Many Small Stepping Stones Improve Habitat Connectivity for the Endangered Taylor's Checkerspot Butterfly (*Euphydryas editha taylori*)

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Abstract

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Habitat fragmentation is a major driver of wildlife population decline globally, and the loss and fragmentation of grassland ecosystems has resulted in the reduction of functional connectivity for many specialist butterflies. These species are highly dependent on connected habitat patches for maintaining genetic diversity and protecting populations from extreme events such as drought or fire. The Taylor's checkerspot, an endangered Pacific Northwest endemic species, has experienced declines in local population abundance across their geographical range due to the loss of grasslands. This loss has been caused by the increasing spread of invasive species, conifer encroachment, the loss of historical fire regimes, and human activities. To support the conservation goals for this species, I developed a movement model and conducted a connectivity analysis to determine how patch size, quantity, and placement influence dispersal probabilities across a portion of the butterfly’s range. Because this species is short lived with a limited flight period, movement over multiple generations may be necessary for colonizing new patches. To account for this, I quantified dispersal potential over 100 generations using a Markov chain approach. Over 100 generations, many small stepping stones produced the highest dispersal probabilities when compared to the addition of fewer, larger patches. The placement and number of these patches differed in their ability to improve immigration versus emigration rates. After 100 years, randomized patch placement supported higher immigration probabilities while randomized and least-cost-path patch placement supported similar emigration probabilities, providing managers with flexibility when selecting sites, which may alleviate budgetary limitations or land-use conflicts. This is especially important in highly developed areas where options for restoring habitat are likely to be limited to small, opportunistically acquired patches.

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Introduction

Habitat loss and fragmentation are primary management priorities for wildlife conservation and leading causes of population decline and extinction globally (Saunders et al. 1991; Debinski and Holt 2000; Steffan‑Dewenter and Tscharntke 2000; Brückmann et al. 2010; Sawyer et al. 2011; Evans et al. 2016). Fragmentation of resource patches isolates individuals and populations and restricts movement across the landscape and between subpopulations (Ewers and Didham 2005; Evans et al. 2016). Fragmentation can separate individuals from food sources and mates and reduce the availability of optimal environmental conditions. These limitations can lead to reduced population sizes making populations more vulnerable to extinction through the loss of genetic diversity and reduced resilience to extreme weather events, disease, and predation (Nieminen et al. 2001; Thomas and Hanski 2004; Bennett et al. 2013). Further, as landscapes become more fragmented, local extinction rates may exceed recolonization rates and suitable habitat may remain unoccupied while isolated populations continue to decline (Nieminen et al. 2001; Dover and Settele 2009).

Butterfly populations are often negatively affected by habitat fragmentation because many species have restricted habitats, specific resource needs, limited dispersal abilities, and exhibit metapopulation dynamics (Hanski 1999; Steffan‑Dewenter and Tscharntke 2000; Thomas and Hanski 2004; Dover and Settele 2009; Brückmann et al. 2010). Metapopulations, defined as a collection of local populations connected through dispersal (MacArthur and Wilson 1967; Levins 1970), rely on interactions among these local populations for the long-term survival of the species (Hanski and Thomas 1994; Hastings and Harrison 1994; Conradt et al. 2000; Thomas and Hanski 2004). Specifically, populations exhibiting metapopulation dynamics persist in collections of occupied and unoccupied habitat patches that, through occasional dispersal, can fluctuate in population size and occupancy over time. In these populations, the processes of local extinction and recolonization of unoccupied patches are influenced by limited connectivity, asynchronous disturbances, and dispersal (Hanski and Thomas 1994; Blomfield et al. 2023; Meyer et al. 2024). Butterflies existing in metapopulations depend on networks of resource patches, specifically, areas containing larval host plants and adult nectar sources within species-specific dispersal distances (Weiss et al. 2013). As fragmentation changes the landscape, resource patches can shrink in size, shift in quality, and become difficult to access (Bonelli et al. 2013).

Adult dispersal plays an important role in butterfly biology (Ehrlich et al. 1984; Weiss et al. 1987; Öckinger 2006), making habitat connectivity an important consideration for butterfly conservation (Brückmann et al. 2010). Dispersal behavior, timing, and distance is highly species-specific, ranging from roughly 15,000 km over multiple generations in a single year for the highly mobile painted lady (*Vanessa cardui* (Linnaeus) 1758), to less than 250 m annually for dispersal-limited species like the frosted elfin (*Callophrys irus*, Godart 1824) (Talavera et al. 2023; Meyer et al. 2024). In species exhibiting metapopulation dynamics, immigration by some individuals into small, occupied patches is important for maintaining genetic diversity. For example, some local populations hold only a single family group of offspring, leading to inbreeding depression without the addition of new individuals. Saccheri et al. (1998) and Nieminen et al. (2001) both found that inbreeding due to these small, local population sizes reduced adult longevity, larval survival, and egg hatching rates in the Glanville fritillary (*Melitaea cinxia*, (Linnaeus) 1758) when compared to crossbred individuals. Additionally, the recolonization of unoccupied habitat patches is important for resource acquisition and safeguarding populations from extreme events, such as drought or fire. In these events, heterogeneity among habitat patches can allow some local populations to persist even while others are extirpated (Hanski and Thomas 1994; Sutcliffe et al. 1997; Conradt et al. 2001).

Agricultural intensification, development, and loss of traditional Indigenous land management practices have led to the decline of natural prairies and grasslands globally (Krebs et al. 1999; Brückmann et al. 2010). Nevertheless, semi-natural grasslands and fragmented landscapes can still be important for the conservation of species, particularly insects (Öckinger 2006; Brückmann et al. 2010). Remaining grassland fragments are increasingly small and isolated, limiting the population sizes and connectivity they can support. In Germany, Brückmann et al. (2010) found that a total loss of grassland connectivity would reduce the richness of specialist butterflies by up to 69%, and many grassland butterfly specialists are threatened or endangered by the loss and fragmentation of grassland ecosystems globally, including the Marsh fritillary (*Euphydryas aurinia*, Rottemburg 1775), Mission blue (*Icaricia icarioides missionensis*, (Hovanitz) 1937), Poweshiek skipperling (*Oarisma poweshiek*, (Parker) 1870), and Oberthür's grizzled skipper (*Pyrgus armoricanus*, Oberthür 1910) (Warren 1994; Öckinger 2006).

The Taylor’s checkerspot (*Euphydryas editha taylori*, (Edwards) 1888) is a federally listed endangered butterfly endemic to rare western grasslands in the Pacific Northwest. The persistence of this species, like the ecosystem of which it is part, is threatened by habitat loss and fragmentation caused by urbanization and development, agricultural conversion, encroachment by conifers, and non-native, invasive vegetation (Crawford and Hall 1997; Stinson 2005;

Department of the Interior 2013; U.S. Fish and Wildlife Service 2022). The Taylor's checkerspot is a non-migratory, univoltine species of nymphalid butterfly with a largely sedentary life cycle (Department of the Interior 2013; U.S. Fish and Wildlife Service 2022). In Washington, adults spend 10-14 days in flight between April and early June, during which time they must find mates and select suitable host plants (*Castilleja hispida*, Benth. or *Plantago lanceolata*, L.) for oviposition. Early instars consume host plants from communal webs for the first three instars between May and July, and diapause for approximately 8 months. During diapause, larvae seek shelter from late summer heat in protected, shaded areas on or near the soil surface. Larvae emerge from diapause in late winter, when they return to foraging a wider array of plant species. After the fifth instar, larvae pupate at the underside of host plants or just below the soil surface, after which adults emerge to begin the cycle once more.

Historically, the Taylor's checkerspot occurred in over 80 sites throughout British Columbia, Washington, and Oregon, over half of which were located in Washington (Department of the Interior 2013). Currently, the species occupies only 11 sites, eight of which are in Washington (Stinson 2005; Potter 2016). This reduction in distribution has largely coincided with the alteration and loss of grassland systems throughout the butterfly's range (Department of the Interior 2013). The South Puget Recovery Region contains the largest area of suitable and potentially suitable habitat within the species' range, and reintroduction and habitat restoration efforts are occurring throughout the region (U.S. Fish and Wildlife Service 2022). The largest population complex of the Taylor's checkerspot occurs on Joint Base Lewis–McChord (JBLM) approximately 27 km south of Tacoma, WA. Here, the species survives in isolated patches within a 3,075 ha area of grassland still supporting a high percentage of native vegetation. All remaining subpopulations within the south Puget Sound ecoregion, both on and off of the military lands, are the product of reintroduction efforts and were previously sourced from females collected from one on-base site (Linders et al. 2020; personal correspondence, Linders 2023).

The Taylor's checkerspot, like other butterflies, is an important indicator species, whose population decline can serve as a reflection of grassland health. Within the south Puget Sound ecoregion, the Taylor's checkerspot can also act as an umbrella species, as restoration and management of checkerspot habitat will also provide indirect benefits for other at-risk species within the region facing a similar set of stressors, including the Mazama pocket gopher (*Thomomys mazama*, (Merriam) 1897), Streaked Horned Lark (*Eremophila alpestris strigata*, Henshaw, 1884), and other at-risk butterflies like the Hoary elfin (*Callophrys polios*, Cook & Watson 1907) and Mardon skipper (*Polites mardon*, W. H. Edwards 1881) (U.S. Fish and Wildlife Service 2022).

Despite dramatic declines in connected, high-quality habitat and the extirpation of historical checkerspot populations, managers lack usable connectivity assessments that could guide the prioritization of management sites and targeted reintroductions. With this study, I aim to support the conservation and recovery of the Taylor's checkerspot butterfly by exploring approaches to increasing functional connectivity across the largest remaining grassland in the species' south Puget Sound range. Specifically, the first objective of this study was to quantify patch connectivity under current vegetation patterns in the South Puget Sound prairie ecoregion. My second objective was to explore how simulated habitat additions of different numbers and sizes of patches affected connectivity.

I hypothesized that dispersal probabilities would increase in previously isolated patches with the implementation of an experimental management scenario using many small stepping stones compared to experimental management scenarios using fewer, larger patches. This is because the placement of many small patches is better able to reduce the gap between habitat patches compared to fewer, larger patches. Additionally, individuals who move from isolated patches into randomly placed larger patches have adequate resource area within these larger patches, making them less likely to continue dispersing to currently occupied patches outside of their starting locations. Larger patches randomly placed outside of likely dispersal routes will also provide fewer dispersal options when compared to higher quantities of randomly placed smaller patches. Additionally, I expected to find the highest dispersal probabilities when patches were optimally arranged along a route that best reduced movement costs when compared to randomized patch placement. I expect these pathways to provide the highest dispersal probabilities because patch placement in these scenarios is within areas with the highest conductivity and least resistance.

To achieve these objectives, I developed a butterfly movement model for a portion of the Taylor’s checkerspot’s Washington range. I then simulated movement among existing habitat patches, quantifying the probabilities of immigration and emigration. Next, I augmented the current habitat patches with additional simulated habitat patches varying in size and number (from one large patch to many small patches). Again, I recorded simulated immigration and emigration rates. After determining the number of patches that produced the most movement, I used an additional connectivity model to arrange the same number of patches in a pattern to create least-cost paths. I compared movement in these least-cost path scenarios to the randomly placed patches I had previously created.

Materials & Methods

Study Area

The South Puget Recovery Region sits at the southern end of the Puget Sound and contains the largest area of suitable and potentially suitable habitat within the distribution range for Taylor's checkerspot. The 91st Division Prairie, nestled within Department of Defense lands and extensively used for a variety of military activities, contains the largest extant prairie and the largest naturally occurring population of Taylor's checkerspot within the Recovery Region. Approximately 0.6 km south of 91st Division Prairie sits Marion Prairie, a small (62 ha), fragmented prairie consisting of 21.7% native annuals (Stinson 2005). This prairie is heavily used for military training and 87% of the area is considered to be in poor condition. Despite this, small, local populations of Taylor's checkerspot within the dispersal range of 91st Division Prairie have historically occurred. For these reasons, I selected to model resistance and connectivity between these two prairies.

Resistance Maps

To develop the spatial layers used for butterfly movement modeling, I used monitoring and management sites to establish a set of optimal habitat patches. I then used two forms of resistance, habitat quality and height-based barriers, to produce two spatial layers used to inform individual movement behavior in the movement model. Vegetation and developed area height was used to generate a spatial layer in which individuals could penetrate or be repelled by barriers of different heights with different probabilities based on boundary survey observations and observed sex-based height limitations (Kaye et al. 2011; Bennett et al. 2013), while habitat quality informed resistance by influencing an individual's movement direction. Empirical data used to inform quality-related movement was extracted from studies on the closely related Baltimore checkerspot (*Euphydryas phaeton*, Drury 1773) (Brown et al. 2017).

To determine quality-based resistance, I built a model to map the quality of the matrix outside of known habitat patches. To develop this resistance layer, I used maximum entropy modeling (Maxent 3.4.4; Phillips et al. 2006), a machine learning method, to develop a categorical resistance layer for the Taylor's checkerspot South Puget Sound range. I chose to use Maxent because it can use both continuous and categorical data, it performs well even with limited training data, it can model geographic distributions using presence-only data, and it has been used to perform species distribution modeling for several other butterfly species (Westwood et al. 2020; Mukherjee and Hossain 2024; Yao et al. 2024).

Seven environmental variables were used in the model, and were selected for their likely influence on movement behavior and habitat quality. Taylor's checkerspot occupancy data from 2013-2022 (EcoStudies Institute, unpub 2023) was used for occurrence points, under the assumption that there is very low resistance where the species is currently found. Vegetation data input into the model included 30 m raster images of existing vegetation type (LANDFIRE 2022a), existing vegetation height (LANDFIRE 2022b), and existing vegetation cover

(LANDFIRE 2022c). Here, existing vegetation type refers to classified, co-occurring terrestrial plant community types, existing vegetation height refers to the average height of the dominant plant community in each cell, and existing vegetation cover refers to the percentage of vegetative cover within each cell. Two categorical vector layers were combined and incorporated in this model to represent soils; Washington state soils (Department of Natural Resources) and JBLM soils (EcoStudies Institute, unpub 2023) where soil type/name was used to differentiate soil classes. Washington state soils data were derived from the Private Forest Land Grading system (PFLG) and soil surveys. Two layers were required for this spatial data, as the Washington state soils layer does not include records on military lands. Additionally, 30 m ground surface elevation (DEM) from the USGS 3D Elevation Program (U.S. Geological Survey) was incorporated into the model. Slope and aspect were both extracted from the DEM and used as additional variables. All layers were clipped to the species' South Puget Sound extent, scaled to 30m, converted to rasters, and the projection and coordinate system for all layers was set to NAD 1983/ UTM Zone 10N.

I used the R package ENMTools (Warren et al. 2021) to check for highly correlated environmental layers (threshold > 0.7) to reduce multicollinearity and improve model interpretability. I used the package ENMeval (Muscarella et al. 2014) to select the appropriate settings for running Maxent, which were as follows: regularization multiplier = 1, cross-validation method = randomkfold, kfolds = 10, features allowed = linear and quadratic. ENMeval was also used to create a bias file based on species occurrence points. This was done to reduce sampling bias under the assumption that the occurrence points extracted from occupancy data were located in areas that are easy to sample and therefore expected to have a higher frequency of points relative to other locations. The bias file was used to preferentially select background points outside of areas with the highest occurrence densities. I generated a total of 10,000 background points. I used a jackknife test to measure variable importance, and selected the model settings that produced the best performing model based on AICc value.

I used the model outputs to create a raster image with the model averages that I then reclassified into categorical quality classes for the final product. Because there are already monitoring and management sites in place, these data were used to generate optimal habitat patches, which were overlaid on top of the matrix map. Where recent management or monitoring had not been conducted, the map was given a categorical value based on the Maxent results for the matrix layer. The final map contained a total of six categories of habitat suitability (Table 1) and was used in the subsequent simulation of the current habitat scenario (Figure 1).

Because adult butterflies have vertical movement restrictions, I created an additional barrier map using vegetation height and anthropogenic development (LANDFIRE 2022b). Four classes of flight-restricting barrier heights were developed using boundary survey observations and available dispersal data on sex-based flight limitations (Grosboll unpub 2011; Bennett et al. 2013; Brown et al. 2017; Kaye et al.). Cells with vegetation less than one meter in height were considered non-barriers with no probability of deflection, whereas vegetation and development at heights ≥ 10 meters were considered impenetrable. A barrier file was then incorporated into the modeling environment with probabilities of deflection and transmission for each barrier type (Table 2).

Movement-only Model

A movement model was developed for adult female Taylor's checkerspot butterflies using HexSim (www.hexsim.net; Schumaker & Brookes, 2018). HexSim is a computational environment developed to simulate wildlife population dynamics and their responses to multiple, interacting stressors. The HexSim framework supports the development of simple to highly complex simulation models and allows for flexible model creation. Additionally, this modeling environment allows for the integration of sparse data and limited mechanisms into simulations. This is advantageous for understanding complex ecological interactions even when data are limited. HexSim is a versatile software, and has been used to create management-focused models for many other at-risk species of varying taxa including birds (Wilsey et al. 2012; Schumaker et al. 2014; Bancroft et al. 2016; Wiens et al. 2017; Heinrichs et al. 2018; Marcot et al. 2025), mammals (Nogeire et al. 2015; Pacioni et al. 2018; Lyons et al. 2018; Heinrichs et al. 2023), amphibians and reptiles (Pomara et al. 2014; Tuma et al. 2016; Rustigian et al. 2023), and fish (Fulford et al. 2011; Snyder et al. 2022). Importantly, HexSim has also been used to develop a movement model for the Fender's blue butterfly (*Icaricia icarioides fenderi*, (Macy) 1931), another at-risk butterfly endemic to the Pacific Northwest (Schumaker 2024). Similarly to the Taylor's checkerspot, this species is a dispersal limited resource specialist that exhibits metapopulation dynamics. I used this modeling platform to explore movement patterns between existing and simulated habitat patches in Marion Prairie and the surrounding grassland. The results of these models were then used in a subsequent connectivity analysis.

The habitat-based resistance map was imported into the HexSim modeling environment as a raster image and the 30-m square pixels were resampled to 30-m hexagons. Hexagons, as opposed to square cells, allows individuals to move in six directions, keeping all neighboring cells equidistant. I used the binary patch map to create a layer consisting only of patch edges. I used this new layer for the initialization of individuals with one individual occupying each edge hexagon for a total of 2372 edge hexagons and individuals populating all simulated scenarios. This initialization method is consistent with the similar Fender's blue connectivity analysis and was used to improve computational efficiency, as the objective of the analysis was to describe inter-patch connectivity (Schumaker 2024). Larger patches contained more edge cells than smaller patches and hence larger patches contained more individuals at the beginning of each simulation than did smaller patches.

I developed the spatially explicit, individual-based movement model using data gathered from checkerspot movement and dispersal studies. To best reflect sex-based differences in flight behavior and accounts of colonization and dispersal events, I used a combination of species-specific and surrogate-species data to inform movement events. Female Taylor's checkerspot adults are the more sedentary sex, frequently observed flying in short, low bursts to and from host or nectar plants (Bennett et al. 2013; Kaye et al. 2011). Still, Bennett et al. (2013) observed a maximum single-day female track length of 288 m in their Oregon. In a study of the closely related Bay checkerspot (*Euphydryas editha bayensis*, Sternitsky 1937), one female was observed dispersing 3 km in four days, with evidence of colonization occurring up to 4.5 km in distance (Harrison 1989). Dispersal >5 km appears to be unlikely in Edith's checkerspots (*Euphydryas editha*, Boisduval, 1852); however, one Bay checkerspot adult was recorded moving 7.6 km in a 1998 report (USFWS 1998; Stinson 2005). In dispersal studies of the Glanville fritillary (*Melitea cinxia*, (Linnaeus) 1758), a species within the same tribe

(Melitaeini), no colonization events were seen >6.8 km and the majority of colonization events were observed within 2.3 km (Nieminen 2004). To capture this variability in the model, individuals were permitted a maximum lifetime movement of 4020 m distributed across 100 iterations of ≤150 m incremental movements. This distance was calculated using a maximum daily flight distance observed *in situ*, multiplied by the average lifespan for adult checkerspots. Each individual moved independently, and individual movement stopped after the individual either reached their maximum distance or maximum movement iterations.

Movements occurred across the classified habitat map, with path lengths and movement direction as a function of habitat quality. In HexSim, percent auto-correlation determines the degree to which the model produces straight-line movements or a true random walk. I assigned the percent auto-correlation for individuals across each landscape class based on empirical Baltimore checkerspot data describing their flight paths and mean turning angles (Brown et al. 2017). Movement was tallied after each iteration and complete path lengths were recorded at the end of every simulation. Movement loops terminated after an individual either reached their maximum dispersal distance or after 100 iterations, whichever came first. I ran 1000 replicate model runs and generated a combined logfile including the number of iterations each individual required to reach their maximum movement distance, the total distance moved, the total distance remaining, current movement distance, and individual path length.

Connectivity Analysis

I analyzed the patch-to-patch dispersal simulated in the butterfly movement model using the utility LINK (Schumaker 2024). LINK is an open-source C-language software utility developed for the purpose of overcoming limitations of other connectivity assessments by incorporating biological and behavioral detail. This software can simulate movements or use movement generated from another program. It has few constraints and simple input requirements including a CSV-formatted patch map and a record of all individual movement events over a given number of replicates. I used a binary patch map and six functional codes to transform the raw movement data into potential and functional connectivity maps and matrices of interpatch dispersal using the LINK utility. For all functions, map geometry was extracted from HexSim and held constant at 1855 rows, 1896 minimum columns, and 1896 maximum columns.

I constructed a compact dispersal record data table from the combined logfile, producing one line movement strings for each individual where: N_i = the individual, and H_1 H_2 H_3... H_N = the hexagon IDs where the individual had moved (Figure 2). I then constructed a linkage table containing movement data connecting pairs of optimal patches. These one line strings of distinct movement records are represented as: X_i = the starting patch, Y_i = the ending patch, N_i = the number of hexagons in path i, and H_1, H_2, H_3… H_N = the associated hexagon IDs. Where a movement began and ended within the same patch, dispersal was recorded as X_i, Y_i, 0. Additionally, I built a dispersal kernel illustrating connected and isolated optimal patches using the LNK data table and produced a matrix report or emergent dispersal kernel with individual movement probabilities to and from a given patch.

Because the dispersal data did not follow a normal distribution, consisted of small sample sizes, and had several outliers, Kruskal-Wallis tests were performed as an alternative to an ANOVA to determine if movements under the habitat addition scenarios were significantly different. A

Dunn's Test was then used to compare scenarios. Each comparison looked at dispersal to and from Marion Prairie, excluding movement between the patches located within the prairie and averaged to avoid overestimating dispersal for scenarios with greater numbers of patches. Specifically, I averaged immigration to Marion Prairie by dividing by the number of patches outside of Marion Prairie, while emigration out of Marion Prairie was averaged based on the number of patches inside Marion Prairie.

Prior to developing and simulating habitat patch addition scenarios, I ran a connectivity analysis for the current habitat scenario to establish a baseline of movement between Marion Prairie patches and neighboring patches of optimal habitat. No movement between these regions was observed across 1000 replicates (mean immigration = 0.000, mean emigration = 0.000, SD immigration = 0.000, SD emigration = 0.000).

I conducted an additional analysis to determine whether any direct movement between the large southwestern and southeastern patches neighboring Marion Prairie occurred with the presence of new patches. No individuals moved between these sites in any of the tested scenarios, so no additional tests were performed for this east-west movement type.

Multi-generation Movement

Because the LINK connectivity analysis only accounted for a single generation of movement, I quantified multi-generational dispersal potential using a Markov chain approach implemented in R with the expm package (Maechler et al. 2010). This used the scenario's matrix of patch-to-patch dispersal probabilities generated with Link, where $P_{g=1}[x,y]$ represented the probability of a butterfly dispersing from patch i to patch j in a single generation. The multi-generational probabilities were calculated using matrix powers, as seen in (1).

$$P_{g=n}[x,y] = \sum_{k=1}^{n} a_{xk}b_{yj} = a_{x1}b_{1y}+a_{x2}b_{2y}+ \dots +a_{xn}b_{yn}, \tag{1}$$

meaning that the second generational probabilities of dispersal for $P_{g=2}[x,y]$ would be found by taking each probability for patch x, multiplying these by the probability of dispersal from that patch to patch y, and taking the total sum of those products. $P_{g=n}[x,y]$ gives the probability that a line of individuals could start in patch x and end up in patch y after n generations, while $\sum_{k=1}^{n} P_{g=n}[x,y]$ represents the probability that a line of individuals could start in patch x and ever visit patch y. For each scenario, I calculated the movement to and from patches within Marion Prairie. These movement probabilities were then averaged for each scenario group.

Scenario Development

After the current habitat simulation and subsequent connectivity analysis were conducted, Marion Prairie was identified as an isolated cluster of patches within the dispersal range of neighboring prairies that are not currently connected through dispersal (Figure 1). Due to its lack of connectivity and its proximity to prairies to both the northwest and northeast, this area was selected as a connectivity management priority. Thus, all further experimentation and analyses were restricted to this area.

I developed experimental habitat management scenarios in which I manipulated the quantity and size of additional habitat patches. While patch arrangement and size varied between scenarios, the total area of new patches was kept constant across all scenarios with a 5% (27.69 ha) increase in total habitat area compared to the current habitat scenario. In this process, I created five scenarios across a gradient of one to thirty additional patches including: a “30-patch” scenario, where thirty 0.92 ha patches were added; a “20-patch” scenario, where twenty 1.38 ha patches were added; a “10-patch” scenario, where ten 2.77 ha patches were added; a “5-patch” scenario, where five 5.54 ha patches were added; and a “1-patch” scenario where a single 27.69 ha patch was added. Five random variations of each scenario were created for a total of 25 simulated landscapes.

New patches were placed randomly in each scenario. Patch placement was restricted to the Marion Prairie buffer and outside of any cell that was already a current patch or barrier. Consistent with the current habitat scenario, 2416 individuals were initiated across the current habitat patch edges for each experimental scenario. Individuals then moved across the unique habitat map associated with their respective scenario consisting of both newly placed and original patches. I replicated each scenario 1000 times and conducted a connectivity analysis for each replicate using the methods previously described for the current habitat scenario.

I conducted an intra-scenario analysis to determine how similar or dissimilar dispersal results were across each scenario group. Each replicate within a scenario group performed similarly to others within the same group (immigration $p = 1.0$, emigration $p > 0.1$). This indicates that within-scenario patch placement did not have a significant influence on dispersal probabilities within any of the five scenario groups. Because of this, scenario group values were averaged, and treated as equal for additional analyses.

"Smart" Scenarios

After examining the results of these experimental simulations, I conducted an additional connectivity analysis using Circuitscape (Hall et al. 2021) to determine whether specific patch placement would support higher dispersal probabilities than randomized patch placement. I used the barrier layer developed for the movement model as the resistance layer, with a high resistance set for all barrier cells and low resistance elsewhere. This resistance layer was used, rather than the quality layer in order to determine the optimal placement of new habitat. This was under the assumption that areas of lesser habitat quality with low-vegetation stature are more practical for restoration management while forested or densely vegetated areas require extensive work to restore and/or may not be possible to restore to optimal conditions. I used the current habitat patch map for the pairwise iteration function, which created a cumulative current map of flow between all patches. Because the barrier layer for this model was considered unchangeable, meaning no new patches could be placed within cells classified as a barrier, areas of higher current indicated possible locations that could host new patches in order to make dispersal more likely. I developed a new habitat map using a combination of the results from this model and the best performing patch size of the previous experiment, keeping the total area of the new habitat consistent with prior scenario development. This simulation was considered a "smart" model, as the expectation was that strategically placed patches, rather than randomly placed patches, would support the greatest amount of dispersal.

Results

Resistance Map

The habitat-based resistance model had high AUC scores for both training (mean = 0.893, SD = 0.0001) and test (mean = 0.893, SD = 0.004) data. Habitat-based resistance values across the South Puget Sound ranged from 0.00 to 0.78, with lower values indicating higher resistance and higher values indicating lower resistance. A total of 17 km^2 of the South Puget Sound extent was predicted to have an occurrence probability of ≥ 0.7, and no areas were given a probability greater than 0.79. I reclassified these results using intervals of resistance ranging from very low resistance to very high resistance which was subsequently combined with the management patch layer and barrier layer previously described.

The results of the analysis of variable contributions indicated that soil type had the highest contribution and permutation importance among variables (Table 3). Similarly, results from the jackknife test of variable importance indicated that the soils variable had the highest gain when used in isolation and decreased gain the most when omitted. This suggests that this variable was the most informative layer for predicting distribution, while existing vegetation type had the second highest gain across jackknife test results. At a suitability threshold of 0.70, Spanaway gravelly sandy loam soil with a slope of 0-3% accounted for 73% of suitable, or low-resistance area, while the same soil type with a slope of 3-15% accounted for an additional 17%. With the same threshold applied, 77% of suitable habitat occurred in the Willamette Valley upland prairie vegetation type.

Habitat Restoration Scenarios

The 30-patch scenario showed the greatest increase in single-generation, patch-to-patch dispersal probabilities to and from Marion Prairie patches (Figure 3). Probabilities of both immigration (mean = 0.004, SD=0.002) and emigration (mean = 0.029, SD=0.006) were significantly greater than those of the current habitat scenario (mean imm = 0.000, mean em = 0.000, SD imm = 0.000, SD em =0.000), 1-patch (mean imm <0.001, mean em <0.001, SD imm<0.001, SD em<0.001), 5-patch (mean imm < 0.001, mean em = 0.007, SD imm<0.001, SD em=0.010), and 10-patch (mean imm <0.001, mean em = 0.012, SD imm<0.001, SD em =0.004) scenarios (p <0.001) (Figure 4A-B). Emigration in the 30-patch scenario also differed significantly from the 20-patch scenario (mean 0.026, SD =0.011, p =0.02), though differences in immigration were not significantly different between the two (mean =0.004 , SD = 0.002, p = 0.99).

The 20-patch scenario supported the second highest rates of dispersal between Marion Prairie and neighboring patches, and differed significantly from the current habitat, 10-patch, 5-patch, and 1-patch scenarios (p < 0.001). The 10-patch scenario differed significantly from the 5-patch, 1-patch, and current habitat scenarios for emigration (p < 0.001), but did not differ significantly from these scenarios in immigration rates (p > 0.1). The 1-patch scenario performed most similarly to the current habitat scenario, and there was no statistically meaningful difference between their immigration or emigration rates (p = 1, p = 0.96), nor was there a significant difference between the current habitat and 5-patch scenarios (p = 0.93, p = 0.87).

"Smart" Scenarios

In the single generation analysis, the "smart" scenario increased both immigration and emigration probabilities when compared to the current habitat scenario and the best performing randomized scenario. The probability of both immigration (0.005) and emigration (0.039) were higher in the Smart 30 scenario than the median of the 30-patch scenario (Figure 5). However, one randomization within the 30-patch scenario group outperformed the Smart 30 scenario in both immigration and emigration and one randomization within the 20-patch scenario group outperformed the Smart 30 scenario in immigration.

Multi-generation Movement

The randomized 30-patch scenario supported the highest overall dispersal probabilities across 100 generations with an immigration probability of 0.025 at year 100 and an emigration probability of 0.241 at year 100 (Figure 6). The randomized 20-patch scenario had the second highest overall immigration probability (0.020) and the third highest emigration probability (0.197). The Smart 30 scenario supported the third highest immigration (0.013) and second highest emigration (0.240) at year 100. The 1-patch scenario supported the least movement, with an immigration probability of 0.000 and an emigration probability of 0.001.

Immigration and emigration values differed by an order of magnitude with higher probabilities of individuals leaving Marion Prairie and ending in neighboring exterior patches across all scenarios when compared to individuals entering Marion Prairie from neighboring patches. However, the pattern of dispersal differed between the two directions of movement. For example, the randomized 30-patch scenario and Smart 30 scenario followed a similarly high trajectory for emigration, while Smart 30 fell below the randomized 30-patch scenario by a value of 0.01 for immigration.

Discussion

The decline of grassland connectivity is a major contributor to the population decline of specialist butterfly species and a driver of reduced species richness at local, regional, and global scales (Saunders et al. 1991; Brückmann et al. 2010). Improving connectivity in fragmented landscapes is necessary for successful conservation management yet the quantity, size, and arrangement of restored habitat patches is species-specific and may differ depending on management priorities (Hill et al. 1996; Schultz and Crone 2005; Dover and Settele 2009). For the Taylor’s checkerspot, adding numerous, small habitat patches between fragmented areas led to the greatest increase in dispersal between these areas when simulated both for a single generation and across a 100-year period. While there is debate regarding whether few large or several small patches are better at conserving species in fragmented landscapes, the appropriate size, quantity, and arrangement of patches for improving at-risk species conservation is species- and system dependent (Bender et al. 1998). The findings of this study are consistent with current connectivity literature, as specialists and small species tend to have a smaller gap threshold and connectivity for these species can be improved by managing these gaps with appropriately spaced stepping stones (With 1997; Sutcliffe et al. 2003; Schultz and Crone 2005; Bentrup 2008; Dover and Settele 2009; Rocha et al. 2021). This indicates that continuous corridors of habitat may not be necessary for the recovery of this species, but rather that continuing to manage current patches and restoring and maintaining smaller stepping stones are both important for the long-term survival of this species, potentially making reconnecting fragmented patches more logistically feasible for land managers.

The results also indicate that managers likely have some flexibility in the placement of newly restored patches. In this study, multi-generation analysis resulted in the highest dispersal probabilities in the scenario group with randomly placed (as opposed to strategically placed) small patches. Immigration rates were notably higher in the randomized 30- and 20-patch scenarios over time, while emigration rates were comparable between the randomly and strategically placed 30-patch scenarios. Thus, it appears that there are many options for increasing connectivity in this landscape and that spreading out stepping stones across the landscape will be more effective than creating a single corridor. This flexibility can allow managers to adapt restoration plans to other quality-measures and stressors impacting dispersal behavior that were not accounted for in this study, such as light pollution, human activity, microclimate conditions, and recent nearby disturbances (Sawyer et al. 2011)

While least-cost-path analysis is a popular method for studying habitat linkage, it may not be equally informative for all species (Sawyer et al. 2011; Leoniak et al. 2012; Avon and Bergès 2016). Despite placing the Smart 30 patches in a direct path from Marion Prairie to the nearest neighboring patches, randomized patch placement supported comparable or higher dispersal probabilities over time. Several factors could have contributed to this. For example, strategic patch placement to create least cost corridors may be more important for larger species with greater dispersal abilities like wolves (Huck et al. 2010, 2011; Carroll et al. 2012), cougars (LaRue and Nielsen 2008), lynx (Huck et al. 2010), swift foxes (Alexander et al. 2016), fishers, and bobcats (Leoniak et al. 2012). Conversely, smaller species with less direct dispersal behaviors and more limited dispersal abilities may benefit from a larger number of movement options. Individuals rarely disperse in a single route (Pinto and Keitt 2009; Sawyer et al. 2011) and some versions of the randomized scenarios may have provided the alternative movement routes necessary for connecting habitat patches across the matrix of varying resistance values and barriers in this study area and given this species' unique dispersal behavior and limitations. Cost methods are also sometimes correlated with Euclidean distance, which may not capture true factors of movement such as mortality risk or behavioral aversion (Pullinger and Johnson 2010; Etherington and Holland 2013). Future research is needed to better identify the appropriateness of using different connectivity modeling methods for various taxa.

Modeled scenario planning and experimental management allows researchers to assess management strategies across broad temporal scales without the labor and time investment associated with field experimentation (Dunning et al. 1995; Schumaker and Brookes 2018). This is particularly important in at-risk ecosystems and with at-risk populations, as is the case for this region and species. As habitat fragmentation continues to threaten this species, improving methods for identifying areas for targeted habitat restoration can help managers efficiently increase habitat connectivity and facilitate dispersal between patches. This research aligns with Priority 1 recovery actions codified in the Species Recovery Plan (U.S. Fish and Wildlife Service 2022) by providing both current and experimental patch-patch functional connectivity metrics and by providing a flexible framework for improving conservation targets as more data become available. Specifically, while the connectivity analysis from this study can provide insights into habitat restoration, the developed movement model can be expanded upon with the addition of further stressors and management scenarios which can then be used to forecast population outcomes for this species.

Connectivity models can also provide useful information about strategic management when empirical data on dispersal behavior is lacking. However, the lack of empirical data can also limit the usefulness of connectivity analyses as the assumptions made in the development of the model may overlook important biological processes influencing resistance and movement. To avoid overly simplified movement events and to incorporate biological nuance, the movement model developed for this study used empirical data to convert the observed turning angles of a surrogate species into autocorrelation. This allowed individuals to interact with a non-binary map with a gradient of resistance that is more biologically realistic than the approach often used in cost analysis and similar connectivity analyses (Dover and Settele 2009; Evans et al. 2020).

Because Hexsim supports the addition of a barrier layer, I was also able to incorporate species- and sex-specific behavioral responses to edge cells and vegetation height (Kaye et al. 2011; Bennett et al. 2013). These behaviors were kept consistent across all modeled scenarios, regardless of the means for determining patch placement. Zones considered available for habitat restoration (new patches) were also kept consistent across all scenarios. Cells in these zones were defined as excluding a barrier value or a current habitat value. Barrier cells were excluded in this way to keep restoration scenarios more realistic and applicable to *in situ* conservation efforts, as areas with more canopy coverage are no longer able to provide the appropriate soil quality to support adequate Taylor's checkerspot resources, and restoration of densely vegetated areas is often much more time and energy intensive. Likewise, current habitat cells were excluded to avoid manipulating patch size.

For model simplicity, life history traits, such as per capita reproduction and mortality rates, were excluded from the movement model. Consequently, model results do not reflect population outcomes but rather explicitly depict changes to inter-patch movement. However, connectivity and gene flow are directly related to population outcomes, and, therefore, one can predict that improving connectivity to isolated patches can provide positive benefits to local population dynamics. Life history traits were also not incorporated into calculations of long-term dispersal trends. Insect dispersal behavior is influenced by weather conditions (e.g., temperature, precipitation, and wind speed) and prior habitat conditions. Habitat fragmentation may modify the quality of remaining resource patches, with smaller patches experiencing edge effects or less than optimal environmental conditions (Saunders et al. 1991; Dover and Settele 2009). While the movement model from this study is non-binary, there could still be important environmental data missing, such as patch heterogeneity, which likely plays an important role in site use and dispersal behavior, and habitat patches may experience different environmental conditions or stressors (Thomas et al. 2001).

While prior studies indicate that adult dispersal is important for maintaining metapopulation dynamics (Harrison 1989; Hill et al. 1996; Gutiérrez et al. 1999; Öckinger 2006; Bonelli et al. 2013; Meyer et al. 2024), it is possible that larval dispersal can also play an important role. Weiss et al. (1987) reported that Edith's checkerspot late instars can move ~10 m a day, though the distance of their movement also plays a role in their growth rates. More studies on larval dispersal are needed to better understand the role it may play in site selection and metapopulation dynamics.

Long-term dispersal trends are also influenced by movement direction. In each analysis of experimental management, emigration rates were consistently higher than immigration rates. This is expected, as individuals from the larger neighboring patches to the east and west of Marion Prairie are more likely to stay within these larger patches than to immigrate into Marion Prairie, whereas individuals starting within Marion Prairie had little to no patch interior to explore or remain in for each movement event and hence tended to move to a new patch. This is similar to observed movement behavior, including in other butterfly studies, with individuals in larger patches being less prone to find patch edges or less likely to leave habitat patches with plentiful resources than individuals persisting in smaller patches whom are more likely to leave in search of additional resources and mates (Hanski and Thomas 1994; Hill et al. 1996; Mennechez et al. 2003; Schultz and Crone 2005). A fragmentation study of the bog fritillary (*Boloria eunomia*, (Esper) 1799) also found that female emigration increased in fragmented landscapes compared to continuous landscapes, potentially to limit male harassment or to distribute the risk of offspring mortality (Mennechez et al. 2003; Turlure et al. 2011; Severns and Breed 2014; U.S. Fish and Wildlife Service 2022). However, immigration into these small patches remains important for prairie metapopulation connectivity, maintaining healthy genetic diversity, and for safeguarding a portion of local populations from extreme events. Therefore, selecting restoration sites that improve both immigration and emigration probabilities over time will likely provide the best conservation outcomes.

The results of suitability modeling and resistance layer development for this study confirm that the occurrence of this species is highly linked to the presence of Spanaway gravelly sandy loam soils and Willamette Valley upland prairie vegetation. These glacial outwash soils are characterized as being very deep, with low slopes and occurring at low elevations (30 to 150 m). Additionally, they are somewhat excessively drained and generally experience dry summers and wet winters. In good condition, these prairie soils support short-statured bunchgrass like Roemer's fescue (*Festuca roemeri* (Elmer)) and native forbs like the common woolly sunflower (*Eriophyllum lanatum* (Pursh) Forbes) and small camas (*Camassia quamash* (Pursh) Greene). However, the soil type that best supports these native prairie vegetation communities is also susceptible to invasion by both native and non-native invaders. Scotch broom (*Cytisus scoparius* (L.) Link) and Himalayan blackberry (*Rubus armeniacus* (Focke)) both grow readily in soils with low water-holding capacity and limited canopy cover, while native Douglas fir (*Pseudotsuga menziesii*, (Mirbel) Franco) has colonized prairie soils where long-term fire suppression has occurred. Encroachment by these species can restrict movement, particularly by height-limited females, by reaching heights > 1 meter and by creating dense vegetation patches that make crawling, a behavior observed in newly emerged females, difficult. While removal of prairie invaders may not immediately create optimal habitat conditions, it may provide additional dispersal pathways through prior movement barriers.

The results from this model support the growing call for expanding grassland conservation, specifically as it pertains to insect conservation in the face of global insect decline (Schultz and Dlugosch 1998; Henderson et al. 2018; Lark 2020; Mason et al. 2021; Scherer et al. 2021; Mallick et al. 2023; Edwards et al. 2025). In a recent study, Edwards et al. (2025) found that common North American butterfly species are declining at an alarming rate, with 13 times as many species declining as increasing. In the Pacific Northwest, more than twice as many common butterfly species are declining rather than increasing, with many of these species associated with or specific to grasslands, including the Sonoran skipper (*Polites sonora*, (Scudder) 1872) and purplish copper (*Lycaena helloides*, (Boisduval) 1852). For grassland specialists, the loss of connectivity in these ecosystems has led to reduced species richness, increased extinction rates, and led to the replacement of these specialists by generalist species (Polus et al. 2007; Brückmann et al. 2010). Understanding the likelihood of improving connectivity for these species with a connectivity analysis such as this one can allow managers to most effectively choose sites to restore and reintroduce individuals to (Day et al. 2020; Diengdoh et al. 2023; Schumaker 2024). During a time of rapid species decline, a combination of modeling and field research is increasingly necessary for finding management solutions that have the best chance of successfully achieving conservation goals under the increasing pressures and limitations placed on wildlife biologists and land managers.

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Tables

Table 1. Final habitat quality resistance classifications based on maximum entropy modeling and known management sites.

Numeric Classification	Interpretation	Area (km^2)
0	Very High Resistance	1102.78
1	High Resistance	1006.88
2	Moderate Resistance	171.51
3	Low Resistance	123.92
4	Very Low Resistance	22.43

Table 2. Probabilities used in creating the habitat barrier file. Available dispersal surveys show that female checkerspots infrequently cross barriers greater than 3m in height. Additionally, no quantitative data exist for the probabilities of female butterflies exiting a matrix landscape after entering it. For this experiment, the same probabilities of transmission and deflection were used to both enter and leave barrier hexagons. Where vegetation and development were <1 meter, unrestricted flight was allowed.

Barrier Class	Heights (meters)	Probability of Deflection	Probability of Attempting	Probability of Succeeding
No Barrier	<1	0	1	1
1	1-2	0.79	.206	1
2	3-4	0.805*	.197	.99
3	5-9	0.926*	.148	.50
4		1	0	0

* Linear interpolation was used for calculating probabilities of deflection for barriers 2 & 3.

Table 3. Variable contributions to the habitat-based resistance model averaged across 10 replicates.

Environmental Variable	Percent Contribution	Permutation Importance
Soils	50.5	92.2
Existing Vegetation Type	37.7	4.4
Existing Vegetation Height	11.5	0.8
Elevation	0.2	1.8
Existing Vegetation Cover	0.1	0.5
Aspect	0	0.2
Slope	0	0

Figures

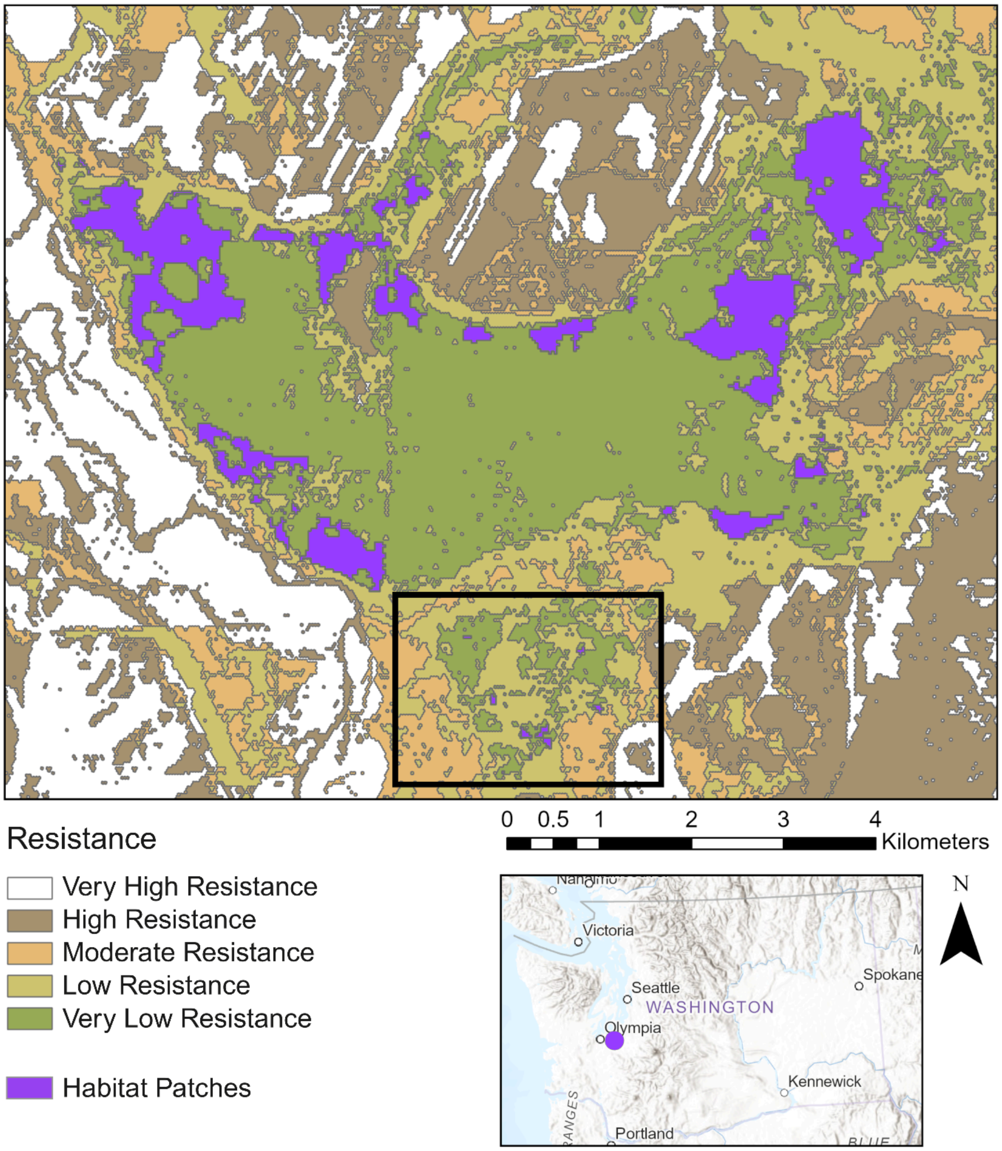


Figure 1. Current habitat map, focused on the largest area of suitable Taylor's checkerspot habitat in the South Puget Sound. Current patches are highlighted in purple, while resistance is categorized from very high to very low. The black box highlights Marion Prairie, an area consisting of small, isolated habitat patches. This area was the focus of all simulated habitat additions.

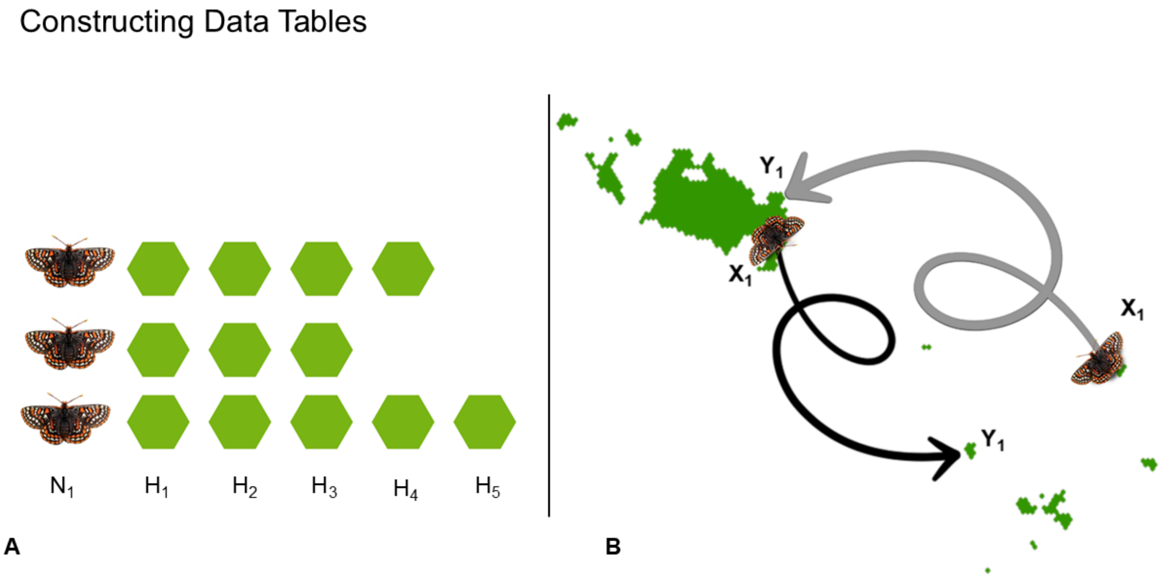


Figure 2. Graphical representation of constructing connectivity data tables where (A) represents compact dispersal records with N_i = the individual, and H_1 H_2 H_3... H_N = the hexagon IDs where the individual had moved. (B) represents linkage table construction where connected pairs of patches are recorded. Here, X_i = the starting patch, Y_i = the ending patch, N_i = the number of hexagons in path i, and H_1, H_2, H_3… H_N = the associated hexagon IDs. The gray arrow represents one individual's movement path while the black arrow represents a second individual's movement path.

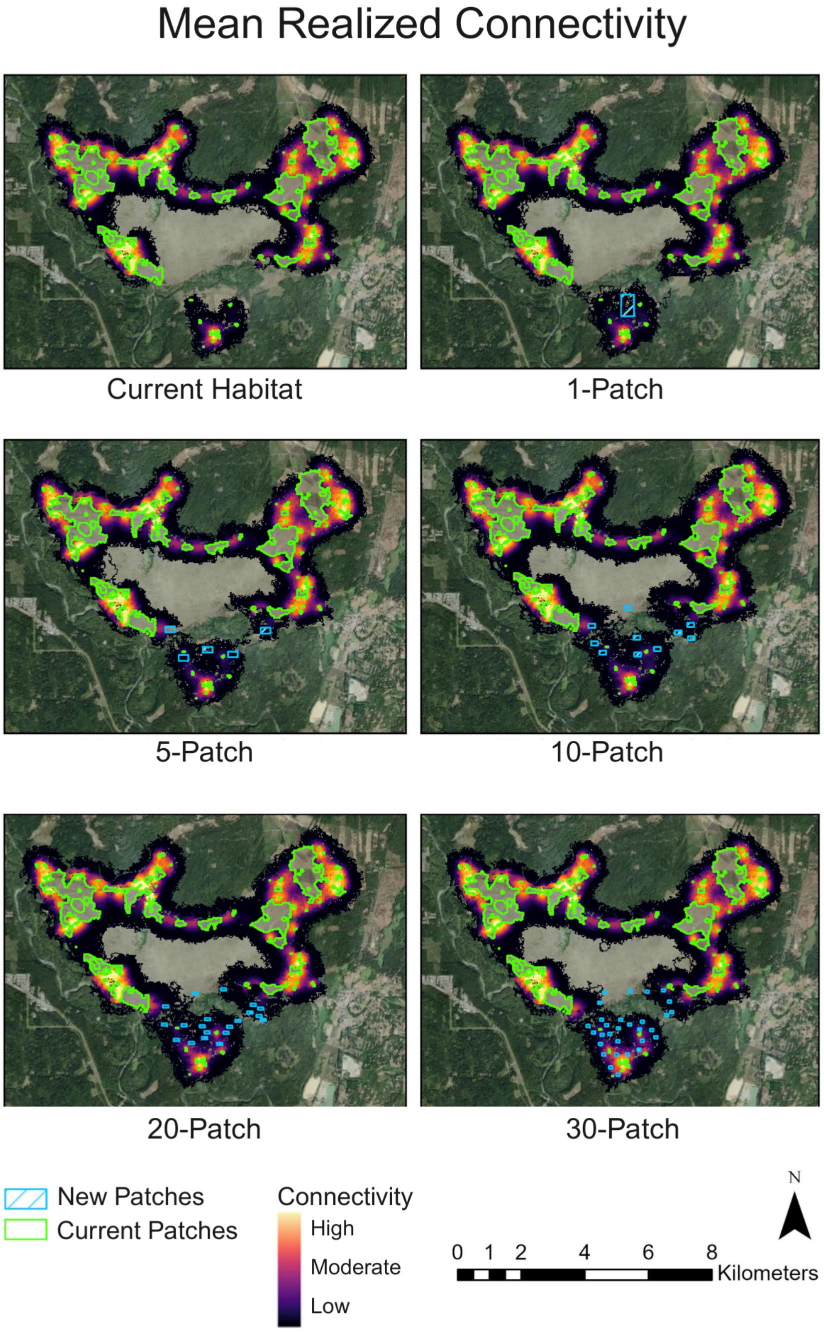
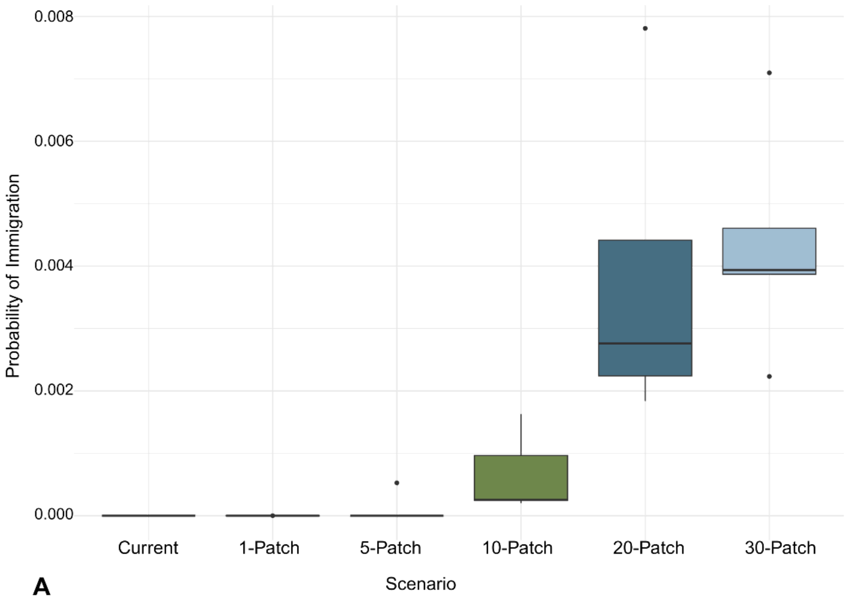


Figure 3. Functional connectivity between all patches averaged across 1000 replicates. Current habitat patches are displayed in green and an example of randomized new patch arrangement is overlaid in blue. Patch-to-patch movement chains are seen avoiding barriers like treelines.



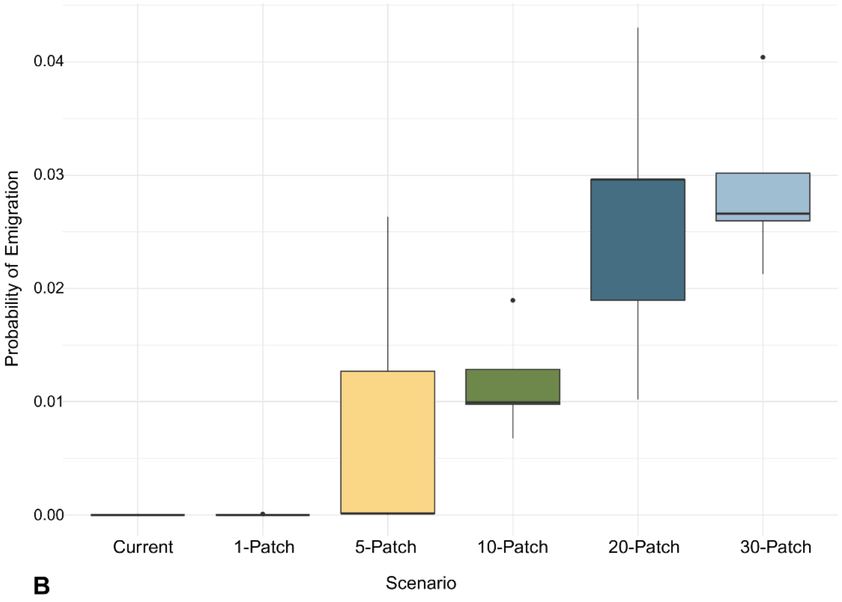


Figure 4. Box-and-whisker plots of the dispersal probabilities for each scenario group with (A) immigration and (B) emigration shown independently. The median of each scenario group is depicted as a horizontal bar, while boxplot whiskers indicate 1.5 times the interquartile range.

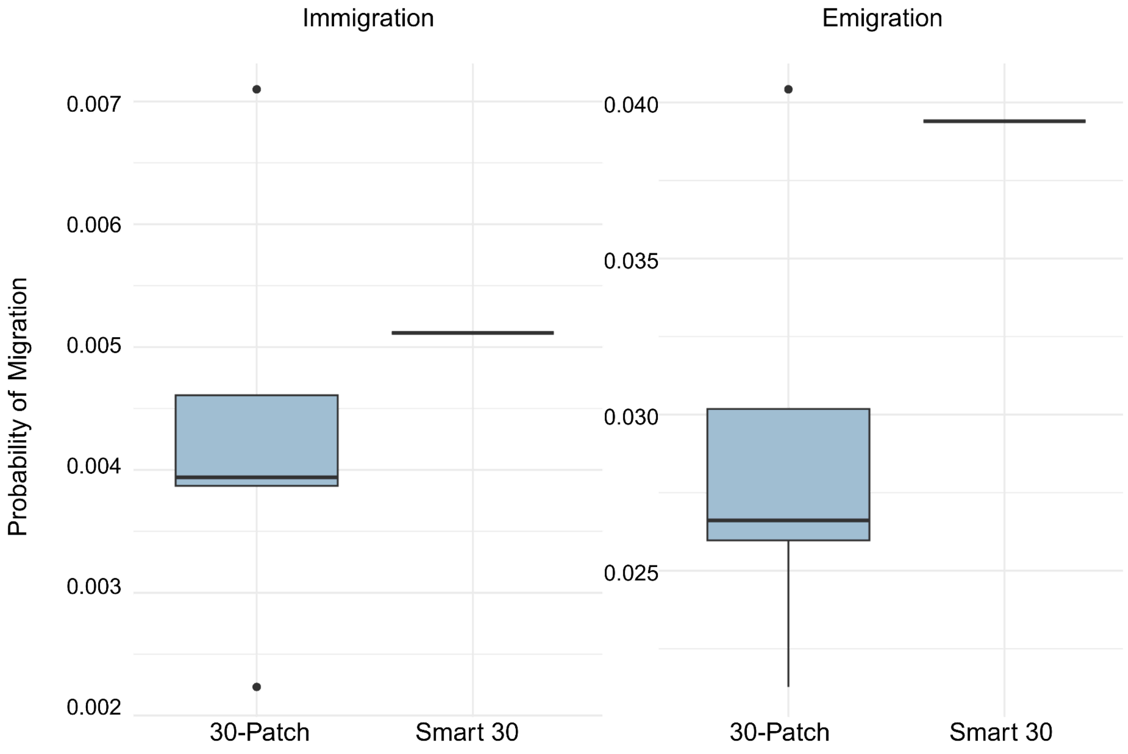


Figure 5. Box-and-whisker plots of the probability of immigration and emigration for the Smart 30 scenario compared with the best performing randomized modeled immigration, the 30-patch scenario.

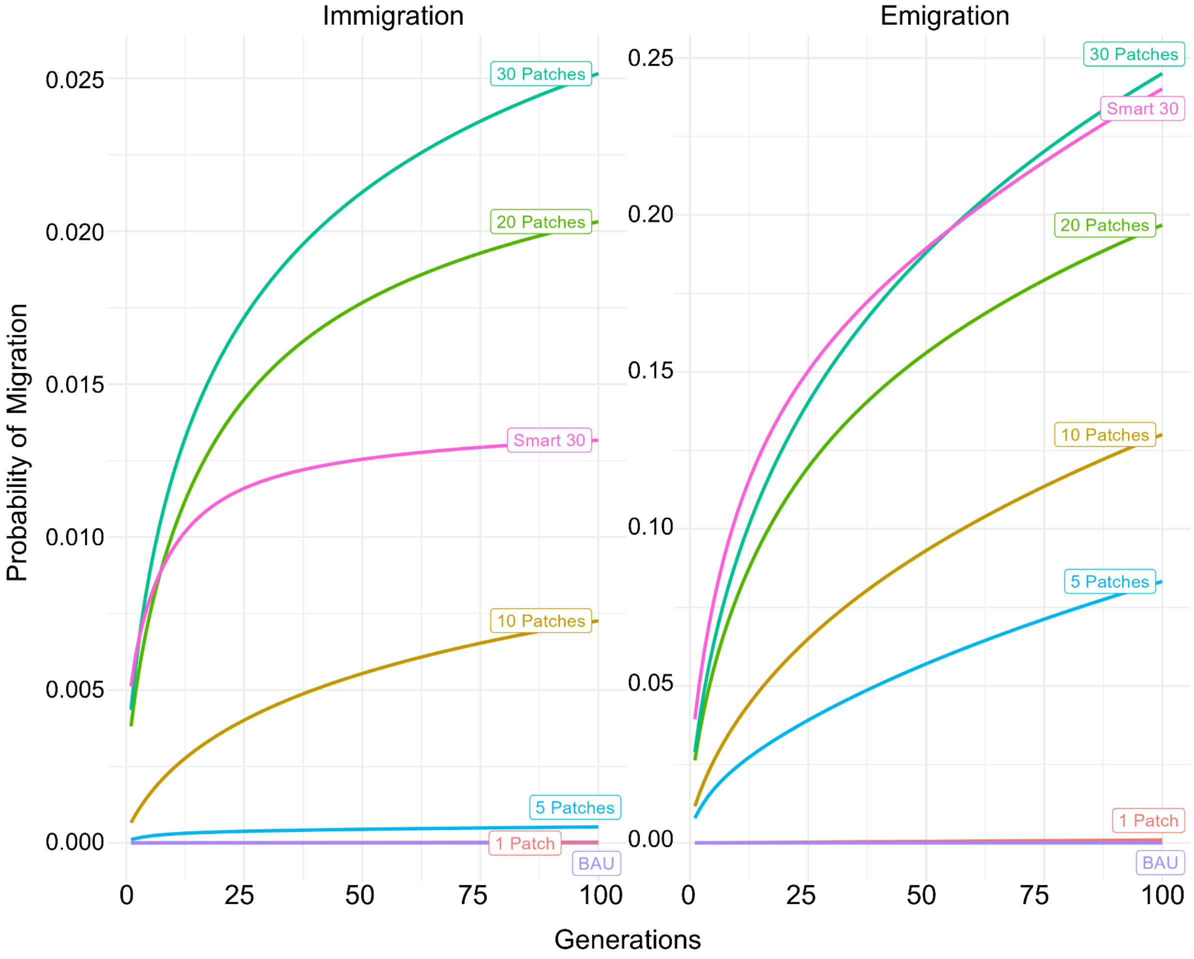


Figure 6. Probabilities of dispersal between Marion Prairie and neighboring patches over 100 generations for each scenario group.

References

Alexander JL, Olimb SK, Bly KLS, Restani M (2016) Use of least-cost path analysis to identify potential movement corridors of swift foxes in Montana. J Mammal 97:891–898. https://doi.org/10.1093/jmammal/gyw032

Avon C, Bergès L (2016) Prioritization of habitat patches for landscape connectivity conservation differs between least-cost and resistance distances. Landsc Ecol 31:1551–1565. https://doi.org/10.1007/s10980-015-0336-8

Bancroft BA, Lawler JJ, Schumaker NH (2016) Weighing the relative potential impacts of climate change and land‐use change on an endangered bird. Ecol Evol 6:4468–4477. https://doi.org/10.1002/ece3.2204

Bender DJ, Contreras TA, Fahrig L (1998) HABITAT LOSS AND POPULATION DECLINE: A META-ANALYSIS OF THE PATCH SIZE EFFECT. Ecology 79:517–533. https://doi.org/10.1890/0012-9658(1998)079[0517:HLAPDA]2.0.CO;2

Bennett VJ, Pack SM, Smith WP, Betts MG (2013) Sex-biased dispersal in a rare butterfly and the implications for its conservation. J Insect Conserv 17:949–958. https://doi.org/10.1007/s10841-013-9577-5

Bentrup G (2008) Conservation Buffers: Design Guidelines for Buffers, Corridors, and Greenways. Department of Agriculture, Forest Service, Southern Research Station, Asheville, NC

Blomfield A, Menéndez R, Wilby A (2023) Population synchrony indicates functional connectivity in a threatened sedentary butterfly. Oecologia 201:979–989. https://doi.org/10.1007/s00442-023-05357-2

Bonelli S, Vrabec V, Witek M, et al (2013) Selection on dispersal in isolated butterfly metapopulations. Popul Ecol 55:469–478. https://doi.org/10.1007/s10144-013-0377-2

Brown LM, Fuda RK, Schtickzelle N, et al (2017) Using animal movement behavior to categorize land cover and predict consequences for connectivity and patch residence times. Landsc Ecol 32:1657–1670. https://doi.org/10.1007/s10980-017-0533-8

Brückmann SV, Krauss J, Steffan‐Dewenter I (2010) Butterfly and plant specialists suffer from reduced connectivity in fragmented landscapes. J Appl Ecol 47:799–809. https://doi.org/10.1111/j.1365-2664.2010.01828.x

Carroll C, McRAE BH, Brookes A (2012) Use of Linkage Mapping and Centrality Analysis Across Habitat Gradients to Conserve Connectivity of Gray Wolf Populations in Western North America. Conserv Biol 26:78–87. https://doi.org/10.1111/j.1523-1739.2011.01753.x

Conradt L, Bodsworth EJ, Roper TJ, Thomas CD (2000) Non-random dispersal in the butterfly Maniola jurtina : implications for metapopulation models. Proc R Soc Lond B Biol Sci 267:1505–1510. https://doi.org/10.1098/rspb.2000.1171

Conradt L, Roper TJ, Thomas CD (2001) Dispersal behaviour of individuals in metapopulations of two British butterflies. Oikos 95:416–424. https://doi.org/10.1034/j.1600-0706.2001.950306.x

Crawford RC, Hall H (1997) Changes in the South Puget Prairie Landscape. Washington Department of Natural Resources and The Nature Conservancy

Day CC, Zollner PA, Gilbert JH, McCann NP (2020) Individual-based modeling highlights the importance of mortality and landscape structure in measures of functional connectivity. Landsc Ecol 35:2191–2208. https://doi.org/10.1007/s10980-020-01095-5

Debinski DM, Holt RD (2000) A Survey and Overview of Habitat Fragmentation Experiments. Conserv Biol 14:342–355. https://doi.org/10.1046/j.1523-1739.2000.98081.x

Department of Natural Resources SCS USDA Forest Service, Washington State University Washington SOILS

Department of the Interior (2013) Endangered and Threatened Wildlife and Plants; Determination of Endangered Status for the Taylor's Checkerspot Butterfly and Threatened Status for the Streaked Horned Lark; Final Rule. Fed Regist 78:

Diengdoh VL, Ondei S, Amin RJ, et al (2023) Landscape functional connectivity for butterflies under different scenarios of land-use, land-cover, and climate change in Australia. Biol Conserv 277:109825. https://doi.org/10.1016/j.biocon.2022.109825

Dover J, Settele J (2009) The influences of landscape structure on butterfly distribution and movement: a review. J Insect Conserv 13:3–27. https://doi.org/10.1007/s10841-008-9135-8

Dunning JB, Stewart DJ, Danielson BJ, et al (1995) Spatially Explicit Population Models: Current Forms and Future Uses. Ecol Appl 5:3–11. https://doi.org/10.2307/1942045

Edwards CB, Zipkin EF, Henry EH, et al (2025) Rapid butterfly declines across the United States during the 21st century. Science 387:1090–1094. https://doi.org/10.1126/science.adp4671

Ehrlich PR, Launer AE, Murphy DD (1984) Can Sex Ratio be Defined or Determined? The Case of a Population of Checkerspot Butterflies. Am Nat 124:527–539. https://doi.org/10.1086/284292

Etherington TR, Holland PE (2013) Least-cost path length versus accumulated-cost as connectivity measures. Landsc Ecol 28:1223–1229. https://doi.org/10.1007/s10980-013-9880-2

Evans DM, Che-Castaldo JP, Crouse D, et al (2016) Species recovery in the United States:

Increasing the effectiveness of the Endangered Species Act

Evans LC, Sibly RM, Thorbek P, et al (2020) The importance of including habitat-specific behaviour in models of butterfly movement. Oecologia 193:249–259. https://doi.org/10.1007/s00442-020-04638-4

Ewers RM, Didham RK (2005) Confounding factors in the detection of species responses to habitat fragmentation. Biol Rev 81:117. https://doi.org/10.1017/S1464793105006949

Fulford RS, Peterson MS, Grammer PO (2011) An ecological model of the habitat mosaic in estuarine nursery areas: Part I—Interaction of dispersal theory and habitat variability in describing juvenile fish distributions. Ecol Model 222:3203–3215. https://doi.org/10.1016/j.ecolmodel.2011.07.001

Grosboll unpub DN (2011) TAYLOR'S CHECKERSPOT (EUPHYDRYAS EDITHA TAYLORI) OVIPOSITION HABITAT SELECTION AND LARVAL HOSTPLANT USE IN WASHINGTON STATE. The Evergreen State College

Gutiérrez D, Thomas CD, León-Cortés JL (1999) Dispersal, distribution, patch network and metapopulation dynamics of the dingy skipper butterfly (Erynnis tages). Oecologia 121:506–517. https://doi.org/10.1007/s004420050957

Hall KR, Anantharaman R, Landau VA, et al (2021) Circuitscape in Julia: Empowering Dynamic Approaches to Connectivity Assessment. Land 10:301. https://doi.org/10.3390/land10030301

Hanski I (1999) Habitat Connectivity, Habitat Continuity, and Metapopulations in Dynamic Landscapes. Oikos 87:209. https://doi.org/10.2307/3546736

Hanski I, Thomas CD (1994) Metapopulation dynamics and conservation: A spatially explicit model applied to butterflies. Biol Conserv 68:167–180. https://doi.org/10.1016/0006-3207(94)90348-4

Harrison S (1989) Long-Distance Dispersal and Colonization in the Bay Checkerspot Butterfly, Euphydryas Editha Bayensis. Ecology 70:1236–1243. https://doi.org/10.2307/1938181

Hastings A, Harrison S (1994) METAPOPULATION DYNAMICS AND GENETICS. 167–188

Heinrichs JA, Aldridge CL, Gummer DL, et al (2018) Prioritizing actions for the recovery of endangered species: Emergent insights from Greater Sage-grouse simulation modeling. Biol Conserv 218:134–143. https://doi.org/10.1016/j.biocon.2017.11.022

Heinrichs JA, Marcot BG, Linnell MA, Lesmeister DB (2023) Characterizing long‐term population conditions of the elusive red tree vole with dynamic individual‐based modeling. Conserv Sci Pract 5:e12938. https://doi.org/10.1111/csp2.12938

Henderson RA, Meunier J, Holoubek NS (2018) Disentangling effects of fire, habitat, and climate on an endangered prairie-specialist butterfly. Biol Conserv 218:41–48.

https://doi.org/10.1016/j.biocon.2017.10.034

Hill JK, Thomas CD, Lewis OT (1996) Effects of Habitat Patch Size and Isolation on Dispersal by Hesperia comma Butterflies: Implications for Metapopulation Structure. J Anim Ecol 65:725. https://doi.org/10.2307/5671

Huck M, Jędrzejewski W, Borowik T, et al (2010) Habitat suitability, corridors and dispersal barriers for large carnivores in Poland. Acta Theriol (Warsz) 55:177–192. https://doi.org/10.4098/j.at.0001-7051.114.2009

Huck M, Jędrzejewski W, Borowik T, et al (2011) Analyses of least cost paths for determining effects of habitat types on landscape permeability: wolves in Poland. Acta Theriol (Warsz) 56:91–101. https://doi.org/10.1007/s13364-010-0006-9

Kaye TN, Stanley AG, Ross D (2011) Dispersal behavior and habitat variation of Taylor's checkerspot butterfly

Kaye TN, Stanley AG, Ross D (2011) Dispersal behavior and habitat variation of Taylor's checkerspot butterfly. Institute for Applied Ecology, Corvallis, Oregon and US Fish and Wildlife Service, Lacey, Washington

Krebs JR, Wilson JD, Bradbury RB, Siriwardena GM (1999) The second Silent Spring? Nature 400:611–612. https://doi.org/10.1038/23127

LANDFIRE USD of the I Geological Survey, and US Department of Agriculture (2022a) Existing Vegetation Type. https://landfire.gov/vegetation/evt. Accessed 4 Dec 2023

LANDFIRE USD of the I Geological Survey, and US Department of Agriculture (2022b) Existing Vegetation Height Layer. https://landfire.gov/vegetation/evh. Accessed 4 Dec 2023

LANDFIRE USD of the I Geological Survey, and US Department of Agriculture (2022c) Existing Vegetation Cover Layer. https://landfire.gov/vegetation/evc. Accessed 4 Dec 2023

Lark TJ (2020) Protecting our prairies: Research and policy actions for conserving America's grasslands. Land Use Policy 97:104727. https://doi.org/10.1016/j.landusepol.2020.104727

LaRue MA, Nielsen CK (2008) Modelling potential dispersal corridors for cougars in midwestern North America using least-cost path methods. Ecol Model 212:372–381. https://doi.org/10.1016/j.ecolmodel.2007.10.036

Leoniak G, Barnum S, Atwood JL, et al (2012) Testing GIS-Generated Least-Cost Path Predictions for Martes pennanti (Fisher) and its Application for Identifying Mammalian Road-crossings in Northern New Hampshire. Northeast Nat 19:147–156. https://doi.org/10.1656/045.019.0201

Levins R (1970) Extinction. Lectures on mathematics in life sciences. American Mathematical Society, Providence

Linders M (2023) Personal Correspondence

Linders M, Lewis K, Curry K (2020) Taylor's checkerspot (Euphydryas editha taylori) Captive Rearing and Translocation: South Puget Sound, Washington, 2018-2019. US Fish and Wildlife Service and Joint Base Lewis-McChord

Lyons AL, Gaines WL, Singleton PH, et al (2018) Spatially explicit carrying capacity estimates to inform species specific recovery objectives: Grizzly bear (Ursus arctos) recovery in the North Cascades. Biol Conserv 222:21–32. https://doi.org/10.1016/j.biocon.2018.03.027

MacArthur RH, Wilson EO (1967) The Theory of Island Biogeography. Princeton University Press, Princeton

Maechler M, Dutang C, Goulet V (2010) expm: Matrix Exponential, Log, "etc." 1.0–0

Mallick B, Rana S, Ghosh TS (2023) Role of herbicides in the decline of butterfly population and diversity. J Exp Zool Part Ecol Integr Physiol 339:346–356. https://doi.org/10.1002/jez.2688

Marcot BG, Schumaker NH, D'Elia J (2025) Response of California condor populations to reintroductions, reinforcements, and reductions in spent lead ammunition pollution. Ecol Model 501:111002. https://doi.org/10.1016/j.ecolmodel.2024.111002

Mason SC, Shirey V, Ponisio LC, Gelhaus JK (2021) Responses from bees, butterflies, and ground beetles to different fire and site characteristics: A global meta-analysis. Biol Conserv 261:109265. https://doi.org/10.1016/j.biocon.2021.109265

Mennechez G, Schtickzelle N, Baguette M (2003) Metapopulation dynamics of the bog fritillary butterfly: comparison of demographic parameters and dispersal between a continuous and a highly fragmented landscape

Meyer RT, Ball NT, McElveen D (2024) Dispersal, population size, and reproduction in a fire-maintained frosted elfin (Callophrys irus) metapopulation. J Insect Conserv 28:165–177. https://doi.org/10.1007/s10841-023-00531-6

Mukherjee SS, Hossain A (2024) Species distribution modelling of the purple leaf blue butterfly (Amblypodia anita) in West Bengal, India, under current environmental conditions. Biodiversity 25:215–222. https://doi.org/10.1080/14888386.2024.2383177

Muscarella R, Galante PJ, Soley‐Guardia M, et al (2014) ENMeval: An R package for conducting spatially independent evaluations and estimating optimal model complexity for MAXENT ecological niche models. Methods Ecol Evol 5:1198–1205. https://doi.org/10.1111/2041-210X.12261

Nieminen M (2004) Structure and dynamics of Melitea cinxia metapopulations. In: On the wings of checkerspots: a model system for population biology. pp 63–91

Nieminen M, Singer MC, Fortelius W, et al (2001) Experimental Confirmation That Inbreeding Depression Increases Extinction Risk in Butterfly Populations. Am Nat 157:237–244. https://doi.org/10.1086/318630

Nogeire TM, Lawler JJ, Schumaker NH, et al (2015) Land Use as a Driver of Patterns of Rodenticide Exposure in Modeled Kit Fox Populations. PLOS ONE 10:e0133351. https://doi.org/10.1371/journal.pone.0133351

Öckinger E (2006) Possible Metapopulation Structure of the Threatened ButterflyPyrgus armoricanus in Sweden. J Insect Conserv 10:43–51. https://doi.org/10.1007/s10841-005-1249-7

Pacioni C, Kennedy MS, Berry O, et al (2018) Spatially-explicit model for assessing wild dog control strategies in Western Australia. Ecol Model 368:246–256. https://doi.org/10.1016/j.ecolmodel.2017.12.001

Phillips SJ, Anderson RP, Schapire RE (2006) Maximum entropy modeling of species geographic distributions. Ecol Model 190:231–259. https://doi.org/10.1016/j.ecolmodel.2005.03.026

Pinto N, Keitt TH (2009) Beyond the least-cost path: evaluating corridor redundancy using a graph-theoretic approach. Landsc Ecol 24:253–266. https://doi.org/10.1007/s10980-008-9303-y

Polus E, Vandewoestijne S, Choutt J, Baguette M (2007) Tracking the effects of one century of habitat loss and fragmentation on calcareous grassland butterfly communities. Biodivers Conserv 16:3423–3436. https://doi.org/10.1007/s10531-006-9008-y

Pomara LY, LeDee OE, Martin KJ, Zuckerberg B (2014) Demographic consequences of climate change and land cover help explain a history of extirpations and range contraction in a declining snake species. Glob Change Biol 20:2087–2099. https://doi.org/10.1111/gcb.12510

Potter AE (2016) Periodic status review for Taylor’s Checkerspot in Washington. Washington Department of Fish and Wildlife, Olympia, Washington

Pullinger MG, Johnson CJ (2010) Maintaining or restoring connectivity of modified landscapes: evaluating the least-cost path model with multiple sources of ecological information. Landsc Ecol 25:1547–1560. https://doi.org/10.1007/s10980-010-9526-6

Rocha ÉGD, Brigatti E, Niebuhr BB, et al (2021) Dispersal movement through fragmented landscapes: the role of stepping stones and perceptual range. Landsc Ecol 36:3249–3267. https://doi.org/10.1007/s10980-021-01310-x

Rustigian HL, Santelmann MV, Schumaker NH (2023) Assessing the potential impacts of alternative landscape designs on amphibian population dynamics. Landsc Ecol 18:65–81

Saccheri I, Kuussaari M, Kankare M, et al (1998) Inbreeding and extinction in a butterfly metapopulation. Nature 392:491–494. https://doi.org/10.1038/33136

Saunders DA, Hobbs RJ, Margules CR (1991) Biological Consequences of Ecosystem Fragmentation: A Review. Conserv Biol 5:

Sawyer SC, Epps CW, Brashares JS (2011) Placing linkages among fragmented habitats: do least-cost models reflect how animals use landscapes?: Least-cost modelling for habitat linkage design. J Appl Ecol 48:668–678. https://doi.org/10.1111/j.1365-2664.2011.01970.x

Scherer G, Löffler F, Fartmann T (2021) Abandonment of traditional land use and climate change threaten the survival of an endangered relict butterfly species. Insect Conserv Divers 14:556–567. https://doi.org/10.1111/icad.12485

Schultz CB, Crone EE (2005) Patch Size and Connectivity Thresholds for Butterfly Habitat Restoration. Conserv Biol 19:887–896. https://doi.org/10.1111/j.1523-1739.2005.00462.x

Schultz CB, Dlugosch KM (1998) Nectar and hostplant scarcity limit populations of an endangered Oregon butter¯y. Springer-Verl

Schumaker NH (2024) A rapid assessment methodology for quantifying and visualizing functional landscape connectivity. Front Conserv Sci 5:1412888. https://doi.org/10.3389/fcosc.2024.1412888

Schumaker NH, Brookes A (2018) HexSim: a modeling environment for ecology and conservation. Landsc Ecol 33:197–211. https://doi.org/10.1007/s10980-017-0605-9

Schumaker NH, Brookes A, Dunk JR, et al (2014) Mapping sources, sinks, and connectivity using a simulation model of northern spotted owls. Landsc Ecol 29:579–592. https://doi.org/10.1007/s10980-014-0004-4

Severns PM, Breed GA (2014) Behavioral consequences of exotic host plant adoption and the differing roles of male harassment on female movement in two checkerspot butterflies. Behav Ecol Sociobiol 68:805–814. https://doi.org/10.1007/s00265-014-1693-z

Snyder MN, Schumaker NH, Dunham JB, et al (2022) Tough places and safe spaces: Can refuges save salmon from a warming climate? Ecosphere 13:e4265. https://doi.org/10.1002/ecs2.4265

Steffan‐Dewenter I, Tscharntke T (2000) Butterfly community structure in fragmented habitats. Ecol Lett 3:449–456. https://doi.org/10.1111/j.1461-0248.2000.00175.x

Stinson DW (2005) WASHINGTON STATE STATUS REPORT FOR THE MAZAMA POCKET GOPHER, STREAKED HORNED LARK, AND TAYLOR'S CHECKERSPOT. Washington Department of Fish and Wildlife

Sutcliffe OL, Bakkestuen V, Fry G, Stabbetorp OE (2003) Modelling the benefits of farmland restoration: methodology and application to butterfly movement. Landsc Urban Plan 63:15–31. https://doi.org/10.1016/S0169-2046(02)00153-6

Sutcliffe OL, Thomas CD, Yates TJ, Greatorex-Davies JN (1997) Correlated extinctions, colonizations and population fluctuations in a highly connected ringlet butterfly metapopulation. Oecologia 109:235–241. https://doi.org/10.1007/s004420050078

Talavera G, García-Berro A, Talla VNK, et al (2023) The Afrotropical breeding grounds of the Palearctic-African migratory painted lady butterflies (Vanessa cardui). Proc Natl Acad Sci 120:e2218280120. https://doi.org/10.1073/pnas.2218280120

Thomas CD, Hanski I (2004a) Metapopulation Dynamics in Changing Environments. In: Ecology, Genetics and Evolution of Metapopulations. Elsevier, pp 489–514

Thomas CD, Hanski I (2004b) Metapopulation Dynamics in Changing Environments. In: Ecology, Genetics and Evolution of Metapopulations. Elsevier, pp 489–514

Thomas JA, Bourn NAD, Clarke RT, et al (2001) The quality and isolation of habitat patches both determine where butterflies persist in fragmented landscapes. Proc R Soc Lond B Biol Sci 268:1791–1796. https://doi.org/10.1098/rspb.2001.1693

Tuma MW, Millington C, Schumaker N, Burnett P (2016) Modeling Agassiz's desert tortoise population response to anthropogenic stressors: Agassiz's Desert Tortoise Population Modeling. J Wildl Manag 80:414–429. https://doi.org/10.1002/jwmg.1044

Turlure C, Baguette M, Stevens VM, Maes D (2011) Species- and sex-specific adjustments of movement behavior to landscape heterogeneity in butterflies. Behavioral Ecology 22:967–975. https://doi.org/10.1093/beheco/arr077

U.S. Fish and Wildlife Service (2022) Draft Recovery Plan for Taylor's Checkerspot Butterfly (Euphydryas editha taylori). Portland, Oregon

U.S. Geological Survey 3D Elevation Program Ground Surface Elevation - 30m

USFWS (1998) Recovery Plan for the Serpentine Soil Species of the San Francisco Bay Area. U.S. Fish and Wildlife Service, Portland, Oregon

Warren DL, Matzke NJ, Cardillo M, et al (2021) ENMTools 1.0: an R package for comparative ecological biogeography. Ecography 44:504–511. https://doi.org/10.1111/ecog.05485

Warren MS (1994) The UK status and suspected metapopulation structure of a threatened European butterfly, the marsh fritillary Eurodryas aurinia. Biol Conserv 67:239–249. https://doi.org/10.1016/0006-3207(94)90615-7

Weiss S, MacDonald B, Longcore T (2013) Prioritization of Information Gaps Critical to Strengthening the Scientific Basis of Habitat Enhancement Planning and Determining Site Readiness for Taylor's Checkerspot Butterfly Strategy and Recommendations to Address Priority Information Gaps. Urban Wildlands Group

Weiss SB, White RR, Murphy DD, Ehrlich PR (1987) Growth and Dispersal of Larvae of the Checkerspot Butterfly Euphydryas editha. Oikos 50:161. https://doi.org/10.2307/3565996

Westwood R, Westwood AR, Hooshmandi M, et al (2020) A field‐validated species distribution model to support management of the critically endangered Poweshiek skipperling (Oarisma poweshiek) butterfly in Canada. Conserv Sci Pract 2:e163. https://doi.org/10.1111/csp2.163

Wiens JD, Schumaker NH, Inman RD, et al (2017) Spatial Demographic Models to Inform Conservation Planning of Golden Eagles in Renewable Energy Landscapes. J Raptor Res 51:234–257. https://doi.org/10.3356/JRR-16-77.1

Wilsey CB, Lawler JJ, Cimprich DA (2012) Performance of habitat suitability models for the endangered black-capped vireo built with remotely-sensed data. Remote Sens Environ 119:35–42. https://doi.org/10.1016/j.rse.2011.12.002

With KA (1997) The Application of Neutral Landscape Models in Conservation Biology: Aplicación de Modelos de Paisaje Neutros en la Biología de la Conservación. Conserv Biol 11:1069–1080. https://doi.org/10.1046/j.1523-1739.1997.96210.x

Yao J, Zhou C, Wang W, et al (2024) Habitat Suitability of Danaus genutia Based on the Optimized MaxEnt Model. Insects 15:971. https://doi.org/10.3390/insects15120971