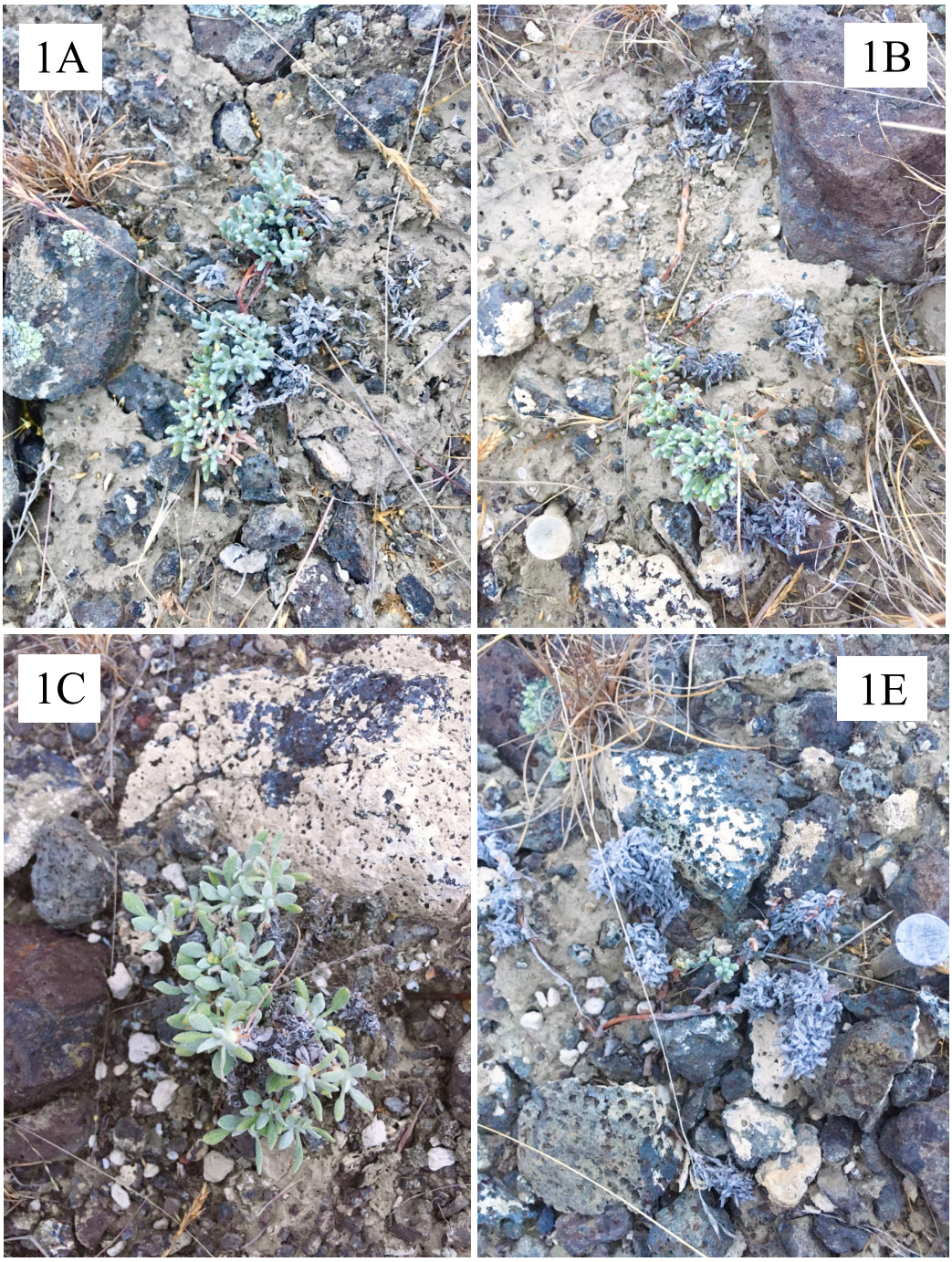


Figure U-1 **2020 Outplanted Seedlings Still Alive at Badger Mountain May 2023**
Photos taken by M. D. Kahn-Abrams



Figure U-2 **2021 Outplanted Seedlings Still Alive at Snow Mountain Site 3 May 2023**
Seedlings 114, 129 and 141 were outplanted at transect SM3-4. Seedling 92 was outplanted at SM3-5. Photos taken by M. D. Kahn-Abrams

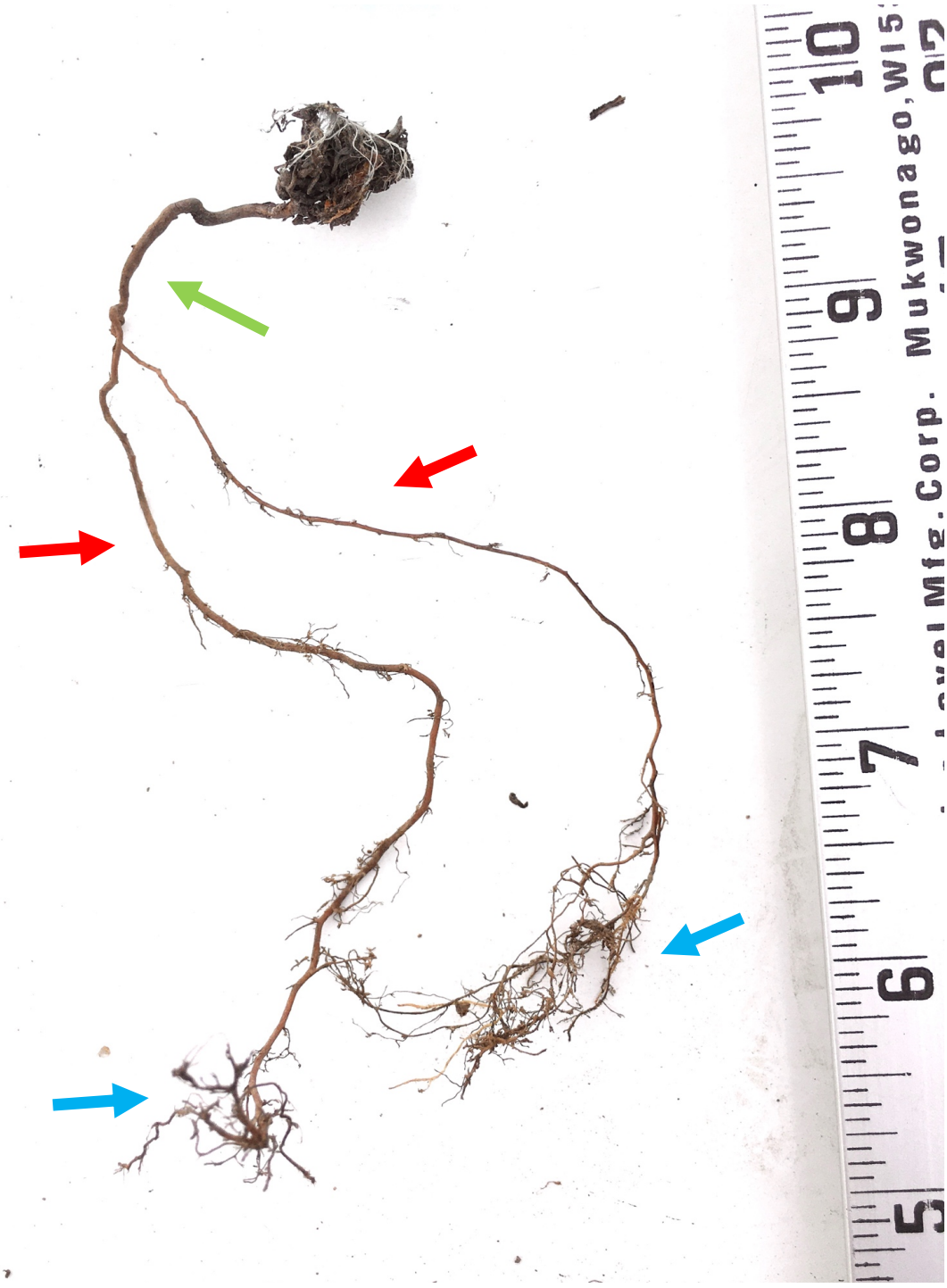


Figure U-3 **Rooting Pattern of Dead Seedling Outplanted in 2021 at Snow Mountain Site 2**
Green arrows indicate main tap root, red arrows indicate secondary/exploratory roots (woody) and blue arrows indicate tertiary/ fine roots. This seedling shows robust root development. Photos taken by M. D. Kahn-Abrams

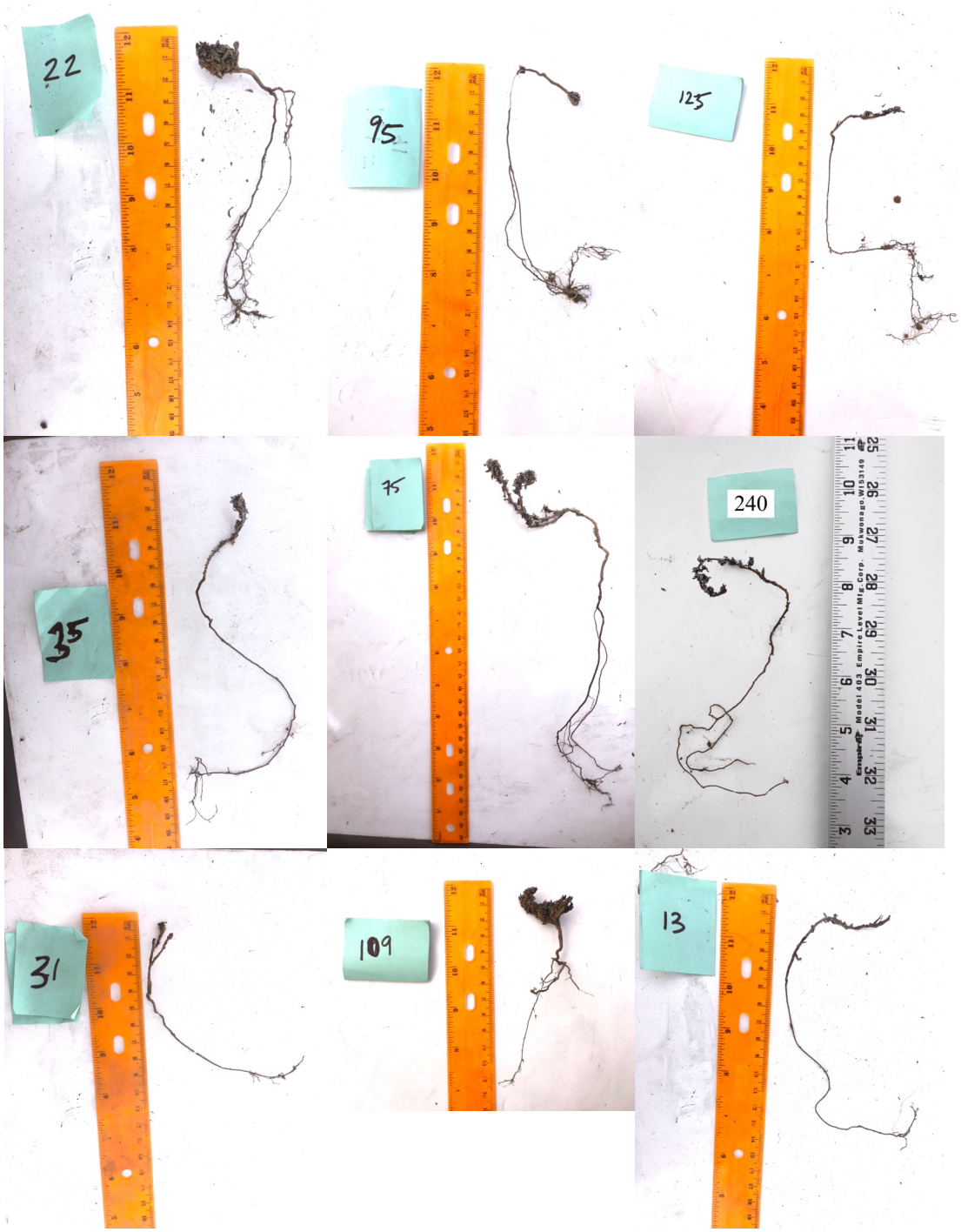


Figure U-4 **Differences in Rooting Patterns of Seedling Outplanted in 2021 at Snow Mountain Sites 2 and 3**
Different rooting patterns were observed in outplanted seedlings at Snow Mountain. Top row shows robust growth of fine roots (22, 95, 125), middle row show robust growth of tap and lateral roots (35, 75, 240), and bottom row shows stunted growth of tap roots and little to no secondary/ lateral or tertiary/ exploratory rooting (31, 109, 13). Photos taken by M. D. Kahn-Abrams

Appendix V: Chapter 2
Part II Pairwise ADONIS Tables of Optimal *E. codium* Habitat Groups and Outplanting Transects at Badger and Snow Mountain 1-3

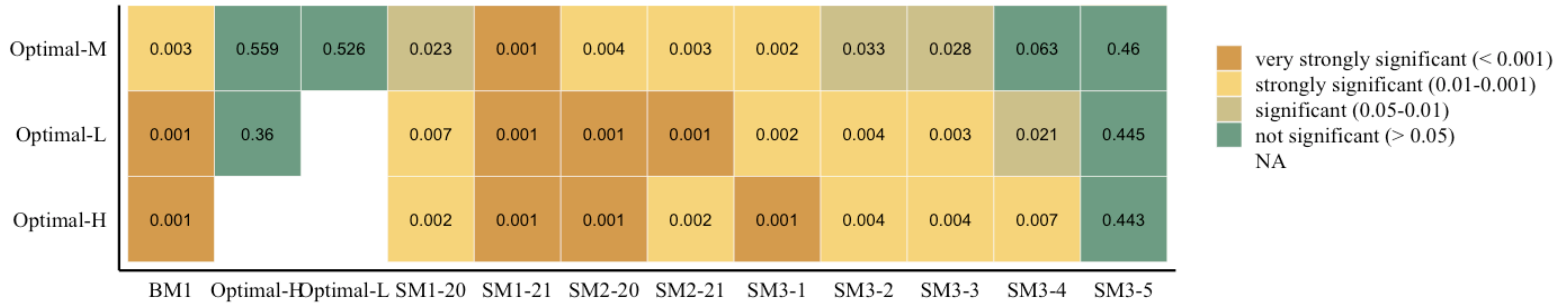


Figure V-1 **Pairwise Comparison of Differences in Soil Surface Composition Between Native Site Cluster Analysis Groups and Outplanting Transects**
Heatmap of p-values resulting from ADONIS pairwise comparison of differences in soil surface composition between Native Site optimal *E. codium* habitat (high, medium, low) groups and at outplanting transects at Badger Mountain (BM), and Snow Mountain (SM) sites 1-3. Tile colors correspond to strength of significance: brown = ≤ 0.001 (very strong significant difference), yellow = 0.01-.001 (strong significant difference), beige = 0.05-0.01 (significant difference), green = no significant difference (p = > 0.05).

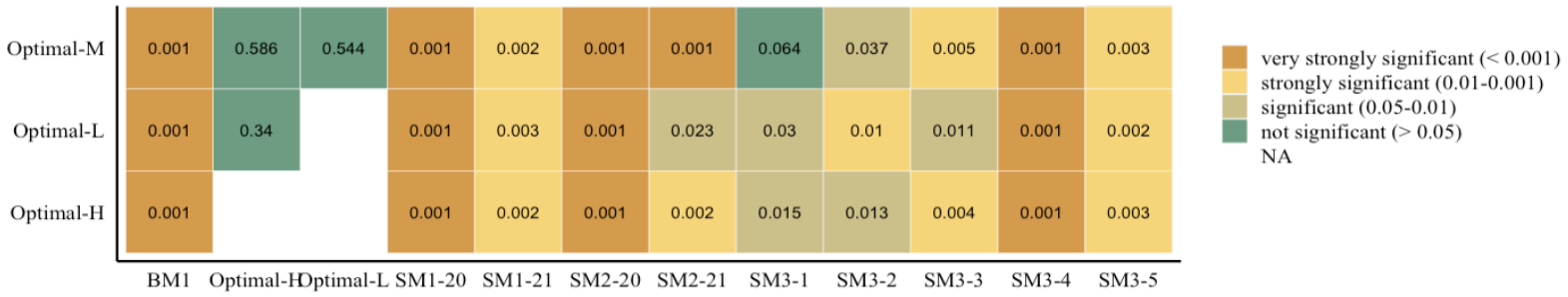


Figure V-2 **Pairwise Comparison of Differences in Soil Surface Rock Fragment Composition Between Native Site Cluster Analysis Groups and Outplanting Transects**
Heatmap of p-values resulting from ADONIS pairwise comparison of differences in soil surface rock fragment composition between Native Site optimal *E. codium* habitat (high, medium, low) groups and at outplanting transects at Badger Mountain (BM), and Snow Mountain (SM) sites 1-3. Tile colors correspond to strength of significance: brown = ≤ 0.001 (very strong significant difference), yellow = 0.01-.001 (strong significant difference), beige = 0.05-0.01 (significant difference), green = no significant difference (p = > 0.05).

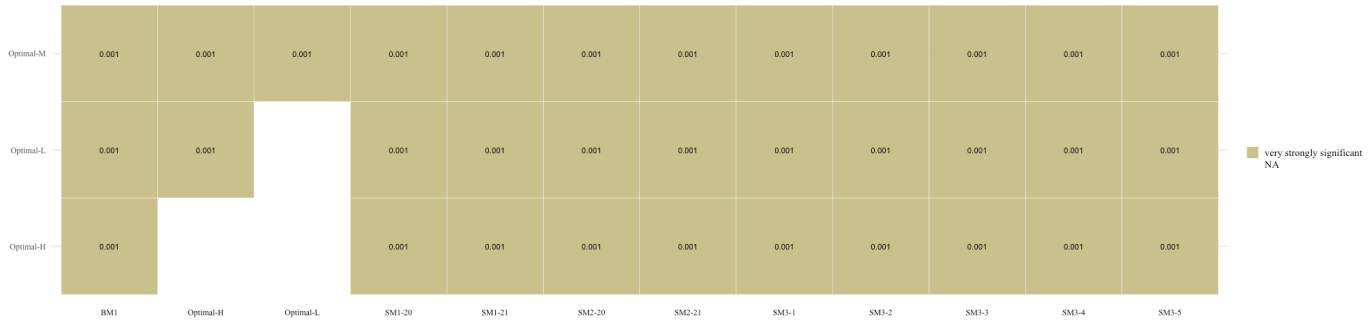


Figure V-3 **Pairwise Comparison of Differences in Vegetation Community Composition Between Native Site Cluster Analysis Groups and Outplanting Transects**
Heatmap of p-values resulting from ADONIS pairwise comparison of differences in vegetation community composition between Native Site optimal *E. codium* habitat (high, medium, low) groups and at outplanting transects at Badger Mountain (BM), and Snow Mountain (SM) sites 1-3. Tile colors correspond to strength of significance: brown = ≤ 0.001 (very strong significant difference), yellow = 0.01-.001 (strong significant difference), beige = 0.05-0.01 (significant difference), green = no significant difference (p = > 0.05).

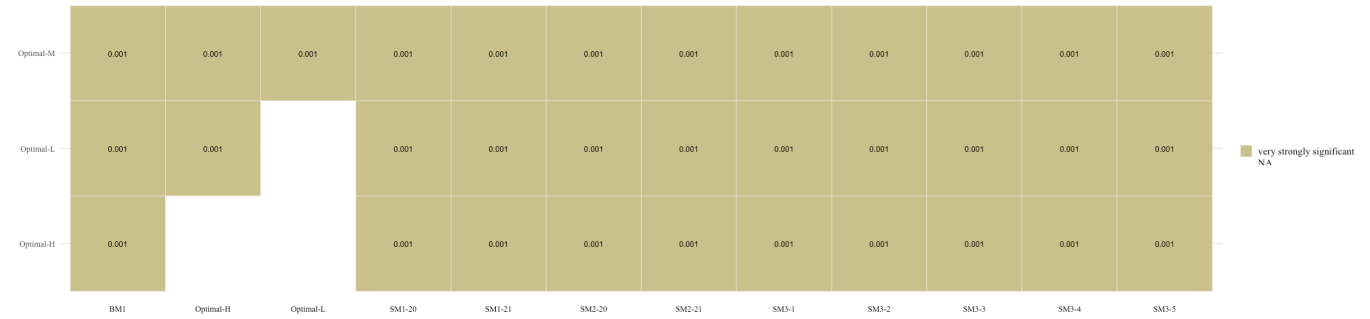


Figure V-4 **Pairwise Comparison of Differences in Vegetation Functional Group Composition Between Native Site Cluster Analysis Groups and Outplanting Transects**
Heatmap of p-values resulting from ADONIS pairwise comparison of differences in vegetation functional group composition between Native Site optimal *E. codium* habitat (high, medium, low) groups and at outplanting transects at Badger Mountain (BM), and Snow Mountain (SM) sites 1-3. Tile colors correspond to strength of significance: brown = ≤ 0.001 (very strong significant difference), yellow = 0.01-.001 (strong significant difference), beige = 0.05-0.01 (significant difference), green = no significant difference (p = > 0.05).

Appendix W: Chapter 2 Part II
Summary Tables of Differences Between *E. codium* Habitat Groups and Outplanting Transects at Badger and Snow Mountain 1-3

Table W-1 **Summary of Differences in Categorical Site Characteristics and Soil Texture Between Native Site Cluster Analysis Groups and Outplanting Transects**
Mode of categorical characteristics in Native Site optimal *E. codium* habitat (high, medium, low) groups and at outplanting transects at Badger Mountain (BM), and Snow Mountain (SM) sites 1-3. Multilpe levels are included when frequencies are the same. Site characteristics include landscape position, hillslope position (SU= summit, SH= shoulder, BS= backslope), slope shape (CC= concave-concave, CL= concave-linear, CV = concave-convex, LC= linear-concave, LL= linear-linear, LV= linear-convex, VC= convex-concave, VL= convex-linear, VV= convex-convex (B), slope complexity (C= complex, S= simple), and aspect (N = north, NE = northeast, E= east, SE= southeast, SW= southwest, W= west, NW= northwest). Mode of soil suface texture is included with catagorical varaiables.

Transect	n	Landscape Position	Hillslope Position	Slope Complex	Slope Shape	Aspect	Soil Texture
Optimal-Medium	24	Mountaintop-Upperthird	SH	S	LL	E+W	Loamy Sand + Sandy Loam
Optimal-Low	28	Mountaintop-Upperthird	SH	C	VL	W	Sandy Loam
Optimal-High	20	Mountaintop-Upperthird	SH	S	LL	E	Loamy Sand
BM1	8	Mountainflank-Lowerthird	FS	C	VL	SW	Silt Loam
SM1-20	8	Mountainbase-Upperthird	BS	C+S	LL	SW	Loam + Sandy Loam
SM1-21	8	Mountainbase-Upperthird	BS	C+S	LL	SW	Loam
SM2-20	8	Mountainflank-Middlethird	BS	S	LL	W	Sandy Loam
SM2-21	8	Mountainflank-Middlethird	SH	C	CV	NW	Sandy Loam
SM3-1	8	Mountainflank-Upperthird	SU	C	VL	NE	Sandy Loam
SM3-2	8	Mountainflank-Upperthird	SU	S	LL	NW	Loam
SM3-3	8	Mountainflank-Upperthird	SU	C	LL	N+NW	Loam
SM3-4	8	Mountainflank-Upperthird	SU	C+S	LL	N	Loam + Sandy Loam
SM3-5	8	Mountainflank-Upperthird	SU	C	LL	NW	Loam

Table W-2 **Summary of Differences in Continuous Site Characteristics Between Native Site Cluster Analysis Groups and Outplanting Transects**
Differences in mean, minimum/maximum (range), and standard deviation (sd) of heat load index (HLI), slope (cm/cm), slope angle (°) and total rock fragment classification between Native Site optimal *E. codium* habitat (high, medium, low) groups and at outplanting transects at Badger Mountain (BM), and Snow Mountain (SM) sites 1-3.

		Heat Load Index			Slope (cm/cm)			Slope Angle (°)			Total RF Fragment Class		
Transect	n	Mean	Range	sd	Mean	Range	sd	Mean	Range	sd	Mean	Range	sd
Optimal-Medium	24	0.71	0.49-0.86	0.11	0.22	0.07-0.53	0.11	11.46	4-27	5.85	56.31	9-75	23.06
Optimal-Low	28	0.68	0.52-0.83	0.11	0.20	0.03-0.41	0.10	12.78	2-22	5.66	53.59	9-75	24.15
Optimal-High	20	0.72	0.52-0.9	0.10	0.20	0.03-0.39	0.11	11.94	2-24	6.97	64.38	32-75	18.88
BM1	8	0.83	0.74-0.89	0.06	0.23	0.13-0.3	0.06	13.62	7-18	3.85	45.83	0-75	33.41
SM1-20	8	0.85	0.83-0.88	0.02	0.21	0.17-0.25	0.03	12.62	10-16	2.07	64.38	32-75	19.67
SM1-21	8	0.80	0.75-0.82	0.03	0.16	0.14-0.18	0.02	6.88	3-8	1.89	45.50	9-75	25.69
SM2-20	8	0.84	0.75-0.9	0.04	0.21	0.16-0.29	0.05	12.88	10-20	3.76	60.51	2-75	28.08
SM2-21	8	0.74	0.71-0.75	0.01	0.21	0.09-0.33	0.07	9.62	4-12	3.02	61.44	9-75	25.89
SM3-1	8	0.67	0.62-0.75	0.05	0.14	0.08-0.2	0.04	8.00	7-10	1.07	53.75	32-75	22.72
SM3-2	8	0.72	0.66-0.75	0.03	0.26	0.06-0.9	0.33	4.75	2-7	1.49	69.69	32-75	15.03
SM3-3	8	0.74	0.71-0.75	0.02	0.09	0.07-0.12	0.02	3.25	0-7	2.19	64.38	32-75	19.67
SM3-4	8	0.73	0.71-0.75	0.02	0.07	0.05-0.1	0.02	2.75	0-5	1.58	75.00	75-75	0.00
SM3-5	8	0.74	0.72-0.76	0.01	0.05	0.02-0.08	0.02	2.00	0-3	1.07	75.00	75-75	0.00

Table W-3 **Summary of Differences in Hydraulic Conductivity Between Native Site Cluster Analysis Groups and Outplanting Transects** Differences in mean, minimum/maximum (range), and standard deviation (sd) of hydraulic conductivity (K) between Native Site optimal *E. codium* habitat (high, medium, low) groups and at outplanting transects at Badger Mountain (BM), and Snow Mountain (SM) sites 1-3.

Transect Differenes in Hydraulic Conductivity (K)				
Transect	**Mean**	**Minimum**	**Maximum**	**sd**
BM1	-2.05×10^{-4}	-1.08×10^{-3}	6.76×10^{-4}	5.96×10^{-4}
Optimal-High	2.03×10^{-3}	-2.41×10^{-3}	1.55×10^{-2}	4.58×10^{-3}
Optimal-Low	1.74×10^{-3}	-2.81×10^{-3}	6.98×10^{-3}	2.22×10^{-3}
Optimal-Medium	2.28×10^{-4}	-3.05×10^{-3}	3.46×10^{-3}	1.76×10^{-3}
SM1-20	-5.60×10^{-4}	-1.73×10^{-3}	5.56×10^{-4}	7.98×10^{-4}
SM1-21	-3.03×10^{-4}	-8.16×10^{-4}	2.09×10^{-4}	3.60×10^{-4}
SM2-20	-4.16×10^{-6}	-1.22×10^{-3}	1.18×10^{-3}	8.57×10^{-4}
SM2-21	1.43×10^{-4}	-1.69×10^{-3}	2.80×10^{-3}	1.63×10^{-3}
SM3-1	1.01×10^{-3}	1.56×10^{-4}	2.49×10^{-3}	7.90×10^{-4}
SM3-2	8.60×10^{-4}	1.48×10^{-4}	2.62×10^{-3}	7.59×10^{-4}
SM3-3	2.61×10^{-4}	-3.17×10^{-4}	1.36×10^{-3}	5.85×10^{-4}
SM3-4	2.56×10^{-4}	-8.46×10^{-5}	1.21×10^{-3}	4.15×10^{-4}
SM3-5	6.61×10^{-4}	1.76×10^{-4}	1.37×10^{-3}	3.99×10^{-4}

Table W-4 **Summary of Differences in Soil Surface Composition Between Native Site Cluster Analysis Groups and Outplanting Transects** Differences in mean, minimum/maximum (range), and standard deviation (sd) soil surface compositional components between Native Site optimal *E. codium* habitat (high, medium, low) groups and at outplanting transects at Badger Mountain (BM), and Snow Mountain (SM) sites 1-3.

		Rock			**Bareground**			**Litter**			**Biocrust**		
Transect	**n**	Mean	Range	sd	Mean	Range	sd	Mean	Range	sd	Mean	Range	sd
BM1	8	38	3-88	28	11	0-38	14	9	0-38	13	25	3-62	24
Optimal-High	20	74	38-88	19	11	0-38	13	3	0-20	5	0	0-3	1
Optimal-Low	28	69	20-88	19	12	0-38	10	7	0-38	8	1	0-20	4
Optimal-Medium	24	71	20-88	23	15	0-62	18	4	0-20	5	0	0-3	1
SM1-20	8	46	20-62	19	15	0-38	12	12	3-38	12	7	0-20	6
SM1-21	8	35	20-62	19	28	10-38	13	18	3-38	10	14	3-20	9
SM2-20	8	40	3-62	26	30	10-88	25	20	3-62	20	4	3-10	2
SM2-21	8	42	10-88	27	31	10-38	13	10	0-20	7	5	0-10	4
SM3-1	8	39	10-62	21	28	10-62	19	8	3-10	3	12	10-20	5
SM3-2	8	53	38-62	13	18	10-38	12	7	3-10	4	13	3-20	6
SM3-3	8	59	38-62	9	22	10-38	11	12	10-20	5	13	3-20	6
SM3-4	8	62	62-62	0	19	10-20	4	12	3-20	6	9	3-20	7
SM3-5	8	78	62-88	13	10	3-20	5	5	3-10	3	6	0-10	4

Table W-5 **Summary of Differences in Soil Surface Rock Fragment Composition Between Native Site Cluster Analysis Groups and Outplanting Transects** Differences in mean, minimum/maximum (range), and standard deviation (sd) soil surface rock fragment compositional components between Native Site optimal *E. codium* habitat (high, medium, low) groups and at outplanting transects at Badger Mountain (BM), and Snow Mountain (SM) sites 1-3.

Transect Differences Soil Surface Rock Fragment Composition

		Bedrock			Boulder			Stone			Cobble			Course Gravel			Medium Gravel			Fine Gravel			Very Fine Gravel		
Transect	**n**	Mean	Range	sd	Mean	Range	sd	Mean	Range	sd	Mean	Range	sd	Mean	Range	sd	Mean	Range	sd	Mean	Range	sd	Mean	Range	sd
BM1	8	12	0-38	17	0	0-0	0	5	0-38	13	39	3-88	30	13	0-38	12	19	0-62	28	1	0-3	1	0	0-0	0
Optimal-High	20	0	0-0	0	0	0-10	2	1	0-20	4	5	0-20	6	22	0-62	20	28	0-62	18	31	3-88	27	10	0-62	15
Optimal-Low	28	0	0-0	0	0	0-0	0	0	0-0	0	14	0-62	17	25	0-62	20	28	0-88	20	21	0-88	20	6	0-62	12
Optimal-Medium	24	0	0-0	0	0	0-0	0	1	0-10	2	7	0-62	15	24	0-62	20	32	10-62	16	25	3-88	25	3	0-10	3
SM1-20	8	0	0-0	0	0	0-0	0	0	0-3	1	47	10-88	32	44	10-88	32	12	0-38	12	1	0-3	1	0	0-0	0
SM1-21	8	0	0-0	0	0	0-0	0	0	0-0	0	29	10-62	18	42	20-62	14	23	0-38	14	1	0-3	1	0	0-0	0
SM2-20	8	0	0-0	0	0	0-0	0	0	0-0	0	62	10-88	30	26	10-38	13	5	0-10	4	8	0-20	8	0	0-0	0
SM2-21	8	6	0-38	13	0	0-0	0	1	0-3	1	32	3-62	18	32	10-62	18	9	0-38	12	16	0-38	18	0	0-0	0
SM3-1	8	0	0-0	0	0	0-0	0	5	0-38	13	5	0-10	4	43	20-62	21	38	10-62	18	9	3-20	6	0	0-0	0
SM3-2	8	0	0-0	0	0	0-0	0	2	0-10	5	5	0-10	4	44	3-88	29	42	20-88	22	5	3-10	3	0	0-0	0
SM3-3	8	0	0-0	0	0	0-0	0	6	0-38	13	19	0-62	21	54	20-88	28	21	3-38	15	7	0-10	4	0	0-0	0
SM3-4	8	0	0-0	0	0	0-0	0	0	0-0	0	15	10-20	5	81	62-88	12	12	3-20	6	2	0-3	1	0	0-0	0
SM3-5	8	0	0-0	0	0	0-0	0	0	0-0	0	4	0-10	4	68	3-88	29	26	10-62	16	8	3-10	3	0	0-0	0

Table W-6 **Summary of Vegetation Community Characteristics Between Native Site Cluster Analysis Groups and Outplanting Transects** Differences between mean, minimum/maximum (range), and standard deviation (sd) of vegetation characteristics between Native Site optimal *E. codium* habitat (high, medium, low) groups and at outplanting transects at Badger Mountain (BM), and Snow Mountain (SM) sites 1-3.

		Species Abundance			Total Cover		
Transect	**n**	Mean	Range	sd	Mean	Range	sd
BM1	8	5.75	5-8	1.04	35.75	3-99	37.57
Optimal-High	20	3.70	3-5	0.66	27.88	4-59	16.54
Optimal-Low	28	4.57	3-7	1.00	39.20	11.5-71	14.64
Optimal-Medium	24	4.88	3-8	1.51	32.96	7-61	13.34
SM1-20	8	11.50	6-15	3.07	46.31	5.5-105.5	32.35
SM1-21	8	13.88	10-20	3.18	51.12	22-100.5	24.24
SM2-20	8	11.50	7-16	3.07	29.19	18-45	10.71
SM2-21	8	11.12	9-13	1.73	41.00	12.5-64.5	19.00
SM3-1	8	11.62	9-14	1.60	41.69	18-71	14.70
SM3-2	8	12.88	10-16	1.81	34.69	26.5-58.5	10.97
SM3-3	8	13.75	12-16	1.58	45.06	30.5-52	8.99
SM3-4	8	14.00	9-17	2.45	51.94	27.5-71.5	15.75
SM3-5	8	11.75	10-15	1.58	37.06	20-52	11.33

Table W-7 **Summary of Vegetation Functional Group Cover Between Outplanting Transects**
Differences between mean, minimum/maximum (range), and standard deviation (sd) of vegetation functional groups between Native Site optimal *E. codium* habitat (high, medium, low) groups and at outplanting transects at Badger Mountain (BM), and Snow Mountain (SM) sites 1-3.

		Shrub			Subshrub			Perennial Forb			Annual Forb			Perennial Graminoid			Annual Graminoid		
Transect	**n**	Mean	Range	sd	Mean	Range	sd	Mean	Range	sd	Mean	Range	sd	Mean	Range	sd	Mean	Range	sd
BM1	8	1.25	0-10	3.54	0.00	0-0	0.00	0.00	0-0	0.00	1.94	0.5-6	1.74	10.81	0.5-20	8.31	21.25	0.5-87.5	33.97
SM1-20	8	1.62	0-10	3.54	4.12	0-10	4.97	11.81	0-29.5	10.82	6.62	1-26.5	8.32	2.00	0-3	1.39	19.62	1-63	22.82
SM1-21	8	12.19	0-37.5	13.19	4.69	0-13.5	5.59	13.88	6-19.5	4.57	4.31	0.5-14.5	4.66	9.12	3-10	2.47	6.44	1.5-12	3.58
SM2-20	8	0.75	0-3	1.39	0.75	0-3	1.39	11.62	0.5-23.5	8.67	5.88	0.5-29.5	10.17	6.19	0-10	4.21	3.50	0.5-13	4.33
SM2-21	8	7.56	0-37.5	13.93	3.44	0-10	4.31	17.62	6.5-49	13.18	1.69	0-5	1.60	8.62	3-20	5.76	1.56	0.5-3.5	1.24
SM3-1	8	0.00	0-0	0.00	9.12	3-20	7.33	21.25	10-36.5	8.24	1.19	0.5-3.5	0.96	9.12	3-10	2.47	0.50	0-1	0.38
SM3-2	8	0.00	0-0	0.00	3.19	0-10	3.02	21.94	14.5-36	6.57	1.12	0.5-1.5	0.35	6.12	0-10	4.26	1.81	0-10	3.33
SM3-3	8	0.00	0-0	0.00	7.88	0.5-20	8.02	26.88	15-43.5	10.51	0.94	0-3	0.98	8.00	0.5-10	3.79	0.88	0.5-1	0.23
SM3-4	8	0.00	0-0	0.00	8.06	0-13.5	5.12	32.44	16.5-49.5	12.25	0.81	0-3.5	1.10	9.56	3-13	2.85	0.56	0-1	0.50
SM3-5	8	0.00	0-0	0.00	1.38	0-3	1.38	26.06	12-40	8.85	1.38	0-3.5	1.38	7.38	3-10	3.62	0.38	0-0.5	0.23

Appendix X: Chapter 2 Part II

Stress Plots of NMDS Ordinations Visualizing Soil Surface, Soil Surface Rock Fragment, Vegetation Community and Vegetation Functional Group Compositions of *E. codium* Habitat Groups and Outplanting Transects at Badger and Snow Mountain 1-3

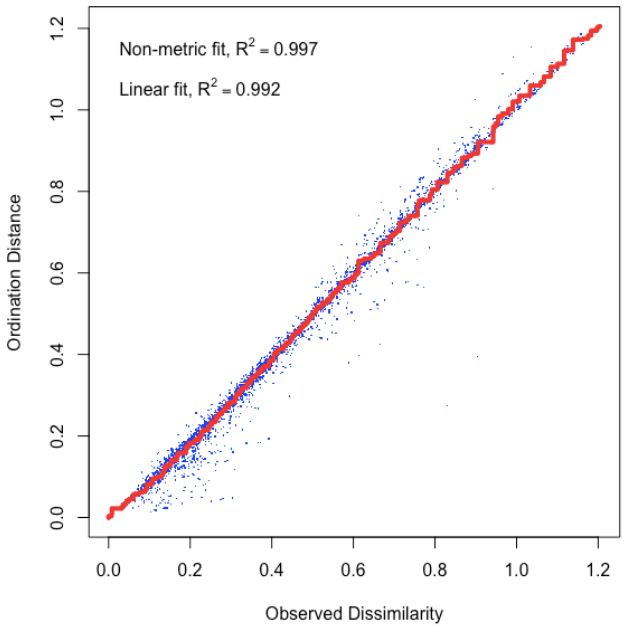


Figure X-1 **NMDS Stress Plot of Soil Surface Composition**
Shepard plot of soil surface composition showing the Euclidean distance between plots in the 3-dimensional ordination space (Ordination Distance).

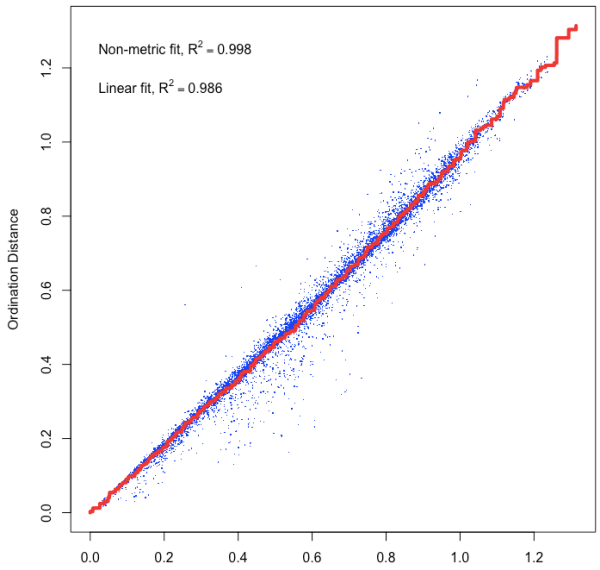


Figure X-2 **NMDS Stress Plot of Soil Surface Rock Fragment Composition**
Shepard plot of soil surface composition showing the Euclidean distance between plots in the 3-dimensional ordination space (Ordination Distance).

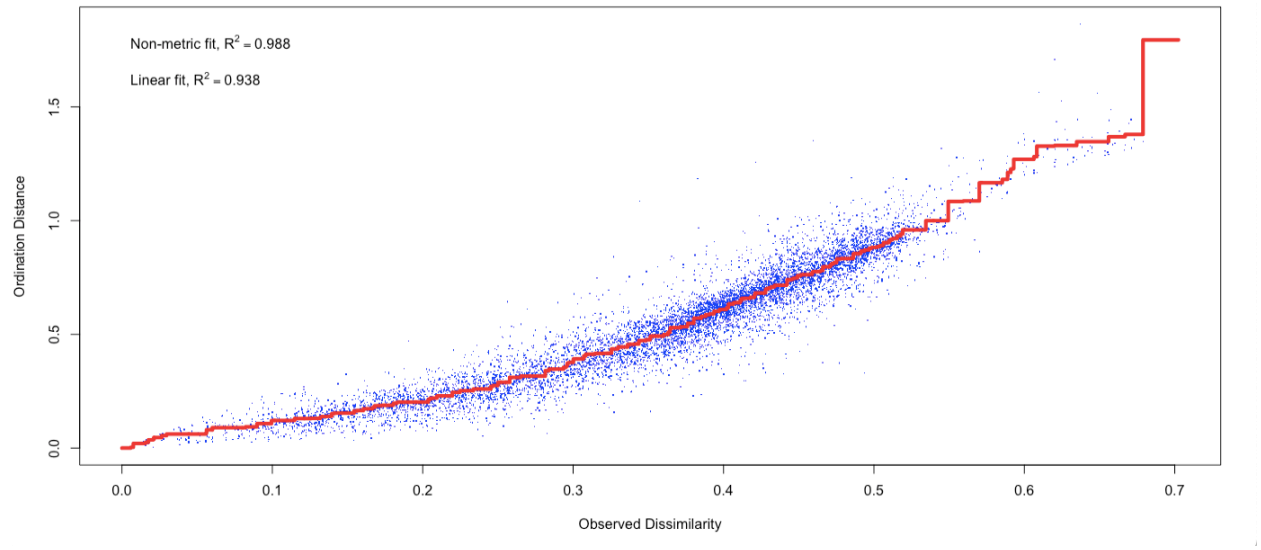


Figure X-3 **NMDS Stress Plot of Vegetation Composition**
Shepard plot of vegetation composition showing the Bray-Curtis distance between plots in the 3-dimensional ordination space (Ordination Distance).

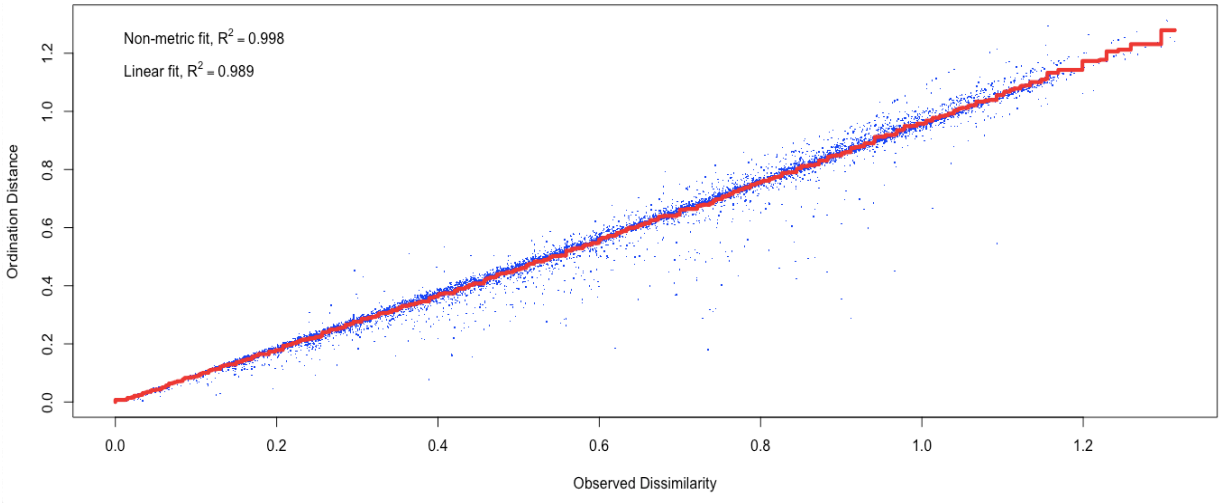


Figure X-4 **NMDS Stress Plot of Vegetation Functional Group Composition**
Shepard plot of vegetation composition functional groups showing the Euclidean distance between plots in the 3-dimensional ordination space (Ordination Distance).

Appendix Y: Chapter 2 Part II
Multigroup Indicator Species Analysis (ISA) Table of *E. codium* Habitat Groups and Outplanting Transects at Badger and Snow Mountain 1-3

Table Y-1 **Multigroup ISA of Soil Surface Rock Fragment Composition *E. codium* Habitat Groups and Outplanting Transects at Badger and Snow Mountain 1-3**
Vegetation species that most characterize Native Site optimal *E. codium* habitat (high, medium, low) groups and outplanting transects at Snow Mountain (SM) site 3. IV_{ij} of 100 means species occurs in all plots. Significant relationships are indicated by asterisks (* = significant, ** = strongly significant, ***= very strongly significant).

ISA of Soil RF Surface Rock Fragment Cover- Multigroup

Cover Class	BM1	Optimal-High	Optimal-Low	Optimal-Medium	SM1-20	SM1-21	SM2-20	SM2-21	SM3-1	SM3-2	SM3-3	SM3-4	SM3-5	IVij	*P*	
Cobble	X				X	X	X	X	X	X	X	X		86.5	0.005	**
Fine Gravel		X	X	X			X	X	X	X	X	X	X	96.0	0.005	**
Very Fine Gravel		X	X	X										96.0	0.005	**
Bedrock	X							X						31.4	0.010	**
Stone	X							X	X	X	X			25.0	0.035	*

Table Y-2 **Multigroup ISA of Vegetation Functional Group Composition *E. codium* Habitat Groups and Outplanting Transects at Badger and Snow Mountain 1-3**
Vegetation species that most characterize Native Site optimal *E. codium* habitat (high, medium, low) groups and at outplanting transects at Badger Mountain (BM) and Snow Mountain (SM) sites 1-3. IV_{ij} of 100 means species occurs in all plots. Significant relationships are indicated by asterisks (* = significant, ** = strongly significant, ***= very strongly significant).

ISA of Vegetation Functional Group

Veg Functional Grp	BM1	Optimal-H	Optimal-L	Optimal-M	SM1-20	SM1-21	SM2-20	SM2-21	IVij	*P*	
Shrub						X		X	35.0	0.005	**
Perennial Forb					X	X	X	X	89.3	0.005	**
Annual Forb	X				X	X	X	X	93.7	0.005	**
Annual Graminoid	X				X	X	X	X	97.1	0.005	**
Subshrub		X	X	X	X	X		X	87.8	0.005	**

Veg Functional Grp	Optimal-H	Optimal-L	Optimal-M	SM3-1	SM3-2	SM3-3	SM3-4	SM3-5	IVij	*P*	
Perennial Forb				X	X	X	X	X	96.3	0.005	**
Annual Forb				X	X	X	X	X	75.1	0.005	**
Annual Graminoid				X	X	X	X	X	63.3	0.005	**

Table Y-3 **Multigroup ISA of Vegetation Composition in *E. codium* Habitat Groups and Outplanting Transects at Badger and Snow Mountain 1-3**
Vegetation species that most characterize Native Site optimal *E. codium* habitat (high, medium, low) groups and outplanting transects at Badger Mountain (BM), and Snow Mountain (SM) sites 1 and 2. IV_{ij} of 100 means species occurs in all plots. Significant relationships are indicated by asterisks (* = significant, ** = strongly significant, ***= very strongly significant).

ISA of Vegetation Composition

Species	Habit	Origin	BM1	Optimal-H	Optimal-L	Optimal-M	SM1-20	SM1-21	SM2-20	SM2-21	IVij	*P*	
Allium acuminatum	Perennial forb	Native					X				25.0	0.030	*
Alyssum alyssoides	Annual forb	Invasive					X	X			54.7	0.005	**
Allium spp	Perennial forb	Native						X			25.0	0.030	*
Artemisia rigida	Perennial shrub	Native						X		X	38.6	0.005	**
Bromus commutatus	Annual graminoid	Invasive					X	X	X	X	84.4	0.005	**
Bromus tectorum	Annual graminoid	Invasive	X								78.6	0.005	**
Collomia grandiflora	Annual forb	Native							X		37.5	0.005	**
Descurainia pinnata	Annual forb	Native	X								31.6	0.015	**
Draba verna	Annual forb	Naturalized	X				X	X	X		73.9	0.005	**
Epilobium brachycarpum	Annual forb	Native					X	X	X	X	68.8	0.005	**
Erodium cicutarium	Annual forb	Invasive	X								62.5	0.005	**
Eriogonum codium	Perennial subshrub	Native		X	X	X					99.4	0.005	**
Erigeron linearis	Perennial forb	Native							X	X	18.7	0.050	*
Eriogonum sphaerocephalum	Perennial subshrub	Native								X	21.9	0.035	*
Eriogonum thymoides	Perennial subshrub	Native					X	X	X	X	34.4	0.005	**
Idahoa scapigera	Annual forb	Native					X	X			67.7	0.005	**
Lagophylla ramosissima	Perennial forb	Native							X		50.0	0.005	**
Lactuca serriola	Biennial forb	Invasive	X						X	X	20.8	0.015	**
Lewisia rediviva	Perennial forb	Native							X	X	75.0	0.005	**
Lomatium canbyi	Perennial forb	Native					X	X			64.3	0.005	**
Lomatium macrocarpum	Perennial forb	Native							X	X	25.0	0.010	**
Microsteris gracilis	Annual forb	Native					X	X		X	29.2	0.030	*
Nestotus stenophyllus	Perennial forb	Native					X		X	X	25.0	0.015	**
Olsynium douglasii	Perennial forb	Native							X	X	68.8	0.005	**
Phlox hoodii	Perennial forb	Native							X	X	43.8	0.005	**
Poa bulbosa	Biennial graminoid	Invasive					X	X	X		61.6	0.005	**
Polemonium micranthum	Annual forb	Native							X	X	23.0	0.020	*
Pseudoroegneria spicata	Perennial graminoid	Native			X	X				X	34.0	0.010	**
Sedum lanceolatum	Perennial forb	Native							X	X	68.8	0.005	**
Taeniatherum caput-medusae	Annual graminoid	Invasive					X	X			93.8	0.005	**
Trifolium macrocephalum	Perennial forb	Native					X	X			50.0	0.005	**
Viola trinervata	Perennial forb	Native					X	X			87.5	0.005	**

Table Y-4 **Multigroup ISA of Vegetation Community Composition in *E. codium* Habitat Groups and Outplanting Transects at Badger and Snow Mountain 1-3**
Vegetation species that most characterize Native Site optimal *E. codium* habitat (high, medium, low) groups and outplanting transects at Snow Mountain (SM) site 3. IV_{ij} of 100 means species occurs in all plots. Significant relationships are indicated by asterisks (* = significant, ** = strongly significant, ***= very strongly significant).

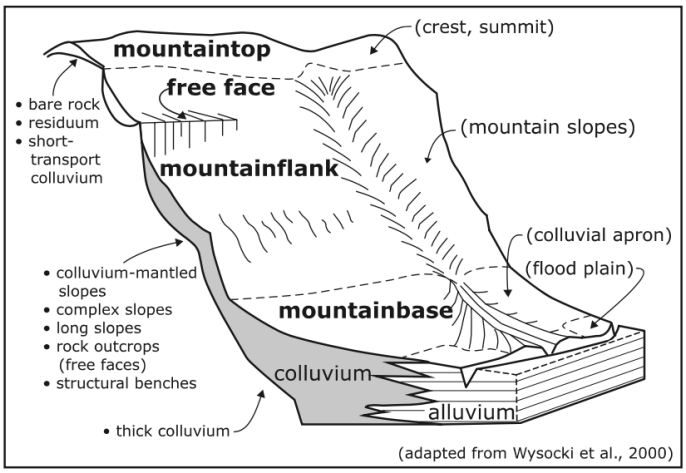
ISA of Vegetation Composition

Species	Habit	Origin	Optimal-H	Optimal-L	Optimal-M	SM3-1	SM3-2	SM3-3	SM3-4	SM3-5	IVij	*P*	
Allium spp	Perennial forb	Native						X			33.9	0.015	**
Antennaria flagellaris	Perennial forb	Native				X	X	X	X	X	70.0	0.005	**
Balsamorhiza hookeri	Perennial forb	Native							X	X	83.2	0.005	**
Bromus commutatus	Annual graminoid	Invasive				X	X	X	X		78.1	0.005	**
Collinsia parviflora	Annual forb	Native				X	X	X	X	X	57.5	0.005	**
Elymus elymoides	Perennial graminoid	Native							X		21.5	0.025	*
Eriogonum codium	Perennial subshrub	Native	X	X	X						98.3	0.005	**
Eriogonum douglasii	Perennial subshrub	Native							X		25.0	0.030	*
Eremogone franklinii	Perennial forb	Native							X		38.8	0.005	**
Eriogonum thymoides	Perennial subshrub	Native				X	X	X	X	X	87.5	0.005	**
Idahoa scapigera	Annual forb	Native				X	X	X	X	X	70.0	0.005	**
Lewisia columbiana	Perennial forb	Native				X	X	X	X	X	70.0	0.005	**
Lewisia rediviva	Perennial forb	Native				X	X	X	X	X	77.5	0.005	**
Lomatium macrocarpum	Perennial forb	Native				X	X	X	X	X	92.5	0.005	**
Microsteris gracilis	Annual forb	Native				X	X				33.3	0.005	**
Nestotus stenophyllus	Perennial forb	Native				X	X	X	X	X	75.0	0.005	**
Olsynium douglasii	Perennial forb	Native				X	X	X	X	X	97.5	0.005	**
Phlox hoodii	Perennial forb	Native						X	X	X	54.2	0.005	**
Pseudoroegneria spicata	Perennial graminoid	Native		X	X						37.8	0.005	**
Sedum lanceolatum	Perennial forb	Native				X	X	X	X	X	77.5	0.005	**
Viola trinervata	Perennial forb	Native				X	X				30.4	0.010	**
Vulpia microstachys	Annual graminoid	Invasive					X	X	X	X	56.9	0.005	**

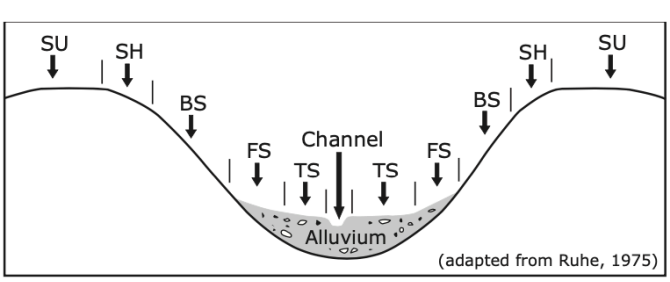
Appendix Z: Chapter 1 & 2 Methods

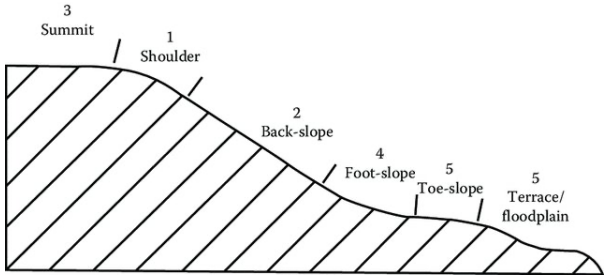
Illustrations of Qualitative Site Assessment Categories from the *Field Book for Describing and Sampling Soils* (Version 3.0)

Landform

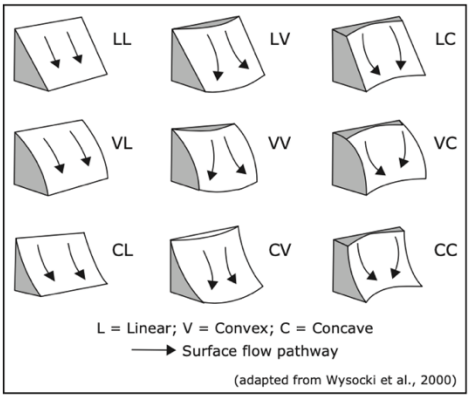


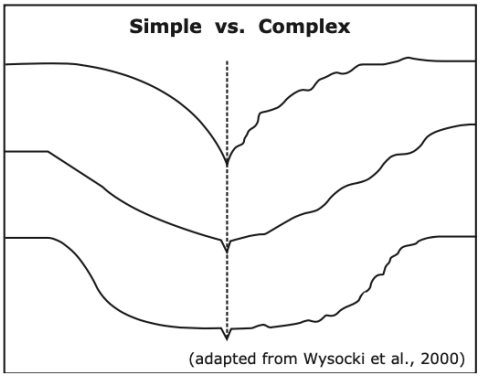
Hillslope





Slope Shape (left) and Complexity (right)





Appendix AA: Chapter 1 & 2 Methods

Data Adjustments and Calculations for Hydraulic Conductivity

For plots where recording continuous infiltration over six minutes required stopping the run to refill the minidisk infiltrometer, multiple runs were consolidated into a single continuous six-minute run (0-360 seconds). To do this, the starting run's volumes were "corrected" and then "sown" together with the ensuing run's volumes (Fig AB-1). The difference between the volume at 30 seconds during the second run and the last volume recorded during the first run was computed ("correction value") (Fig AB-1B and 2B) . The "correction value" was then added to all volumes of the first run ("corrected values"), resulting in the last volume of the first run equaling the volume of the second run at 30 seconds. The starting volume and volume at 30 seconds in the second run were then dropped from the data set, and the "corrected" first run was "sown" together with the unchanged values of the second run starting with the volume at 60 seconds. One extra data point was collected at six minutes and thirty seconds (390 seconds) for each run after the mini disk infiltrometer was refilled, resulting in one volume for each time point between 0 and 360 seconds (n=13) once time points 0 and 30 from the second run were deleted from the data set. The collection of infiltration data using a mini disk infiltrometer is intended to reflect the volume of water infiltrating continuously through the soil profile over a given period of time. Deleting the difference between the starting volume and volume after 30 seconds from the second run removes data reflecting the infiltration of water back through the soil profile where it has already infiltrated during the first run. Retaining the volume of water recorded after the first 30 seconds best reflects steady state infiltration and the continuation of the infiltration rate observed during the first run, while overcoming computational challenges posed by the need to refill the minidisk infiltrometer during data collection.

For plots where three to four runs occurred during the six-minute sampling period, only the final run's raw data values were retained. All proceeding run's values received accumulative correction values (Fig AB-1 2A-C). An independent correction value was calculated for each run except the first run, based on the difference between the starting volume and volume after 30 seconds. These correction values were successively and accumulatively added to all runs raw data values except the final run. For each plot, the first run's volumes were "corrected" by adding all computed "correction values" from all the successive runs. The second run's volumes were "corrected" by adding only the "correction values" from successive runs and not the volume computed from its own run data. This continued successively for all runs except the final run. This ensured the final volume of each run equaled the volume of the successive run at 30 seconds. Unchanged final run values and proceeding run's "corrected" values were then "sown" together into a continuous six-minute run (0-360 seconds). Due to errors in data collection that resulted in not enough extra data points collected to account for the number of starting run values dropped from the data set, five plots have data for only five minutes and thirty seconds (0-330 seconds) while one plot only has data recorded for five minutes (300 seconds). Similarly, one plot (n=1) contains an extra data point (six minutes and thirty seconds or 390 seconds).

Unsaturated hydraulic conductivity (HC) was calculated from field measurements taken in dry soil of cumulative infiltration verses time, in accordance with methods outline by Zhang 1997 and adapted by Meter Group (Meter 2020-2021) (Fig W-1). The results are fit with the function:

$$I = C_1 t + C_2 t \quad \text{(Equation X)}$$

where C_1(m × s^{-1}) is a parameter related to soil sorptivity, and C_2(m × s^{-1}) is hydraulic conductivity. Fitted infiltration verses time values are graphed to produce an XY (scatter) plot (Fig X). This is used to calculate C_1, which is the slope of this line.

Unsaturated hydraulic conductivity for soil (K) is computed:

$$K = \frac{C_1}{A} \quad \text{(Equation X)}$$

where C_1 is the slope of the curve of the cumulative infiltration versus the square root of time and A is a value derived from the van Genuchten parameters for a given soil type, the suction rate used during sample collection, and the radius of the infiltrometer disk. The van Genuchten parameters for the 12 soil texture classes were calculated by Carsel and Parrish (1988). A is computed from Equations X and X:

$$A = \frac{11.65\left(n^{0.1}-1\right)\exp\left[2.92(n-1.9)\alpha h_0\right]}{(\alpha r_0)^{0.91}} \quad n \geq 1.9 \quad \text{(Equation X)}$$

$$A = \frac{11.65\left(n^{0.1}-1\right)\exp\left[7.5(n-1.9)\alpha h_0\right]}{(\alpha r_0)^{0.91}} \quad n \leq 1.9 \quad \text{(Equation X)}$$

n and α are the van Genuchten parameters for the soil, r_o is the disk radius, and h_o is the suction at the disk surface. The Mini Disk Infiltrometer was set to –5 cm of suction during data collection, and has a radius of 2.25 cm. Soil surface hand texture classifications for each plot were utilized to select the soil texture class from which associated n, α and A values were determined.

Meter. 2020-2021. Mini Disk Infiltrometer Manual. Meter Group, Inc. USA. Meter Group AG. https://www.labcell.com/media/24285/20421_mini_disk_manual_web.pdf

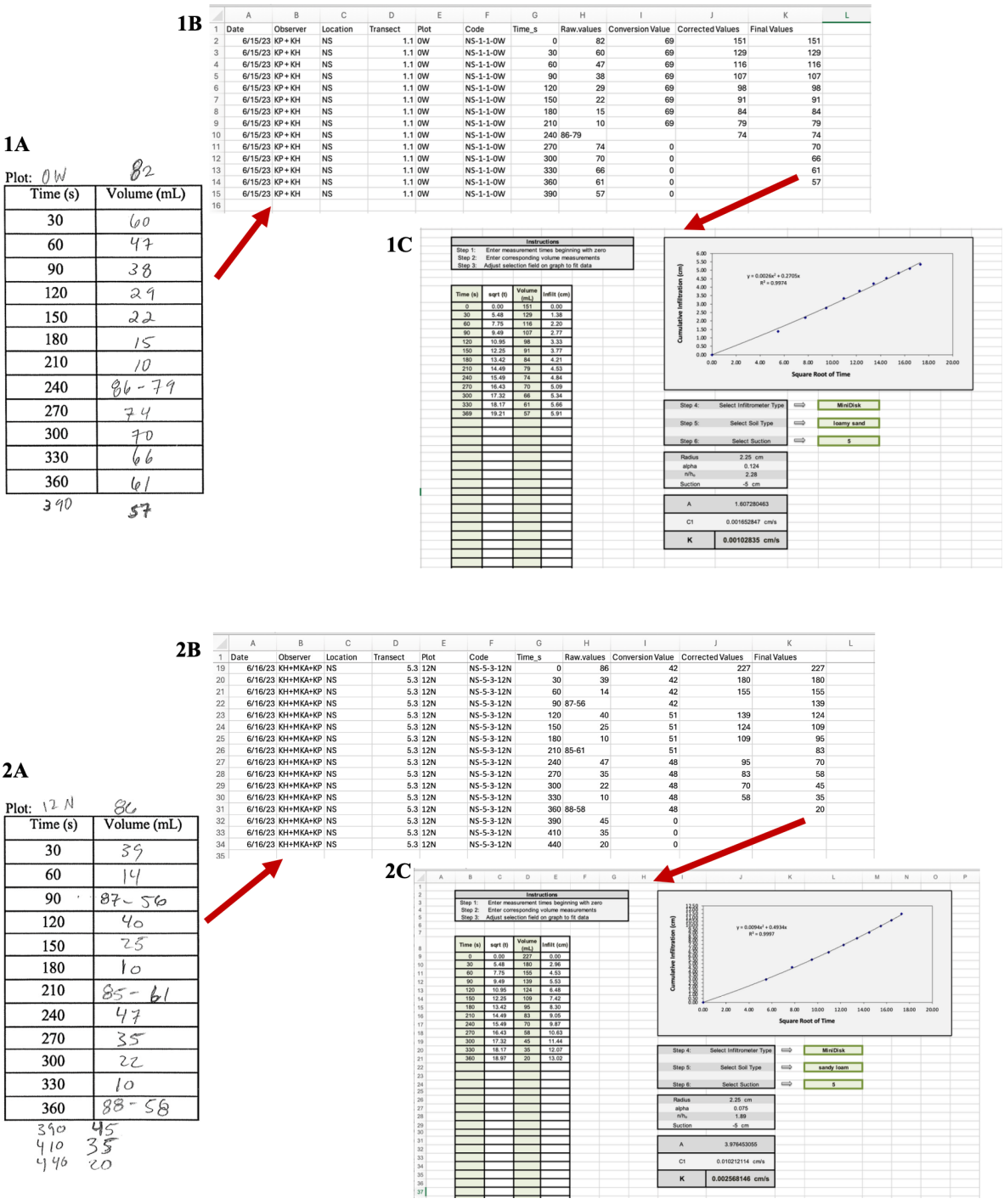


Figure AB-1 **Method for Preparing Water Infiltration Field Data for Analysis.** Method for taking two runs of soil water infiltration taken in the field, adjusting the values and "sowing" the runs together to form one continuous run from 0-390 second (1A-C). Method for taking three runs of field infiltration data, adjusting values and "sowing" runs together (2A-C).

Appendix AB: Chapter 1 & 2 Methods

R script to Calculate Hydraulic Conductivity from Mini Infiltrometer Data

```
#Calculating Hydraulic Conductivity ----
#Based on function created by Jon Bakker 2/2024 + updated by J.Bakker 1/2025
#Rewritten by Maya Kahn-Abrams for data analysis (ERCO project) 12/27/2024 + 3/28/25

#Load packages----
library(tidyverse)
library(broom)
library(dplyr)


# 1. Load data-----
##Load plot info into object "plots"----
plots <- read_csv(here("Data/NS_Infil_040124_MKA_FINAL_plots.csv"))
plots <- plots %>%
  mutate(ID = Code,
         Suction = ifelse(Suction > 0, -Suction, Suction))

#read transect numbers as characters
plots$Transect <- as.character(plots$Transect)

#remove plots that do not have infiltration values
plots <- plots %>%
  filter(!Notes == "Infil data not collected")

##Load measurements into object "measurements"----
measurements <- read_csv(here("Data/NS_Infil_010925_JB_FINAL_meas.csv"))

measurements <- measurements %>%
  mutate(ID = Code) %>%
  select(!Code)

##Load Van Genuchten table into object "VanG"----
VanG <- read_csv(here("Data/NS_Infil_040124_MKA_FINAL_VanG.csv"))

#2. Combine data files and calculate variables----
raw_data <- plots %>%
  merge(y = measurements, by = "ID") %>%
  group_by(ID) %>%
  mutate(Infiltration = (max(Volume_ml) - Volume_ml) / (pi * Radius_cm^2)) %>%
  ##JDB - for some reason the square-root of time was not calculating correctly here
  ##JDB - so I moved it into the loop
  ungroup()
```

```
#3. Fit curve to Time-Infiltration data and save key parameters----
IDs <- unique(raw_data$ID)
output <- c()

for(i in 1:length(IDs)) {
  temp_data <- raw_data %>%
    filter(ID == IDs[i]) %>%
    mutate(sqrt_time = sqrt(Time_s))
  temp_mod <- lm(temp_data$Infiltration ~ 0 + I(sqrt_time^2) + sqrt_time, data = temp_data)
  temp_res <- data.frame(ID = IDs[i],
                         estimate = tidy(temp_mod) %>%
                           filter(term == "I(sqrt_time^2)") %>%
                           select(estimate),
                         R2adj = glance(temp_mod)$adj.r.squared)
  output <- rbind(output, temp_res)
}

output <- output %>%
  rename("C1" = estimate)

## Combine C1 with other parameters and calculate K
HC.ns <- plots %>%
  merge(y = output, all = TRUE) %>%
  merge(y = VanG, all.x = TRUE, all.y = FALSE) %>%
  mutate(K = C1 / A) %>%
  select(Code, Location, Transect, Plot, ID, C1, R2adj, K)

# 4. Extract cumulative volume entering soil in 300 seconds ##JDB
#infil_300 <- raw_data %>%
  #filter(Time_s == 300) %>%
 # dplyr::select(Code, Infiltration) %>%
 # rename("Volume_300" = Infiltration)

# 5. Combine HC with infiltration ##JDB
#HC.ns <- HC.ns %>%
#  merge(y = infil_300)

# 4. Clean up data frame and environment----
#filter out test
HC.ns <- HC.ns %>%
  filter(!Code == "None")

#delete unnecessary objects
rm(measurements)
```

```
rm(output)
rm(plots)
rm(raw_data)
rm(temp_data)
rm(temp_mod)
rm(temp_res)
rm(VanG)
#rm(infil_300)
```

Appendix AC: Chapter 1 & 2 Methods
R script for Heat Load Index Function (Zeleny and Lin 2021)

```
#Calculating Heat Load ----
#Based on function created by David Zeleny & Tsung-Yi Lin (last updated 1/2021)
#Rewritten by Maya Kahn-Abrams for data analysis (ERCO project) 04/03/2024

#selected equation #2 because slope < 60 degrees

heatload <- function (aspect, slope, latitude, method = 'heatload', units = 'degrees', equation = 2)
{
  if (units == 'degrees') {
    aspect <- aspect/180*pi
    slope <- slope/180*pi
    aspect[slope == 0] <- 0
    latitude <- latitude/180*pi }

  A <- if (method == 'heatload') abs (pi - abs (aspect - (5*pi/4))) else pi - abs (aspect-pi)
  S <- slope
  L <- if (length (latitude) == 1) rep (latitude, length (A)) else latitude
  if (equation == 1) res <- exp (-1.467 +1.582*cos(L)*cos(S) -1.500*cos(A)*sin(S)*sin(L) -
0.262*sin(L)*sin(S) +0.607*sin(A)*sin(S))
  if (equation == 2) res <- exp (-1.236 +1.350*cos(L)*cos(S) -1.376*cos(A)*sin(S)*sin(L) -
0.331*sin(L)*sin(S) +0.375*sin(A)*sin(S))
  if (equation == 3) res <- +0.339 +0.808*cos(L)*cos(S) -0.196*sin(L)*sin(S) -
0.482*cos(A)*sin(S)
  return (res)
}
```

Appendix AD: Chapter 3

Current Status and Demographic, Environmental, and Genetic Stochasticity of Umtanum Desert Buckwheat (*Eriogonum codium*)

On December 20, 2013, the U.S. Fish and Wildlife Service (US FWS) listed Umtanum desert buckwheat (*Eriogonum codium)* as a threatened species under the Endangered Species Act of 1973 (US Fish and Wildlife 2022). The species has a recovery priority number of five, indicating it is a species (versus a subspecies), faces a high degree of threat, and has a low potential for recovery (US FWS 2013a). This species will be considered "recovered" when there is "the presence of resilient and self-sustaining populations that conserve existing genetic diversity in the species' natural geographic range within protected sites, and these populations are not substantially threatened by wildfire, nonnative plant species, or other threats". In 2013, the US FWS designated critical habitat for the species (US FWS 2013b).

The main cause of the species' decline is the loss of individuals and degradation of its habitat by wildfires and invasive plant species. Umtanum desert buckwheat is a narrow endemic restricted to a small area of approximately 4.8 acres (<1 mile) on a narrow discontinuous band of lithosol soils on the eastern end of Umtanum Ridge in Hanford Reach National Monument (HRNM) (Reveal et al. 1995, Dunwiddie et al. 2000, US FWS 2022, Fertig 2022). The historical range of Umtanum desert buckwheat is unknown but in addition to lithosol soils, hot dry summers and cold winters in semi-arid shrub-steppe are the assumed to be the primary habitat and environmental requirements for the species (US FWS 2013a). It is a long- lived perennial with individuals estimated to be older than 100 years, and the single population is small and in decline due to extremely low recruitment. Even with high flower production and germination rates, seedling mortality is high, and growth between individuals and years is highly variable (Dunwiddie et al. 2000, Caplow et al. 2007). In 1995, although there was a wide range of sizes and age classes in the population, fewer plants than expected were documented in the smallest size classes (< 100 cm^2 crown) compared to a typical size distribution, indicating recruitment is insufficient to support a self-sustaining population (Reveal et al. 1995, Dunwiddie et al. 2000). During nine years of demographic monitoring from 1997 to 2006, only five seedlings survived beyond 1 year and only one seedling survived 5 years to produce flowers (Caplow et al. 2007). The estimated population of 5,228 plants in 1997 has decreased significantly to 3,016 plants by 2019 (42% decline) (Fertig 2020, 2022).

Estimates of this species' viability[20] are based on the concepts of resiliency, redundancy, and representation (US FWS 2022). The species has low resiliency despite the single extant population being above the estimated minimum viable population (MVP) size, because of the poor condition of its habitat due to invasive species and demographic factors of low recruitment. There is only one population, so redundancy is non-existent. The species is a narrow endemic occupying a small area with little ecological differentiation, likely resulting in little genetic diversity and low representation. Because this species' viability is low from low resiliency, redundancy, and representation, its extinction risk remains high as its single population is unable to withstand stochastic and catastrophic events. Its recovery strategy seeks to improve i. resiliency by establishing populations of sufficient size and productivity to withstand stochastic

[20] defined as "the likelihood of persistence over the long term" (US FWS 2022)

events, ii. redundancy by establishing a sufficient number of populations to provide a safety margin to withstand catastrophic events, and iii. representation by expanding the ecological diversity and preserving the genetic diversity of the species. US FWS estimates that recovery criteria could be met by 2047, based on the conservative assumption that all recovery plan actions are fully funded and implemented as currently outlined, including cooperative efforts by all partners needed to achieve recovery.

Environmental stochasticity

The estimated 42% decline in the Umtanum desert buckwheat's population from 1997 to 2019 is largely due to the drastic effects of environmental stochasticity on the low growth rate (<1% annual decline) of the single vulnerable population. Fire is the primary stochastic event that threatens this species, and two wildfire events in the last 20 years have resulted in the destruction of a significant portion of the population (US FWS 2019). Adult individuals are negatively affected by fire, with high mortality for completely burned and partially burned individuals following fire. Unlike fire adapted species which exhibit vigorous resprouting of new growth post fire, Umtanum desert buckwheat is sensitive to heat and easily killed- even singed but not visibly charred plants have died within a year after fire (Listing Assignments 2010). Direct and indirect losses of plants from wildfires have been significant; a fire in 1996 killed an estimated 10-20% of the entire population, while the Silver Dollar Fire in 2017 completely burned 42% of Natural Heritage Program permanent monitoring plots and leaving only 37% of plots unburned (Shank 2019). Post fire both completely burned, and most partially burned individuals of Umtanum desert buckwheat died, while remaining individuals experienced significant decreases in both seed viability and germination with increased fire exposure (Listing Assignments 2010, Shank 2019).

Repeated fires have resulted in a decline in habitat quality as the subsequent invasion of annual grasses has become established in and adjacent to the *E. codium* population and pose a significant threat. Cheatgrass (*Bromus tectorum)* and other invasive annual grasses compete for resources, especially vernally available soil moisture critical to seedling establishment, and increases the fine fuel load resulting more frequent high intensity fires and shortened fire intervals, continuing the destruction of Umtanum desert buckwheat's single population. Increasingly periodic stochastic wildfire events constitute catastrophizes with significant negative impacts on the long-term viability of this population, rapidly accelerating projected decreases in long term population growth, and pushing this species into an extinction vortex. Finally, the adaptability of this species to climate change is predicted to be low and regional models of climatic shifts in the Columbia Basin predict increased summer and winter temperatures and decreased precipitation and winter snowfall by 2040 (Littell et al. 2009). Physiological climate change related stress resulting from current trends of decreased rainfall combined with increased temperatures, may exceed this species range of tolerance beyond survivable limits, further fueling rapid species decline, and adversely effecting individuals across all age classes.

Demographic stochasticity

Using a Population Viability Analysis (PVA) model, Caplow et al. 2007 reported the stochastic growth rate for the population as measured from 1997-2006 was 0.9935, with minimal recruitment. This indicated that although very close to stable, Umtanum desert buckwheat is in a very gradual annual decline of about 2/3 of one percent. The model forecasted little to no risk of a 90% population decline within the next 100 years, a 13 % chance of a 50% decline over the next 50 years, and a 72 % chance of a 50% decline within the next 100 years. The elasticity analysis indicated that stasis of stage 4 (> 500 cm^2 crown, elasticity=0.468) plants had the single greatest impact on population growth rate (Table 2). In addition, stasis of stage 3 (200- 500 cm^2 crown, elasticity=0.226) and stage 2 (>200 cm2 crown, elasticity=0.164) plants had the second and third strongest effects on population growth. Overall, seedling dynamics (recruitment and survival) had very little impact on population growth rate and the populations' decline was predicted to be gradual and expected to take several decades to accumulate significant impacts. However, this model did not account for environmental stochastic events like wildfire and drought.

Population trends for Umtanum desert buckwheat have declined from 1995 to 2019. Using the revised 1995 population estimate of 6,041 reproductive and vegetative plants, abundance has decreased by close to 50% to 3,016 plants in stages 2, 3 or 4 found alive in 2019. This rapid decline exemplifys how the negative effects of demographic stochasticity and low population growth rates act synergistically with environmentally stochastic events to quickly push vulnerable species toward rapid population decline and possible extinction.

Table 1. Average transition matrix for *Eriogonum codium*. Each value represents the mean of nine observed transitions from 1997 through 2006, except for stage 1 (seedlings). Values in this column are the mean from only seven observed transitions because no seedlings were observed in 2002 or 2005. The transitions representing stasis (remaining in the same stage from one year to the next) are shown in bold.

		Stage at time t			
		1	2	3	4
Stage at time t+1	1	--	0.010	0.094	0.416
	2	0.070	**0.820**	0.070	0.018
	3	0.000	0.114	**0.805**	0.056
	4	0.000	0.023	0.109	**0.912**
	mortality	93.0%	4.3%	1.5%	1.4%

Table 2. Elasticies of the mean matrix (Table 1) for *Eriogonum codium*. Each value represents the proportional sensitivity of the population growth rate to small changes in vital rates. Column sums are the cumulative elasticities for each stage.

		Stage at time t			
		1	2	3	4
Stage at time t+1	1	0	0.0001	0.0015	0.0106
	2	0.0123	**0.1644**	0.0159	0.0067
	3	0	0.0281	**0.2258**	0.0248
	4	0	0.0067	0.0354	**0.4676**
	Sum	**0.0123**	**0.1993**	**0.2786**	**0.5097**

Table 1& 2 (Caplow et al 2007)

Genetic stochasticity

Due to Umtanum desert buckwheat's small population and highly restricted range, it is likely that this species is either currently experiencing or is at high risk of genetic stochasticity. It is possible that observed low rates of reproductive success are indicators of inbreeding depression, in which the limited number of reproducing individuals (Table 1) may have extremely low genotypic variability, resulting in low fecundity and seedling survival. The genetic variability between individuals and subpopulations, and any potential relationships

between observed rates of high seedling mortality and low genetic variability, are currently unknown as no population wide genetic work has been done on this species. As the three subpopulations are confined to a highly restricted range within a mile of each other, it is likely that individuals are derived from the same ancestorial population or individuals, which could result in low numbers of unique genetic adaptations to variable environmental conditions at the population level. However, limited genetic work done by Grady 2012 found this species to have high levels of polytomy, indicating genetic diversity from past evolutionary trajectories may be retained within the genome on even a limited number of individuals. Polytomy is thought to indicate a generalist model of edaphic driven endemism and could be functionally important to both this species plasticity to changing environmental conditions and managers ability to stabilize its current population decline (Rajakaruna 2004, Grady 2012).

As this species is long lived and can take five years or more to reach reproductive maturity, the reduction of the population by 50% over the past twenty-five years has increased the likelihood that genetic stochasticity is negatively affecting the population. As indicated in Tables 1 and 2, high mortality rates for adults in stage 3 or stage 4 of the population can have significant effects on demographic stochasticity, which can spiral into an F extinction vortex leading and genetic drift. Environmental stochastic events such as wildlife that removed significant portions of this species effective population of actively reproductive adults, could result in genetic stochasticity as both heterozygotic variability and heritable variability are reduced with in the single population. Finally, as current assisted migration and out planting attempts are utilizing seed stock from only three individuals grow in a nursery from wild seed, these significant genetic bottlenecks could have powerful consequences for the adaptability of future populations to successfully established at other locations. Seed increase breeding from a low number of individuals combined with the genetic bottleneck wild-adapted traits undergo during nursery production, means genetic stochasticity and genetic drift could have powerful effects on individual fitness and this species ability to adapt and persist in a changing climate.

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