

As Above so Below? Trampling Effects on Alpine and Subalpine Soil Seed Banks

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Abstract

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Subalpine and alpine meadows are a popular recreation destination, but heavy visitation results in off-trail vegetation trampling. Repairing trampling damage in the alpine and subalpine is a challenge because plant growth is slow, transporting materials to the restoration site is difficult, and restoration is resource-intensive. Climate-change-driven shifts towards hotter, drier growing seasons may make restoration even harder. Where nonnative species invasion risk is low, the soil seed bank could be a convenient, low-cost tool to buffer restored areas against climate change impacts by increasing diversity. I evaluated the size and composition of the germinable soil seed bank and compared it to aboveground vegetation communities in trampled and intact areas across an elevation gradient at Paradise, Mount Rainier National Park. I also investigated differences in soil characteristics between trampled and intact areas to evaluate potential barriers to seedling establishment and growth. Soils from the top 5 cm and from 5-10 cm below the surface of intact areas had higher seed density and species richness than the top 5 cm of trampled

areas, with reductions in seed density in trampled areas increasing with elevation. Invasive and lowland species comprised 0.2% of the germinable soil seed bank. The aboveground vegetation communities of trampled areas at lower elevations resembled intact communities at high elevations. The soil seed bank community differed from the standing vegetation for both intact and trampled areas, and was dominated by *Juncus* and *Carex* species. Soil analysis showed that trampling increased compaction and pH while reducing percent organic matter and micronutrients. Abundant seeds in the soil seed bank but low overlap with the standing vegetation shows that the soil seed bank has potential to supplement, but not replace, restoration planting or seeding. Restoration practices to restore soil structure may be necessary to facilitate soil seed bank germination and seedling establishment.

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CHAPTER 1

Introduction

Mount Rainier National Park's Paradise Meadows provide easy access to iconic subalpine wildflowers and parkland, breathtaking views of the Cascade Range, and opportunities for outdoor recreation and education. Over 2 million visitors are drawn to Paradise annually (NPS, 2024), and park visitors ranked viewing the meadows and wildflowers as a primary reason for visiting during the snow-free season (Simmons 2001). However, high foot traffic and off-trail hiking result in unofficial trails and loss of sensitive subalpine and alpine plant communities (Fritzke, 1992; Rochefort and Gibbons, 1992).

Trampling damage is a widespread problem in alpine areas across the world (Moritsch and Muir, 1993; Conlin and Ebersole, 2001; Klug et al., 2002; Zabinski et al., 2002; Willard et al., 2007; Zhang et al., 2012). The Organic Act requires the National Park Service to protect the habitats and organisms living in the parks for future generations (1916 NPS Organic Act, 54 U.S.C. § 100101(a)). Therefore, Mount Rainier officials have been combating trampling damage for decades by planting plugs of native meadow species in disturbed areas (Rochefort and Gibbons, 1992). The plugs survive but grow slowly, and restored areas have lower diversity and foliar cover than intact areas years after restoration (B. Fallon, pers. comm.). Restoration that looks incomplete is vulnerable to repeated trampling (Moritsch, 1992; Zabinski and Cole, 2000). Additionally, climate change is expected to make restoration harder, and alpine and subalpine habitats are predicted to experience more extreme climate change effects than lowland ecosystems (Mote et al., 2005; Pepin et al., 2015; Lamprecht et al., 2018; Wershow and DeChaine, 2018). At Mount Rainier, climate change is predicted to bring warmer temperatures and decreased snowpack (Ford, 2012). While a longer growing season could speed plant growth,

extreme heat with lower water availability may also reduce planting survival and growth, making restoration more difficult and labor-intensive.

Restoration practitioners at Mount Rainier and other high-elevation recreation areas need restoration techniques that are resilient to the effects of climate change, as well as information about conditions that could be limiting current restoration practices. For this thesis, I focus on how propagule availability and soil conditions may be limiting restoration, though microclimate conditions, and biotic interactions can also limit restoration progress (Zabinski and Cole, 2000). While the park supplies some propagules by planting plugs, restoration is more resilient to climate change when it uses diverse methods, genetic material, plant ages, and timing (Aplet and McKinley, 2017; Wilsey, 2021; Zabin et al., 2022). However, implementing diverse restoration practices can be labor-intensive and may not be feasible as land managers balance multiple priorities.

I address the extent to which propagules are present in the soil seed bank and whether soil conditions may be limiting current restoration. In Chapter 2, I examine (1) How does seed density differ between trampled and intact areas over an elevation gradient and across depths of intact areas? (2) How do soil seed bank communities compare across trampling levels, elevations, and soil depths? And (3) How does trampling affect soil compaction and nutrient levels? In Chapter 3 I address (1) How does trampling change the composition of aboveground communities? (2) How does trampling affect soil seed bank density and community composition of upper soil layers? And (3) Is the soil seed bank community similar to aboveground vegetation and which species drive community differences? Chapters 2 and 3 are written as separate manuscripts for later submission to peer-reviewed journals.

CHAPTER 2

Off-trail trampling alters soil seed banks and nutrients across elevational gradients in alpine and subalpine ecosystems

Abstract

Human trampling is a common threat to alpine and subalpine areas. Soil seed banks may be a useful tool to aid restoration, but trampling has varying effects on soil seed bank density and composition. Trampling can also impact soil conditions such as compaction and nutrients which can limit seedling recruitment. In this study, I compared the germinable soil seed bank density, composition, and soil conditions between trampled and intact areas at Paradise Meadows, Mount Rainier National Park, across an elevation gradient and sampling depths. Soil from intact areas had on average 15,332 seedlings per m² while trampled areas had 2458. Relative to intact areas, the soil seed bank community of trampled areas differed in composition, was less varied, and contained fewer species. *Juncus* and *Carex* species were common across all elevations and sample depths, but the litter layer from intact areas was dominated by pink mountain heather (*Phyllodoce empetriformis*). Trampled area soils were more compacted and less acidic with lower organic matter and micronutrient levels than intact areas. The soil seed bank of intact or trampled areas contains enough seeds from native species to supplement trampled area restoration, but soil structure and nutrients may limit seedling germination and establishment *in situ*.

Introduction

The soil seed bank may strengthen ecosystem resilience by providing a diverse assemblage of species that can regenerate following disturbance (Hoyle et al., 2013; Plue et al.,

2021). Because alpine soil seed banks tend to harbor relatively few invasive species (Hoyle et al., 2013), leveraging regeneration from the soil seed bank could be a useful tool to increase vegetation cover and diversity to improve restoration efforts' resilience (Aplet and McKinley, 2017; Kiss et al., 2018). However, soil seed bank utility for restoration depends on the abundance of seeds, the number and identity of species present, and their potential to establish and grow.

Reproduction using seeds may play a minor role in alpine ecosystems, with plants relying more heavily on vegetative reproduction (Billings and Mooney, 1968; Laughlin, 2023). However, some studies suggest seedling establishment is more common than vegetative reproduction in disturbed alpine areas (Chambers, 1995). The germinable soil seed banks of intact alpine and subalpine areas may contain hundreds to tens of thousands of seeds per square meter, with species richness ranging from nine to 27 species (Chambers, 1993; Zabinski et al., 2000; Klug et al., 2002; Ma et al., 2009, 2010; Venn and Morgan, 2010; Hoyle et al., 2013).

The soil seed bank could serve as a source of seeds to restore alpine areas damaged by recreation, which is a common challenge for alpine land management (Therrell et al., 2006). Alpine and subalpine areas can be important tourism destinations, and high visitor use can result in heavy foot traffic and off-trail hiking which kill vegetation and can lead to erosion (Willard and Marr, 1971; Fritzke, 1992; Rochefort and Gibbons, 1992; Eagan et al., 2004). Willard and Marr (1971) and Willard et al. (2007) surveyed trampling damage recovery over 40 years and suggest that passive restoration of trampled alpine areas could take hundreds of years even when areas are protected from re-trampling.

Soil seed banks in heavily trampled sites may contain fewer seeds than intact areas due to damage, erosion, or seed runoff (Isselin-Nondedeu and Bédécarrats, 2007), with seed density declining with increasing distance from intact vegetation (Zabinski et al., 2000). A comparison of

soil seed banks in passively restored and grazed, eroded alpine grasslands showed more degraded areas had fewer seeds and lower species richness than recovering areas (Wellstein et al., 2024). However, this effect is not consistent across studies. Devegetated alpine areas in Colorado receive higher seed rain than intact areas (Chambers, 1993) which could result in more seeds in the soil seed bank in trampled areas. Additionally, some studies have found more seeds in the soils of alpine and mountain trails and adjacent areas than in intact areas, though these differences are driven by a few prolific seeders and may vary by microhabitat (Klug et al., 2002; Jolivet et al., 2022).

Trampling can affect the soil seed bank community composition and may facilitate invasive or lowland species migration, which would affect its utility in restoration. For example, Zabinski et al., (2000) found that subalpine campsites with more disturbance had fewer species in the soil than intact areas. Trampled soils may also contain more early seral species than intact areas (Roovers et al., 2006). Similarly, foot traffic on mountain trails could facilitate transportation and dispersal of nonnative or lowland species that could produce a restored community that differs from the surrounding intact area or outcompete subalpine and alpine species (Liedtke et al., 2020; Jolivet et al., 2022). Understanding the composition of the soil seed bank in trampled and intact areas is important to ensure its use in restoration does not facilitate a state shift in the vegetation (Ma et al., 2019) or shift towards a community that is more vulnerable to changes (Larson and Suding, 2022).

In alpine and subalpine habitats, soil seed banks are most dense in the top 5 cm (Chambers, 1993; Zabinski et al., 2000; Roovers et al., 2006; Ma et al., 2010, although see Ma et al., 2009), but burial depth, elevation, temperature and moisture conditions, and species-specific seed longevity affect seed bank input and losses (McGraw, 1987; Long et al., 2015; An et al.,

2020). Despite changes in standing vegetation community across an elevational gradient that could affect seed rain input to the soil seed bank, the effect of elevation on alpine and subalpine soil seed banks is less pronounced (Venn and Morgan, 2010; Luo et al., 2017). At higher elevations, seeds may remain viable in the soil for longer (Cavieres and Arroyo, 2001), but soil seed bank density has also been shown to decline with increasing elevation (Luo et al., 2017). In intact subalpine soil seed banks, Zabinski et al. (2000) found no difference in seed abundance or species richness between the litter layer and top 5 cm of soil, though some species were only found in one layer or the other. Differences in seed dormancy or viability may also affect community composition across seed bank depths and elevations (Shiferaw et al., 2018).

Regeneration of trampled areas may also be limited by soil factors (Zabinski and Cole, 2000), which can affect soil seed bank abundance, species richness, and seed persistence (Long et al., 2015; Luz et al., 2018). Trampling intensifies erosion of seed- and organic-matter-rich upper soil layers as elevation and slope increase (Fritzke, 1992). Foot traffic causes compaction (Weaver and Dale, 1978). Compaction reduces pore space, decreases water and air permeability, slows water infiltration, and increases erosion and loss of soil organic matter, which affect plant growth and seedling establishment (Batey, 2009; Yang and Zhang, 2011). Loss of organic matter also reduces levels and availability of soil nutrients (Dhaliwal et al., 2019), although the effects of trampling on soil nutrients in alpine areas have not been widely studied.

For this study, I evaluated the effect of trampling on soil seed banks and soil properties at Paradise meadows, Mount Rainier National Park. Despite extensive restoration efforts throughout the meadows using plugs, observations of seedlings in restored areas are uncommon (B. Fallon, pers. comm.). I aimed to identify whether trampling effects on the soil seed bank or soil properties could be limiting regeneration. Specifically, I addressed (1) How does seed

density differ between trampled and intact areas over an elevation gradient and across depths of intact areas? (2) How do soil seed bank communities compare across trampling levels, elevations, and soil depths? And (3) How does trampling affect soil compaction and nutrient levels?

Methods

Study Site

This study was conducted in subalpine and alpine areas at Paradise, Mount Rainier National Park. Mount Rainier is a 4392 m tall active stratovolcano in the Cascade Mountains (Crawford et al. 2009). The Paradise visitor center and parking lot is 1650 m above sea level and the most widely used day-hike trails in the area reach an elevation of 2200 m (NPS 2024).

Paradise is located on the south side of Mount Rainier, with slope aspects ranging from southwest to southeast. During the snow-free growing season from late July to early October (Frappier, 2004), mean low and high daily temperatures range from 4.4 to 14.4 °C, while they range from -3.9 to 3.9 °C during the snow season (daily 1991-2020 values; PRISM 2026). Most precipitation in Paradise falls as snow (NPS 2025). Paradise receives an average of 307.5 cm of snow-water-equivalent annually, while 30.2 cm of rain fall during the growing season (PRISM 2026).

The Paradise area spans the subalpine to alpine ecotone from closed-canopy subalpine forest to rocky alpine scree slopes with sparse vegetation (Rochefort and Gibbons, 1992). The subalpine forests are comprised of *Abies lasiocarpa*, *Tsuga mertensiana*, and *Callitropsis nootkatensis* (Rochefort and Peterson, 1996). Subalpine meadow communities are primarily comprised of *Lupinus latifolius*, *Valeriana sitchensis*, *Bistorta bistortoides*, *Carex spectabilis*,

and *Castilleja parviflora*. Shrub-heath communities span the subalpine to alpine gradient and are often dominated by *Phyllodoce empetrifloris*, *Cassiope mertensiana*, *Vaccinium deliciosum*, *Lupinus latifolius*, *Phyllodoce glanduliflora*, and *Festuca viridula* (Henderson, 1973).

Mount Rainier attracts over 2 million visitors per year (NPS 2026), and Paradise is the most-visited site in the park (Simmons et al., 2001). Lower elevation trails within approximately half a mile of the parking lot and visitor center are paved; the remaining trail network is unpaved, with rock perimeters and rope-and-rebar fencing to delineate the trail. Despite these measures, off-trail hiking has created unofficial trails and trampled patches throughout the meadows (Fritzke, 1992; Rochefort and Gibbons, 1992).

Site Selection and Soil Sampling

I used satellite imagery, Google Street View, and existing National Park Service social trail and restoration datasets to locate areas with trampling damage next to areas with intact vegetation. Potential sites were selected to represent the range of vegetation communities across the elevation gradient at Paradise, and were grouped as low (1675-1775 m), medium (1775-1900 m), and high elevation (1900-2075 m). Potential sites underwent archeological surveys as required by Mount Rainier National Park permits, then were surveyed to ensure they were large enough to contain the sampling design and had no evidence of previous restoration. Sites that satisfied these conditions were selected to maximize distance between sites.

This selection process produced 15 sites (Figure 2-1)—four low, six medium, and five high elevation—for inclusion in the study. Appendix 1-1 shows photos of each site. Fewer sites at low elevation satisfied the criteria for inclusion because trampling damage in the lower Paradise meadows is less severe than at higher elevations. Two low elevation sites contained an unpaved road used by NPS vehicles. While these roads do not experience the same volume of

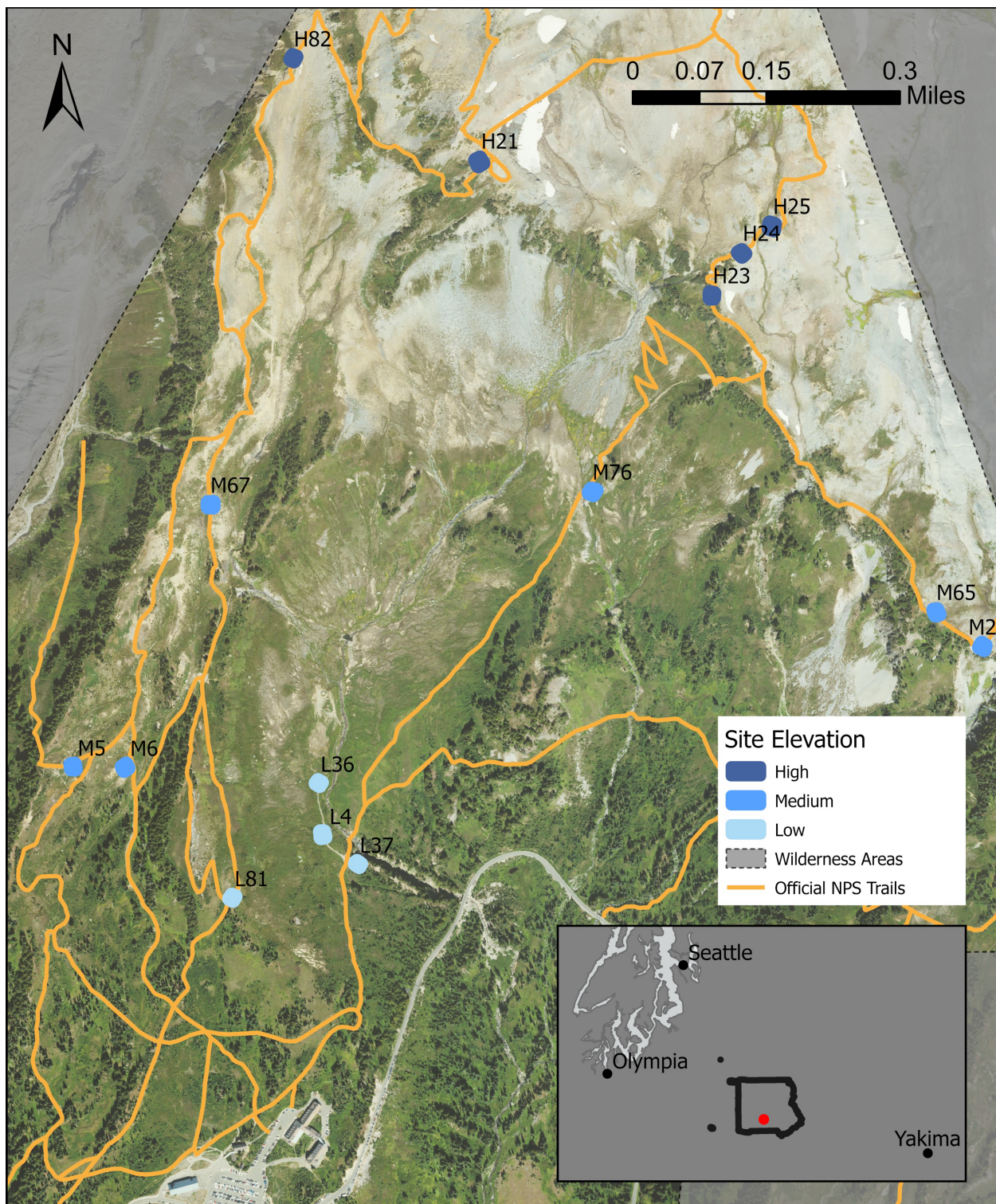


Figure 2-1. Sites selected for soil sampling at Paradise, Mount Rainier National Park. Sites are labeled with their unique identifiers, where “L,” “M,” and “H” stand for low, medium, and high, respectively.

foot traffic as the other sites, vehicle use also results in soil compaction and vegetation loss (Weaver and Dale, 1978), and would likely require similar restoration techniques to areas trampled by human foot traffic.

Trampled and intact areas were evaluated using trampling condition classes developed by Rochefort and Swinney (2000). Trampled areas were characterized by areas of low moss, vascular vegetation, and litter cover, with exposed bare soil and rock in a pattern continuous with an established trail (condition classes 3 and 4). In contrast, adjacent intact areas had higher vegetation cover and leaf litter with little to no trampling evidence (condition classes 0-2).

At each site, two parallel 2 x 8 m belt transects were established 3 m apart, with one in a trampled area and the other in the adjacent intact meadow (Figure 2-2). Within each transect, three plots were established 2-3 m apart. Plots in trampled areas were 1 m from the intact vegetation boundary to reduce seed rain from intact areas into trampled area soil seed bank samples. Occasionally, trampled area plot placement was adjusted to avoid placement on official trails, in instances where the trampled area was less than 3 m wide, or to avoid intact patches within trampled areas. This ensured trampled area sampling represented areas that would be restoration priorities. In the intact area, plots were 2-4 m from the vegetation boundary to reduce edge effects. For both intact and trampled areas, plots that fell on areas that lacked soil (such as boulders) were relocated within the transect to ensure soil samples could be collected.

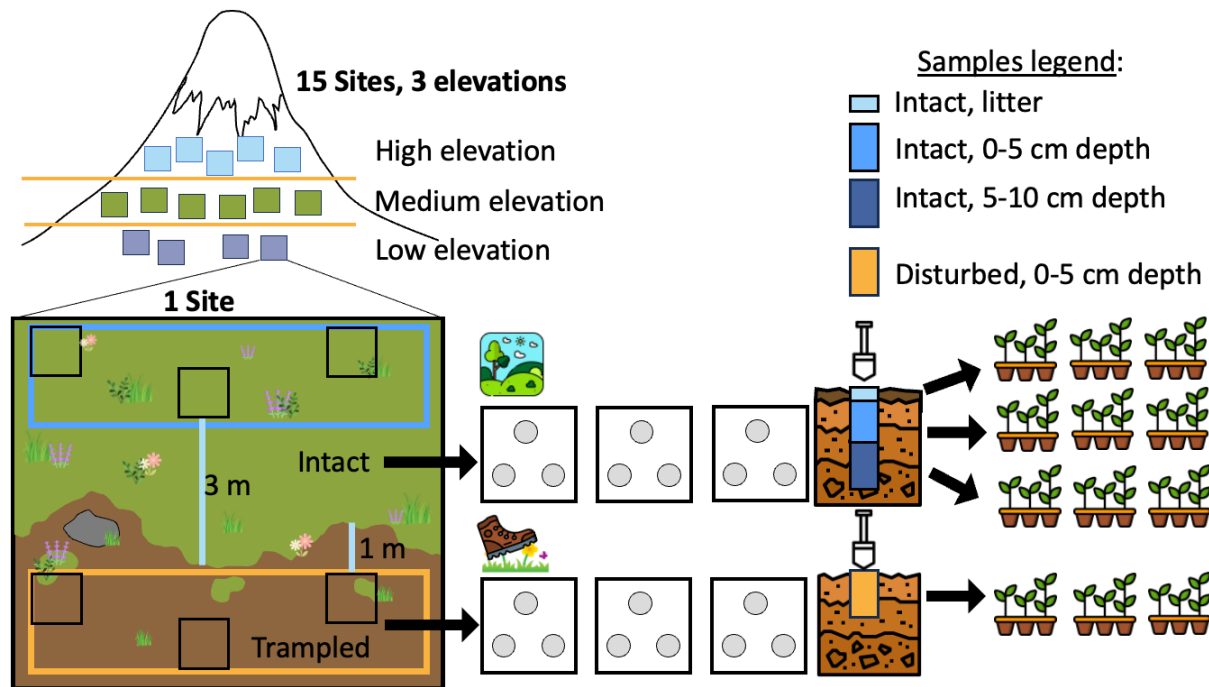


Figure 2-2. Schematic of sampling design. Icons were sourced from flaticon.com.

In August 2024, I surveyed the aboveground vegetation in each plot; these data are reported in Chapter 3. I sampled soil from each plot in late September 2024 to capture the full potential community present following summer seed rain (Bertiller, 1992) and when the soil seed bank could be utilized to supplement fall restoration plantings. Soil was sampled from three equally spaced locations within each plot using a 5 cm diameter bulk density sampler. Samples from each hole were stored in separate bags. A penetrometer (Humboldt H-4205, dial-type pocket penetrometer) with a 6.3 mm foot was used to measure the unconfined compressive strength (hereafter “compaction”) of the soil surface at each sampling location.

I sampled the top 5 cm of soil in trampled areas and the top 10 cm of soil in intact areas. Intact areas were sampled deeper because erosion may have removed upper layers from trampled areas, and I therefore wondered if trampled areas would more closely resemble deeper soils of intact areas. Litter was separated from mineral soil, where present; litter was absent from all

trampled areas and from 10 intact plots. Mineral soil samples from intact areas were divided into 0-5 cm and 5-10 cm deep layers.

Soil Sample Preparation for Seed Bank Study

Soil samples were stored indoors in plastic bags in cool conditions for up to a week, then opened to dry for 3-4 weeks. Mineral soil samples were sieved to remove rocks and organic matter greater than 4 mm. Litter samples were not sieved. Samples of the same depth from the same plot were aggregated such that each site had nine soil samples (three trampled 0-5 cm, three intact 0-5 cm, three intact 5-10 cm) and up to three litter samples. This produced 170 aggregate samples: 45 from the 0-5 depth in trampled areas (15 sites x 3 plots), 45 from the 0-5 depth in intact areas, 45 samples from the 5-10 cm depth in intact areas, and 35 from the litter layer in intact areas (15 sites x 3 plots, minus 10 plots with no litter).

For each aggregate sample, 120 cm³ of soil was measured, moistened with 25 mL of deionized water, and cold stratified at 5 °C for 12 weeks. Litter samples were aggregated and the full litter volume was moistened before stratification.

After cold stratification, each sample was spread evenly over a 25 x 25 cm germination flat filled with 4 cm of Sunshine Mix #4 (Sun Gro Horticulture) potting media. I also prepared 15 control flats that contained potting media but no sample to detect air or soil-borne seed contamination. In total, there were 185 flats (170 flats containing a soil or litter sample and 15 control flats). Flats were uniquely identified so that observers were blind to sample identity during data collection. All flats were placed in a greenhouse maintained between 20-22 °C and watered as needed to keep soil surfaces lightly moist.

Germination Data Collection

Germination testing began in February 2025. Samples were checked for new seedlings twice weekly for the first six weeks, weekly for the next eight months, then once every two weeks until the study concluded after 13 months. Once seedlings developed their first set of true leaves, they were assigned a temporary morphotype name to distinguish them from other species, removed from the flat, and potted to grow until identification to species was possible. Unidentified morphotypes were re-checked every one to two months as plants developed identifiable features. Seedlings that died prior to identification to species were assigned the most specific possible taxonomic level, and assigned unique names to distinguish distinct morphotypes.

Plants were identified as they flowered. Some morphotypes did not flower during the 13 months of the study; these could often be identified to species or genus based on non-reproductive features. Two very common species, *Juncus mertensianus* and *Carex spectabilis*, did not flower during the study, and their identity was inferred using a combination of their leaf morphology, comparison of their abundance in the soil seed bank to their collection frequency in herbaria records (CPNWH 2026), and the composition of aboveground vegetation plots. Some samples had too many *Juncus* spp. germinants to grow to maturity. For these samples, I potted up to three *Juncus* spp. seedlings each data collection event and grew them for identification; remaining seedlings were counted and removed from samples without potting. This group was analyzed as a separate taxon from other *Juncus* species during analysis, but may have contained common *Juncus* species including *J. mertensianus* and *J. drummondii*.

Species that arrived through airborne seed contamination were identified by their presence in control flats or in the soil of other pots in the greenhouse. Seedlings of these species

were excluded from all summaries and analyses. A list of weed species and their total abundances in the sample flats is shown in Appendix 1-2.

Soil Nutrient Analysis

I used the remaining soil from the samples for soil chemistry and nutrient analysis. Samples from the same disturbance and depth were aggregated across plots within each site to produce 45 samples: trampled 0-5 cm depth, intact 0-5 cm depth, and intact 5-10 cm depth. Four sample aggregates did not contain sufficient soil for analysis, resulting in 41 samples submitted for analysis. Samples were sent to Soiltest Farm Consultants (Moses Lake, WA), who measured pH, electrical conductivity, organic matter, nitrate, ammonium, phosphorus, potassium, calcium, magnesium, sodium, sulfur, zinc, iron, manganese, copper, and boron.

Statistical Analysis

All analysis was completed in R version 4.5.2 (R Core Team 2025). I compared the effects of trampling, elevation, and sample depth on seedling abundance, species richness, community composition, soil nutrients, and compaction of the samples using three sets of comparisons.

The first comparison, hereafter the “Top 5 cm Comparison,” evaluated the effect of trampling and elevation on the 0-5 cm depth samples from intact and trampled areas. Analyses for this comparison included disturbance, elevation, and their interaction, while controlling for site differences. For the soil seed bank response variables, this comparison explores whether the soil seed bank of intact areas has persisted in trampled areas and the same processes of seed accumulation and loss are occurring across both areas. The elevation term tests whether patterns are consistent across the elevation gradient. For the soil condition response variables, this

comparison evaluates whether plants roots would experience similar soil conditions in top 5 cm of trampled areas as they would in intact areas.

The second comparison, hereafter the “5-10 cm Comparison”, tested whether trampled soils resemble deeper soils from intact areas by comparing 0-5 cm depth samples from trampled areas with the 5-10 cm depth samples from intact areas. The models for this comparison used the same structure as for the Top 5 cm Comparison.

The third comparison, hereafter the “Intact Comparison,” evaluated whether deeper soils have fewer seedlings or different community compositions by comparing the three strata (litter, 0-5 cm, 5-10 cm) within intact areas. Models for this comparison included sample depth, elevation, and their interaction, while controlling for site differences. This comparison explores how seed longevity, movement, and size dynamics affect the soil seed bank and how soil nutrient availability changes along the soil profile.

Seedling Abundance

Average seedling counts per flat for each disturbance-depth combination were converted to seedlings per m² to allow comparison with other studies. Counts were converted by multiplying the average seedling count per flat by the average pre-sieved total soil volume collected for that combination, then dividing by 120 (the volume used for the germination tests) to get the average number of seedlings expected in a plot’s aggregate sample. This average was divided by 58.9 cm², the soil surface area covered by the top of the three, 5 cm diameter sample cores to get seeds per cm², then multiplied by 10,000 to convert to m². Seedling counts per flat were used for all other analyses.

I used generalized linear mixed models to evaluate the effect of trampling, elevation, and sampling depth on seedling abundance. Absent litter samples were excluded from these analyses.

For the Top 5 cm and the 5-10 cm Comparisons, models included site as a random effect. For the Intact Comparison, models included plot nested within site as random effects. Models for all three comparisons used the negative binomial distribution with a log link. I evaluated model fit by inspecting DHARMA simulated residuals and testing for overdispersion and zero inflation (Hartig, 2024). I used likelihood ratio tests to calculate the statistical significance of each model term (Bolker, 2025). For significant terms, I used the emmeans package to make pairwise comparisons using the Tukey adjustment for multiple comparisons (Lenth and Piaskowski, 2017). For these and all other comparisons, tests were considered significant when P values were less than 0.05, and marginally significant when $0.05 < P < 0.10$.

Community Composition

I used permutational analysis of variance (PERMANOVA, `vegan::adonis2`) to evaluate whether community composition differed between samples (Oksanen et al., 2001). I relativized seedling counts by the maximum count observed for each species, then calculated the Bray-Curtis distance between samples. Relativizing by the maximum prevents community analysis from being weighted towards strongly dominant species and obscuring composition differences resulting from turnover among less common species by weighting very common and uncommon species more similarly. For the Intact Comparison, litter samples that could not be collected were included and analyzed as having seedling counts of zero for all species. Excluding missing litter samples would have resulted in an unbalanced design which is not currently supported by `adonis2`. I added a dummy variable to all observations to permit inclusion of flats with zero seedlings. PERMANOVA model terms matched the terms used in the seedling abundance analyses for each of the three comparisons, and I restricted permutations to account for correlation among sites and plots.

When there were differences between groups, I explored how communities differed using three post-hoc analyses: pairwise PERMANOVAs, analysis of dispersion using PERMDISP, and follow-up pairwise PERMDISP. For the Top 5 cm Comparison and 5-10 cm Comparison, I combined trampling and elevation terms to create a factor with six levels (i.e. trampled at low elevation, intact at low elevation, etc.). For the Intact Comparison, I combined the elevation and depth terms to create a factor with nine levels. PERMDISP (`vegan::betadisper`) is a permutation-based technique that tests whether groups differ in the dispersion of observations around their mean (Anderson, 2006; Anderson et al., 2008; Bakker, 2024). The combined results of PERMANOVA and PERMDISP show whether differences between communities were driven by differences in means and/or differences in dispersion. Post-hoc analyses used unrestricted permutations.

I visualized community differences using nonmetric multidimensional scaling (NMDS, `vegan::metaMDS`), an ordination technique that configures the community Bray Curtis distance matrix into a graph such that distances between points visually represent differences in community composition between observations (Oksanen et al., 2001). NMDS plots were created using three dimensions, and the first two dimensions are displayed in the results. NMDS used 40 tries and up to 100 tries with 300 iterations per try (McCune and Grace, 2002; Bakker, 2024).

I explored the causes of community differences by comparing the species richness and evenness across trampling status, elevations, and depths; summarizing the dominant and most widespread species among groups; and conducting an Indicator Species Analysis (ISA). For samples with seedlings, I analyzed differences in species richness using generalized linear mixed models with the same model structures as for seedling abundance. The models for species richness used the Poisson distribution with a log link. These models excluded samples that had

zero seedlings to explore differences in community composition (samples with no seedlings lack a community). I used correlation tests to evaluate the relationship between species richness and species evenness.

I evaluated the most widespread and dominant species for each disturbance-depth combination. Widespread species were defined as species that were in at least 10% of samples across the entire study. I summarized the percent of flats that each widespread species was found in for each disturbance-depth combination. I defined dominant species as the species that was the most common in each sample. Samples with co-dominant species were counted once for each species. When evaluating dominant species, samples with only one seedling were excluded from calculations. For each dominant species, I summed the number of samples of each disturbance-depth combination that the species was dominant for, then divided the sum by the total number of samples within each disturbance-depth combination. This produced a list of the most common dominant species for each disturbance-depth.

I conducted ISA (`indicspecies::multipatt`) for the Top 5 cm Comparison and the Intact Comparison (de Cáceres and Legendre, 2009). Group combinations were created using the same disturbance-elevation or depth-elevation factors as for the post-hoc PERMANOVA and PERMDISP tests. Combinations were restricted to single levels and combinations of levels that matched in one element of their treatment (e.g., the same trampling status, depth, or elevation) and were continuous for ordered variables (e.g., the combination of low and medium elevations was permitted, but not the combination of low and high elevations). Species were considered strong indicators if their indicator value was greater than 0.5 and their P value was less than 0.05. ISA used unrestricted permutations.

Soil Compaction and Nutrients

I analyzed the effect of trampling on soil compaction and nutrients. For compaction, the three values from each plot were averaged for analysis. The penetrometer's maximum measurable value was 6 kg/cm²; if measurements exceeded the maximum, 6 kg/cm² was used for analysis. I used a linear mixed model to test the effect of disturbance, elevation, and their interaction on compaction with site as a random effect. Values were log-transformed for analysis to meet the homogeneity of variances assumption.

Organic matter, pH, and electrical conductivity were analyzed separately using linear mixed models to evaluate the effect of the combination of disturbance and depth (a factor with three levels), elevation, and their interaction, with site as a random effect. Electrical conductivity was log transformed to meet model assumptions of normally distributed errors.

Many of the soil nutrients were correlated, so I used a principal component analysis (PCA) to reduce the data into uncorrelated dimensions using scaled values for nitrate, ammonium, phosphorus, potassium, calcium, magnesium, sodium, sulfur, zinc, iron, manganese, copper, and boron. The first three axes of the PCA on soil nutrients accounted for 73.1% of the variation in the data, and roughly corresponded with the primary macronutrients potassium, nitrogen, and phosphorus (Table 2-1; Appendix 1-3, Figure 1-3-1). The first axis (PC1) had high loadings across potassium and most secondary macronutrients and micronutrients (except Na and S). PC2 represented nitrogen, with high loadings for both ammonium and nitrate. PC3 corresponded with phosphorus and sulfur, which were inversely related: higher levels of phosphorus were associated with lower levels of sulfur. I used linear mixed models with the same model structure as for organic matter to evaluate the effect of disturbance-depth, elevation, and their interaction on each PC, with site as a random effect.

Table 2-1. First three principal components' loadings and percent variation explained. Bold values show the highest magnitude loadings that have the largest impact on each PC. Loadings for all principal components are in Appendix 1-3, Table 1-3-1.

Nutrient	PC1 (46.4%)	PC2 (16.9%)	PC3 (9.8%)
NO ₃ -N	0.098	0.573	0.190
NH ₄ -N	0.194	0.498	0.189
Bray P	0.006	0.239	-0.647
K	0.357	0.179	0.104
S	-0.093	-0.214	0.652
Zn	0.350	-0.225	-0.001
Fe	0.324	-0.171	-0.163
Mn	0.347	0.079	-0.044
Cu	0.301	-0.247	-0.140
B	0.301	-0.231	0.005
Ca	0.351	0.081	0.130
Mg	0.353	0.107	0.089
Na	0.200	-0.263	0.020

Results

Over the 13-month germination period, a total of 3901 seedlings of 67 non-weed species germinated from the 170 samples. An intact, high-elevation, 5-10 cm depth sample had the highest seedling count with 446 seedlings. Thirteen trays had zero seedlings: three from intact, high-elevation, 5-10 cm depth samples, and 10 from trampled 0-5 cm samples. Seventy five percent of trays had less than 24 seedlings, and 90% of trays had less than 48 seedlings.

Seedling Abundance

There was an average of 9602 seedlings per m² for a 5-cm-thick soil sample (average excludes litter layer), though seedling density varied due to trampling. Intact 0-5 cm plots had an average of 15,332 seedlings per m², and trampled areas had an average of 2458 seedlings per m².

Top 5 cm Comparison: Samples in intact areas had 6.0 ± 1.2 (estimate $\pm$ s.e.) times more seedlings than trampled areas from the same depth (Table 2-2, Figure 2-3). Seedling counts did not differ across elevations overall, but there was a significant elevation-trampling

interaction. For trampled sites, seedling counts declined with increasing elevation, though only low and high elevations differed significantly. However, for intact sites, seedling counts were similar across elevations.

5-10 cm Comparison: The intact, 5-10 cm samples had 2.9 ± 1.3 times more seedlings than trampled areas. There was no effect of elevation on seedling abundance, but there was a significant interaction between trampling and elevation. While seedling abundance declined with increasing elevation for trampled sites, it increased with elevation for intact sites. At medium and high elevations, intact samples had significantly more seedlings than trampled samples.

Intact Comparison: Among intact samples, there were significant differences in seedling counts between sample depths, but no significant differences across elevations, and no significant depth-elevation interaction (Table 2-3). The 0-5 cm depth had 1.6 ± 1.2 times more seedlings than litter ($P = 0.034$) and 2.0 ± 1.2 times more seedlings than 5-10 cm depth samples ($P < 0.001$).

Table 2-2. ANOVA results showing main effects of the GLMM for the Top 5 cm and 5-10 cm Comparisons.

Term	NumDF	DenDF	F	P value
Top 5 cm Comparison				
Disturbance	1	72	80.848	< 0.001 ***
Elevation	2	12	1.166	0.345
Disturbance * Elevation	2	72	3.180	0.048 *
5-10 cm Comparison				
Disturbance	1	72	23.488	< 0.001 ***
Elevation	2	12	0.140	0.871
Disturbance * Elevation	2	72	6.077	0.004 **

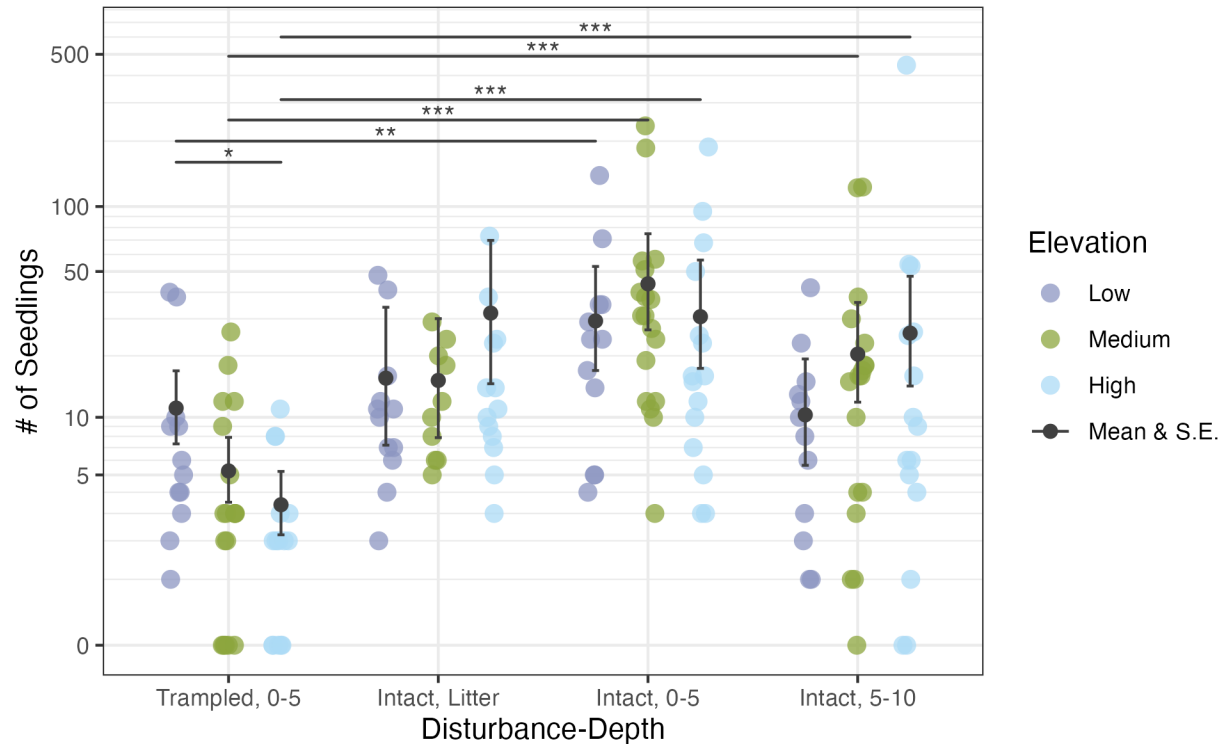


Figure 2-3. Seedling abundance per sample across trampling status, depths, and elevation. The y-axis scale is log-transformed. Black points and whiskers show the GLMM predicted mean and standard error above points showing observed counts. Model predictions are averaged across the three models for all estimates except litter. The lines at the top indicate statistically significant pairwise differences for the Top 5 cm (lower lines) and 5-10 cm Comparisons (upper lines), where “*” = $0.05 < p < 0.01$, “**” = $0.01 < p < 0.001$, “***” = $p < 0.001$. A table of P values and estimates for all contrasts are shown in Appendix 1-4.

Table 2-3. ANOVA results showing main effects of the GLMM on seedling abundance for the Intact Comparison.

Term	NumDF	DenDF	F	P value
Depth	2	104.3	9.201	< 0.001***
Elevation	2	11.5	0.196	0.825
Depth * Elevation	4	104.3	0.881	0.478

Community Composition

PERMANOVA and NMDS

Top 5 cm Comparison: Communities differed significantly between trampled and intact sites and between elevations (Table 2-4). There was a marginally significant interaction between elevation and trampling. Pairwise contrasts showed communities from top 5 cm of soil differed significantly between intact and trampled areas for all elevations (Figure 2-4; Appendix 1-5,

Table 1-5-1). The soil seed bank communities from intact samples were significantly more dispersed than communities from trampled areas (PERMDISP: $F(1, 88) = 51.319$, $P < 0.001$), and there were marginally significant differences in dispersion among elevations (PERMDISP: $F(2, 87) = 2.872$, $P = 0.062$). There was also a significant combined effect of elevation and trampling (PERMDISP: $F(5, 84) = 12.604$, $P < 0.001$). For each elevation, trampled areas were significantly less dispersed than intact areas (Appendix 1-5, Table 1-5-1). Low elevation sites were marginally significantly more dispersed than medium elevation sites for both trampled and intact areas.

Table 2-4. PERMANOVA results for the Top 5 cm Comparison of community composition.

Term	Df	Sum Of Sqs	R ²	F	P value
Elevation	2	0.363	0.056	1.569	0.026 *
Site	12	1.390			
Disturbance	1	0.687	0.106	12.747	< 0.001***
Disturbance: Elevation	2	0.178	0.027	1.649	0.059 .
Residual	72	3.878	0.597		
Total	89	6.495	1.000		

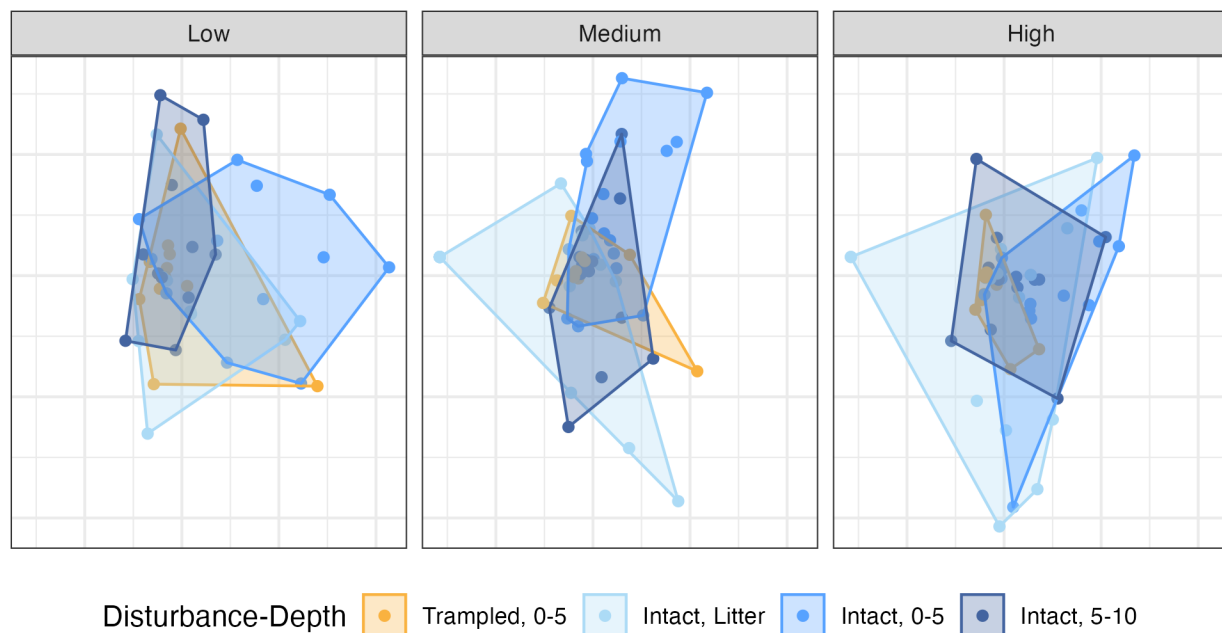


Figure 2-4. NMDS plots (stress = 0.178) showing the soil seed bank community of each disturbance-depth combination. Plots show points from an NMDS run using data from all samples, subset by elevation for each panel.

5-10 cm Comparison: The communities of trampled areas and deeper intact areas' samples differed due to trampling and elevation (Table 2-5). All elevations differed from each other (Appendix 1-5, Table 1-5-2). As with the Top 5 cm Comparison, community differences in the 5-10 cm Comparison between trampled and intact areas were due in part to differences in dispersion (PERMDISP: $F(1, 88) = 14.211$, $P < 0.001$). There were also differences between elevations (PERMDISP: $F(2, 87) = 4.424$, $P = 0.015$). Pairwise contrasts showed that low elevation sites were significantly more dispersed than medium and high elevation sites (Appendix 1-5, Table 1-5-2).

Table 2-5. PERMANOVA results for the 5-10 cm Comparison of community composition.

Term	Df	Sum Of Sqs	R ²	F	P value
Elevation	2	0.319	0.055	1.492	0.057 .
Site	12	1.283			
Disturbance	1	0.209	0.036	3.913	<0.001 ***
Disturbance: Elevation	2	0.150	0.026	1.408	0.143
Residual	72	3.844	0.662		
Total	89	5.806	1.000		

Intact Comparison: Among soil seed bank communities from intact plots, there were composition differences among elevations, depths, and their interaction (Table 2-6). For low elevation sites, the 0-5 cm depth differed from 5-10 cm and litter (Appendix 1-5, Table 1-5-3). At middle elevations, all sample depths differed, and at high elevations, litter differed from 5-10 cm and there were marginally significant differences between litter and 0-5 cm depths. Communities' dispersion differed between depths (PERMDISP: $F(2,132) = 12.075$, $P < 0.001$), but not elevations (PERMDISP: $F(2, 132) = 0.659$, $P = 0.519$). There was a significant combined effect of depth and elevation (PERMDISP: $F(8, 126) = 4.796$, $P < 0.001$). At low elevations, dispersion was higher in the 0-5 cm depth samples than 5-10 cm, and at high elevation, 5-10 cm

depths were more dispersed than litter. At medium elevations, both differed: dispersion was higher in the 0-5 cm depth samples than 5-10 cm, and 5-10 cm depths were more dispersed than litter (Appendix 1-5, Table 1-5-3). Because PERMANOVA showed that elevations differed, but PERMDISP shows they did not differ in dispersion, this means differences along the elevation gradient were due to differences in means rather than dispersion between plots.

Table 2-6. PERMANOVA results for the Intact Comparison of community composition.

Term	Df	Sum Of Sqs	R ²	F	P value
Elevation	2	0.560	0.048	1.672	0.027 *
Site	12	2.010			
Depth	2	0.771	0.066	5.549	<0.001 ***
Depth: Elevation	4	0.484	0.041	1.743	0.007 **
Site: Plot	30	2.118	0.180	1.016	<0.001 ***
Residual	84	5.836	0.495		
Total	134	11.780	1.000		

Species Richness and Evenness

Five species on average germinated from each sample. Intact, 0-5 cm samples had the highest species richness, followed by intact litter and intact 5-10 cm. Trampled sites had the lowest species richness (Appendix 1-6).

Top 5 cm Comparison: Species richness in intact areas was 2.1 ± 1.1 times higher than trampled areas (Table 2-7). There were no significant effects of elevation on species richness, and no significant interaction between elevation and disturbance.

5-10 cm Comparison: Intact areas' 5-10 cm samples had 1.3 ± 1.1 times higher species richness than trampled areas. There were no differences across elevations, and no significant disturbance-elevation interactions.

Table 2-7. ANOVA results showing main effects of the GLMM on species richness for the Top 5 cm and 5-10 cm Comparisons. Trends are shown in a figure in Appendix 1-6.

Term	NumDF	DenDF	F	P value
Top 5 cm Comparison				
Disturbance	1	63.6	40.510	< 0.001***
Elevation	2	12.5	0.708	0.512
Disturbance: Elevation	2	63.6	0.793	0.457
5-10 cm Comparison				
Disturbance	1	62.4	3.385	0.071 .
Elevation	2	11.7	0.253	0.781
Disturbance: Elevation	2	62.2	0.806	0.451

Intact Comparison: Among intact plots, species richness in 0-5 cm depth samples was 1.6 ± 1.1 times higher than the 5-10 cm sample depth ($P < 0.001$) and 1.4 ± 1.1 times higher than litter ($P < 0.001$, Table 2-8). There were no significant differences across elevations, and no significant interaction.

Table 2-8. ANOVA results showing main effects of the GLMM on species richness for the Intact Comparison.

Term	NumDF	DenDF	F	P value
Depth	2	77.3	13.747	< 0.001 ***
Elevation	2	12.4	0.290	0.754
Depth: Elevation	4	77.2	0.750	0.561

There was a strong negative correlation between seedling abundance and species evenness across all samples (correlation test: $R = -0.667$, $t(142) = -10.653$, $P < 0.001$). The top eight most common species comprised 88% of the seedlings, and *Juncus* species seedlings vastly outnumbered all other species, accounting for 68% of all germinants (Figure 2-5). *Juncus* seedlings that were potted and grown to identifiable stage were exclusively *J. mertensianus* and *J. drummondii*. A full species list, and total abundance for each for each disturbance-depth combination can be found in Appendix 1-7.

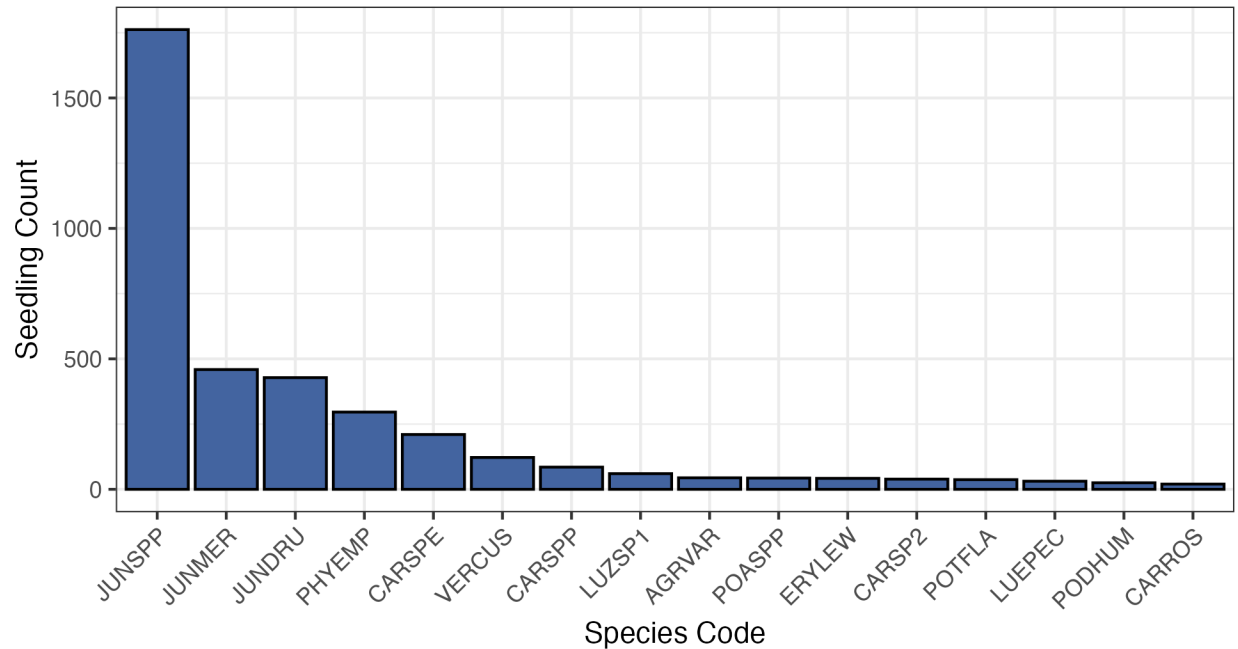


Figure 2-5. Seedling abundance of the most common 16 species. These species encompass 95% of all seedlings that germinated. Species codes: JUNSP = *Juncus* spp., JUNMER = *Juncus mertensianus*, JUNDRU = *J. drummondii*, PHYEMP = *Phyllodoce emetiformis*, CARSPE = *Carex spectabilis*, VERCUS = *Veronica cusickii*, CARSPP = *Carex* spp., LUZSP1 = *Luzula* sp. 1, AGRVAR = *Agrostis variabilis*, POASPP = *Poa* species, ERYLEW = *Erythranthe lewisii*, CARSP2 = *Carex* sp. 2, POTFLA = *Potentilla flabellifolia*, LUEPEC = *Luetkea pectinata*, PODHUM = *Podagrostis humisifolia*, CARROS = *Carex rossii*.

Widespread and Dominant Species

Juncus drummondii, *Juncus mertensianus*, and *Carex spectabilis* were the most widespread species across sampling depths and trampling status, and they tended to also be the dominant species within a sample (Table 2-9). However, *Juncus* species were not among the dominant species in litter samples; instead, litter was dominated by *Phyllodoce empetrifomis*, *Carex spectabilis*, and *Veronica cusickii*. *C. spectabilis* was among the most common dominant species for all depths in intact areas and in trampled areas, across elevations. Within the top 5 cm of samples from intact and trampled areas, both *J. mertensianus* and *J. drummondii* were widespread and dominant at low and middle elevations (Table 2-10). However, at high

elevations, *J. mertensianus* was the most widespread species, and while *J. drummondii* was found in 37% of trays, it was the dominant species for only one sample.

Table 2-9. Frequency of the widespread species found in at least 10% of all samples for each disturbance-depth combination. Values show the percent of samples each species was in for each group. Top three most common dominant species for each group across elevations are shown in bold with a "(D)". *Sagina saginoides* was not found in at least 10% of all samples, but in trampled areas it was tied with *Carex spectabilis* for the third most common dominant species, dominant in 8.3% of samples.

Species	Trampled, 0-5	Intact, 0-5	Intact, 5-10	Intact, Litter
Graminoids				
<i>Agrostis variabilis</i>	17.8	24.4	11.1	11.4
<i>Carex</i> sp. 2	0	24.4	6.7	8.6
<i>Carex</i> species	8.9	44.4	26.7	22.9
<i>Carex spectabilis</i>	17.8 (D)	80.0 (D)	33.3 (D)	57.1 (D)
<i>Juncus drummondii</i>	37.8 (D)	71.1 (D)	57.8	31.4
<i>Juncus mertensianus</i>	40 (D)	68.9	55.6 (D)	22.9
<i>Juncus</i> spp. ¹	35.6	62.2 (D)	42.2 (D)	17.1
<i>Luzula</i> sp. 1	6.7	37.8	24.4	8.6
Poaceae species	4.4	17.8	11.1	5.7
Shrubs & Subshrubs				
<i>Luetkea pectinata</i>	11.1	8.9	6.7	17.1
<i>Phylodoce empetriformis</i>	13.3	46.7	17.8	77.1 (D)
Forbs				
<i>Erythranthe lewisii</i>	17.8	22.2	4.4	14.3
<i>Veronica cusickii</i>	0	28.9	17.8	22.9 (D)

¹ *Juncus* species was comprised of *J. drummondii* and *J. mertensianus*.

Table 2-10. Frequency of the widespread species found in at least 10% of 0-5 cm depth samples (intact and trampled) for each elevation. The top three most common dominant species for each elevation are shown in bold next to a “(D)”. There was a five-way tie for the third-most common dominant species at low elevation between *Carex rosii*, *C. spectabilis*, *Juncus* species, *Potentilla flabellifolia*, and *Sagina saginoides*, each dominant in 4.3% of samples.

Species	Low	Medium	High
Graminoids			
<i>Agrostis variabilis</i>	45.8	5.6	20.0
<i>Carex</i> sp. 2	20.8	13.9	3.3
<i>Carex</i> species	41.7	19.4	23.3
<i>Carex spectabilis</i>	50.0	55.6	40.0 (D)
<i>Juncus drummondii</i>	70.8 (D)	58.3 (D)	36.7
<i>Juncus mertensianus</i>	58.3 (D)	61.1 (D)	43.3 (D)
<i>Juncus</i> spp. ¹	45.8	66.7 (D)	30.0 (D)
<i>Luzula</i> sp. 1	16.7	11.1	40.0
Poaceae species	16.7	8.3	10.0
Shrubs & Subshrubs			
<i>Luetkea pectinata</i>	0	8.3	20.0
<i>Phyllodoce empetrifomis</i>	20.8	27.8	40.0
Forbs			
<i>Erythranthe lewisii</i>	20.8	30.6	6.7
<i>Veronica cusickii</i>	12.5	11.1	20.0

¹ *Juncus* spp. was comprised of *J. drummondii* and *J. mertensianus*.

Indicator Species

The ISA comparing trampled areas to intact areas' 0-5 cm depths identified 12 indicator species (see Appendix 1-8 for indicator values, P values, and notes about unknown species).

Sagina saginoides was an indicator for low elevation, trampled sites. *Agrostis variabilis* was an indicator of low elevation sites regardless of disturbance history. *Potentilla flabellifolia* and *Carex* sp. 2 were indicators of intact areas at low elevation. *Luzula* sp. 1 was an indicator for intact areas at high elevation. *Carex spectabilis*, all *Juncus* species (*Juncus drummondii*, *Juncus mertensianus*, and unidentified *Juncus* spp.), *Phyllodoce empetrifomis*, and *Veronica cusickii* were strong indicators for intact areas across all elevations.

The ISA comparing sample depths of intact areas identified eight indicator species. *Agrostis variabilis* and *Carex* sp. 2 were indicators of the 0-5 cm depth at low elevation.

Phyllodoce empetriiformis was an indicator for litter at all elevations, while *Carex spectabilis* and *Juncus drummondii* were indicators for the 0-5 cm depth at all elevations. *Juncus mertensianus* was an indicator for soil samples (0-5 and 5-10 cm) at medium elevation, and *Luzula* sp. 1 was an indicator for soil samples at high elevation.

Soil Compaction and Nutrients

Trampling altered soil structure and chemistry. Trampled soils had significantly higher compaction (ANOVA: $F(1, 72) = 14.541$, $P < 0.001$), with mean compaction values 1.3 ± 1.1 times higher than intact sites (Figure 2-6). There were no differences in compaction due to elevation ($F(2, 12) = 1.636$, $P = 0.235$) or the interaction of elevation and trampling ($F(2, 72) = 0.476$, $P = 0.624$).

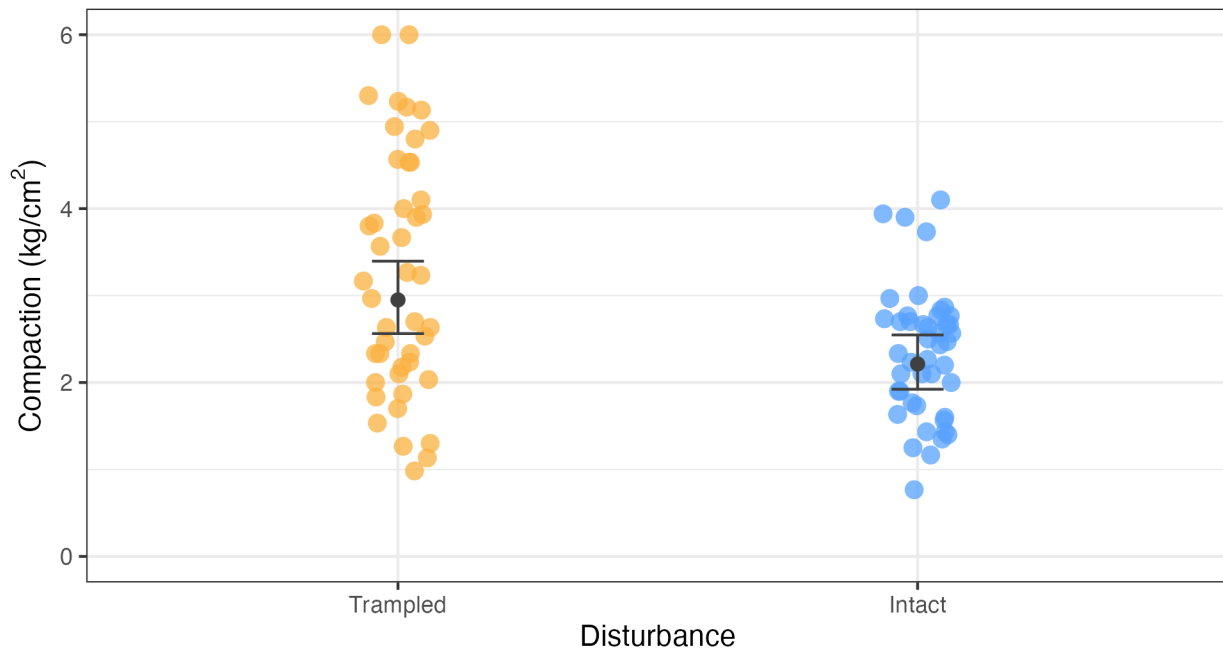


Figure 2-6. Soil surface compaction in trampled and intact sites.

There were significant differences in pH between disturbance-depths and elevations (Table 2-11). Trampled soils had higher pH than both intact depths. Low elevation sites had lower pH than middle elevations (Figure 2-7).

Organic matter differed between disturbance-depth combinations and elevations. Intact 0-5 cm samples had higher percent organic matter content than trampled and 5-10 cm depth samples. Intact 5-10 cm depths also had marginally significantly more organic matter than trampled soil. Low elevations had higher percent organic matter than medium elevation samples. See Appendix 1-3 for all pairwise contrasts.

There were also significant differences in the soil electrical conductivity (EC) between disturbance-depths and elevations. Intact soils had higher EC than trampled soils, and intact 0-5 cm samples had higher EC than 5-10 cm depth samples. Low elevation samples had higher EC than both medium and high elevations.

There were significant micronutrient (PC1) differences between disturbance-depths and elevations (Table 2-12; Figure 2-8). Intact area samples had higher micronutrient levels than trampled areas, and intact, 0-5 cm depths had higher micronutrient levels than 5-10 cm depths.

There were marginally significant nitrogen (PC2) differences between disturbance-depths, but no effect of elevation on nitrogen (Table 2-12; Figure 2-8).

The phosphorus-sulfur axis (PC3) differed between disturbance-depths and with the interaction between disturbance-depth and elevation (Table 2-12; Figure 2-8). At low elevations, intact samples from 0-5 cm had lower phosphorus and higher sulfur than trampled areas and 5-10 cm intact areas, whereas at high elevations trampled areas had higher phosphorus and lower sulfur than intact area samples from both depths.

Table 2-11. ANOVA results showing main effects for the LMERS on pH, organic matter, and electrical conductivity.

Term	NumDF	DenDF	F	P value
pH				
Disturbance - Depth	2	17.477	7.934	0.004 **
Elevation	2	7.973	4.880	0.041 *
Disturbance - Depth: Elevation	4	17.150	0.238	0.913
Organic Matter				
Disturbance - Depth	2	22.140	16.252	< 0.001 ***
Elevation	2	12.950	3.868	0.048 *
Disturbance - Depth: Elevation	4	21.949	1.100	0.381
Electrical Conductivity				
Disturbance - Depth	2	20.426	29.564	< 0.001 ***
Elevation	2	11.102	7.131	0.010 *
Disturbance - Depth: Elevation	4	20.213	2.207	0.105

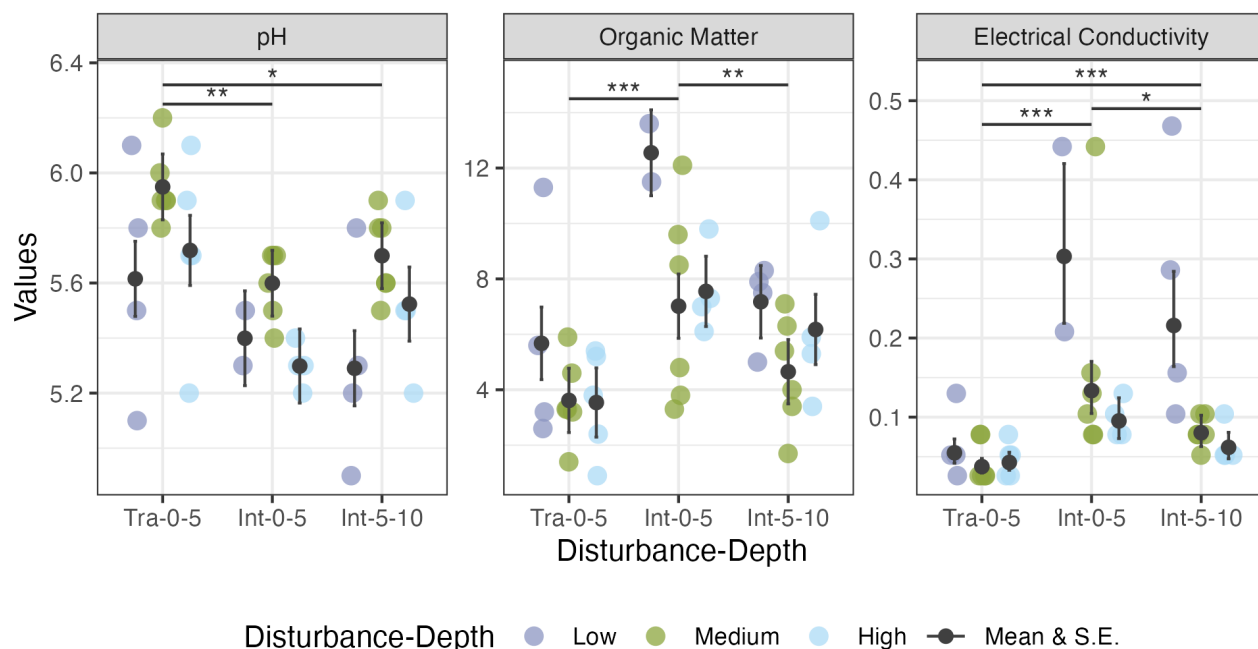


Figure 2-7. Soil pH, percent organic matter, and electrical conductivity (mmhos/cm) for each disturbance-depth combination. X-axis labels use abbreviations “Tra” = trampled and “Int” = intact followed by the sample depth. Lines with stars indicate statistical significance for disturbance-depth pairwise contrasts only; see Appendix 1-3 (Tables 1-7-2, 1-7-3, and 1-7-4) for pairwise contrasts for elevation.

Table 2-12. ANOVA results showing main effects of the LMERs on first, second, and third principal components. See Appendix 1-3 for pairwise contrast results tables.

Term	NumDF	DenDF	F	P value
PC1: Micronutrients & Potassium				
Disturbance-Depth	2	22.091	26.708	< 0.001 ***
Elevation	2	11.935	9.579	0.003 **
Disturbance-Depth: Elevation	4	21.779	1.337	0.288
PC2: Nitrogen				
Disturbance-Depth	2	21.961	2.868	0.078 .
Elevation	2	12.050	0.174	0.843
Disturbance-Depth: Elevation	4	21.678	2.006	0.129
PC3: Phosphorus & Sulfur				
Disturbance-Depth	2	19.544	4.548	0.024 *
Elevation	2	11.206	2.213	0.155
Disturbance-Depth: Elevation	4	19.480	12.743	< 0.001 ***

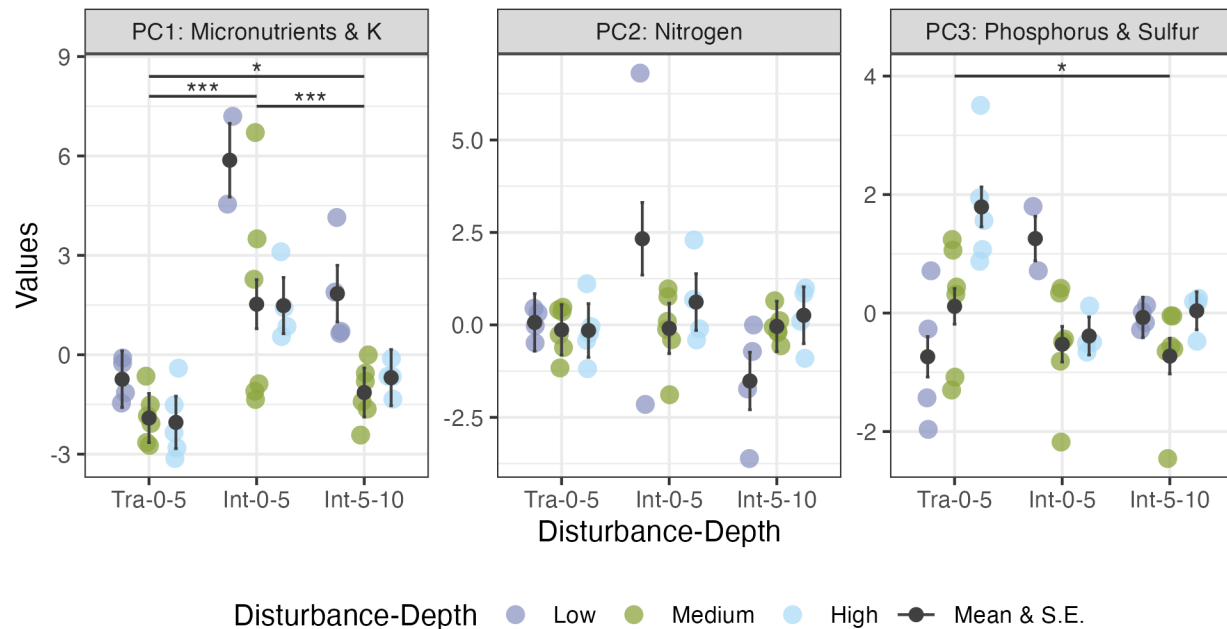


Figure 2-8. Micronutrient, nitrogen, and phosphorus-sulfur PCs for each disturbance-depth and elevation. Higher values of PC1 and PC2 were associated with higher micronutrients and nitrogen, respectively. Higher values of PC3 were associated with higher sulfur and lower phosphorus. Lines with stars indicate statistical significance for disturbance-depth pairwise contrasts only; see Appendix 1-3 (Tables 1-3-5, 1-3-6, and 1-3-7) for pairwise contrasts for elevation. Graphs comparing each nutrient across intact and trampled samples are presented in Appendix 1-3 (Figure 1-3-2).

Discussion

This study showed that trampling lowers the soil seed bank density, alters the soil seed bank community, and changes soil structure and chemistry. Intact area soils had a higher seedling density, were more species rich, and generally more varied than trampled areas. The upper 5 cm of soil had the highest seedling abundance and species richness. While *Juncus* species were by far the most abundant taxa, communities differed between soil layers and elevations, and the dominant species of soil samples differed from that of litter samples. Trampled areas also had different soil structure and chemistry from intact areas, with higher pH, reduced organic matter, and reduced micronutrient levels.

Seed Density (Question 1): The seedling abundances from intact areas in this study are among the higher estimates reported from other alpine and subalpine soil seed bank studies using similar methods, which report counts typically between 1500 to 8000, but ranging from 150 to over 30,000 (Klug et al., 2002; Ma et al., 2009; Venn and Morgan, 2010; Luo et al., 2017; Ludewig et al., 2021; Wellstein et al., 2024). Among the intact samples, I saw the most seedlings in the 0-5 cm depth, which is consistent with other soil seed bank studies (Chambers, 1993; Roovers et al., 2006; Luo et al., 2017).

Trampled areas had fewer seedlings than intact area soils of either depth, and the communities of both areas differed. Seedling abundance in trampled areas declined with increasing elevation, whereas in intact areas elevation did not affect seedling abundance for the top 5 cm. Additionally, the difference in seedling abundance between trampled and deeper intact area samples increased with increasing elevation. These differences may be due to higher erosion rates at higher elevations due to steeper slopes and lower vegetation cover that removed more of the upper layer of soil from trampled areas (Quinn et al., 1980). While most of the sampled areas

did not have clear evidence of erosion deeper than a few centimeters, I did not directly estimate erosion depth for this study. Additional factors that could also be affect seed abundance in trampled areas at higher elevations including increased loss of seed rain due to higher slopes, increased exposure to temperature extremes, or abrasive effects of trampling on seeds. Future studies could investigate whether and how these factors interact with elevation to affect soil seed bank abundance in trampled areas.

Seed Bank Community Composition (Question 2): The soil seed bank was dominated by a few species, shown by the strong negative relationship between species evenness and seedling abundance: samples that had more seedlings tended to have lower species evenness because they were dominated by *Juncus* species. Several other soil seed bank studies have shown that soils tend to have one or a few very common species, frequently *Juncus* and *Carex* (Klug et al., 2002; Roovers et al., 2006; Bossuyt and Honnay, 2008; Luo et al., 2017; Ludewig et al., 2021). Ingersoll and Wilson (1993) studying soil seed banks in the subalpine areas of the Oregon Cascade Mountains found that *J. drummondii* and *J. mertensianus* comprised 75% of the total seedlings, similar to the portion observed in this study (68%).

The seedling community composition differed between sample depths in intact areas. *Phyllodoce empetrifomis* was an indicator species of litter for all elevations and was the dominant species in the most litter samples, whereas graminoids including *Carex* and *Juncus* species were more common in soil samples. Ingersoll and Wilson (1993) similarly found *P. empetrifomis* was uncommon in the soil seed bank. The relatively lower abundance of *P. empetrifomis* in the soil suggests it has relatively lower seed longevity, which may be due to this species' preference for later successional communities (Franklin and Dyrness, 1973). Conversely, *Juncus* and *Carex* were common across all sample depths which is likely related to their

preference for early succession communities (Franklin and Dyrness, 1973; Jumpponen et al., 1999). *Juncus drummondii* and *Carex spectabilis* have been reported as abundant early colonizers of disturbed areas at Sunrise, Mount Rainier (Frank and Del Moral, 1986). Therefore, the most common species in the soil might be well-adapted to colonize open trampled areas for the beginning phases of restoration (Tilley et al., 2022). *Carex spectabilis*, *Juncus drummondii*, and *J. mertensianus*, as well as other species common in the soil including *Luetkea pectinata*, *Veronica cusickii*, *Erethranthe lewisii*, and *Luzula* species are often-planted restoration species at Mount Rainier and therefore may be lower priority for restoration plantings.

Soil Impacts (Question 3): Although the soil seed bank contains seeds and species for restoration, soil compaction and nutrient differences between trampled and intact sites could make seedling establishment more challenging in trampled areas. Compaction reduces water and air permeability and slows infiltration rates (Gregory et al., 2006; Batey, 2009; Yang and Zhang, 2011), which could affect water availability for seedling establishment. Compaction can also reduce rooting depth and growth rates (Alessa and Earnhart, 2000), further lowering water and nutrient availability in trampled soil and slowing plant growth (Rokich et al., 2001; Bassett et al., 2005). These effects could become more extreme with lower annual snowpack and hotter, drier summers predicted with climate change (Ford, 2012).

Trampled soils also had lower micronutrient levels than intact soils, which may be due to their lower percent organic matter. These trends mostly matched those of other similar studies (Zabinski and Cole, 2000; Singh et al., 2020). Kalahroudi et al. (2023) observed similar percent organic matter, electrical conductivity, and pH values in their untrampled control plots to this study's intact plots. They also found that high trampling frequency reduced microbial respiration. Compaction also affects the microbial community composition and diversity (Zabinski and Cole,

2000; Liu et al., 2023), which could affect plant nutrient uptake (Miransari, 2013). Trampled plots had higher pH, a finding that differs from other studies on trampling effects on soil chemistry (Yaşar Korkanç, 2014; Li et al., 2020). Less acidic soils in trampled areas could suggest higher nutrient availability for plants, although plants in this habitat are likely adapted to low pH.

Trampling showed no effect on nitrogen levels for this study. However, an ideal soil nitrogen testing procedure involves chilling samples following collection, then drying and analyzing them with days of collection to get an accurate assessment of soil nitrogen at the time of sampling (Stenberg et al., 1998; Cain et al., 1999). For this study, samples were analyzed for nutrients after having been dried, sieved, and stored in a cool, dark environment for several months. Therefore, nitrogen levels likely changed between collection and analysis. Additionally, nitrogen is mobile in the soil, so soil from a single sampling event may not accurately represent season-long nitrogen levels (Cain et al., 1999). Studies aiming to quantify soil nitrogen in the future would benefit from collecting samples throughout the season and using sampling protocols that yield more accurate estimates.

Conclusions and Implications for Management: The abundance of seedlings in the soil seed bank of both intact and trampled areas suggest it has some utility for restoration. This study found that the soil seed bank is not harboring invasive or lowland species that could further damage sensitive alpine and subalpine ecosystems. Four nonnative seedlings germinated from the 0-5 cm depth from intact areas (two *Taraxacum officianale*, one *Lactuca serriola*, and an unidentified *Cirsium* species). Three seedlings typically found at lower elevations (two *Persicaria lapathifolia* seedlings and a *Plectritis congesta* seedling) germinated from litter samples. These represent 0.2% of all seedlings that germinated.

While this study shows that seeds are present and may be abundant in the soil, land managers report that seedlings are rare in trampled areas (B. Fallon, pers. comm.). Seedling observations are uncommon even following restoration plantings that disturb the soil surface and expose seeds to light or moisture that might stimulate germination. This study suggests that the reason for the lack of seedlings is likely not lack of seeds. I found seedling abundance varied across sites, so it is possible seedlings are missing from restored areas due to chance low seed density in those areas. However, other causes of low seedling abundance *in situ* include a lack of seed germination or seedling mortality following germination before seedlings are observed by land managers. The stable greenhouse temperatures and watering regime for this study aimed to stimulate germination of as many seeds as possible from the samples, but these conditions are not representative of *in situ* germination conditions. Soil samples for this study were placed in consistently moist, warm growing conditions in a thin layer to expose as many seeds as possible to light. Even if buried seeds in the soil are exposed to light through digging during restoration, unseasonably warm or cold temperatures, or early or late snow or frost, could cause lower germination rates *in situ* than I observed for this study. Alternatively, seeds may be germinating from restored areas after being exposed by digging, but dying before they could be observed. Even if restored areas are well-protected from repeat trampling, the same factors that could affect germination rates could cause early seedling mortality. If seedlings survive unpredictable early season conditions, low summer precipitation and heat waves could also prevent seedling establishment.

Future studies could address whether lack of germination or poor seedling survival is driving low seedling recruitment in restored areas by comparing soil seed banks of areas that have recently been planted with trampled areas that have not been restored to see if seed

abundance rates differ between areas. Lower abundance in restored areas would suggest seeds are germinating out of the soil (Ma et al., 2009). While not tested for this study, applying common dormancy-breaking treatments including smoke water or gibberellic acid to soils *in situ* then observing germination could also test whether low seedling abundance is due to germination requirements not being met. Seedling surveys of restored areas earlier in the season could reveal if seedlings are present before they are typically observed by restoration crews planting in late summer.

Determining why seedling recruitment is low in restored areas is important because this study showed the soil seed bank could be a significant seed source. Both trampled and intact areas contained more seedlings in the top 5 cm of soil (2458 and 15,332 seedlings per m², respectively) than are typically sown for alpine area restoration. For example, Roberts and Seastedt (2019) sowed 1300 pure live native grass seeds per m² in an alpine road obliteration project which resulted in 40% of the reference site's cover after four years. Lima et al. (2025) sowed 250-500 seeds per m² for trampled area restoration in Acadia National Park but did not see substantial effects.

Compaction and nutrient deficiencies could slow the growth of plugs transplanted into restoration sites. Restoration plantings disturb the soil, which may reduce surface compaction. Future studies could test whether soil disturbance from plantings is sufficient to alleviate compaction by comparing compaction of restored and non-restored trampled areas. Although the plants at Paradise are adapted to low-nutrient, alpine and subalpine soils, the plant litter accumulation and breakdown processes in intact areas are disrupted by trampling. Restoration techniques that return soil compaction, pH, and organic matter to intact levels may facilitate plant growth that restores natural soil creation processes. This could be addressed by adding

organic matter to the soil. For example, Lima et al. (2025) found that adding an organic planting media with erosion control without seeding or planting was a more effective treatment than planting plugs of native species or sowing seeds into areas without soil restoration. Also, adding organic matter including compost and peat to trampled subalpine campsites in northeastern Oregon led to restored areas with higher vegetation cover than areas with no soil amendments (Cole, 2013). While abundant seeds exist in the soil seed bank for potential use in restoration, future work testing how to improve soil conditions to promote seed germination and seedling survival *in situ* is needed.

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CHAPTER 3

Alpine and Subalpine Soil Seed Banks and Their Similarity to Aboveground

Vegetation: Implications for Climate-Resilient Restoration

Abstract

Restoration efforts are more resilient to climate change impacts with increased biological, methodological, and temporal diversity, though achieving this diversity in practice is challenging for practitioners. The soil seed bank has been proposed as a buffer against climate change effects, and could be a convenient, low-cost tool to increase the diversity of restoration efforts in alpine and subalpine ecosystems where nonnative species invasion risk is low. I compared soil seed bank and standing vegetation communities at Mount Rainier National Park and assessed how elevation and disturbance affect each to evaluate the potential of using soil seed banks to restore areas damaged by off-trail hiking. Trampled standing vegetation communities were distinct from intact communities at low elevation, but more closely resembled high elevation assemblages. With increasing elevation, trampled communities were less variable but also more similar to adjacent intact areas. While seeds were abundant in the soil seed bank, with 2458 seeds per m² in trampled and 19,987 seeds per m² in intact areas, the plant community in the soil seed banks differed from the aboveground community in both intact and trampled areas. The soil seed bank was dominated by early successional species such as native *Juncus* and *Carex*, and contained some species often used for restoration. However, it lacked other species common in intact meadows. This study shows that the soil seed bank has potential to supplement, but not replace, restoration planting or seeding.

Introduction

Alpine and subalpine areas—the areas above treeline and the meadow-forest mosaic ecotone below it—are predicted to experience more extreme climate change effects compared to lowland ecosystems (Mote et al., 2005; Pepin et al., 2015, 2022; Lamprecht et al., 2018; Wershow and DeChaine, 2018). Climate change is predicted to make summer heat waves more extreme and decrease snowpack, which could expose alpine plants to early and late season frosts (Ford, 2012; Gobiet et al., 2014; Inouye, 2020; Sethi et al., 2020). These extremes may make restoration in the alpine and subalpine more difficult. If the soil seed bank contains adequate seeds of desired species, it could be a tool to increase restoration efforts' resilience to climate change by expanding restored area species richness and diversifying revegetation methods.

Off-trail hiking is a widespread problem in alpine areas and other outdoor recreation destinations that causes degradation to sensitive ecosystems, soil compaction, erosion, and areas largely devoid of vegetation (Willard and Marr, 1971; Fritzke, 1992; Rochefort and Gibbons, 1992; Eagan et al., 2004). Passive restoration of alpine trampling damage may take hundreds of years even when areas are protected from re-trampling (Willard and Marr, 1971; Ebersole, 2002; Willard et al., 2007). Active restoration can speed recovery, but plant survival is low and growth in the subalpine and alpine is slow. Moritsch and Muir (1993) transplanted meadow sod mats and reported 19-44% survival after three years for subalpine social trail restoration in Yosemite, California. For subalpine campground restoration in Oregon, survival and cover of restoration plugs and seedlings peaked four years after restoration then declined through the seventh year of monitoring (Cole and Spildie, 2006). Ten years following restoration, planted areas had the same total cover as they did the first year (Cole, 2013).

Species are expected to track their climate envelope and migrate upward as climate changes (Lenoir et al., 2008; Chen et al., 2011, although see Maclean and Early, 2023; Rubenstein et al., 2023). Land managers may need to either accept or direct change by using lower elevation species or species with wider thermal tolerances in restoration (Butterfield et al., 2017), or resist change by managing increasing competition from lowland species (Chiara et al., 2024) or compensating for lower fitness of the current species pool as conditions get hotter (Magness et al., 2022; Schuurman et al., 2022). However, abiotic and biotic factors interact to influence species assemblages such that disturbance in environments with lower abiotic stress, such as low elevation habitats, can allow species adapted to high abiotic stress to persist (Darwin 1859, Louthan et al., 2015). Disturbance and elevation can interact to lower range limits for high elevation species (Chardon et al., 2019), which could support inclusion of high-elevation species in trampled area restoration. High elevation species may be adapted to the low competition levels and abiotically stressful conditions of trampled areas. Understanding how elevation and disturbance interact can inform species selection for climate resilient restoration.

Restoration is more resilient when it uses more diverse species, genetics, functional traits, methods, or timing (Aplet and McKinley, 2017; Wilsey, 2021; Zabin et al., 2022). However, diversifying restoration techniques and species can be challenging for land managers to implement due to limited seed availability, staffing resources, and funding (Cooke et al., 2019; Galatowitsch, 2023; Andres et al., 2024). The soil seed bank may buffer communities from increasingly frequent extreme climate events by supplying genetic and species diversity (Hoyle et al., 2013; Kiss et al., 2018; Plue et al., 2021; Auffret et al., 2023). Using the soil seed bank to supplement other restoration methods could increase the resilience of alpine restoration efforts

with relatively low effort from restoration practitioners (Aplet and McKinley, 2017; Kiss et al., 2018).

The germinable soil seed banks of intact alpine and subalpine areas may contain hundreds to tens of thousands of seeds per square meter, and can vary in species richness (Chambers, 1993; Zabinski et al., 2000; Klug et al., 2002; Ma et al., 2009, 2010; Venn and Morgan, 2010; Hoyle et al., 2013; Ludewig et al., 2021; Chapter 2 of this thesis). The effect of trampling on alpine and subalpine seed banks is also variable, with some studies finding higher seed density in trampled than intact areas (Klug et al., 2002; Roovers et al., 2006; Jolivet et al., 2022) and others showing the opposite (Zabinski et al., 2000; Wellstein et al., 2024).

The soil seed bank and seed rain have shown some promise in restoration. For example, a road reclamation project in Colorado showed that volunteer species from seed rain or the soil seed bank contributed 17-23% of the restored vegetation cover and six additional species after four years (Roberts and Seastedt, 2019). However, a concern with utilizing the soil seed bank for restoration is that foot traffic on mountain trails could facilitate transportation and dispersal of nonnative or lowland species that are not desired in the restored community (Liedtke et al., 2020; Jolivet et al., 2022). While some studies have found invasion risk via the soil seed bank in alpine and subalpine areas is low (Hoyle et al., 2013; Ludewig et al., 2021), the community in the soil seed bank often differs from that of the aboveground community to varying degrees (Ma et al., 2010, 2019; Venn and Morgan, 2010).

Understanding the density and species composition of the soil seed bank, and its similarity to intact reference communities, can inform whether the soil seed bank can increase a restoration effort's climate change resilience, and prioritize species selection for species that are not in the soil seed bank (Ludewig et al., 2021). I explored the potential utility of the soil seed

bank in restoration of trampled subalpine and alpine areas at Paradise, Mount Rainier National Park by answering the following questions: (1) How does trampling change the composition of aboveground communities? (2) How does trampling affect soil seed bank density and community composition? (3) Is the soil seed bank community similar to aboveground vegetation and what species drive community differences?

Methods

Study Site

This study was conducted in subalpine and alpine areas at Paradise, Mount Rainier National Park. Mount Rainier is a 4392 m tall active stratovolcano in the Cascade Mountains (Crawford et al. 2009). The Paradise visitor center and parking lot is 1650 m above sea level and the most widely used day-hike trails in the area reach an elevation of 2200 m (NPS 2024). Paradise is located on the south side of Mount Rainier, with slope aspects ranging from southwest to southeast. During the snow-free growing season from late July to early October (Frappier, 2004), mean low and high daily temperatures range from 4.4 to 14.4 °C, while they range from -3.9 to 3.9 °C during the snow season (daily 1991-2020 values; PRISM 2026). Most precipitation in Paradise falls as snow (NPS 2025). Paradise receives an average of 307.5 cm of snow-water-equivalent annually, while 30.2 cm of rain fall during the growing season (PRISM 2026).

The Paradise area spans the subalpine to alpine ecotone from closed-canopy subalpine forest to rocky alpine scree slopes with sparse vegetation (Rochefort and Gibbons, 1992). The subalpine forests are comprised of *Abies lasiocarpa*, *Tsuga mertensiana*, and *Callitropsis nootkatensis* (Rochefort and Peterson, 1996). Subalpine meadow communities are primarily comprised of *Lupinus latifolius*, *Valeriana sitchensis*, *Bistorta bistortoides*, *Carex spectabilis*,

and *Castilleja parviflora*. Shrub-heath communities span the subalpine to alpine gradient and are often dominated by *Phyllodoce empetrifloris*, *Cassiope mertensiana*, *Vaccinium deliciosum*, *Lupinus latifolius*, *Phyllodoce glanduliflora*, and *Festuca viridula* (Henderson, 1973).

Mount Rainier attracts over 2 million visitors per year (NPS 2026), and Paradise is the most-visited site in the park (Simmons et al., 2001). Lower elevation trails within approximately half a mile of the parking lot and visitor center are paved; the remaining trail network is unpaved, with rock perimeters and rope-and-rebar fencing to delineate the trail. Despite these measures, off-trail hiking has created unofficial trails and trampled patches (Fritzke, 1992; Rochefort and Gibbons, 1992).

Site Selection

I used satellite imagery, Google Street View, and existing social trail and restoration datasets shared and maintained by the National Park Service to locate areas with trampling damage next to areas with intact vegetation. Potential sites were selected to represent the range of vegetation communities across the elevation gradient at Paradise, and were grouped as high (1900-2075 m), medium (1775-1900 m), and low elevation (1675-1775 m). Potential sites underwent archeological surveys as required by Mount Rainier National Park permits, then were surveyed to ensure they were large enough to contain the sampling design and had no evidence of previous restoration. Remaining potential sites that satisfied these conditions were selected to maximize distance between sites.

This selection process produced 15 sites (Figure 3-1)—four low, six medium, and five high elevation sites—for inclusion in the study. Fewer sites at low elevation satisfied the criteria for inclusion in the study because trampling damage in the lower Paradise meadows is less severe than at higher elevations. Two low elevation sites contained an unpaved road used

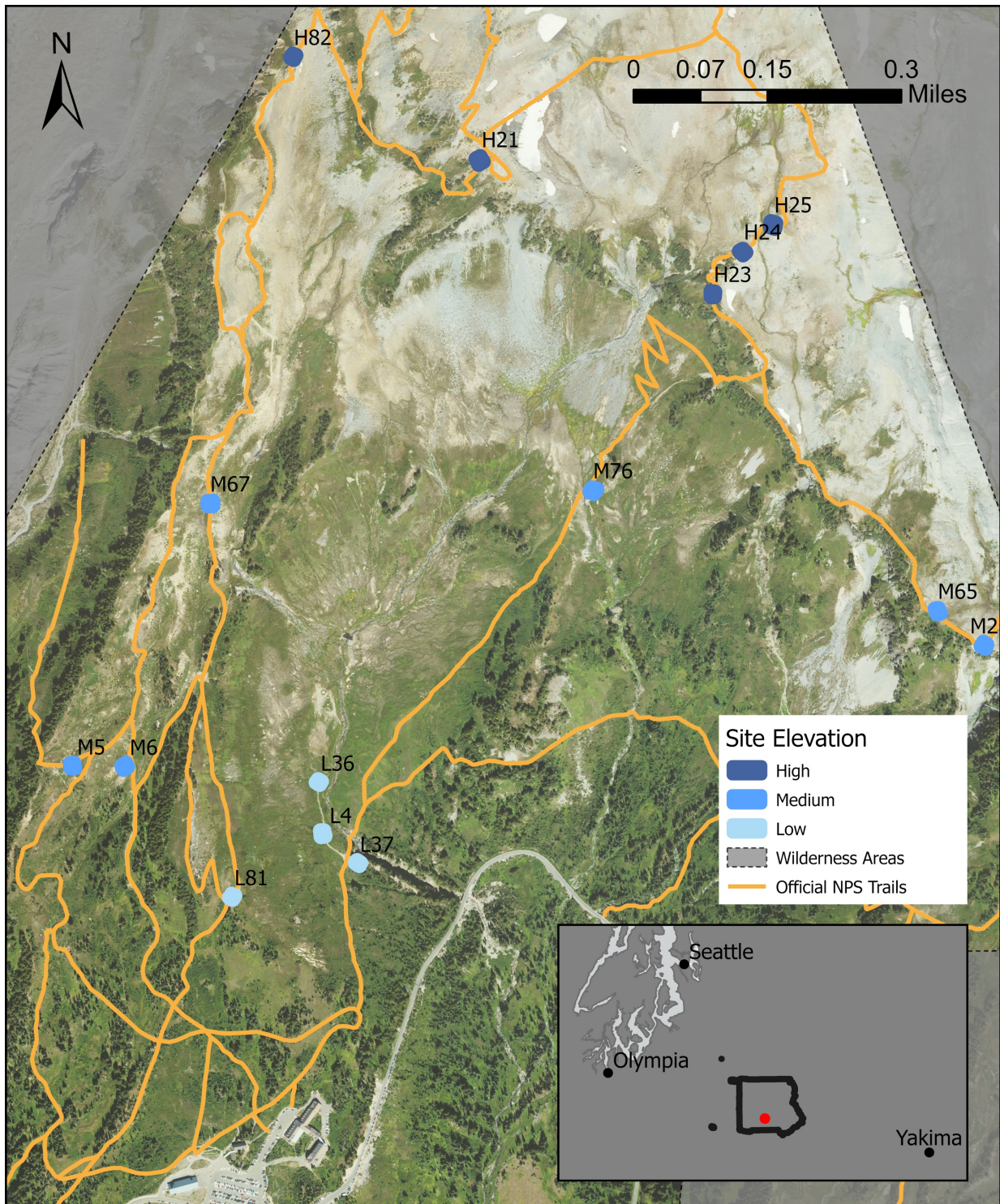


Figure 3-1. Sites selected for soil sampling at Paradise, Mount Rainier National Park. Sites are labeled with their unique identifiers, where “L,” “M,” and “H” stand for low, medium, and high, respectively.

infrequently by NPS vehicles. While these roads do not experience the same volume of foot traffic as the other sites, vehicle use also results in soil compaction and vegetation loss (Weaver and Dale, 1978), and would likely require similar restoration techniques to areas trampled by human foot traffic.

Trampled and intact areas were evaluated using trampling condition classes developed by Rochefort and Swinney (2000). Trampled areas were characterized by areas of low moss, vascular vegetation, and litter cover, with exposed bare soil and rock in a pattern continuous with an established trail (condition classes 3 and 4). In contrast, adjacent intact areas had higher vegetation cover and leaf litter with little to no trampling evidence (condition classes 0-2).

Aboveground Community Surveys and Soil Sampling

At each site, two parallel 2 x 8 m belt transects were established 3 m apart, with one in a trampled area and the other in the adjacent intact meadow (Figure 2-2). Within each transect, three plots were established 2-3 m apart. Plots in trampled areas were 1 m from the intact vegetation boundary to reduce seed rain from intact areas into trampled area soil seed bank samples. Occasionally, trampled area plot placement was adjusted to avoid placement on official trails, in instances where the trampled area was less than 3 m wide, or to avoid intact patches within trampled areas. This ensured trampled area sampling represented areas that would be restoration priorities. In the intact area, plots were 2-4 m from the vegetation boundary to reduce edge effects. For both intact and trampled areas, plots that fell on areas that lacked soil (such as boulders) were relocated within the transect to ensure soil samples could be collected.

In August 2024, I visually estimated the foliar cover of each vascular plant species in each plot to the nearest percent, and nearest tenth of a percent if less than 1%. Unknown species were classified to the lowest taxonomic level possible and photographed.

I sampled soil from each plot in late September 2024 to capture the full potential community present following summer seed rain (Bertiller, 1992) and when the soil seed bank could be utilized to supplement fall restoration plantings. Soil was sampled from three equally spaced locations within each plot using a 5 cm diameter bulk density sampler. Samples from each hole were stored in separate bags. I sampled the top 5 cm of soil and litter layer when present. When present, litter was collected and stored separately. Litter was absent from trampled plots and 10 intact plots. The top 5 cm of soil from trampled and intact areas were evaluated because it would be easiest to stimulate germination from these layers for restoration. I also sampled soil 5-10 cm below the intact soil surface. For discussion of the 5-10 cm depth samples and comparison of intact area soil depths, see Chapter 2.

Seed Bank Study Sample Preparation and Germination Data Collection

Soil samples were stored indoors in plastic bags in cool conditions for up to a week, then opened to dry for 3-4 weeks. Mineral soil samples were sieved to remove rocks and organic matter greater than 4 mm. Litter samples were not sieved. Samples of the same depth from the same plot were aggregated such that each site had six soil samples (three trampled 0-5 cm and three intact 0-5 cm) and up to three litter samples. This produced 125 aggregate samples: 45 from the trampled areas (15 sites x 3 plots), 45 from the 0-5 intact areas, and 35 from the litter layer in intact areas (15 sites x 3 plots, minus 10 plots with no litter).

For each aggregate sample, 120 cm³ of soil was measured, moistened with 25 mL of deionized water, and cold stratified at 5 °C for 12 weeks. Litter samples were aggregated and the full litter volume was moistened before stratification.

After cold stratification, each sample was spread over germination flats filled with potting media and placed in a greenhouse. I also prepared 15 control flats that contained potting

media but no sample to detect air or soil-borne seed contamination. Flats were checked twice weekly for the first six weeks, once weekly for the next eight months, then once every two weeks until the study concluded after 13 months. As seedlings germinated, they were logged as a morphotype that described their resemblance to other seedlings, then identified to the lowest taxonomic level when they produced identifiable features. See Chapter 2 for germination and seedling count data collection details.

Statistical Analysis

All analyses were completed in R version 4.5.2 (R Core Team 2025). For all comparisons, tests were considered significant when P values were less than 0.05, and marginally significant when $0.05 < P < 0.10$.

Aboveground Community

I used permutational analysis of variance (PERMANOVA, `vegan::adonis2`) to evaluate whether aboveground community composition differed between trampled and intact areas (Oksanen et al., 2001). I relativized the percent cover estimates by the maximum value observed for each species, then calculated the Bray-Curtis distance between plots. I added a dummy variable to all plots to permit inclusion of plots with zero foliar cover. The PERMANOVA model tested the effect of trampling, elevation, and their interaction on the aboveground plant community. I restricted permutations to account for correlation among sites and plots.

I explored how communities differed using three post-hoc analyses: pairwise PERMANOVAs, analysis of dispersion using PERMDISP, and follow-up pairwise PERMDISPs. PERMDISP analyses were done using the `betadisper` function in the `vegan` package. This permutation-based analysis tests whether groups differ in the dispersion of observations around their mean (Anderson, 2006; Anderson et al., 2008; Bakker, 2024). The combined results of

PERMANOVA and PERMDISP show whether differences between communities were driven by differences in means or also differences in dispersion. I visualized community differences using nonmetric multidimensional scaling (NMDS, `vegan::metaMDS`) an ordination technique that configures the community Bray Curtis distance matrix into a graph such that distances between points visually represent differences in community composition between observations (Oksanen et al., 2001). NMDS used 40 tries and up to 100 tries with 300 iterations per try (McCune and Grace, 2002; Bakker, 2024).

I explored which species drive community differences between trampled and intact areas using indicator species analysis (ISA) with the `multipatt` function of the `indicspecies` package (Cáceres and Legendre, 2009). I combined trampling and elevation terms to create a grouping term with six levels (i.e. trampled at low elevation, intact at low elevation, etc.). Combinations were restricted to single levels and combinations of levels that matched in one element of their treatment (i.e. the same trampling status or elevation) and were continuous for ordered variables (i.e. low and medium but not low and high elevations). Species were considered strong indicators if their indicator value was greater than 0.5 and their P value was less than 0.05. Permutations were not restricted to account for random effects of site or plot for the post hoc pairwise ANOVAs, PERMDISP analyses, or ISA.

Soil Seed Bank Community

Litter samples were germinated separately from soil samples but seedling counts from litter were summed with their corresponding soil sample for analysis. Species in the flats that arrived through airborne seed contamination were identified by their presence in control flats or in the soil of other pots in the greenhouse. Seedlings of these species were excluded from all summaries and analyses.

I used generalized linear mixed models to evaluate the effect of trampling and elevation on seedling abundance and species richness. Trays with zero seedlings were excluded from the species richness analysis. The models included disturbance, elevation and their interaction, with site as a random effect, using the negative binomial distribution and a log link. I evaluated model fit by inspecting DHARMA simulated residuals and testing for overdispersion and zero inflation (Hartig, 2024). I used likelihood ratio tests to calculate the statistical significance of each model term (Bolker, 2025). For significant terms, I used the emmeans package to make pairwise comparisons using the Tukey adjustment for multiple comparisons (Lenth and Piaskowski, 2017).

As with the aboveground vegetation analysis, I compared soil seed bank community composition using PERMANOVA, with post hoc pairwise PERMANOVA and PERMDISP tests. Community differences were visualized using NMDS.

Comparison of Aboveground and Soil Seed Bank Communities

I compared the aboveground vegetation community composition to the soil seed bank community. Species or groups shared between both communities were renamed for taxonomic consistency. For unknown species in each dataset, I used photos and seedlings to determine if the species were different, and designated unique names to different taxa. Plants that were identified to species in one community but could not be identified to species in the other community were combined under the less-specific group (e.g. Multiple *Pedicularis* species were identified in the field but *Pedicularis* seedlings could not be distinguished in the soil seed bank, so they were both called *Pedicularis* spp. when comparing the two communities). Appendix 2-1 lists species found in each community and how they were named for the aboveground vs. soil seed bank comparisons.

To account for different measures of species abundance between the aboveground and soil seed bank communities, abundance data were converted to a presence-absence matrix and analyzed using Jaccard dissimilarity. I compared the effect of community type (soil seed bank or aboveground), elevation, and their interaction using PERMANOVA for intact and trampled areas separately. I analyzed intact and trampled areas separately because I expected the two to have different patterns of seed accumulation and loss due to differences in standing vegetation density and erosion rates. I included a dummy variable for communities with zero plants and restricted permutations to account for correlation within sites and plots. Post hoc analyses included pairwise PERMANOVAs, PERMDISP, and ISA. Each ISA compared the two community types but not elevations.

Results

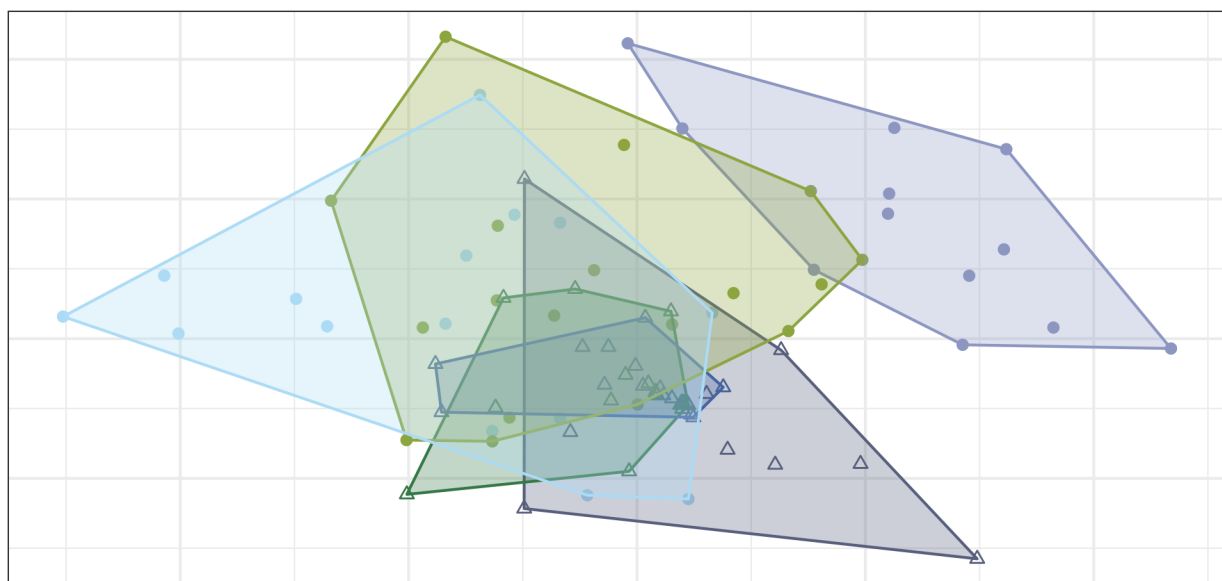
Aboveground Community

Both trampling and elevation affected aboveground community composition (Table 3-1). Trampled and intact areas were more similar with increasing elevation (Figure 3-2). However, there were also significant differences in dispersion between trampled and intact plots (PERMDISP: $F(1, 88) = 48.968$, $P < 0.001$), among elevations (PERMDISP: $F(2, 87) = 4.950$, $P = 0.009$), and the combined effect of the two (PERMDISP: $F(5, 84) = 12.82$, $P < 0.001$). At low elevations, there were no differences in dispersion between intact and trampled areas, but at medium and high elevations, trampled areas were less dispersed than intact areas (see Appendix 2-2 for PERMANOVA and PERMDISP pairwise contrasts). Together, the results from the pairwise PERMANOVA and PERMDISP tests show that trampled and intact areas at low elevation sites differ due to differences in their means rather than their dispersion, while at middle and high elevations, trampled and intact communities may differ due to their means and

their dispersion. Trampled, low elevation communities differed from all other communities, but NMDS showed these communities overlapped more with high elevation areas (both trampled and intact) than low elevation, intact areas.

Table 3-1. PERMANOVA results comparing the aboveground community composition across trampled and intact areas and across elevations.

Term	Df	Sum Of Sqs	R ²	F	P value
Elevation	2	1.345	0.084	2.065	<0.001 ***
Site	12	3.908			
Disturbance	1	1.789	0.112	15.824	<0.001 ***
Disturbance: Elevation	2	0.802	0.050	3.549	<0.001 ***
Residual	72	8.138	0.509		
Total	89	15.982	1.000		



Elevation-Disturbance

- Low-Trampled
- High-Trampled
- Medium-Intact
- Medium-Trampled
- Low-Intact
- High-Intact

Figure 3-2. NMDS plot (stress = 0.159) comparing trampled (open triangles and lighter hues) and intact (filled circles and darker hues) aboveground communities from low and high elevation bands. Plots show points from an NMDS run using data from all plots.

Trampling reduced the species richness of the aboveground community. If any plants were present, the average species richness of trampled areas was 5.9 compared to 11.1 in intact

areas. The dominant species also differed. Two of the three dominant species in intact areas were shrubs *Phyllodoce empetriformis* (26% of plots) and *Vaccinium deliciosum* (15%), while trampled areas' dominant species included *Carex spectabilis* (18%) and *Luetkea pectinata* (11%). *Lupinus latifolius* was in the top three dominant species for 22% of intact plots and 43% of trampled plots. Besides these species, dominant species tended to differ between plots; other species were dominant in three plots (6.7%) or fewer.

Lupinus latifolius, *Carex spectabilis*, and *Luetkea pectinata* were also widespread across all plots, regardless of elevation or trampling status (Table 3-2). *Juncus drummondii* was widespread across trampled areas at low elevation, and relatively common in both trampled and intact areas at medium and high elevation. *Erigeron glacialis* was common in low elevation plots regardless of trampling, and only in intact areas of medium and high elevations. *Bistorta bistortoides* was consistently in fewer trampled plots than intact plots.

Indicator species analysis identified 17 indicator species. *Eucephalus ledophyllus* was an indicator for low elevation sites regardless of disturbance. All other indicators were associated with intact areas, differing in whether they were associated with one, two, or all elevations (Appendix 2-2).

Table 3-2. Species present in 10% or more of the aboveground plots, by disturbance and elevation. Columns show the percent of plots that contained each species for each trampling-elevation combination. The sample size for trampled and intact areas for each elevation is half the elevation's sample size.

	Low (n = 24)		Medium (n = 36)		High (n = 30)	
Species	Trampled	Intact	Trampled	Intact	Trampled	Intact
<i>Abies lasiocarpa</i> ¹	16.7	33.3	11.1	22.2	6.7	13.3
<i>Anemone occidentalis</i>	8.3	58.3	22.2	27.8	6.7	13.3
<i>Antennaria lanata</i>	8.3	8.3	11.1	33.3	0	33.3
<i>Bistorta bistortoides</i>	16.7	58.3	5.6	38.9	6.7	20
<i>Carex nigricans</i>	16.7	41.7	22.2	77.8	20	26.7
<i>Carex spectabilis</i>	50	50	55.6	72.2	33.3	53.3
<i>Castilleja parviflora</i>	8.3	16.7	11.1	44.4	13.3	53.3
<i>Erigeron glacialis</i>	41.7	41.7	0	27.8	0	20
<i>Eucephalus ledophyllus</i>	25	33.3	0	16.7	0	0
<i>Festuca viridula</i>	25	8.3	0	16.7	6.7	46.7
Poaceae sp. 1	25	16.7	11.1	5.6	0	13.3
<i>Hieracium triste</i>	41.7	8.3	33.3	55.6	13.3	26.7
<i>Juncus drummondii</i>	41.7	0	22.2	50	6.7	13.3
<i>Ligusticum</i> species	8.3	66.7	5.6	22.2	0	33.3
<i>Luetkea pectinata</i>	16.7	8.3	44.4	55.6	53.3	80
<i>Lupinus latifolius</i>	75	83.3	77.8	88.9	80	100
<i>Luzula piperi</i>	0	0	22.2	27.8	6.7	20
<i>Oreostemma alpigenum</i>	16.7	0	16.7	33.3	33.3	40
<i>Phlox diffusa</i>	0	0	11.1	27.8	13.3	26.7
<i>Phyllodoce empetrifolia</i>	25	83.3	11.1	66.7	13.3	33.3
<i>Potentilla flabellifolia</i>	41.7	66.7	5.6	61.1	0	13.3
<i>Vaccinium deliciosum</i>	16.7	83.3	0	33.3	13.3	33.3
<i>Valeriana sitchensis</i>	33.3	83.3	5.6	11.1	0	0
<i>Veronica cusickii</i>	41.7	58.3	33.3	77.8	33.3	86.7

¹Less than 2% cover in all plots except one low elevation, intact area plot with 6.5% cover

Soil Seed Bank Community

Seedling Abundance

Over the 13-month germination period, a total of 2645 seedlings of 64 species germinated from the litter and top 5 cm of the trampled and intact soils. An intact, medium-elevation sample had the highest seedling count with 235 seedlings. While some sites had very high counts, 90% of trays had less than 69 seedlings, and 75% of trays had less than 33 seedlings. Ten trays had 0 seedlings, all from trampled, 0-5 cm samples.

There was an average of 11,474 seedlings per m² for a 5-cm-thick soil sample (including litter, if present), though seedling density varied due to trampling. Samples from intact areas had 8.9 ± 1.2 (estimate $\pm$ s.e.) times more seedlings than trampled areas (Table 3-3), with 19,987 seedlings per m² germinating from intact areas compared to 2546 seedlings per m² in trampled areas. Seedling counts did not differ across elevations overall, but there was a significant trampling-elevation interaction. For trampled sites, seedling counts declined with increasing elevation, though only low and high elevation sites differed significantly (Figure 3-3). For intact sites, seedling counts were similar across elevations.

Table 3-3. ANOVA results showing main effects of the GLMM comparing seedling abundance in trampled and intact areas.

Term	NumDF	DenDF	F	P value
Disturbance	1	72	141.317	< 0.001 ***
Elevation	2	12	1.181	0.340
Disturbance: Elevation	2	72	3.566	0.033 *

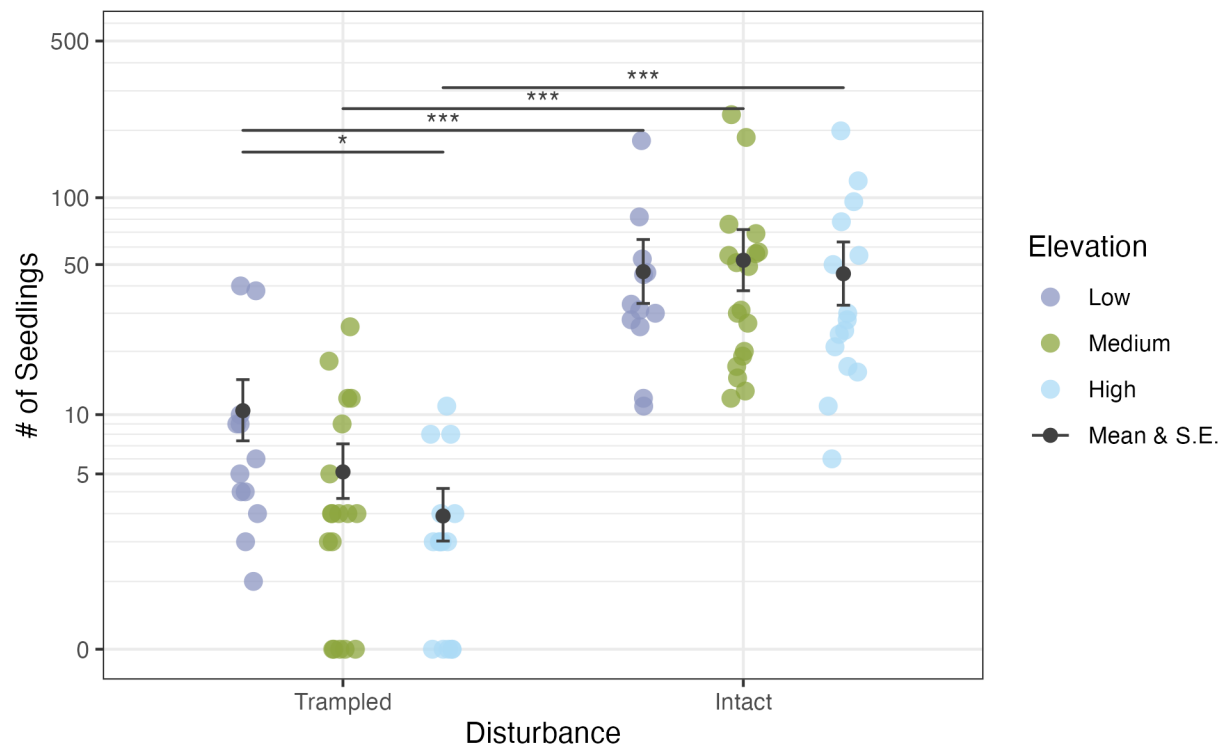


Figure 3-3. Seedling abundance per sample from the top 5 cm of litter and soil from trampled and intact areas. The y-axis scale is log-transformed. Black points and whiskers show the GLMM predicted mean and standard error above points showing observed counts. The lines at the top indicate statistically significant pairwise differences where “*” = $0.05 < p < 0.01$, “***” = $p < 0.001$. Table of P values and estimates for all contrasts are shown in Appendix 2-3.

Community Composition

The soil seed bank community differed between trampled and intact areas (Table 3-4, Figure 3-4) and intact area communities were more dispersed than trampled areas (PERMDISP: $F(1, 88) = 95.401$, $P < 0.001$). All elevations also differed from each other, though this was due to differences in means rather than dispersion (PERMDISP: $F(2, 87) = 2.163$, $P = 0.121$).

Table 3-4. PERMANOVA results comparing the community composition of intact and trampled area samples.

Term	Df	Sum Of Sqs	R ²	F	P value
Elevation	2	0.658	0.046	1.443	0.050 .
Site	12	2.733			
Disturbance	1	2.226	0.157	19.377	< 0.001 ***
Disturbance: Elevation	2	0.283	0.020	1.232	0.215
Residual	72	8.272	0.584		
Total	89	14.172	1		

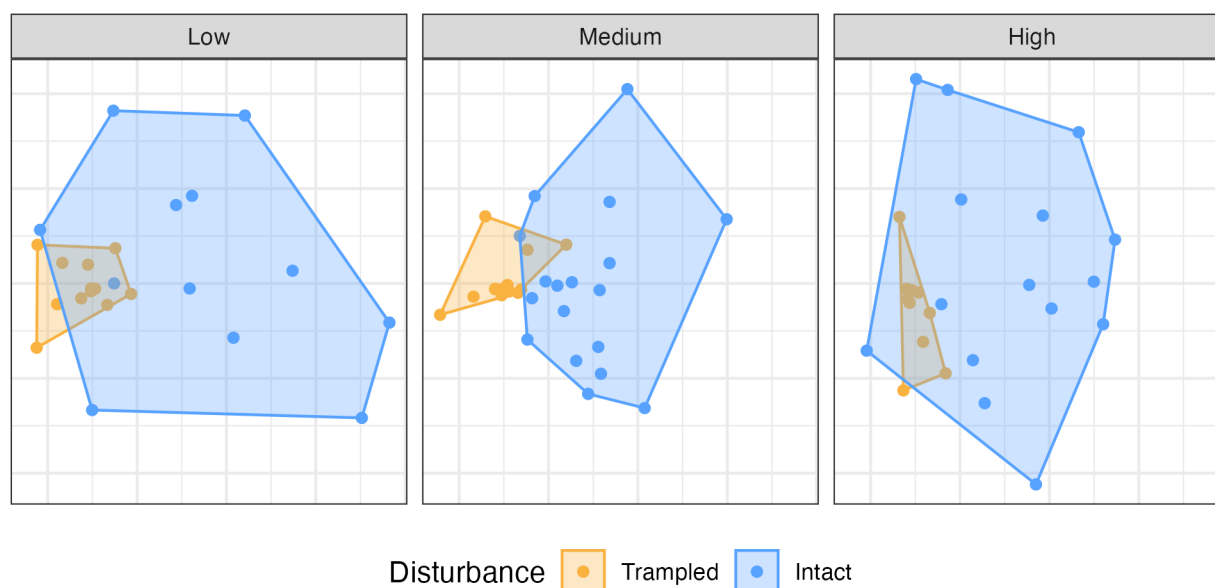


Figure 3-4. NMDS plot (stress = 0.163) showing the soil seed bank community of intact and trampled areas. Pairwise PERMANOVAs showed there were significant differences between all elevations (low vs. medium: $P = 0.033$, low vs. high: $P = 0.019$, and medium vs. high: $P = 0.017$). Plots show points from an NMDS run using data from all samples, subset by elevation for each panel.

Intact areas had 2.6 ± 1.1 times higher species richness in intact than trampled areas (Table 3-5). There were no significant effects of elevation on species richness, and no significant interaction between elevation and disturbance.

Table 3-5. ANOVA results showing main effects of the GLMM comparing species richness in trampled and intact areas.

Term	NumDF	DenDF	F	P value
Disturbance	1	64.3	75.670	< 0.001 ***
Elevation	2	12.8	0.836	0.456
Disturbance: Elevation	2	64.3	1.567	0.217

Comparison of Aboveground and Soil Seed Bank Community

Across the standing vegetation and top 5 cm of the soil seed bank (including litter), 24 species—roughly 40% of species in each community—were common to both communities. Eighteen of these species occurred in more than one flat and plot (Table 3-6). Total species richness was similar in both communities: there were 61 species aboveground and 57 in the soil

Table 3-6. List of species (or genera) common to the soil seed bank and aboveground communities. For each community type (soil seed bank or aboveground), columns show the percent of intact and trampled trays or plots the species occurred in. The sample size for each group is shown in the column header. The rightmost “Sum” column is the total number of trays or plots the species occurred in across community types. A cross-walk of species names from the two community types is provided in Appendix Table 2-1-1.

	Soil Seed Bank			Aboveground			Both
Species	Intact (n = 45)	Trampled (n = 45)	Sum (n = 90)	Intact (n = 45)	Trampled (n = 45)	Sum (n = 90)	Sum (n = 180)
Graminoids							
<i>Carex nigricans</i>	8.9	4.4	51.1	20.0	6.7	35.6	21.1
<i>Carex preslii</i>	4.4	6.7	4.4	11.1	5.6	7.8	6.7
<i>Carex rosii</i>	15.6	4.4	2.2	4.4	10.0	3.3	6.7
<i>Carex spectabilis</i>	86.7	17.8	60.0	46.7	52.2	53.3	52.8
<i>Juncus drummondii</i>	73.3	37.8	24.4	22.2	55.6	23.3	39.4
<i>Juncus mertensianus</i>	71.1	40.0	2.2	6.7	55.6	4.4	30.0
<i>Luzula</i> species	40.0	6.7	20.0	11.1	23.3	15.6	19.4
Poaceae species	20.0	4.4	4.4	2.2	12.2	3.3	7.8
Shrubs and Subshrubs							
<i>Cassiope mertensiana</i>	11.1	0	8.9	2.2	5.6	5.6	5.6
<i>Luetkea pectinata</i>	17.8	11.1	51.1	40.0	14.4	45.6	30.0
<i>Phylodoce empetriformis</i>	66.7	13.3	60.0	15.6	40.0	37.8	38.9
<i>Spirea splendens</i>	8.9	2.2	2.2	6.7	5.6	4.4	5.0
<i>Vaccinium</i> species	17.8	6.7	46.7	8.9	12.2	27.8	20.0
Forbs							
<i>Epilobium alpigenum</i>	11.1	2.2	11.1	0	6.7	5.6	6.1
<i>Erigeron</i> species	6.7	6.7	28.9	11.1	6.7	20.0	13.3
<i>Pedicularis</i> species	6.7	0	20.0	8.9	3.3	14.4	8.9
<i>Potentilla flabellifolia</i>	15.6	0	46.7	13.3	7.8	30.0	18.9
<i>Veronica cusickii</i>	31.1	0	75.6	35.6	15.6	55.6	35.6

seed bank. Aboveground community plots had 9.2 species per plot on average, and soil seed bank 5.6 species per sample.

Intact Areas

Aboveground and soil seed bank communities differed significantly for intact areas. There were also significant differences due to elevation, and there was a significant interaction between elevation and community type (Table 3-7). These differences were mostly due to differences in means between the two communities, but aboveground communities were also slightly more dispersed than the soil seed bank (Figure 3-5, PERMDISP: $F(1, 88) = 3.761$, $P = 0.056$). There were no dispersion differences between elevation (PERMDISP: $F(2, 87) = 2.146$, $P = 0.123$), or due to the interaction between community type and elevation (PERMDISP: $F(5, 84) = 0.802$, $P = 0.551$).

Table 3-7. PERMANOVA results comparing intact areas' aboveground and soil seed bank communities across elevations. See Appendix 2-4 for pairwise contrasts.

Term	Df	Sum Of Sqs	R ²	F	P value
Elevation	2	1.734	0.064	1.676	0.009 **
Site	12	6.207			
Community	1	5.424	0.201	27.362	< 0.001 ***
Community: Elevation	2	1.080	0.040	2.724	0.007 **
Site: Plot	30	4.207	0.156		
Residual	42	8.325	0.309		
Total	89	26.976	1.000		

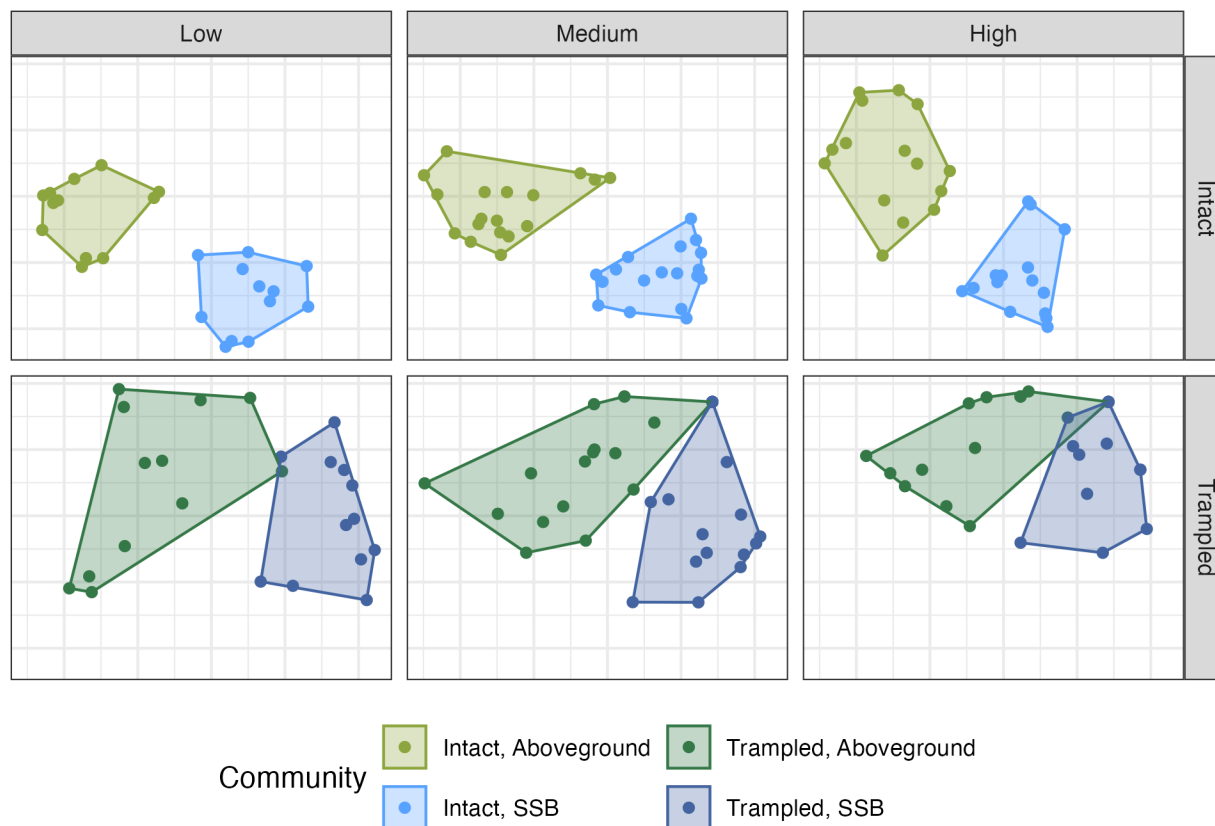


Figure 3-5. NMDS plots (stress = 0.148) comparing aboveground and soil seed bank (SSB) communities from intact and trampled areas. Plots show points from an NMDS run using data from all plots and soil samples, subset by elevation and trampling status for each panel.

Indicator species analysis identified 21 indicators of the aboveground and soil seed bank communities for intact areas. No species were indicators for both aboveground and soil seed bank communities. For a full list, see Appendix 2-4. Indicators of aboveground communities included *Lupinus latifolius*, *Veronica cusickii*, *Carex nigricans*, *Luetkea pectinata*, *Bistorta bistortoides*, *Potentilla flabellifolia*, *Vaccinium* species (including both *V. deliciosum* and *V. membranaceum*), *Anemone occidentalis*, *Oreostemma alpigenum*, *Valeriana sitchensis*, and *Antennaria lanatum*. Indicators of the intact soil seed bank included *Juncus mertensianus*, *J. drummondii*, *Erythranthe lewisii*, and *Agrostis variabilis*.

Trampled Areas

Within trampled areas, the soil seed bank and aboveground communities differed, and there were differences across elevations (Table 3-8). Low elevation sites differed from medium and high elevation sites (pairwise PERMANOVA: $P = 0.007$ and $P < 0.001$, respectively), and there were marginally significant differences between medium and high elevations (pairwise PERMANOVA: $P = 0.077$). There was a marginally significant elevation-community interaction; the soil seed bank and aboveground communities of trampled areas were more similar to each other with increasing elevation (Figure 3-5). Differences between the soil seed bank and aboveground communities were not due to dispersion (PERMDISP, $F(1, 88) = 1.697$, $P = 0.196$). However, there were dispersion differences between elevations (PERMDISP, $F(2, 67) = 6.027$, $P = 0.004$). Low elevations were more dispersed than both middle ($P = 0.003$) and high ($P = 0.002$) elevations.

Table 3-8. PERMANOVA results comparing trampled areas' aboveground and soil seed bank communities across elevations.

Term	Df	Sum Of Sqs	R ²	F	P value
Elevation	2	1.510	0.057	1.681	0.050 *
Site	12	5.390			
Community	1	3.389	0.128	15.815	< 0.001 ***
Community: Elevation	2	0.649	0.024	1.5137	0.097 .
Site: Plot	30	6.638	0.250		
Residual	42	9.000	0.339		
Total	89	26.576	1.000		

Indicator species analysis showed seven indicator species for trampled aboveground or soil seed bank communities separately, with no indicators for both. *Carex spectabilis*, *Luetkea pectinata*, *Lupinus latifolius*, *Veronica cusickii*, and *Hieracium triste* were identified as indicators for the aboveground community of trampled areas. *Juncus mertensianus* and *Juncus* species

(seedlings that were not grown to maturity but likely belonged to *J. mertensianus* or *J. drummonii*) were indicators for the soil seed bank community of trampled areas.

Discussion

Aboveground (Question 1): Trampled and intact areas had distinct communities at low elevation, but as elevation increased, the trampled community was increasingly a subset of the intact community. This aligns with predictions from the “Species Interactions-Abiotic Stress Hypothesis” (Louthan et al., 2015) that suggests abiotic conditions drive species compositions in abiotically stressful environments such as alpine ecosystems, while biotic interactions drive composition in ecosystems with lower abiotic stress. At higher elevations, trampling resulted in a community that was a subset of those present in the intact areas. However, at low elevations, where biotic interactions such as competition contribute more to community composition, trampling may reduce competition, leading trampled and intact communities to be distinct. Low elevation trampled communities more closely resembled high elevation intact and trampled communities than low elevation intact communities. This suggests that trampling may have reduced competitive interactions to facilitate persistence of species that would otherwise be competitively excluded at low elevations.

Unlike with the aboveground community, in the soil seed bank, there was not an elevation-disturbance interaction. Rather, the effect of disturbance was consistent across elevations, suggesting that when competition plays a smaller role, disturbance results in a reduced community from the intact area. Therefore, the resemblance of trampled area aboveground communities at low elevation to high elevation communities suggests trampling may not promote lowland or invasive species expansion into the meadows. Instead, higher

elevation species may be suitable to use in restoration because they are adapted to the lower competition and harsher abiotic conditions of trampled areas.

The species able to persist in trampled areas across elevations included *Carex spectabilis*, *C. nigricans*, *Luetkea pectinata*, *J. drummondii*, and *Veronica cusickii*. These species may be able to tolerate altered soil and microclimate conditions associated with trampled areas and are already often used in Mount Rainier's restoration plantings. *Eucephalus ledophyllus* was an indicator for trampled and intact areas at low elevations. This species was absent from the soil seed bank and therefore may not colonize trampled areas without active intervention, but it may be a useful addition to restoration plantings.

Soil Seed Bank (Question 2): Differences between communities were not due to invasive or lowland species. Three potentially nonnative species germinated from the 0-5 cm depth from intact areas (*Taraxacum officianale*, *Lactuca serriola*, and an unidentified *Cirsium* species), and three seedlings typically found at lower elevations (two *Persicaria lapathifolia* seedlings and a *Plectritis congesta* seedling). These represent 0.2% of all seedlings that germinated. This suggests using the soil seed bank for restoration is unlikely to facilitate species shifts which supports the findings of similar studies (Hoyle et al., 2013; Ludewig et al., 2021). The lack of invasive species in the soil seed bank and aboveground plots may also be due to National Park Service management practices. The parks devote considerable resources to invasive species management to address outbreaks quickly and maintain historic species assemblages due to Organic Act obligations. High elevation ecosystems with fewer protections or higher invasive species pressure may have higher rates of nonnative species in the soil seed bank.

The abundance of seedlings in the soil seed bank of both intact and trampled areas suggest it has some utility for trampled area restoration. While harvesting soil from intact areas for restoration may not be scalable, salvaging plants from areas undergoing necessary renovation or repairs is a common practice at Mount Rainier and other national parks, and transplants from intact areas are used to restore backcountry sites where greenhouse plants cannot be transported (Cole and Spildie, 2006; Therrell et al., 2006). This study highlights the potential benefit of utilizing both the top 5 cm of litter and soil as well as the plants from salvage areas for restoration.

Aboveground vs. Soil Seed Bank (Question 3): Community overlap between the soil seed bank and standing vegetation was low overall, though the communities shared many species. The soil seed bank was dominated by *Juncus* and *Carex* species, a finding common in similar studies (Ingersoll and Wilson, 1993; Klug et al., 2002; Roovers et al., 2006; Bossuyt and Honnay, 2008; Luo et al., 2017; Ludewig et al., 2021). Other studies of soil seed banks across many ecosystems have similarly found that seed banks tend to be comprised of different species from the aboveground vegetation (Venn and Morgan, 2010). *Juncus* and *Carex* are common in early succession communities in the Cascade Range (Franklin and Dyrness, 1973; Jumpponen et al., 1999), and *J. drummondii* and *C. spectabilis* were abundant early colonizers of disturbed areas at Sunrise, Mount Rainier (Frank and Del Moral, 1986). At Sunrise, species including *Lupinus latifolius*, *Oreostemma alpigenum*, and *Ligusticum grayi* did not recolonize disturbed areas for two to three decades; these species were also absent or uncommon in the soil seed bank in this study. Therefore, the soil seed bank may hold early-seral species while the standing vegetation represents a later successional phase. Species that are abundant in the soil seed bank may be lower priorities for restoration because they may recolonize without assistance if they

can be stimulated to germinate and establish. This would allow limited resources to be used to replant species absent from the soil.

The soil seed bank lacked some species that are very common in the standing vegetation. For example, *Lupinus latifolius*, *Bistorta bistortoides*, *Valeriana sitchensis*, *Eucephalus ledophyllus*, *Anemone occidentalis*, *Oreostemma alpigenum*, and *Antennaria lanatum* did not appear in the seed bank but are widespread at Paradise Mt Rainer. *L. latifolius* is hypothesized to have poor or episodic seed production (Frank and Del Moral 1986), and its large seeds may not persist as long in the soil as smaller seeded species (Shiferaw et al., 2018). Other species including *Veronica cusickii*, *Potentilla flabellifolia*, and *Luetkea pectinata* were present but relatively uncommon in the soil seed bank.

However, the soil seed bank and standing vegetation had 18 species in common. Most of these were present both in trampled and intact soils. The partial overlap in the two communities and abundance of seeds suggests the soil seed bank could be a tool to supplement, but not replace, restoration plantings. Restoration efforts could facilitate seed germination and seedling establishment, and supplement by planting desired species that are missing or uncommon in the soil seed bank but present in the intact community. Because standing and soil communities differ, the soil seed bank may contribute to increased diversity in the restored community during initial recovery phases. While thousands of seedlings germinated under greenhouse conditions for this study, future research is needed to increase germination and establishment *in situ*.

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CHAPTER 4

Conclusion and Implications for Management

The soil seed bank holds abundant native seeds, suggesting that seed availability is likely not limiting restoration at Mount Rainier. While trampling reduced seed bank density compared to intact samples, soil seed banks in both areas contain more seeds per m² than typical restoration seeding rates. The soil seed bank community from all depths was dominated by *Juncus drummondii* and *J. mertensianus*, but *Carex spectabilis*, *Phyllodoce empetrifomis*, and *Veronica cusickii* were also abundant and common across Paradise meadows. *Juncus* species are common early successional species that are likely to succeed in trampled areas, and many of the other species in the soil seed bank are often used in restoration plantings.

Comparison of the aboveground communities in trampled and intact areas across the elevation gradient at Paradise showed that high-elevation species may also be able to persist in trampled areas at lower elevations. *Eucephalus ledophyllus* was highlighted as an indicator for both trampled and intact areas at low elevations and could be included in outplanting assemblages. Future research could compare growth rates of early and later successional species in trampled areas to further inform species selection.

Despite some species in common, overall, the soil seed bank community and aboveground community of intact areas remained distinct. This means restoration efforts aiming to restore a community that matches the surrounding intact area will need to supplement germination from the soil seed bank by planting or seeding desired species. Species absent from the soil seed bank include *Lupinus latifolius*, *Bistorta bistortoides*, *Valeriana sitchensis*, *Eucephalus ledophyllus*, *Anemone occidentalis*, *Oreostemma alpigenum*, and *Antennaria lanatum*.

Soil conditions may be a barrier to seedling establishment and growth of plugs planted in trampled areas. Trampled areas were more compacted, had higher pH, and had lower organic matter than intact areas. Compaction causes an array of issues for plant growth including slowing root growth, reducing water infiltration, and changing the soil microbial community. Addressing compaction may speed plug growth rates and increase recruitment from the soil seed bank. Additional research is needed on methods to alleviate compaction and restore soil conditions to match those of intact areas.

APPENDIX 1: SUPPLEMENTAL MATERIALS FOR CHAPTER 2

Appendix 1-1: Site Photos



Figure 1-1-1. Site L4, trampled area.



Figure 1-1-2. Site L37.



Figure 1-1-3. Site L39.



Figure 1-1-4. Site L81.



Figure 1-1-5. Site M2.



Figure 1-1-6. Site M5.



Figure 1-1-7. Site M6.



Figure 1-1-8. Site M65.



Figure 1-1-9. Site M67.



Figure 1-1-10. Site M76.



Figure 1-1-11. Site H21.



Figure 1-1-12. Site H23.



Figure 1-1-13. Site H24



Figure 1-1-14. Site H25.



Figure 1-1-15. Site H82.

Appendix 1-2: Weed List

Table 1-2-1. List of weed species and the number of each counted across all trays. Counts do not include seedlings that were seen growing in up-potted seedling containers as weeds. These species were omitted from all analyses.

Species	Count	Notes
<i>Salix</i> spp.	280	May include more than one species. Not identified to species, only shoots and leaves available.
<i>Populus trichocarpa</i>	233	Cottony seeds visible in and around greenhouse
<i>Pseudognaphalium</i> sp.	212	Grows abundantly outside the greenhouse
<i>Oxalis corniculata</i>	93	Species is abundant in the greenhouse
Unknown woody sp. 1	63	Hypothesized to be a <i>Salix</i> sp.; not grown to identifiable stage, but species was abundant in the greenhouse
<i>Epilobium</i> sp.	38	Grows abundantly outside the greenhouse
<i>Erigeron canadensis</i>	27	Plant identified using more mature plants outside greenhouse
<i>Spergularia rubra</i>	25	Grows abundantly outside the greenhouse
Unknown woody sp. 2	17	No grown to identifiable stage, but species was abundant in the greenhouse
<i>Poaceae</i> sp. 7	8	Did not flower
<i>Cardamine hirsuta</i>	6	Grows abundantly outside the greenhouse
<i>Juncus bufonis</i>	4	Grows outside the greenhouse
<i>Rorippa palustris</i>	4	Has been collected from Seattle and Union Bay
<i>Fragaria</i> sp.	4	Genus uncertain; very hairy petioles, ternately compound leaves with serrate margins. Closely resembled ornamental <i>Fragaria</i> sp. growing at the Center for Urban Horticulture outside the Isaacson basement. Did not resemble any native Rosaceae species.
<i>Betula</i> sp.	2	Not identified to species, only shoots and leaves available.

Appendix 1-3: Soil Nutrient PCA Loadings, Pairwise Contrasts, and Graphs

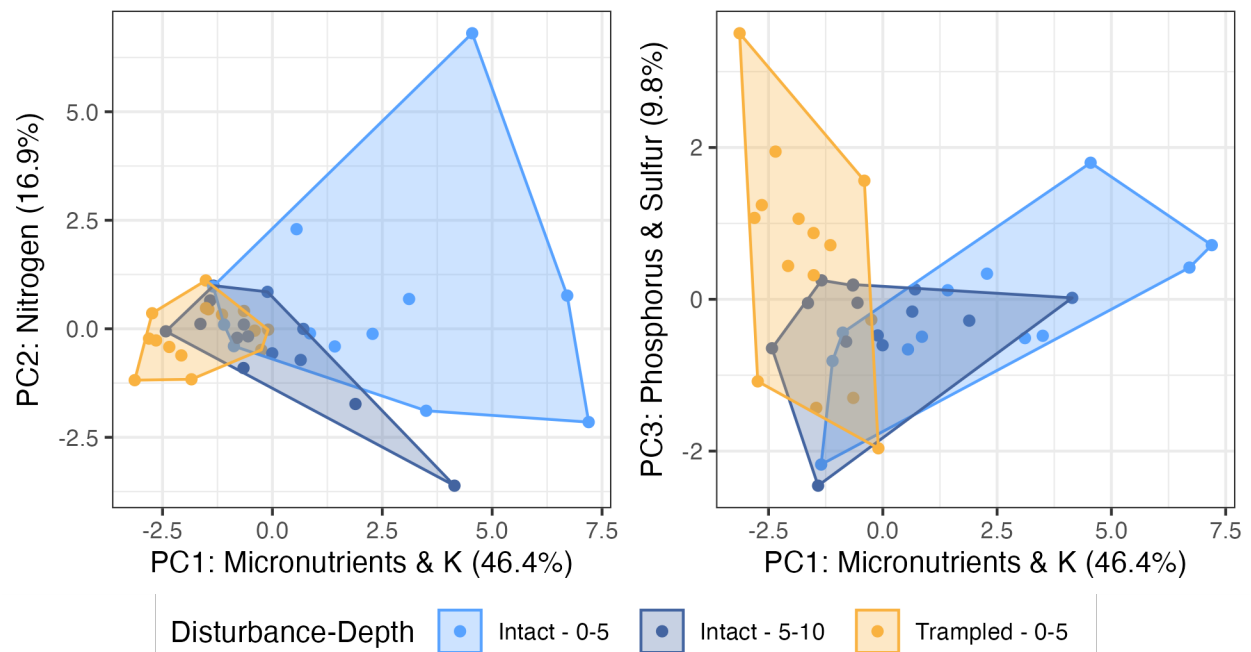


Figure 1-3-1. Plots of the first three PCA axes. The percent values for each axis show the percent variation explained by each principal component.

Table 1-3-1. PCA loadings for soil nutrients. The first three PCs are shown in Table 1-1.

Nutrient	PC1	PC2	PC3	PC4	PC5	PC6	PC7	PC8	PC9	PC10	PC11	PC12	PC12
Rel. Import.	0.464	0.169	0.098	0.082	0.053	0.042	0.035	0.022	0.012	0.010	0.007	0.005	0.001
Nutrient Loadings													
NO3-N	0.098	0.573	0.190	0.323	0.012	0.058	0.049	0.206	0.145	0.469	0.147	0.452	0.082
NH4-N	0.194	0.498	0.189	0.310	0.114	0.155	0.127	0.072	-0.264	-0.355	-0.113	-0.561	0.037
Bray P	0.006	0.239	-0.647	0.237	-0.448	-0.505	-0.019	0.017	-0.060	-0.078	-0.032	-0.022	0.004
K	0.357	0.179	0.104	-0.232	-0.051	-0.127	-0.136	0.040	0.446	-0.379	0.411	0.034	-0.473
S	-0.093	-0.214	0.652	0.221	-0.441	-0.413	0.194	0.013	-0.068	-0.202	-0.050	0.135	0.050
Zn	0.350	-0.225	-0.001	0.137	0.096	-0.175	0.172	-0.246	-0.414	0.367	0.568	-0.185	-0.126
Fe	0.324	-0.171	-0.163	0.239	-0.190	0.484	-0.029	-0.063	-0.294	-0.402	0.058	0.503	0.053
Mn	0.347	0.079	-0.044	-0.059	0.147	-0.111	0.505	-0.572	0.245	0.016	-0.414	0.141	-0.001
Cu	0.301	-0.247	-0.140	-0.063	0.237	-0.160	0.441	0.721	0.048	-0.062	-0.064	0.037	0.128
B	0.301	-0.231	0.005	0.161	-0.524	0.362	-0.022	0.095	0.368	0.340	-0.152	-0.373	-0.049
Ca (ppm)	0.351	0.081	0.130	-0.288	-0.057	-0.150	-0.349	0.144	-0.433	0.210	-0.479	0.108	-0.360

Table 1-3-2. Soil pH pairwise contrasts. The interaction was not significant, so only pairwise contrasts for disturbance-depth and elevation are shown.

Contrast	Estimate	SE	t ratio	P value
Intact, 0-5 - Intact, 5-10	-0.102	0.098	-1.043	0.558
Intact, 0-5 - Trampled, 0-5	-0.357	0.097	-3.670	0.004 **
Intact, 5-10 - Trampled, 0-5	-0.254	0.087	-2.918	0.021 *
Low - Medium	-0.336	0.116	-2.882	0.033 *
Low - High	-0.106	0.124	-0.852	0.678
Medium - High	0.230	0.106	2.172	0.120

Table 1-3-3. Soil electrical conductivity pairwise contrasts. The interaction was not significant, so only pairwise contrasts for disturbance-depth and elevation are shown. Estimates shown on the log scale.

Contrast	Estimate	SE	t ratio	P value
Intact, 0-5 - Intact, 5-10	0.505	0.182	2.773	0.029 *
Intact, 0-5 - Trampled, 0-5	1.323	0.180	7.333	< 0.001 ***
Intact, 5-10 - Trampled, 0-5	0.819	0.161	5.091	< 0.001 ***
Low - Medium	0.808	0.262	3.085	0.023 *
Low - High	0.992	0.278	3.566	0.009 **
Medium - High	0.184	0.241	0.760	0.734

Table 1-3-4. Soil organic matter pairwise contrasts. The interaction was not significant, so only pairwise contrasts for disturbance-depth and elevation are shown. Estimates shown on the log scale.

Contrast	Estimate	SE	t ratio	P value
Intact, 0-5 - Intact, 5-10	3.086	0.861	3.586	0.005 **
Intact, 0-5 - Trampled, 0-5	4.816	0.854	5.642	< 0.001 ***
Intact, 5-10 - Trampled, 0-5	1.730	0.761	2.275	0.082 .
Low - Medium	3.419	1.258	2.719	0.044 *
Low - High	2.744	1.335	2.056	0.138
Medium - High	-0.676	1.160	-0.582	0.832

Table 1-3-5. Pairwise contrasts for PC1 (Micronutrients & Potassium). The interaction was not significant, so only pairwise contrasts for disturbance-depth and elevation are shown.

Contrast	Estimate	SE	t ratio	P value
Intact, 0-5 - Intact, 5-10	3.012	0.642	4.691	< 0.001 ***
Intact, 0-5 - Trampled, 0-5	4.571	0.634	7.205	< 0.001 ***
Intact, 5-10 - Trampled, 0-5	1.558	0.570	2.733	0.032 *
Low - Medium	2.891	0.713	4.055	0.004 **
Low - High	2.819	0.760	3.709	0.007 **
Medium - High	-0.072	0.644	-0.111	0.993

Table 1-3-6. Pairwise contrasts for PC2 (Nitrogen). Neither elevation nor the interaction was significant, so only pairwise contrasts for disturbance-depth are shown.

Contrast	Estimate	SE	t ratio	P value
Intact, 0-5 - Intact, 5-10	1.313	0.561	2.342	0.070 .
Intact, 0-5 - Trampled, 0-5	0.939	0.554	1.694	0.229
Intact, 5-10 - Trampled, 0-5	-0.374	0.497	-0.753	0.735

Table 1-3-7. Pairwise contrasts for PC3 (Phosphorus & Sulfur).

Elevation	Contrast	Estimate	SE	t ratio	P value
Low	Intact, 0-5 - Intact, 5-10	1.144	0.434	2.637	0.039 *
Low	Intact, 0-5 - Trampled, 0-5	1.808	0.434	4.168	0.001 **
Low	Intact, 5-10 - Trampled, 0-5	0.664	0.330	2.015	0.134
Medium	Intact, 0-5 - Intact, 5-10	0.201	0.269	0.746	0.740
Medium	Intact, 0-5 - Trampled, 0-5	-0.639	0.269	-2.373	0.068 .
Medium	Intact, 5-10 - Trampled, 0-5	-0.840	0.269	-3.119	0.014 *
High	Intact, 0-5 - Intact, 5-10	-0.424	0.330	-1.286	0.419
High	Intact, 0-5 - Trampled, 0-5	-1.861	0.327	-5.690	< 0.001 ***
High	Intact, 5-10 - Trampled, 0-5	-1.437	0.327	-4.394	< 0.001 ***

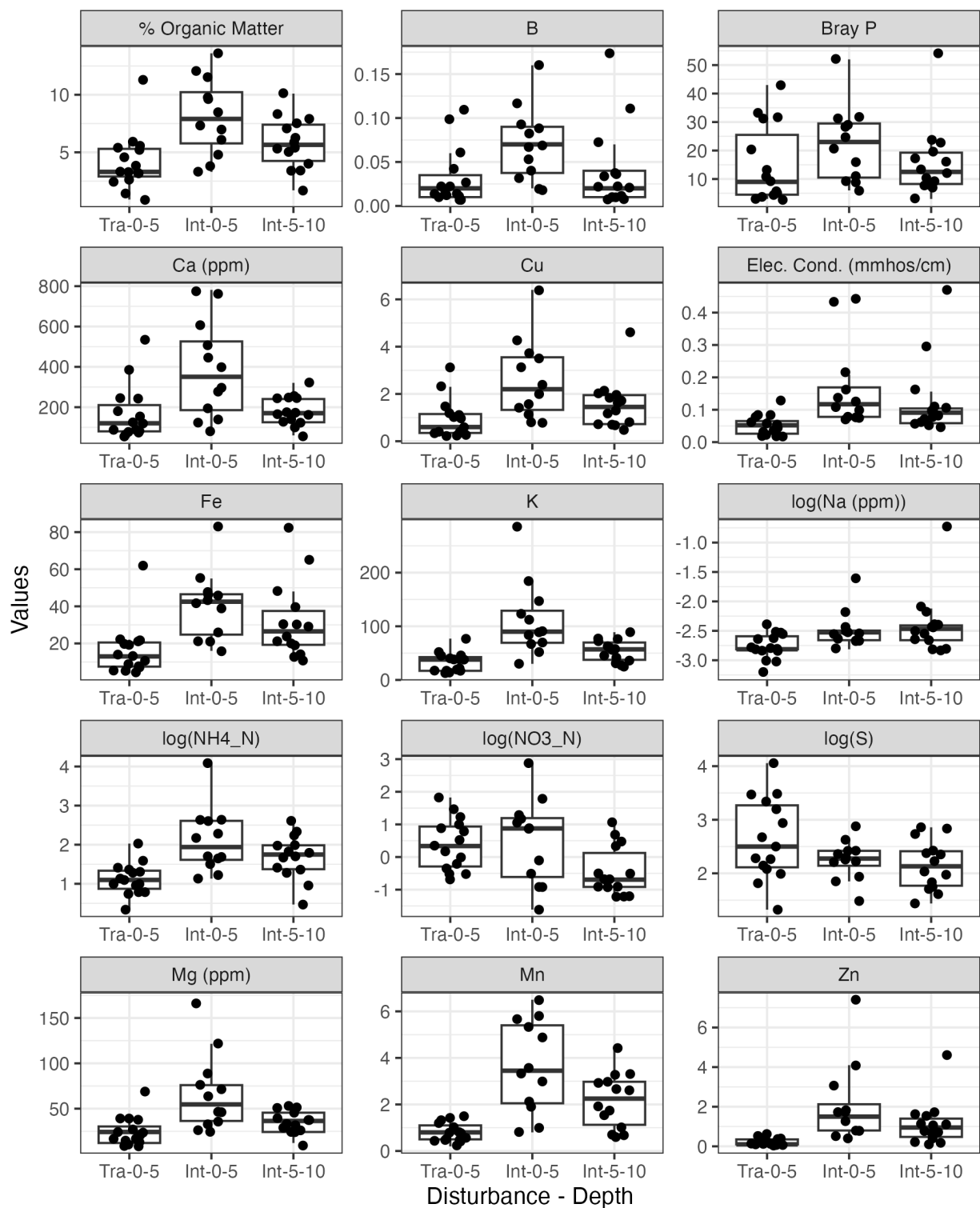


Figure 1-3-2. Soil nutrient test results. Units for all nutrients are mg/kg unless otherwise shown

Appendix 1-4: Seedling Abundance Pairwise Contrasts

Table 1-4-1. Pairwise contrasts for GLMMs for the Top 5 cm and 5-10 cm Comparisons shown in Table 1-2.

Group	Contrast	Estimate	SE	Z ratio	P value
Top 5 cm Comparison					
High	Intact - Trampled	2.245	0.365	6.146	< 0.001 ***
Medium	Intact - Trampled	2.091	0.320	6.532	< 0.001 ***
Low	Intact - Trampled	1.036	0.378	2.737	0.006 **
Intact	Low - Medium	-0.261	0.490	-0.534	0.855
Intact	Low - High	0.115	0.509	0.226	0.972
Intact	Medium - High	0.376	0.460	0.819	0.691
Trampled	Low - Medium	0.794	0.506	1.567	0.260
Trampled	Low - High	1.324	0.536	2.469	0.036 *
Trampled	Medium - High	0.531	0.495	1.071	0.532
5-10 cm Comparison					
High	Intact - Trampled	1.987	0.418	-0.206	< 0.001 ***
Medium	Intact - Trampled	1.363	0.376	3.621	< 0.001 ***
Low	Intact - Trampled	-0.091	0.444	-0.206	0.837
Intact	Low - Medium	-0.444	0.636	-0.697	0.765
Intact	Low - High	-0.718	0.660	-1.089	0.521
Intact	Medium - High	-0.274	0.594	-0.462	0.889
Trampled	Low - Medium	1.011	0.645	1.567	0.260
Trampled	Low - High	1.360	0.676	2.011	0.109
Trampled	Medium - High	0.349	0.623	0.560	0.841

Appendix 1-5: Soil Seed Bank PERMANOVA Results

Table 1-5-1. Pairwise PERMANOVA and PERMDISP contrasts for the combined effect of elevation and trampling for the Top 5 cm Comparison.

Group	Contrast	P values	
		PERMANOVA	PERMDISP
High	Intact - Trampled	< 0.001 ***	< 0.001 ***
Medium	Intact - Trampled	< 0.001 ***	< 0.001 ***
Low	Intact - Trampled	< 0.001 ***	0.002 **
Intact	High - Low	0.010 **	0.082 .
Intact	High - Medium	0.002 **	0.995
Intact	Medium - Low	0.019 *	0.078 .
Trampled	High - Low	0.014 *	0.166
Trampled	High - Medium	0.002 **	0.660
Trampled	Medium - Low	0.155	0.072 .

Table 1-5-2. Pairwise PERMANOVA and PERMDISP contrasts for the combined effect of elevation and trampling for the 5-10 cm Comparison.

Contrast	P values	
	PERMANOVA	PERMDISP
High - Low	0.002 **	0.020 *
High - Medium	0.010 *	0.642
Medium - Low	0.007 **	0.006 **

Table 1-5-3. Pairwise PERMANOVA and PERMDISP contrasts for the combined effect of elevation and sample depth for the Intact Comparison.

Group	Contrast	P value	
		PERMANOVA	PERMDISP
Litter	High vs Low	0.274	0.191
	High vs Medium	0.031 *	0.650
	Medium vs Low	0.013 *	0.260
0-5 cm	High vs Low	0.022 *	0.176
	High vs Medium	0.002 **	0.625
	Medium vs Low	0.009 **	0.050 *
5-10 cm	High vs Low	0.020 *	0.680
	High vs Medium	0.015 *	0.192
	Medium vs Low	0.523	0.108
High	0-5 cm vs Litter	0.072 .	0.146
	0-5 cm vs 5-10 cm	0.345	0.092 .
	5-10 cm vs Litter	0.044 *	0.005 **
Medium	0-5 cm vs Litter	< 0.001 ***	0.067 .
	0-5 cm vs 5-10 cm	0.016 *	0.006 **
	5-10 cm vs Litter	0.008 **	< 0.001 ***
Low	0-5 cm vs Litter	0.004 **	0.233
	0-5 cm vs 5-10 cm	0.021 *	0.016 *
	5-10 cm vs Litter	0.138	0.372

Appendix 1-6: Soil Seed Bank Species Richness Graph

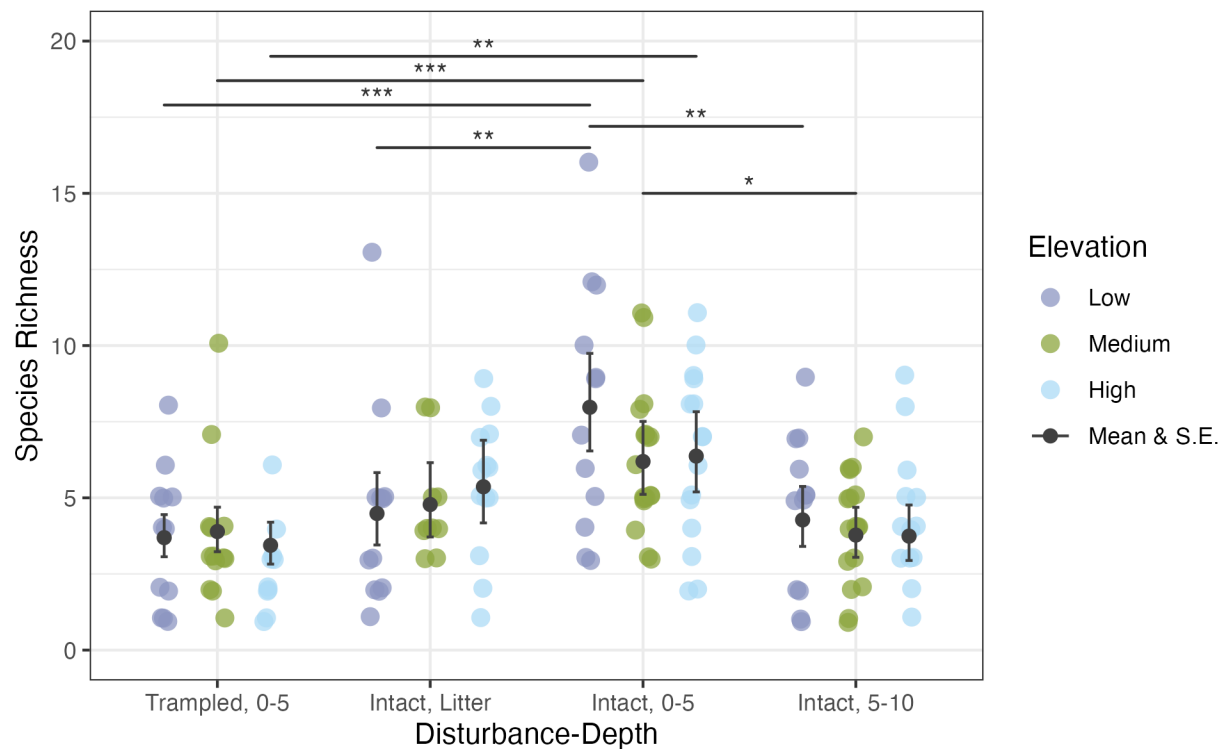


Figure 1-6-1. Species richness by elevation and disturbance-depth combination. Black points and whiskers show the GLMM predicted mean and standard error above points showing observed species richness for each sample. Main effect results are presented in Table 1-7. Model predictions are averaged across the three models for all estimates except litter. The lines at the top indicate statistically significant pairwise differences where “*” = $0.05 < p < 0.01$, “**” = $0.01 < p < 0.001$, “***” = $p < 0.001$.

Appendix 1-7: Seedling Counts by Species, Disturbance-Depth

Table 1-7-1. Seedling counts by species for each disturbance-depth combination. Table is sorted by the intact, 0-5 cm depth counts.

Species	Trampled, 0-5	Intact, Litter	Intact, 0-5	Intact, 5-10	Sum
Graminoids					
<i>Juncus</i> spp.	53	53	868	788	1762
<i>Juncus mertensianus</i>	45	13	235	166	459
<i>Juncus drummondii</i>	60	53	211	104	428
<i>Carex spectabilis</i>	12	63	105	30	210
<i>Carex</i> spp.	4	20	48	13	85
<i>Luzula</i> sp. 1	6	4	30	20	60
<i>Agrostis variabilis</i>	12	6	20	6	44
Poaceae spp.	2	4	29	8	43
<i>Carex</i> sp. 2	0	3	31	5	39
<i>Podagrostis humilis</i>	0	14	8	3	25
<i>Carex rossii</i>	3	2	7	8	20
<i>Carex preslii</i>	4	1	8	2	15
<i>Carex nigricans</i>	4	2	2	0	8
<i>Carex</i> sp. 5	0	2	4	0	6
Graminoid spp.	0	0	3	1	4
Poaceae sp. 4	0	1	2	0	3
Poaceae sp. 6	0	1	1	1	3
<i>Luzula</i> sp. 2	1	1	0	1	3
Poaceae sp. 8	0	0	1	1	2
<i>Luzula</i> spp.	0	0	2	0	2
<i>Danthonia intermedia</i>	0	1	0	0	1
<i>Juncus</i> sp. 3	0	1	0	0	1
<i>Poa stenantha</i>	0	1	0	0	1
Poaceae sp. 1	0	1	0	0	1
Poaceae sp. 5	0	1	0	0	1
<i>Agrostis</i> sp. 2	0	1	0	0	1
Shrubs and Subshrubs					
<i>Phyllodoce empetriformis</i>	7	184	79	26	296
<i>Luetkea pectinata</i>	10	11	5	5	31
<i>Vaccinium</i> sp. 1	2	4	1	6	13
<i>Cassiope mertensiana</i>	0	5	5	2	12
<i>Spiraea splendens</i>	1	1	4	0	6
<i>Vaccinium</i> sp. 2	1	2	0	3	6
<i>Vaccinium</i> spp.	0	0	2	0	2

Table 1-7-1. Continued.

Species	Trampled, 0-5	Intact, Litter	Intact, 0-5	Intact, 5-10	Sum
Forbs					
<i>Veronica cusickii</i>	0	41	45	36	122
<i>Erythranthe lewisii</i>	15	6	19	2	42
<i>Potentilla flabellifolia</i>	0	16	17	4	37
<i>Sagina saginoides</i>	17	0	0	0	17
<i>Veronica wormskjoldii</i>	7	2	3	0	12
Forb spp.	0	6	1	4	11
<i>Epilobium lactiflorum</i>	1	3	2	4	10
<i>Micranthes tolmeii</i>	2	2	4	0	8
<i>Pedicularis</i> spp.	0	3	3	2	8
<i>Senecio vulgaris</i>	1	1	2	2	6
<i>Erigeron</i> sp. 2	3	2	0	0	5
<i>Erigeron</i> sp. 1	1	2	0	0	3
Ranunculaceae sp. (L4)	0	0	3	0	3
<i>Anaphalis margaritacea</i>	0	2	0	0	2
<i>Chamaenerion angustifolium</i>	0	2	0	0	2
Forb sp. 2	0	2	0	0	2
Monocot sp.	0	1	1	0	2
<i>Persicaria lapathifolia</i>	0	2	0	0	2
<i>Taraxacum officinale</i>	0	0	1	1	2
<i>Achillea millefolium</i>	0	1	0	0	1
<i>Agoseris</i> sp. 1	0	0	1	0	1
<i>Agoseris</i> sp. 2	0	0	1	0	1
<i>Allium</i> sp.	1	0	0	0	1
Asteraceae sp.	0	0	0	1	1
<i>Castilleja</i> sp.	0	0	1	0	1
<i>Cirsium</i> sp.	0	0	1	0	1
<i>Epilobium ciliatum</i>	0	1	0	0	1
<i>Epilobium minutum</i>	0	0	0	1	1
<i>Lactuca serriola</i>	0	0	1	0	1
<i>Plectritis congesta</i>	0	1	0	0	1
<i>Trifolium</i> spp.	0	0	1	0	1

Appendix 1-8: Indicator Species Analysis

Table 1-8-1. Indicator species analysis results for comparisons of trampled and intact area samples from the top 5 cm of soil across elevations. IV = indicator value, the square root of the indicator value described in (Dufrêne and Legendre, 1997). “Poaceae species,” “*Carex* species,” and “*Juncus* species” refer to seedlings that germinated but died before identification. “*Carex* species” is likely *Carex spectabilis*, *Carex* sp. 2 did not flower during the study but was distinct from other *Carex* species, and “*Luzula* sp. 1” is likely *L. piperi* or *L. spicata*.

Species	IV	P value
Group: Low (Trampled and Intact)		
<i>Agrostis variabilis</i>	0.547	0.010
Group: Low Intact		
<i>Carex</i> sp. 2	0.571	0.005
Poaceae species	0.532	0.005
<i>Potentilla flabellifolia</i>	0.588	0.005
Group: Low Trampled		
<i>Sagina saginoides</i>	0.577	0.005
Group: High Intact		
<i>Luzula</i> sp. 1	0.564	0.015
Group: Intact (All Elevations)		
<i>Carex spectabilis</i>	0.849	0.005
<i>Carex</i> species	0.642	0.005
<i>Juncus drummondii</i>	0.736	0.005
<i>Juncus mertensianus</i>	0.758	0.005
<i>Juncus</i> species	0.762	0.005
<i>Phyllodoce empetriformis</i>	0.656	0.010
<i>Veronica cusickii</i>	0.537	0.005

Table 1-8-2. Indicator species analysis results for comparisons of the intact area, comparing depths and elevations. IV = indicator value.

Species	IV	P value
Group: Low, 0-5		
<i>Agrostis variabilis</i>	0.512	0.005
<i>Carex</i> sp. 2	0.506	0.005
Group: 0-5 cm (All Elevations)		
<i>Carex spectabilis</i>	0.652	0.005
<i>Carex</i> species	0.520	0.005
<i>Juncus drummondii</i>	0.644	0.005
Group: Medium Elevation (0-5 and 5-10 cm)		
<i>Juncus mertensianus</i>	0.629	0.015
Group: High Elevation (0-5 and 5-10 cm)		
<i>Luzula</i> sp. 1	0.582	0.005
Group: Litter (All Elevations)		
<i>Phyllodoce empetrifomis</i>	0.630	0.005

APPENDIX 2: SUPPLEMENTAL MATERIALS FOR CHAPTER 3

Appendix 2-1: Crosswalk Table

Table 2-1-1. Crosswalk for Taxonomic Consistency between Aboveground and Soil Seed Bank Communities. “SSB” stands for soil seed bank. The leftmost column shows the species code used to refer to the taxa in “Aboveground species” and “SSB Species”. The counts on the left show the number of plots (AG) or flats (SSB) each species or species group was present in, and the “Sum” column shows the total number of occurrences of the taxon across both communities.

Spp Code	Aboveground Species	SSB Species	Notes	# Plots	# Flats	Sum
ACHMIL	<i>Achillea millefolium</i>	<i>Achillea millefolium</i>		1	1	2
AGOSPP	<i>Agoseris</i> sp. 1 (hairless), <i>Agoseris</i> sp. 2 (fuzzy)	<i>Agoseris</i> sp. 1, <i>Agoseris</i> sp. 2		12	1	13
CARNIG	<i>Carex nigricans</i>	<i>Carex nigricans</i>		32	6	38
CARPRE	<i>Carex preslii</i>	<i>Carex preslii</i>		7	5	12
CARROS	<i>Carex rossii</i>	<i>Carex rossii</i>		3	9	12
CARSPE	<i>Carex spectabilis</i>	<i>Carex spectabilis</i>		48	47	95
CASMER	<i>Cassiope mertensiana</i>	<i>Cassiope mertensiana</i>		5	5	10
CASSPP	<i>Castilleja parviflora</i>	<i>Castilleja</i> sp.		23	1	24
CHAANG	<i>Chamaenerion angustifolium</i>	<i>Chamaenerion angustifolium</i>		1	2	3
EPIALP	<i>Epilobium alpinum</i>	<i>Epilobium lactiflorum</i>	This taxon was divided into many species. Used old name (group) for AG-SSB comparisons.	5	6	11
ERISPP	<i>Erigeron glacialis</i>	<i>Erigeron</i> sp. 1, <i>Erigeron</i> sp. 2		18	6	24
JUNDRU	<i>Juncus drummondii</i>	<i>Juncus drummondii</i>		21	50	71
JUNMER	<i>Juncus mertensianus</i>	<i>Juncus mertensianus</i>		4	50	54
LUEPEC	<i>Luetkea pectinata</i>	<i>Luetkea pectinata</i>		41	13	54
LUZSP1	<i>Luzula piperi</i> , <i>Luzula spicata</i>	<i>Luzula</i> sp. 1	<i>Luzulas</i> in SSB resembled <i>L. spicata</i> or <i>L. piperi</i> , so treated as same group	14	21	35
PEDSPP	<i>Pedicularis bracteosa</i> , <i>Pedicularis contorta</i> , <i>Pedicularis ornithorhynchos</i> , <i>Pedicularis racemosa</i> , <i>Pedicularis</i> sp.	<i>Pedicularis</i> sp.		13	3	16

Table 2-1-1. Continued.

Spp Code	Aboveground Species	SSB Species	Notes	# Plots	# Flats	Sum
PHYEMP	<i>Phyllodoce empetrifomis</i>	<i>Phyllodoce empetrifomis</i>		34	36	70
POASPP	Poaceae sp.	Poaceae sp.	Unidentifiable grass (may contain multiple undistinguishable species)	3	11	14
POTFLA	<i>Potentilla flabelifolia</i>	<i>Potentilla flabelifolia</i>		27	7	34
RANSPL4	Ranunculaceae sp.	Ranunculaceae sp.	Unidentified Ranunculaceae verified to be same from AG as SSB using photos	1	1	2
SPISPL	<i>Spirea splendens</i>	<i>Spirea splendens</i>		4	5	9
TAROFF	<i>Taraxacum officinale</i>	<i>Taraxacum officinale</i>		1	1	2
VACSPP	<i>Vaccinium deliciosum</i> , <i>Vaccinium membranaceum</i>	<i>Vaccinium deliciosum</i> , <i>Vaccinium membranaceum</i>	Could not distinguish species in SSB	25	11	36
VERCUS	<i>Veronica cusickii</i>	<i>Veronica cusickii</i>		50	14	64
AGRSP2		<i>Agrostis</i> sp. 2		0	1	1
AGRVAR		<i>Agrostis variabilis</i>		0	21	21
ALLISP		<i>Allium</i> sp.		0	1	1
ANAMAR		<i>Anaphalis margaritacea</i>		0	2	2
CARSP2		<i>Carex</i> sp. 2		0	12	12
CARSP5		<i>Carex</i> sp. 5		0	4	4
CARSPP		<i>Carex</i> spp.	Died before ID	0	28	28
CIRSP		<i>Cirsium</i> sp.		0	1	1
DANINT		<i>Danthonia intermedia</i>		0	1	1
EPICIL		<i>Epilobium ciliatum</i>		0	1	1
ERYLEW		<i>Erythranthe lewisii</i>		0	21	21
FORBSP2		Forb sp. 2	Died before ID; distinct from other unknown forbs	0	1	1
FORBSPP		Forb spp.	Died before ID	0	6	6
GRAMSPP		Graminoid spp.	Died before ID, may contains several graminoid groups	0	2	2
GRASS1		Poaceae sp. 1	Verified species differed from field unknowns using photos	0	1	1
GRASS4		Poaceae sp. 4	Verified species differed from field unknowns using photos	0	3	3

Table 2-1-1. Continued.

Spp Code	Aboveground Species	SSB Species	Notes	# Plots	# Flats	Sum
GRASS5		Poaceae sp. 5	Verified species differed from field unknowns using photos	0	1	1
GRASS6		Poaceae sp. 6	Verified species differed from field unknowns using photos	0	2	2
GRASS8		Poaceae sp. 8	Verified species differed from field unknowns using photos	0	1	1
JUNSPP		<i>Juncus</i> sp. 3		0	46	46
JUNSPP		<i>Juncus</i> spp.		0	46	46
LACSER		<i>Lactuca serriola</i>		0	1	1
LUZSP2		<i>Luzula</i> sp. 2	Verified species differed from field unknowns using photos	0	2	2
LUZSPP		<i>Luzula</i> sp.	Unknown <i>Luzula</i> species that did not contain the other <i>Luzula</i> groups	0	1	1
MICTOL		<i>Micranthes tolmiei</i>		0	8	8
MONOSP		Monocot sp.	Died before ID	0	2	2
PERLAP		<i>Persicaria lapathifolia</i>		0	2	2
PLECON		<i>Plectritis congesta</i>		0	1	1
POASTE		<i>Poa stenantha</i>		0	1	1
PODHUM		<i>Podagrostis humilis</i>		0	5	5
SAGSAG		<i>Sagina saginoides</i>		0	4	4
SENVUL		<i>Senecio vulgaris</i>		0	4	4
TRISPP		<i>Trifolium</i> spp.		0	1	1
VERWOR		<i>Veronica wormskjoldii</i>		0	4	4
ABILAS	<i>Aibes lasiocarpa</i>			15	0	15
AGOSP3	<i>Agoseris</i> sp. 3 (wooly)			1	0	1
ANEOCC	<i>Anemone occidentalis</i>			20	0	20
ANTLAN	<i>Antennaria lanata</i>			15	0	15
ARNLAT	<i>Arnica latifolia</i>			8	0	8
BISBIS	<i>Bistorta bistortoides</i>			21	0	21
CALLEP	<i>Caltha leptosepala</i>			1	0	1

Table 2-1-1. Continued.

Spp Code	Aboveground Species	SSB Species	Notes	# Plots	# Flats	Sum
ELYSP	<i>Elymus</i> sp.			3	0	3
EMPNIG	<i>Empetum nigrum</i>			3	0	3
ERECAP	<i>Eremogone capillaris</i>			1	0	1
ERYSP	<i>Erythronium</i> sp.			5	0	5
EUCLED	<i>Eucephalus ledophyllus</i>			10	0	10
FESVIR	<i>Festuca viridula</i>			15	0	15
GAUHUM	<i>Gaultheria humifusa</i>			2	0	2
GRAMHa	Poaceae sp. (Hairy)		Not common enough to collect	3	0	3
GRAMPu	Poaceae sp. (Purple)		Not common enough to collect	10	0	10
GRAMSp	Poaceae sp. 1		Not common enough to collect	2	0	2
GRAMTa	Poaceae sp. (Tall)		Not common enough to collect	6	0	6
HIETRI	<i>Hieracium triste</i>			28	0	28
JUNCOM	<i>Juniperus communis</i>			2	0	2
LIGSPP	<i>Ligusticum</i> sp.			19	0	19
LUPLAT	<i>Lupinus latifolius</i>			76	0	76
LUZSP3	<i>Luzula</i> sp. 3		Shiny leaves, not flowering	3	0	3
MICSP	<i>Micranthes</i> sp. 1			2	0	2
OREALP	<i>Oreostemma alpigenum</i>			22	0	22
PENCON	<i>Penstemon confertus</i>			1	0	1
PHLALP	<i>Phleum alpinum</i>			3	0	3
PHLDIF	<i>Phlox diffusa</i>			13	0	13
PHYGLA	<i>Phyllodoce glanduliflora</i>			2	0	2
POATall	<i>Poa</i> sp. (Tall)			2	0	2
PRIJEF	<i>Primula jeffreyi</i>			1	0	1
SENTRI	<i>Senecio triangularis</i>			7	0	7
SORSIT	<i>Sorbus sitchensis</i>			2	0	2
TSUMER	<i>Tsuga mertensiana</i>			1	0	1
VALSIT	<i>Valeriana sitchensis</i>			17	0	17

Table 2-1-1. Continued.

Spp Code	Aboveground Species	SSB Species	Notes	# Plots	# Flats	Sum
VERCAL	<i>Veratrum californicum</i>			4	0	4
XERTEN	<i>Xerophyllum tenax</i>			1	0	1

Appendix 2-1: Aboveground Post Hoc Test Results

Table 2-1-1. Pairwise PERMANOVA and PERMDISP contrasts for the combined effect of elevation and trampling.

Group	Contrast	P values	
		PERMANOVA	PERMDISP
High	Intact - Trampled	< 0.001 ***	< 0.001 ***
Medium	Intact - Trampled	< 0.001 ***	< 0.001 ***
Low	Intact - Trampled	< 0.001 ***	0.579
Intact	High - Low	< 0.001 ***	0.721
Intact	High - Medium	< 0.001 ***	0.713
Intact	Medium - Low	< 0.001 ***	0.964
Trampled	High - Low	0.004 **	0.001 ***
Trampled	High - Medium	0.505	0.386
Trampled	Medium - Low	0.004 **	0.007 **

Table 2-1-2. Indicator species analysis results for comparisons of aboveground vegetation in trampled and intact areas across elevations. IV = indicator value, the square root of the indicator value described in (Dufrêne and Legendre, 1997).

Species	IV	P value
Group: Low Elevation (Intact and Trampled)		
<i>Eucephalus ledophyllus</i>	0.507	0.015
Group: Low Intact		
<i>Anemone occidentalis</i>	0.592	0.005
<i>Ligusticum</i> species	0.633	0.005
<i>Vaccinium deliciosum</i>	0.770	0.005
<i>Senecio triangularis</i>	0.608	0.005
<i>Valeriana sitchensis</i>	0.902	0.005
<i>Veratrum californicum</i>	0.577	0.005
Group: Medium Intact		
<i>Epilobium alpinum</i>	0.527	0.005
Group: High Intact		
<i>Festuca viridula</i>	0.586	0.010
Group: Low and Medium Intact		
<i>Phyllodoce empetrifomis</i>	0.797	0.005
<i>Bistorta bistortoides</i>	0.597	0.005
<i>Potentilla flabellifolia</i>	0.684	0.005
Group: Medium and High Intact		
<i>Carex spectabilis</i>	0.666	0.040
<i>Castilleja parviflora</i>	0.628	0.015
Group: Intact Areas (All Elevations)		
<i>Lupinus latifolius</i>	0.815	0.005
<i>Veronica cusickii</i>	0.825	0.005
<i>Antennaria lanatum</i>	0.501	0.040

Appendix 2-2: Soil Seed Bank Pairwise Contrasts

Table 2-2-1. Pairwise contrasts for GLMMs comparing seedling abundance from the soil seed bank of trampled and intact areas.

Contrast	Group	Estimate	SE	Z ratio	P value
Intact - Trampled	Low	1.492	0.343	4.347	< 0.001 ***
Intact - Trampled	Medium	2.323	0.292	7.954	< 0.001 ***
Intact - Trampled	High	2.750	0.335	8.211	< 0.001 ***
Low - Medium	Intact	-0.068	0.423	-0.160	0.986
Low - High	Intact	0.041	0.440	0.093	0.995
Medium - High	Intact	0.108	0.397	0.273	0.960
Low - Medium	Trampled	0.763	0.444	1.721	0.197
Low - High	Trampled	1.299	0.472	2.752	0.016 *
Medium - High	Trampled	0.536	0.438	1.224	0.439

Appendix 2-3: Aboveground-Soil Seed Bank Pairwise Comparison Contrasts

Table 2-3-1. Pairwise PERMANOVA contrasts comparing the soil seed bank and standing vegetation communities of intact areas. PERMDISP pairwise contrasts were not completed because there were no significant differences in dispersion.

Group	Contrast	P value
High	Soil seed bank - Aboveground	< 0.001 ***
Medium	Soil seed bank - Aboveground	< 0.001 ***
Low	Soil seed bank - Aboveground	< 0.001 ***
Soil seed bank	High - Low	0.051 .
Soil seed bank	High - Medium	< 0.001 ***
Soil seed bank	Medium - Low	0.021 *
Aboveground	High - Low	< 0.001 ***
Aboveground	High - Medium	0.004 **
Aboveground	Medium - Low	< 0.001 ***

Table 2-3-2. Indicator species analysis results comparing intact areas' soil seed bank and standing vegetation communities.

Species	IV	P value
Group: Aboveground		
<i>Carex nigricans</i>	0.660	0.005
<i>Castilleja</i> species	0.616	0.005
<i>Luetkea pectinata</i>	0.616	0.01
<i>Lupinus latifolius</i>	0.954	0.005
<i>Oreostemma alpigenum</i>	0.516	0.005
<i>Veronica cusickii</i>	0.732	0.005
<i>Anemone occidentalis</i>	0.558	0.005
<i>Antennaria lanatum</i>	0.516	0.005
<i>Bistorta bistortoides</i>	0.615	0.005
<i>Ligusticum</i> species	0.615	0.005
<i>Potentilla flabellifolia</i>	0.592	0.005
<i>Vaccinium</i> species	0.581	0.015
<i>Hieracium triste</i>	0.577	0.005
<i>Valeriana sitchensis</i>	0.516	0.005
Group: Soil Seed Bank		
<i>Juncus mertensianus</i>	0.830	0.005
<i>Juncus drummondii</i>	0.742	0.005
<i>Agrostis variabilis</i>	0.537	0.005
<i>Carex</i> species	0.730	0.005
<i>Juncus</i> species	0.816	0.005
<i>Carex</i> sp. 2	0.516	0.005
<i>Erythranthe lewisii</i>	0.537	0.005

Table 2-3-3. Indicator species analysis results comparing trampled areas' soil seed bank and standing vegetation communities

Species	IV	P value
Group: Aboveground		
<i>Carex spectabilis</i>	0.581	0.005
<i>Luetkea pectinata</i>	0.560	0.005
<i>Lupinus latifolius</i>	0.882	0.005
<i>Veronica cusickii</i>	0.596	0.005
<i>Hieracium triste</i>	0.537	0.005
Group: Soil Seed Bank		
<i>Juncus mertensianus</i>	0.586	0.005
<i>Juncus</i> species	0.596	0.005