Environmental driver effects on population growth rates vary by rarity type and variation in demographic rate sensitivity

by

Sarah Herzog-Ramirez

B.S., University of Idaho, 2017
M.S., South Dakota State University, 2020

AN ABSTRACT OF A DISSERTATION

submitted in partial fulfillment of the requirements for the degree

DOCTOR OF PHILOSOPHY

Division of Biology
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Abstract

Abiotic and biotic drivers, such as climate or herbivores, influence populations; however, their effects could vary by population or rarity type (range size, habitat specificity, and population density). I examined how the effects of drivers on vital rates could impact population growth due to variation of population growth sensitivity to demographic rates. I found significant variation in effects of neighbors on population growth rate, which is driven primarily by variation in sensitivity to demographic rates across populations. Further, results from a climate warming experiment suggests variation in life history across populations is partly driven by temperature differences. In a separate study, I test the niche breadth hypothesis, which postulates that driver effect sizes should decrease with range size. I estimated the effects of abiotic (climate and fire) and biotic (insect and mammal herbivory) drivers across nearly one hundred tallgrass prairie plant species of varying range size. I found biotic driver effects increase with range size, counter to the niche breadth hypothesis but in accordance with other recent work. Additionally, I model population growth rate for 15 tallgrass prairie species varying in rarity type to examine how the impacts of drivers vary across rarity types, and how these drivers, in combination with dispersal ability, might impact climate change induced range shifts. I found effects of climate, fire, and grazing have minimal effects on population growth rate for all species. However, I found strong deviations in dispersal for species varying in habitat specificity and dispersal ability. In total, our results emphasize effects of drivers can vary across populations and across rarity types. Without taking these differences into this consideration, management and conservation practices could have unanticipated effects.

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Major Professor
Dr. Allison Louthan

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Abiotic and biotic drivers, such as climate or herbivores, influence populations; however, their effects could vary by population or rarity type (range size, habitat specificity, and population density). I examined how the effects of drivers on vital rates could impact population growth due to variation of population growth sensitivity to demographic rates. I found significant variation in effects of neighbors on population growth rate, which is driven primarily by variation in sensitivity to demographic rates across populations. Further, results from a climate warming experiment suggests variation in life history across populations is partly driven by temperature differences. In a separate study, I test the niche breadth hypothesis, which postulates that driver effect sizes should decrease with range size. I estimated the effects of abiotic (climate and fire) and biotic (insect and mammal herbivory) drivers across nearly one hundred tallgrass prairie plant species of varying range size. I found biotic driver effects increase with range size, counter to the niche breadth hypothesis but in accordance with other recent work. Additionally, I model population growth rate for 15 tallgrass prairie species varying in rarity type to examine how the impacts of drivers vary across rarity types, and how these drivers, in combination with dispersal ability, might impact climate change induced range shifts. I found effects of climate, fire, and grazing have minimal effects on population growth rate for all species. However, I found strong deviations in dispersal for species varying in habitat specificity and dispersal ability. In total, our results emphasize effects of drivers can vary across populations and across rarity types. Without taking these differences into this consideration, management and conservation practices could have unanticipated effects.

Table of Contents

List of Figures

elevation). In a-e, we show demographic rates and population growth rate values from unmanipulated control (Control) vs. neighbor removal treatments (Removal), such that positive effects of a neighbor removal treatment (i.e., removal value larger than control value) indicate competition. Panels a-d show the effect of neighbors on predicted demographic rates for the mean size class using the best-fit models for each demographic rate (which we also used to construct the IPMs). Panel e shows the difference between deterministic growth rate for neighbor removal vs. control treatment, predicted using integral projection models (IPMs) constructed from neighbor removal data. In a-e, error bars show 95% confidence intervals on the fixed effect estimates of the demographic rate function (a-d) or 95% confidence intervals derived from incorporating parameter uncertainty into the demographic rate functions used to construct the IPM (e). In panel e, we show the critical value of one using a grey horizontal line. In panel f, we show the effect of neighbor removal treatments on population growth rate (population growth rate without neighbors- population growth rate with neighbors, such that positive values indicate competition). No effect of neighbor removal, a value of zero, is indicated by the gray horizontal line. Error bars indicate the 95% confidence intervals on the difference between population growth rate in the control vs. removal treatment. Letters above each error bar indicate the statistical significance (assessed using overlap of 95% confidence intervals) of differences in neighbor response in pairwise comparisons between populations. Populations sharing the same letter experience similar effects of neighbors (i.e., the 95% confidence interval on the difference between neighbor effects overlaps zero) and populations with different letters experience statistically significant differences neighbor effects on population growth rate (i.e., the 95% confidence interval on the difference between

List of Tables

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Dedication

To my family and friends. Those that have been long-time supporters, those that have passed during my time in Kansas, and those newly gained.

Preface

Chapters 2-4 of this dissertation have been prepared and formatted for submission to peer-reviewed journals. Chapter 2 (with Lara Kueppers of UC Berkeley Energy and Resources and Energy Group as a co-author) is currently in press at *Oikos* (DOI: 10.1111/oik.10928). Chapters 3 and 4 will be submitted for publication following the defense; Ellen Welti (Smithsonian) will be a co-author on Chapter 3 & Lauren Sullivan (Michigan State University) will be a co-author on Chapter 4.

Chapter 1 - Background

Populations and species are affected by multiple environmental drivers, ranging from climatic drivers such as temperature and precipitation, to biotic drivers such as herbivores, predators, or pollinators. Quantifying the impacts of those drivers on population dynamics and species distributions is critical to predicting changes in future species assemblages and biodiversity with climate change (Clark et al. 2001, Allen et al. 2015, Iler et al. 2021, Hamann et al. 2021). However, the impacts of environmental drivers on population dynamics and distributions can vary dramatically both within (Louthan et al. 2018) and across species (Franklin et al. 2016). For example, if only some populations within a species' range are strongly affected by a biotic driver such as pollination, we would expect that reductions in pollinator density could result in extirpation only at those populations—and thus truncation of the species' range in only those areas. Alternatively, if only some species respond strongly to climatic drivers, we would expect that those species will suffer high local extirpation and eventual global extinction risk in a future climate, whereas those that respond less strongly to climatic drivers might have low extinction risk in a future climate. In this dissertation, we quantify the relative effect of biotic and climatic drivers across populations and species at three levels of organization: within and across species, as well as in the context of species range shifts with climate change.

Within species, one commonly cited framework for considering how the effects of drivers might vary across species is the stress gradient hypothesis (SGH) (Bertness and Callaway 1994). The SGH predicts that the effect of one particular biotic driver, interactions with neighboring species, should shift systematically along abiotic gradients. Namely, in areas that are assumed to be less stressful (e.g., warm or wet conditions), the SGH predicts that neighbors act as competitors. In contrast, more stressful (e.g., colder or dryer) neighbors should have

facilitative effects (e.g., alpine species could benefit from additional neighbors due to increased shelter from harsh temperatures). Thus, the SGH predicts that the effect of one biotic driver should vary within a species' range. While this hypothesis predicts neighbor responses at the level of fitness (i.e., population growth rate), the vast majority of tests of this hypothesis only test the SGH at the level of fitness correlates (e.g., survival, reproduction, or spatial patterns in distributions). Thus, we have a poor sense of how the effect of neighbors on population growth rate should vary within a particular species.

Across species, multiple hypotheses predict when and where environmental drivers should most strongly impact population dynamics; in this work, we focus on two hypotheses. The niche breadth hypothesis predicts species with larger ranges should have broad environmental tolerance, meaning that they can maintain a high population growth rate under a variety of environmental conditions (Sexton et al. 2017). In this scenario, a species' lack of response to environmental drivers drives range size: because species are able to tolerate a variety of environmental conditions without substantial reductions in population size, they can occur over a large geographic area (Slatyer et al. 2013). Thus, the niche breadth hypothesis suggests population response to environmental drivers should decrease with a species' range size. An alternative hypothesis, proposed by Opler (1974), predicts the opposite pattern (at least for biotic drivers). Opler (1974) compared insect herbivore species richness across the *Quercus* (oak) genus. He found that for individual trees, insect herbivore species richness found on that tree increases as tree species' range size increases. Opler explains that as a tree's range size increases, the tree species will intersect the ranges of an increasing number of potential herbivore species. When the tree species contacts each new potential herbivore species, herbivores could adapt to consume the tree and spread throughout the tree's range, resulting in high herbivore species

richness – and thus larger impacts on population growth rate-- on any one individual host tree. In contrast to the niche breadth hypothesis, Opler's hypothesis predicts that the effect of biotic drivers such as insect herbivores should increase with species' range size.

Within the context of ongoing climate change, one of the most conservation-relevant species-level responses to drivers concerns whether species will be able to shift their ranges in response to climate change. For example, assuming rare species respond strongly to climate (according to the niche breadth hypothesis), we expect rare species will be unable to shift their ranges to keep pace with climate change. By contrast, if common species' population dynamics do not respond to climate, it seems likely that common species will be able to maintain populations, and perhaps shift their ranges, in the face of climate change. It is particularly important to consider rare species as they account for most of the biodiversity and functional richness in communities (Preston 1948, Brown 1984, Leitão et al. 2016, Enquist et al. 2019). Rare species offer novel functional traits, providing distinct ecosystem services relative to common species (Cardinale et al. 2006), or can offer functional redundancy through providing similar function as common species but providing stability to the ecosystem (Tucker et al. 2011, Jain et al. 2014).

Species' range size is not the only determinant of its rarity. A "rare" species can have restricted range size, narrow habitat requirements, low population densities, or some combination of these three (Rabinowitz 1981). Lower density species tend to have shorter lifespans (i.e., annual/biannual life histories) (Farnsworth 2007), meaning their populations should respond more strongly to climate variation (Morris et al. 2008). The niche breadth hypothesis predicts species with larger niches (i.e., larger ranged species) should experience weaker population responses to environmental drivers (Sexton et al. 2017). Recent work has found in the fossil

record, geographic range size played a primary role in determining extinction risk, and habitat breadth a secondary role, whereas local abundance had little effect (Harnik et al. 2012). However, we have little sense of whether these different rarity types might differ in their ability to track climate change and thus avoid climate change-caused extinction in the modern era. As climate change progresses, species extinction will depend on whether species can shift ranges to track climatic conditions, often to higher elevations or latitudes.

Shifts in species range are the product of both the response of population dynamics to climate variability at any one site—which the niche breadth hypothesis predicts should vary systematically across species-- as well as dispersal. The ability of a propagule to reach a hospitable habitat is limited by a) dispersal ability relative to distance between suitable habitat patches and b) the population size at the source population. Low-density rare species have smaller population sizes and thus produce fewer propagules, likely limiting the speed of range shifts. Small ranged species experience less environmental variation across their range, potentially leading to strong climate-driven declines in population size at extant populations. Unless this limitation in climatic tolerance is counterbalanced by high dispersal ability, we would expect limited range shifts. Habitat specialist species have few appropriate habitat patches, meaning that they must be able to not only disperse long distances to reach a habitat patch, but must be lucky enough to land in a small fragment of appropriate habitat. We know little about how rarity type affects species' dispersal ability or overall ability to shift ranges, let alone how species that are rare in multiple ways will shift their ranges. Understanding how species will shift their ranges with climate change is particularly important in fragmented systems, where optimal habitat might be sparse.

In this dissertation, we focus on the relative importance of environmental drivers within and among species on population dynamics and species range shifts. To do so, we examine two study systems. For within species effects of environmental drivers (Chapter 2) we use a relatively common and widespread alpine plant, *Sedum lanceolatum* Torr. (Crassulaceae), across multiple populations and elevations, paired with a climate manipulation experiment, to examine the effects of neighbors on demographic rates and how these effects might result in varying impacts on population growth due to changes in sensitivity of population growth rate to demographic rates. Our second study system focused on the tallgrass prairies of the Great Plains. For both Chapters 3 and 4, we utilized long-term plant cover data collected at an experimental grassland in the Flint Hills of Kansas, USA. In Chapter 3, we use these long-term data to examine the effects of abiotic (climate and fire) and biotic (bison and grasshoppers) drivers on demographic rates across nearly a hundred native plant species with varying niche (range) size. In Chapter 4, we combine these data with additional plant cover data from northern range limits to create population models, combined with dispersal estimates, that estimate the impacts of rarity type (range size, habitat specificity, and local population density) on climate change induced range shifts.

Chapter 2 - Neighbor effects on population growth rate differ among populations due to variation in demographic rate sensitivities in *Sedum lanceolatum*

2.1 Abstract

Population growth rates will respond to an environmental driver only if the driver impacts demographic rate(s) and the population is sensitive to impacted demographic rate(s). If populations vary in the sensitivity of population growth rate to demographic rates, the effect of an environmental driver on population growth rate could vary across populations, even if the effect of the driver on demographic rates does not vary across populations. Here, we use five years of demographic data of a common alpine plant, including data from a neighbor removal experiment and a climate warming experiment, to quantify the relative contribution of neighbor effects on demographic rates vs. sensitivity of population growth rate to demographic rates to across-population variation in neighbor effects on population growth rate. We find neighbor effects on population growth rate vary significantly across populations, and this effect is driven primarily by variation in sensitivity of population growth rate to demographic rates across populations. Further, results from our climate warming experiment suggests variation in sensitivity across populations is partly driven by temperature differences. Our results highlight the importance of considering changes in the sensitivity of population growth rate to demographic rates across space, and show how changes in sensitivity can contribute to spatial variation in the effects of a driver on population growth rate.

2.2 Introduction

Responses of species' population dynamics to their environment arise from effects of the environment on the demographic rates that comprise population growth rate (e.g., annual survival, growth, and reproduction). For example, neighbors could reduce a focal species' survival, growth, and/or reproduction, potentially resulting in a negative effect of neighbors on population growth rate (Goldberg 1987, Hubbell et al. 2001, Graff et al. 2007). Alternatively, effects of an environmental driver might differ across demographic rates. For example, previous work has found neighbors can decrease some demographic rates while increasing (e.g., Morris and Wood 1989, Del Moral and Bliss 1993, Gustafsson and Ehrlén 2003) or having minimal effects on others (e.g., Fréville and Silvertown 2005, Sozio and Mortelliti 2016). Neighbors can also increase some demographic rates strongly, while increasing others weakly or not at all (e.g., Griffith 2010). This variation in the effect of a driver across demographic rates make it difficult to predict the net impact of neighbors (or any other driver) on population growth rate.

Population growth rates are only impacted by an environmental driver if population growth rate is sensitive to the impacted demographic rate(s). For example, neighbor effects on population growth rate will be negative and strong only if neighbors reduce one or more demographic rates and population growth rate is sensitive to those demographic rate(s). By contrast, neighbor effects on population growth rate will be weak if population growth rate is not very sensitive to the demographic rates that neighbors affect. Thus, even if neighbors have strong effects on multiple demographic rates, neighbors will exert minimal effects on population growth rate if population growth rate is not sensitive to those demographic rates (similar to climate effects found in some bird species; Reed et al. (2013); McLean et al. (2016)). Complicating matters, the sensitivity of population growth rate to demographic rates could vary across

populations, potentially modulating the impact of neighbors on population growth rate (Morris and Doak 2005, Louthan et al. 2018). Thus, the effect of neighbors on population growth rate in a given population could be high because neighbors strongly influence survival in that population (and population growth rate is moderately sensitive to survival). Alternatively, neighbor effects could be strong if population growth rate is very sensitive to survival at that population (and neighbors moderately affect survival). Of course, both mechanisms (population-specific effects of neighbors on demographic rates and changes in sensitivity of population growth rate to demographic rates) could simultaneously generate variation in neighbor effects on population growth rate, or even act in opposition to one another to result in no among-population variation in neighbor effects.

While the effect of neighbors on population growth rate has been well-studied, and can differ substantially across populations (Malkinson and Tielbörger 2010), most studies of neighbor effects do not parse the impact of each of these two mechanisms (population-specific effects of neighbors on demographic rates vs. changes in the sensitivity of population growth rate to demographic rates), let alone identify what factors might drive changes in sensitivity. One of the few studies quantifying the contribution of geographical variation in sensitivity to the effect of neighbors on population growth rate showed that sensitivity was the primary driver of geographical variation in neighbor effects on population growth rate (Louthan et al. 2018). However, this study did not identify which environmental driver(s) elicited geographical variation in sensitivities. Such information is important for inferring generalities: if spatial variation in rainfall drivers generates spatial variation in sensitivities, but spatial variation in soil type does not, we would expect that the impacts of neighbors would often differ across rainfall gradients, but not across soil types. Further, understanding how climate might generate variation

in sensitivities could help us predict how the impact of neighbors might change in a future climate.

A common ecological framework for how we might expect neighbor effects to vary across space is the stress-gradient hypothesis, which predicts neighbor effects change from facultative in more-stressful environments to competitive in less-stressful environments (Bertness and Callaway 1994). While the stress-gradient hypothesis predicts neighbor effects on population growth rate (i.e., fitness), most studies testing this hypothesis examine components of population growth rate (i.e., demographic rates such as survival or reproduction; e.g., Kawai and Tokeshi (2007)); Daleo and Iribarne (2009) or emergent patterns arising from population growth rate responses (e.g., spatial distributions; Tewksbury and Lloyd (2001); Holzapfel et al. (2006)). We lack a robust understanding not only of how neighbor effects on multiple demographic rates together influence population growth rate and whether these effects are consistent with the stress-gradient hypothesis, but also an understanding of whether population-level effects of neighbors are generated by underlying variation in the sensitivity of population growth rate to demographic rates. Such variation could operate in addition to (or in opposition to) any differential effects of neighbors on demographic rates across populations.

Here, we use the common Rocky Mountain succulent *Sedum lanceolatum* Torr. (Crassulaceae) to ask how the effect of neighbors on population growth rate changes across populations and what drives these responses. We use five years of detailed demographic data from four populations spanning a substantial elevational gradient, paired with five years of neighbor removal experiments at each of these populations, to quantify neighbor impacts on demographic rates and on population growth rate. We also use additional demographic data from a watering and heating experiment at a separate location to explore the drivers of among-

population variation in demographic rates and population growth rates. We ask four key questions: 1) how do demographic rates and population growth rate vary among populations?; 2) how do neighbor effects on demographic rates and population growth rate vary among populations?; 3) do population-specific effects of neighbors on population growth rate arise from population-specific effects of neighbors on demographic rates, changes in sensitivity of population growth rate to demographic rates across populations, or both?; and 4) does climate drive among-population variation in demographic rates and population growth rate?

2.3 Methods

We adopted a three-pronged approach to quantify how the effect of neighbors on *S. lanceolatum* varies across populations. First, to quantify variation in demographic rates across populations, we conducted a demographic study of four populations in the United States' Rocky Mountain West in 2011-2015 (Fig. 1, white dots). Second, at each of these four populations, we experimentally removed neighbors annually and used these data to quantify neighbor effects on demographic rates and population growth rate at each population. Finally, to better understand the drivers of underlying variation in population growth rate across elevations, we estimated *S. lanceolatum* demographic rates and population growth rate in the heating and watering treatments of the Alpine-Treeline Warming Experiment at Niwot Ridge Long-Term Ecological Research Site (ATWE, Fig. 1, triangle). We use ATWE data to estimate temperature and precipitation effects on demographic rates and population growth rate. We outline each of these three data sources in more detail below.

2.3.1 Study system

Sedum lanceolatum, the yellow stonecrop, is a perennial succulent that can have >50 rosettes composed of small (< ~3 cm) leaves and flowers occurring on terminal cymes on short (> ~20 cm) inflorescences (Clausen 1975). *Sedum lanceolatum* individuals are patchily distributed across a broad elevational range (1700-4048 m) in sandy, rocky soils of the Western United States(Clausen 1975); maximum elevation of mountains in this region is ~4250 m. The species' lightweight seeds can undergo long-distance dispersal, but most are dropped close to the parent plant (Clausen 1975). *Sedum lanceolatum* has been found to have higher number of leaves and rosettes at high elevations, but higher inflorescence and plant height at lower elevations (Jolls 1980).

Our study was conducted in mountainous regions of Colorado and Wyoming, where *S. lanceolatum* is common. At the outset of our study in 2011, we identified four populations of *S. lanceolatum,* two at low (L1, L2; ~2500m) and two at high elevations (H1, H2; ~3275m), separated by at least 2km. Our four populations span approximately half of the species' elevational range, and are not peripheral populations (Fig. 2.1). Here, we define a population as a discrete group of individuals spatially separated from other discrete groups of individuals. These four populations differ systematically in temperature, with higher temperatures at L1 and L2 than at H1 and H2 (App. Table 1) but all had very similar habitat (open canopy and shallow slopes). In 2011-2015, we conducted demographic censuses and a neighbor removal experiment, both described in detail below, at each of these populations. In addition to work at these four populations, we also collected data at the nearby Niwot Ridge Long-term Ecological Research Site, within an ongoing climate manipulation experiment (Fig. 2.1; described in detail below).

The habitat was very similar to those in our other four populations; elevation was similar to that of our two high populations.

2.3.2 Demographic rates and population growth rate across populations

We quantified variation in demography across four *S. lanceolatum* populations (L1, L2, H1, and H2) in 2011-2015. In 2011, during peak fruiting in late summer and early fall, we marked and mapped 1341 individuals across the four populations along 2-4 permanent transects at each population (transects were <50 m at all populations), measuring size (sum of volumes, height x area, across all rosettes), and counting fruits for each individual. We returned annually during peak fruiting to score survival, measure size, and count fruits. Altogether, we collected data on 6705 individual x transitions, including data on very small plants and seedlings. We used these data to estimate five size-dependent demographic rates: annual survival, mean size after one year of growth, variance in size after one year of growth, probability of fruiting, and number of fruits given a plant fruited. Note that while vegetative reproduction is common, occurring when individual rosettes take root after separating from primary stems, connections between parent and vegetative offspring are apparent above ground. Thus, any vegetative reproduction is subsumed into our estimates of growth.

To quantify seedlings per fruit (i.e., the number of seedlings present each year per fruits in the year prior), we had to know both the number of seeds per fruit and the number of seedlings per seed. To estimate the number of seeds per fruit at each elevation, we collected all fruits from 71 haphazardly selected plants across our four populations in 2010, 2011, and 2012. For a subset of these plants (n = 25, arrayed across all populations), we weighed the total seed mass and counted the total seed number under a microscope, then used a linear regression to ask whether seed mass differed across elevations (n=25, R^2= 0.14). We tested for effects of elevation, rather

than population, due to limited data. Elevation was marginally significant (P=0.061), with higher seed mass at lower elevations. We then estimated the elevation-specific number of seeds per fruit by combining data on seed mass per fruit in our 71 plants with the elevation-specific estimates of seeds number per seed mass derived from the regression.

To estimate the elevation-specific number of seedlings per seed, we conducted a seed addition experiment at each population in 2014. At each population, we established five paired 10 cm x 10 cm plots (10 plots total) that were proximate to one another and 30 cm from any marked plants; one of the pair was randomly assigned to a seed addition treatment and the other to an unmanipulated control treatment. In 2014, we sprinkled 50 *S. lanceolatum* seeds, collected from nearby plants, within the seed addition treatments. In 2015, we counted the number of seedlings in all plots, calculating seedlings per seed as: (seedling number in seed addition plots – seedling number in control plots)/50. This procedure corrects our estimates for any background germination from a seedbank or dispersal from outside the plot. In three of the 20 plot pairs, we found adult *S. lanceolatum* individuals with fruits. These three plots were removed from analyses to prevent possible background seed additions from biasing our results, resulting in 17 plot pairs in our experiment. If seedling number was higher in control than in seed addition plots (occurs in 2/17 pairs), we estimated seedlings per seed as zero. Finally, we multiplied seedlings per seed by number of seeds per fruit, from the regression described in the previous paragraph, to estimate seedlings per fruit for each elevation. Hereafter, we call the data collected at these four populations described in this section the "demography" data.

We used a model selection approach (Bartoń 2020) to assess whether *S. lanceolatum* demographic rates varied across populations using our demography data. For each demographic rate, we compared all possible subsets of a global mixed model that contained a fixed effect of

log-transformed size, a fixed categorical effect of population, and a random effect of year, retaining the random effect in all model comparisons (Table 2.1). We used generalized linear mixed models with a binomial distribution for survival and probability of fruiting, and a linear mixed model for growth, variance in growth, and the log transformed number of fruits given fruiting (i.e., if fruiting occurs, the number of fruits produced, hereafter, "number of fruits"). We used AICc (Hurvich and Tsai 1989) to select a best-fit model for each demographic rate; a likelihood ratio approach to test for significance of coefficients showed similar results (Supplemental Information).

We then used these best-fit demographic rate models to create an integral projection model (IPM; Easterling et al. (2000)) for each of our four populations, which we used to estimate deterministic population growth rate. We incorporated parameter uncertainty in the fixed effect estimates of our demographic rate functions by sampling 500 sets of parameter estimates from a multivariate normal distribution parametrized using the variance-covariance matrix of fixed effect coefficients. We present 95% confidence intervals calculated across these 500 replicates; thus, confidence intervals represent uncertainty associated with parameter uncertainty of our demographic rates. Our discretized IPM had 100 evenly spaced meshpoints and used log-transformed size as a size metric; bounds on the kernel were equivalent to the largest and smallest plant sizes in our datasets. To handle eviction problems, we renormalized transition probabilities to fit within the confines of the matrix (Williams et al. 2012). No complete eviction (where all probability is outside of the minimum or maximum limits of our kernel) events occurred in our analyses. Seedlings enter the kernel with a mean size reflective of all observed seedlings across all populations. While in the main text we present results derived from model selection, we conducted supplemental analyses designed to assess whether model selection

limited our ability to detect neighbor effects on population growth rate. Namely, in Supplemental Information we show results of a likelihood ratio test that assesses significance of coefficients in our models and we show IPMs constructed using the global (rather than best fit) model for each demographic rate; results are very similar.

2.3.3 Neighbor effects on demographic rates and population growth rate across populations

To quantify neighbor effects on S. lanceolatum demographic rates, we conducted a neighbor removal experiment at each of the same four populations from 2011-2015. We call the data collected in this experiment the "neighbor removal experiment" data. In 2011, we marked and mapped 719 individuals that were >= 30 cm apart along permanent transects, arrayed roughly equally across small, medium, and large size classes and across populations, just proximate to the transects described in the previous section. We randomly assigned each individual to either a neighbor removal or an unmanipulated control treatment; small, medium, and large plants were roughly equally distributed among treatments. Starting in 2011, every year we removed all above-ground biomass from a 15 cm radius around neighbor removal treatment plants, taking care not to disturb the soil. In 2011, during peak fruiting in late summer and early fall, we measured size and counted fruits of all these individuals. Until 2015, we returned annually during peak fruiting to score survival, measure size, and count fruits, replacing any individuals that died with newly marked individuals to maintain similar numbers of individual transitions each year. All together, we collected data on 3595 individual x transitions, which we used to estimate the same five size-dependent demographic rates as we did for our demography data. Note that we did not collect separate estimates of seedlings per fruit for neighbor removal

treatments. The removal experiment data and demography data are available at Herzog et al. (2023).

While our 'demography' data and 'neighbor removal experiment' data were collected at the same populations (but in separate transects) and data collection methods were similar, we safeguard against artefacts by always comparing treatments in the removal experiment data to one another, rather than comparing removal treatment data to demography data.

We used our removal experiment data to test for effects of neighbors on demographic rates. We repeated the model selection approach described in the previous section with two modifications: 1) we added a neighbor treatment term into our global model (i.e., control vs. neighbor removal); 2) we added an interaction term between population and neighbor treatment into our global model. We then conducted model selection and used the best-fit models to construct an IPM, this time constructing IPMs for each combination of population and neighbor treatment. For both control and removal treatments, we use the mean seedling size and elevation-specific value for seedlings per fruit observed in the demography data but multiplied removal treatment seedlings per fruit values by two to correspond with observed values more accurately (neighbor removal appears to increase germination; A. Louthan, pers. obs.; this multiplication does not affect our conclusions, see Appendix A).

Our IPM estimates the net effect of neighbors on population growth rate. This approach allows for simultaneous effects of neighbors on multiple demographic rates and can allow for positive effects of neighbors on some demographic rates, negative effects on others, or even no effect of neighbors on demographic rates. In our subsequent analyses, we represent the net effect of neighbors at each population as the difference between each population's deterministic growth rate in control vs. removal treatments predicted by the IPMs.

Drivers of population-specific effects of neighbors on population growth rate

To examine which demographic rates are driving population growth across our four populations, we calculated the sensitivity of population growth rate to demographic rates at each population, using data from the control treatment of the neighbor removal data. For each demographic rate, we increased or decreased all meshpoints' demographic rate values by 5% and calculated the sensitivity as the resultant change in population growth rate, divided by the average change in the demographic rate across size classes; we then averaged the two sensitivities (from the up and down perturbations) to get a population specific sensitivity for each demographic rate. We repeated this process for 500 sets of parameter estimates, as described in the *Demographic rates and population growth rate across populations* section. Thus, confidence intervals on these sensitivities represent uncertainty in the demographic rate parameters. We assume that if the confidence intervals on sensitivities are non-overlapping, those sensitivities differ significantly from one another. To test whether variation in sensitivity of population growth rate to demographic rates contributes to among-population variation in neighbor effects on population growth rate, we recalculate neighbor effect on population growth rate when the one demographic rate that contains a neighbor treatment x population interaction term, variance in growth, is replaced with a demographic rate that does not contain that interaction term (Supplemental Information).

2.3.4 Climate drivers of demographic rates and population growth rate

We collected demographic data within the ATWE experiment, a heating and watering experiment at Niwot Ridge Long-Term Ecological Research site, to isolate the climatic drivers of demographic rate variation across populations. The ATWE experiment consisted of replicated factorial manipulations of heating and watering at three sites; we worked at the "Alpine" site

(40° 3’16” N, 105° 35’37” W, 3540 m), only ~200 m higher than the high elevation populations described in the previous sections (Fig. 1). At this site in 2008, twenty plots with a 3m diameter were assigned to one of four treatments: 1) an unmanipulated control; 2) heated; 3) watered; or 4) heated and watered (hereafter, “heated + watered”). Heating, begun in 2009, was accomplished with active infrared heaters and increased soil temperatures by ~1.5°C at 5-10 cm soil depth during the snow-free season (Jabis et al. 2020), approximately half the difference in temperature between L1 and L2 vs. H1 and H2 during the growing season (App. Tables 1 and 2). Watering, begun in 2010, was accomplished by weekly hand watering of 2.5 mm of water and increased local June-September precipitation by approximately 20% of 1951-1980 mean annual precipitation at the site (Jabis et al. 2020). We used species composition studies in these plots, collected between 2009-2012 as part of the ATWE experiment (Winkler et al. 2016), to identify plots in which *S. lanceolatum* was potentially present in 2013.

To quantify heating and watering effects on *S. lanceolatum,* starting in 2013 we conducted demographic censuses in plots in which *S. lanceolatum* was or had been present in 2009-2012. Namely, if *S. lanceolatum* was recorded in a plot sometime between 2009-2012, we randomly selected a 50x50 cm subset of the plot in which to search exhaustively for all *S. lanceolatum* individuals. If that subset did not contain *S. lanceolatum*, we randomly selected another subset of the plot until we found a subset that did contain *S. lanceolatum* (or until we had exhausted all subsets and found no *S. lanceolatum)*. In each of the subsets where we found *S. lanceolatum*, during peak fruiting in early Fall 2013, we marked and mapped all *S. lanceolatum* individuals, measuring size and counting fruits. In total, we measured 231 individuals across 15 plots, arrayed across control, heating, watering, and heating + watering treatments (82, 61, 44, and 44 individuals, respectively). We returned in 2014 during peak fruiting to score survival,

measure size, and count fruits. We used these data to estimate the same five size-dependent demographic rates described in the prior section, though we did not separately estimate seedlings per fruit. Hereafter, we call data collected at ATWE "climate experiment data." These data are available through the ATWE data portal (Herzog et al. 2023).

We then tested for effects of heating and watering treatments on population growth rate. Namely, we repeated the approach described in the "*Demographic rates and population growth rate across populations*" section, with four modifications: 1) we added two additional terms into our global model: heating and watering (note heating + watering climate treatment was coded as receiving both the heating and watering treatment); 2) we removed terms for population identity; 3) we replaced the random year effect with a random effect of plot; 4) we constructed IPMs for each climate treatment, again incorporating uncertainty in the fixed effect parameter estimates into our projections. We estimate climate treatment effects on population growth rate as the difference between deterministic growth rate in control vs. heating (or vs. watering, or vs. heating + watering). For these IPMs, we use estimates of seedlings per fruit from the high elevation demography data and seedling mean size reflective of the demography data.

2.4 Results

2.4.5 Population effects on demographic rates and population growth rate

For analyses using demography data, demographic rates differed across populations. Namely, a term for population identity was present in the best fit model for all demographic rates. Plants at both L1 and L2 had substantially lower survival than plants at the H1 and H2 populations, though survival was similar between L1 and L2 and H1 and H2 (Fig. 2a). Mean growth (i.e., change in size after one year of growth) was highest at population L1, second

highest at L2, with H1 and H2 showing lowest growth (Fig. 2.2b). Probability of fruiting was low at all populations for plants of the mean size class.; population H2 had the lowest probability of fruiting, H1 second lowest, followed by L1 then L2 (Fig. 2.2c). Lower elevation populations tended to produce more fruits than high elevation populations (Fig. 2.2d). Finally, variance in growth was higher at L1 and L2 than at H1 and H2 (App. Table A.3). Seedlings per fruit was higher at H1 and H2 than at L1 and L2 (1.83 vs. 0.38).

We did not find systematic variation in population growth rate across populations. Confidence intervals at all population growth rates overlap (L1, L2, H2) or are slightly above (H1) unity, suggesting population numbers are stable at all elevations (Fig. 2.2e). Though population growth was stable (i.e., 0.9-1.12) at all populations, different demographic rates generated stable values in different populations. For example, H1 and H2 have high survival (Fig. 2a) and seedlings per fruit, but lower growth and number of fruits (Fig. 2.2b and d). By contrast, L1 and L2 have low survival rates (Fig. 2.2a) and seedlings per fruit, but high growth and number of fruits (Fig. 2.2b and d).

2.4.6 Neighbor effects on demographic rates and population growth rate

Neighbors affected multiple demographic rates and the direction of the neighbor removal effect varied across demographic rates. Neighbor removal treatment was included in the best fit model for probability of survival, growth, and variance in growth (App. Table A.4). Neighbors increased the probability of survival but reduced mean growth (Fig. 2.3a-b), with population-specific effects of neighbors on variance in growth (App. Table A.4). Namely, the presence of neighbors increased variance in growth at L1, strongly decreased variance in growth at L2, and weakly decreased variance in growth at H1 and H2. For all other demographic rate models, the best fit model does not include an interaction between neighbor removal treatment and

population (App. Table A.4). We note that with only four populations, it may be difficult to detect differential effects of neighbors across populations.

At all populations, neighbors acted as competitors, and the effect of neighbors on population growth rate varied across populations. For all populations, removal of neighbors resulted in an increase in population growth rate, indicating neighbors were acting as competitors. Neighbor effects on population growth rate were highest at H1, intermediate at H2 and L2, and lowest at L1 (Fig. 2.3e). Removal of neighbors significantly increased population growth rate at populations L2, H1, and H2, with no significant effect of neighbor removal at population L1 (Fig. 2.3f). Similarly, the effect of neighbors on population growth rate was marginally significantly larger at H1 and H2 than at L1 (H1 vs. L1 95% confidence interval (CI) on the difference between neighbor effects on population growth rate is 0.03-0.46; H2 vs. L1 CI: 0.01-0.43) and significantly higher at L2 than L1 (CI: 0.0765, 0.453); neighbor effects on population growth rate did not significantly differ between other population pairs (Fig. 2.3f).

Drivers of population-specific effects on neighbors on population growth rate

The demographic rates in the (unmanipulated) control treatment from the removal experiment data exhibited similar variation across populations as did the demographic rates in the (unmanipulated) demography data. Namely, populations with the highest demographic rate values in the control treatment also exhibited the highest values in the demography data (with identical patterns for second-, third-, and fourth-highest values) for all vital rates except for probability of survival (which only deviates slightly from this pattern; Figs. 2.2 and 2.3). The congruence between plant performance in the demography data and control treatments suggests that neighbor effects on population growth rate observed in the removal experiment include underlying variation in demographic rates across populations.

We found populations vary in the sensitivity of population growth rate to demographic rates. Population growth rates of L1 and L2 are significantly more sensitive to seedlings per fruit than are H1 and H2 (Fig. 2.4, 95% confidence intervals do not overlap), though sensitivities of population growth rate to other demographic rates do not differ significantly across populations (Fig. 2.4).

Differential effects of neighbors on population growth rate across populations (Fig. 2.3f) could arise from variation in neighbor effects on demographic rates and/or variation in the sensitivity of population growth rate to demographic rates. Given that the effect of neighbors on demographic rates varies across populations for one demographic rate (i.e., the best fit model for variance in growth includes a removal treatment x population term; App. Table A.4) and there are significant differences in the sensitivity of population growth rate to demographic rates across populations (Fig. 2.4), either of these phenomena could generate differential effects of neighbors on population growth rate across populations. To test whether variation in sensitivity is sufficient to drive among-population variation in demographic rates, we removed the interaction between population and treatment in the variance in growth rate model and recalculated population growth rate (Appendix A). We still see differential effects of neighbors on population growth rate across populations (App. Fig. A.1), suggesting that differences in sensitivity are sufficient to drive among-population variation in neighbor effects on population growth rate.

2.4.7 Climate effects on demographic rates and population growth rate

Experimental manipulations of climate impacted demographic rates, and the directions of these effects were consistent with elevational variation in demographic rates observed in the demography data. Using the climate experiment data, we found that the heating treatment was

included in the best-fit model for three out of five demographic rates: survival, probability of fruiting, and number of fruits, whereas the watering treatment was only included in one: variance in growth (App. Table A.5). Heating reduced survival (Fig. 2.5a), increased probability of fruiting (Fig. 2.5c), and strongly increased number of fruits (Fig. 2.5d). Variance in growth was higher in the watering treatment than in the control treatment (App. Table A.5). The best fit model for growth had neither watering nor heating included. Negative effects of warmer temperatures on survival are consistent with the lower survival at lower elevations observed in our demography data (Fig. 2.2a). Positive effects of warmer temperatures on probability of fruiting and number of fruits are consistent with higher probabilities of fruiting and number of fruits at lower elevations in our demography data (Fig 2.2c and d, App. Table A.3). Population growth rate was (non-significantly) higher in the heating treatment and the heating + watering treatment than in the control treatment.

2.5 Discussion

We first discuss the effect of population, then neighbor removal treatment, on demographic rates and population growth rate, highlighting how our results compare to findings from other species. We then discuss the among-population variation in neighbor effects on population growth rate, and the role of variation in sensitivity of population growth rate to demographic rates in driving these responses. We end by discussing whether similar responses might mediate effects of environmental drivers in other species and how these effects might inform conservation priorities.

Population growth rate is similar across populations in *S. lanceolatum*, with the confidence intervals of all populations' population growth rate overlapping (or slightly greater than) unity. With all values and confidence intervals above or near unity, these results reflect

stable population sizes at all population, reflective of the long-term persistence of this species over temporal changes in environmental conditions (Dechaine and Martin 2005). We do not see any evidence that the two lower-elevation populations are suffering from higher temperatures under climate change (as other studies do; e.g., Dulamsuren et al. 2017, Anderson and Wadgymar 2020, Berio Fortini et al. 2022). We note that elevational patterns in the demographic rate estimated with the least certainty, seedlings per fruit, are not entirely reflective of past work finding lower seedlings per adult at high elevations in this species (Jolls and Bock 1983), perhaps because of higher fruits per adult in high elevations (Fig. 2.2c, d, similar findings to past work in this species; Jolls (1980)).

The effects of neighbors were positive for some demographic rates and negative for others. These results are consistent with previous findings showing that neighbors increase some demographic rates while decreasing others (e.g., Williams and Crone 2006, Nomoto and Alexander 2021). Most studies so far have only measured neighbor effects on one or a few demographic rates (Aarssen and Keogh 2002, Maestre et al. 2005, Moll and Brown 2008), but those studies that have often found mixed effects, possibly attributable to life history tradeoffs (e.g., increased allocation to fruiting under competition comes at the expense of plant growth; Lyu and Alexander (2023)). Additionally, these results match other studies finding environmental drivers (e.g. climate) may have differential effects on demographic rates (Reed et al. 2013). Our study is yet another example showing that measuring only one demographic rate's response to neighbors will not allow inference at the level of population growth rate or fitness.

Our findings were largely inconsistent with the predictions of the stress gradient hypothesis (negative effects of neighbors at low elevation, positive effects at high elevation). First, we see no evidence for differential effects of neighbors across populations on most

demographic rates (i.e., no support for a population x neighbor removal term). Further, the effects of neighbors on population growth rate were, on average, more negative at higher elevations (Fig. 2.3f), in direct contrast to the predictions of the stress gradient hypothesis (Callaway et al. 2002, Maestre et al. 2009). Note our low elevation populations were not near the lower edge of the species' elevational range, so it may be near the lower range limit, the effect of neighbors becomes more negative (which would be consistent with the stress gradient hypothesis); similarly, our high elevation populations were not at the higher elevation range limit. At the outset of our study, we did establish two very low elevation sites at ~2100 m elevation, much closer to the lower elevational limit of the species' range, but these burned down in the 2012 High Park Fires less than a year after their establishment. In addition, if we had been able to measure neighbor effects at a higher number of populations or had sufficient data to test for size-specific effects of a population x neighbor interactions or effects of neighbors on seedling vital rates, we might have seen evidence for differential effects of neighbors on vital rates across populations, perhaps consistent with the stress gradient hypothesis.

Despite little change in the effect of neighbors on demographic rates among populations, we do see significant differences in the effect of neighbors on population growth rate. The lack of an interaction term between population and neighbor effect for almost all demographic rates, paired with significant differences in neighbor effects on population growth rates across populations, strongly suggest that changes in sensitivity of population growth rate to demographic rates across populations are the primary driver of neighbor effects on population growth rate. Supporting this analysis, when we remove terms for population x neighbor removal from variance in growth (the only demographic rate that contains such a term), we still see significant differences in neighbor effects on population growth rate (App. Fig. A.1). Few studies

have quantified the role of life history variation (i.e., variation in sensitivity of population growth rate to demographic rates) in mediating population response to environmental conditions, but such studies do show life history variation can be important. For example, Lyu and Alexander (2023) found the contribution of demographic rates to effects of neighbors on population growth rate differed across elevations, with survival and seedling establishment contributing to among-population variation in neighbor effects on population growth rate. However, it is unclear whether among-population variation in sensitivity to these demographic rates or neighbor effects on these demographic rates were the primary driver of these differences. Louthan et al. (2018) found effects of aridity on population growth rate can modulate the effect size of multiple environmental drivers (including neighbors). In this study, the effect size of neighbors on demographic rates did not change with aridity, but the effect size of neighbors on population growth rate did, entirely mediated by effects of aridity on the species' demographic rates and concomitant changes in sensitivity. Together, these previous studies (Louthan et al. 2018, Lyu and Alexander 2023) and the current study suggest that changes in sensitivity across populations could strongly modify the impact of driver effects across space.

Our results further suggest that changes in sensitivity across populations might be predictable. Experimental warming treatments affect demographic rates in the same direction as do (warmer) lower elevation populations (as compared to cooler higher elevation populations), suggesting that at least some of among-population variation in demographic rates is due to temperature. Thus, we would expect similar patterns of variation in sensitivity across any temperature gradient (elevational or latitudinal). The congruence between our findings across populations and within the climate experiment suggests that at least some of the variation in demographic rates across populations arises from plastic responses (though there may also be

adaptation to local climate conditions at low elevations). Thus, populations might be able to adapt to future climate conditions due to plasticity (similar to trait responses; e.g., Anderson and Gezon (2015)), in addition to any genetic adaptation to climate change.

While our study quantifies the impacts of neighbors on population growth rate, similar arguments can be made for other environmental drivers, with substantial conservation implications. For example, our results suggest that the effect of a management action on population growth rates could vary across populations simply because populations differ in the sensitivity of population growth rate to the demographic rates affected by the management action. Of course, stronger effects of that management action on a demographic rate at some populations (and in addition to differences in the intensity of the management action itself across populations) could further modify the effect of a management action on population growth rates. Similarly, perhaps changes in sensitivity to demographic rates across species' ranges might result in differential impacts of climate change in population growth rate across a species range, even in the absence of variation in warming rates across a species' range or in population-specific demographic rate responses to warming. However, we know little about whether variation in sensitivities to demographic rates among populations are common, let alone how general any patterns are. Morris and Doak (2005) have shown sensitivities and elasticities to demographic rates vary across populations in the wide-ranging *Silene acaulis* but found environmental variables such as elevation are not predictive of sensitivity patterns. Future work predicting population-specific driver impacts would benefit substantially from identifying how patterns in sensitivity change across species' ranges.

2.6 Data availability

Demography and neighbor removal data and are available at Dryad (https://doi.org/10.5061/dryad.63xsj3v7z). Climate experiment data are available on the Alpine Treeline Warming Experiment data storage platform (doi:10.15485/2008461).

2.7 Tables

Table 2.1: Fixed-effect parameters for demographic rates of *Sedum lanceolatum* used in our IPMs. In all cases x is size in year t, and y is the size in the following year (t+1), both log transformed. Population is represented by s and conditional number of fruits is indicated by N_f. Note, here we use the same notation for coefficients ($\boldsymbol{\beta}$) of each demographic rate, however these are unique to each demographic rate.

Demographic rate	Global model
Growth	$y = \beta_0 + \beta_1 x + \beta_2 pop. + \varepsilon$
Variance in growth	$var\big(y(t)\big) = \beta_0 + \beta_1 x + \beta_2 pop. + \varepsilon$
Probability of surviving	$logit\big(p(x)\big) = \beta_0 + \beta_1 x + \beta_2 pop + \varepsilon$
Probability of fruiting	$logit\big(p(x)\big) = \beta_0 + \beta_1 x + \beta_2 pop + \varepsilon$
Conditional number of fruits	$\log(N_f) = \beta_0 + \beta_1 x + \beta_2 pop + \varepsilon$

2.8 Figures

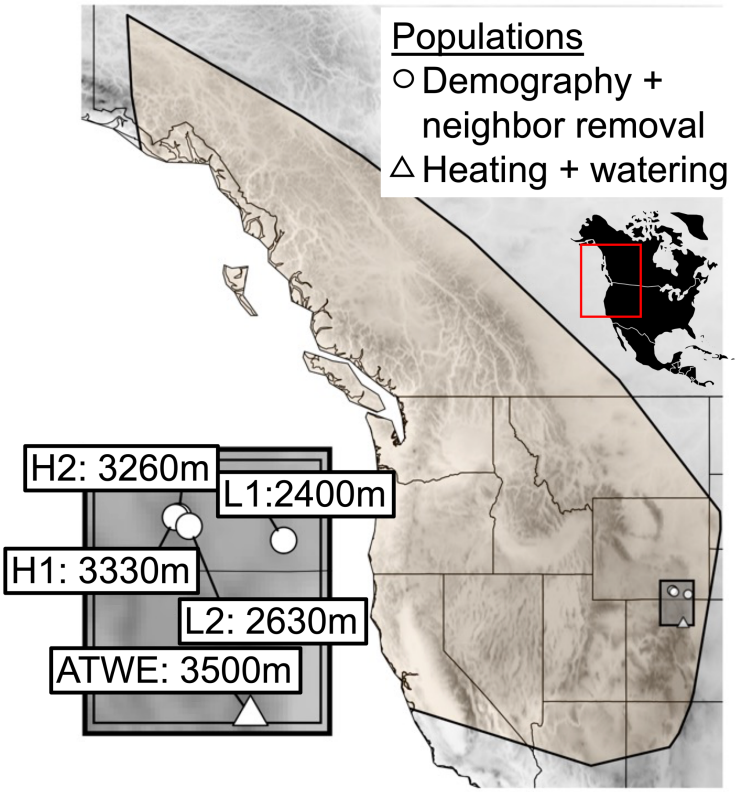

Figure 2.1: Range of *Sedum lanceolatum* (light orange polygon) derived from a minimum convex hull around occurrence records (GBIF.org, 2022), with locations of populations included in this study indicated as white circles (demography and neighbor removal data; Wyoming) or white triangles (climate treatments; ATWE indicates Alpine-Treeline Warming Experiment; Colorado). Inset maps show zoomed out study area, with the extent of the large map framed in red, or, in the black framed area, the zoomed in study area, noting populations and their respective elevations, with extent of inset map noted by black rectangle. Elevation is indicated with gray shading, with darker shades indicating higher elevations. Note points for H1 and H2 overlap due to geographic proximity of populations.

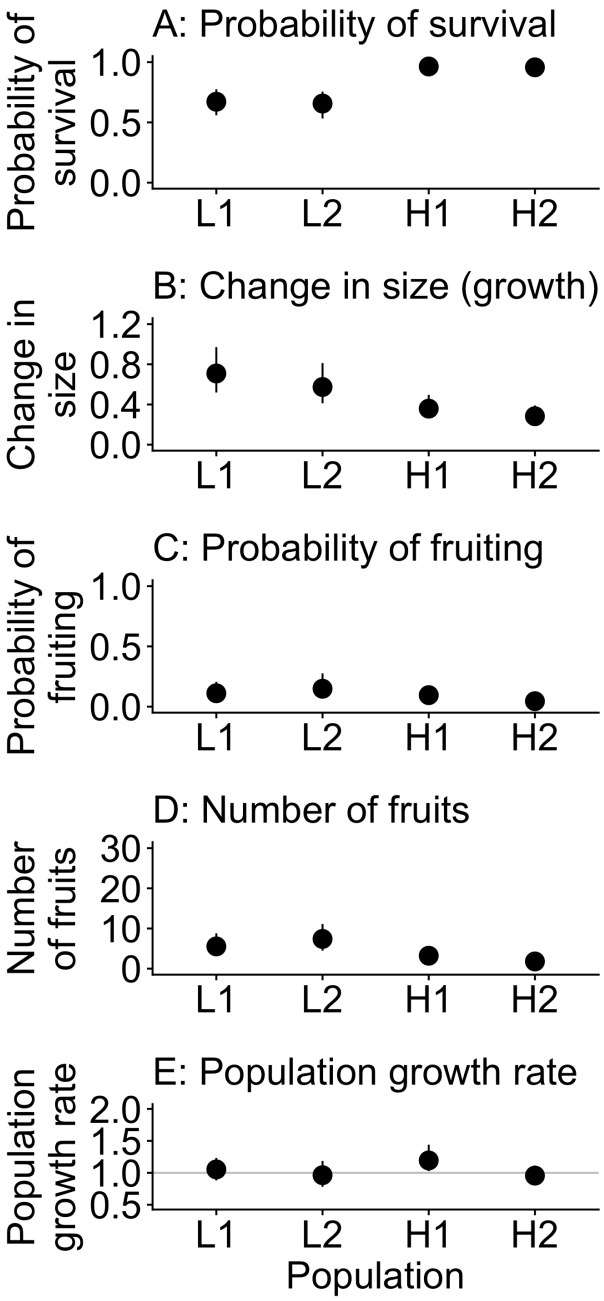

Figure 2.2: Population growth rate and demographic rates calculated using demography data at four populations. Panels a-d show predicted demographic rates for the mean size class using the best fit models for each demographic rate (which we also used to construct the IPMs). Panel e shows predictions of deterministic growth rate from integral projection models (IPMs) constructed using demography data for our four populations (L1, L2, H1, H2; "L" suffix indicates low and "H" indicates high elevation). We show the critical value of one with a grey horizonal line. Error bars show 95% confidence intervals on the fixed effect estimates (b-e) or 95% confidence intervals derived from incorporating parameter uncertainty into the demographic rate functions used to construct the IPM (a). We show size-specific responses and observed data in App. Fig. A.2.

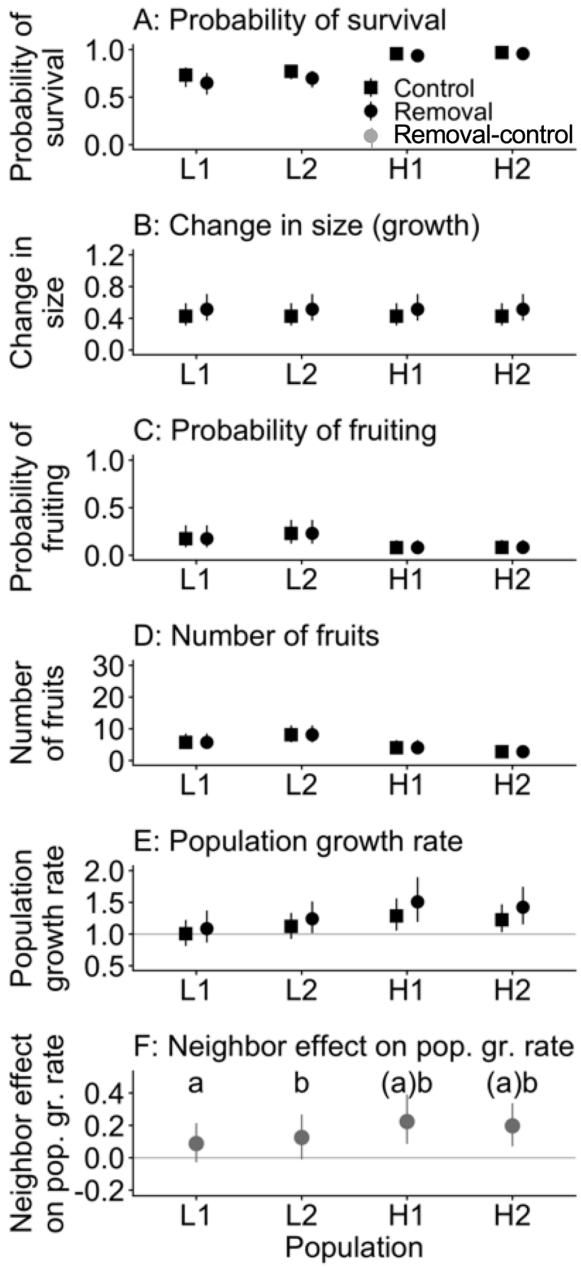

Figure 2.3: Effects of neighbor removal treatment on population growth rate and demographic rates across populations (L1, L2, H1, H2; "L" suffix indicates low and "H" indicates high elevation). In a-e, we show demographic rates and population growth rate values from unmanipulated control (Control) vs. neighbor removal treatments (Removal), such that positive effects of a neighbor removal treatment (i.e., removal value larger than control value) indicate competition. Panels a-d show the effect of neighbors on predicted demographic rates for the mean size class using the best-fit models for each demographic rate (which we also used to construct the IPMs). Panel e shows the difference between deterministic growth rate for neighbor removal vs. control treatment, predicted using integral projection models (IPMs) constructed from neighbor removal data. In a-e, error bars show 95% confidence intervals on the fixed effect estimates of the demographic rate function (a-d) or 95% confidence intervals derived from incorporating parameter uncertainty into the demographic rate functions used to construct the

IPM (e). In panel e, we show the critical value of one using a grey horizontal line. In panel f, we show the effect of neighbor removal treatments on population growth rate (population growth rate without neighbors- population growth rate with neighbors, such that positive values indicate competition). No effect of neighbor removal, a value of zero, is indicated by the gray horizontal line. Error bars indicate the 95% confidence intervals on the difference between population growth rate in the control vs. removal treatment. Letters above each error bar indicate the statistical significance (assessed using overlap of 95% confidence intervals) of differences in neighbor response in pairwise comparisons between populations. Populations sharing the same letter experience similar effects of neighbors (i.e., the 95% confidence interval on the difference between neighbor effects overlaps zero) and populations with different letters experience statistically significant differences neighbor effects on population growth rate (i.e., the 95% confidence interval on the difference between neighbor effect does not overlap zero); letters within parentheses indicate marginal significance. Pop. gr. rate indicates population growth rate. We show size-specific responses and observed data in App. Fig. A.3.

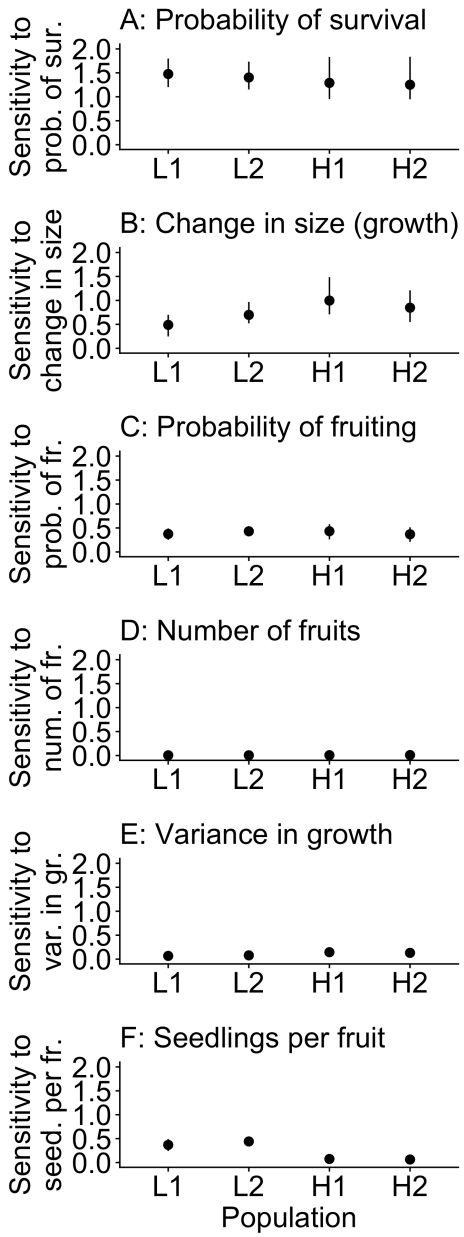

Figure 2.4: Sensitivity of population growth rate to demographic rates across our four populations (L1, L2, H1, H2; "L" suffix indicates low and "H" indicates high elevation) to demographic rates for the mean size class. We estimate sensitivities via perturbation. Error bars indicate 95% confidence intervals on sensitivities, derived from incorporating parameter uncertainty into the demographic rate functions used to construct the IPM. Prob. stands for probability, fr. for fruit, num. for number, var. for variance, and seed. for seedlings. We show size-specific sensitivities in App. Fig. A.4.

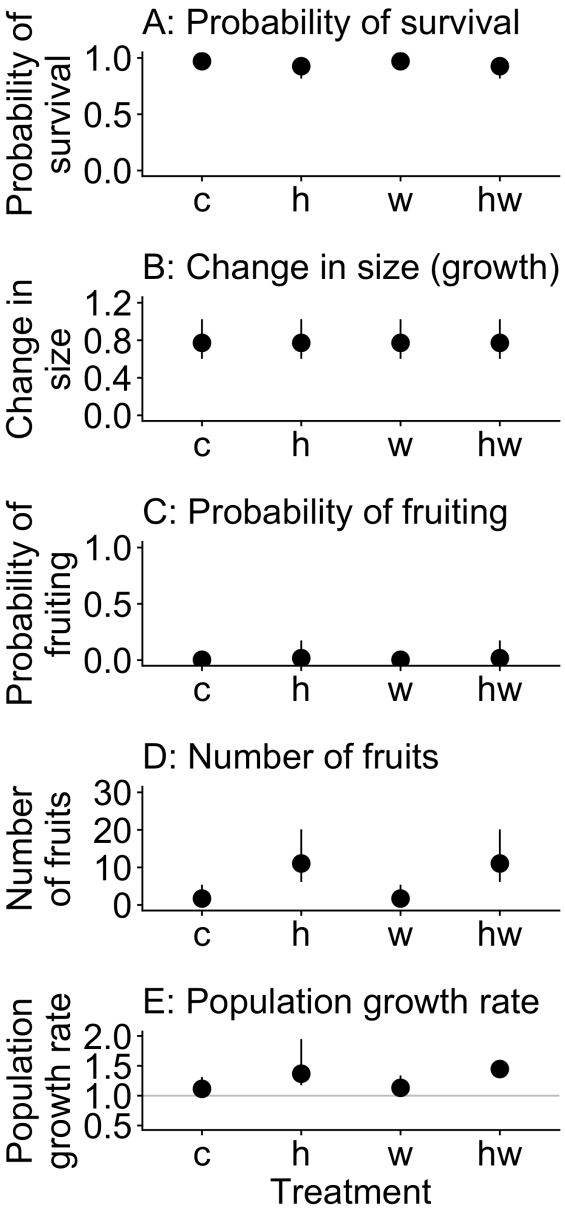

Figure 2.5: Effects of four climate treatments on population growth rate and demographic rates. In all panels, c represents the control treatment, h = heating, w = watering, and hw = heating + watering. Panels a-d show predicted demographic rates values for the mean size class using the best-fit models for each demographic rate (which we also used to construct the IPMs). Panel e shows deterministic growth rate predicted using integral projection models (IPMs) constructed from climate experiment data. We show the critical value of one with a grey horizonal line. Error bars show 95% confidence intervals on the fixed effect estimates (a-d) or 95% confidence intervals derived from incorporating parameter uncertainty into the demographic rate functions used to construct the IPM (e). Note that a watering treatment term was not present in the best fit model for any presented demographic rates, but is present for the best fit model for variance in growth. Additionally, neither heating nor watering was included in the best fit model for growth (b), making all values equal. We show size-specific responses and observed data in App. Fig. A.5.

Chapter 3 - Effects of insect, not mammalian, herbivory on plant population dynamics increase with plant range size

3.1 Abstract

Understanding how species respond to environmental drivers and how these responses vary across species are fundamental ecological questions and inform management under a changing climate and changing communities. The niche breadth hypothesis predicts species with larger niche breadths should experience less change in population growth due to variations of drivers than species with smaller ranges, however previous work has provided mixed support. We use long term plant cover data collected within bison and fire manipulations in a tallgrass prairie system to examine the effects of abiotic (climate and fire) and biotic (bison and grasshoppers) drivers on demographic rates across nearly a hundred native plant species with varying niche (range) sizes. While bison have large impacts on plant populations, there is no relationship with range size, nor do we find any relationship between fire effects and range size. Climate had a significant, albeit weak, increase in effect size with plant range size for colonization. The effect of grasshopper abundances on change in plant cover increased with plant range size. Our results call into question the applicability of the niche breadth hypothesis and emphasize the importance of considering biotic drivers when predicting plant population response patterns, particularly of species with a large range.

3.2 Introduction

Species vary widely in their geographic range size, but the drivers of these differences are often unclear (Lester et al. 2007). One commonly cited hypothesis, the niche breadth hypothesis, suggests that species with broad environmental tolerances should exhibit larger ranges. According to this hypothesis, because species can tolerate a variety of environmental conditions, they can occur over a large geographic area (Slatyer et al. 2013). Additionally, the niche breadth hypothesis predicts that species with a larger geographic range should be able to maintain a high population growth rate under a variety of environmental conditions (Sexton et al. 2017).; i.e., their population dynamics will respond less strongly to environmental drivers than will populations of species with a smaller range. Here we define a driver as a factor that has the potential to affect population growth rate. Empirical tests of the niche breadth hypothesis often assess whether corollaries of population growth rate, such as diet breadth or habitat specificity, show support for the niche breadth hypothesis (Slatyer et al. 2013), with only a few studies quantifying patterns in population growth rate (Pohlman et al. 2005, Sheth and Angert 2014, Pearse et al. 2022).

To achieve a large range size, species should be able to maintain population growth rates high enough avoid local extirpation under a wide variety of abiotic conditions (such as temperature, precipitation, or soil characteristics), biotic conditions (such as herbivores, prey availability, or pollinators), or both. Corollaries of population growth rate responses to abiotic drivers such as habitat breadth or thermal limits tend to show strong support for the niche breadth hypothesis (Laube et al. 2013, Slatyer et al. 2013). In contrast, corollaries of population growth rate responses to biotic drivers such as diet breadth show weaker (Slatyer et al. 2013) or no support (Laube et al. 2013) for this hypothesis. Direct measurements of population growth rate

response to abiotic drivers have generally shown support for the niche breadth hypothesis (Figure 3.1, panel A). We lack tests of the niche breadth hypothesis using direct measurements of population growth rate responses to biotic drivers, meaning that it is not clear whether biotic drivers more strongly impact population growth rate in species with small or large ranges (Figure 3.1A).

An alternative hypothesis proposed by Opler (1974) suggests that the effect of biotic drivers on population growth rate could increase with species range size. Opler compared insect herbivore species richness across members of the oak (*Quercus)* genus. He found insect herbivore species richness on individual trees increases as the tree species' range size increases. Such an effect could be explained by the species-area relationship of island biogeography theory (MacArthur and Wilson 2001): as a host's range size increases, it will encounter an increasing number of potential herbivore species. Potential herbivores will adapt to the newly encountered host species and may spread throughout a host's range, resulting in high herbivore species richness on hosts with larger range sizes. Similar findings have been shown in pathogens, where animals with larger ranges have higher pathogen species richness (Choo et al. 2023). If increasing herbivore or parasite richness results in larger herbivore or pathogen impacts on population growth rate, such an effect would lead to higher impacts of biotic drivers on population growth rate in species with larger ranges than in species with smaller ranges. Consistent with Opler's prediction, recent work by Louthan et al. (*in press*) found the effect of biotic drivers on population growth rate increased with range size (Figure 3.1, panel B). However, this meta-analysis combined data from a variety of studies with widely varying monitoring protocols and experimental designs. The lack of standardized tests of biotic driver

effects on population growth rates for many species limits our ability to test how biotic driver effects vary across species ranges.

In this study, we use long-term plant population measurements collected at a single site (and thus subject to near identical environmental conditions) for 95 species over multiple decades. To test the niche breadth hypothesis, we compare the effect of two abiotic drivers (annual variation in climate and fire frequency), and two biotic drivers (grasshopper and bison herbivory) across 95 species found at Konza Prairie Biological Station (KPBS) of differing range size, using long-term data and experiments from KPBS. To test the Opler hypothesis, we examine the effects of grasshopper herbivory on plant population growth rate. We additionally examine the impacts of bison on plant population growth rate. Opler's hypothesis predicts that plant responses to grasshopper herbivory should increase with plant range size, because there are >50 grasshopper species at KPBS. By contrast, we do not expect to see any change in bison effect size because this type of herbivory only includes one herbivore species (Figure 3.1, panel B).

3.3 Methods

3.3.8 Study site

We studied plants at Konza Prairie Biological Station (KPBS), a 3,500-ha untilled native tallgrass prairie in the Flint Hills of NE Kansas, USA, with moderate temperatures (from 1983-2023, 850 mm precipitation/year, 13°C mean annual temperature (Nippert 2024). The Flint Hills is one of the largest remaining fragments of the critically imperiled tallgrass prairie ecosystem (Sampson and Knopf 1994). Aboveground biomass is predominantly perennial warm-season grasses including big bluestem (*Andropogon gerardii*), little bluestem (*Schizachyrium*

scoparium), and Indian grass (*Sorghastrum nutans*), however, forb species comprise most of the diversity in the region (Towne 2002).

Our abiotic and biotic drivers are all likely to strongly influence population dynamics. Climate conditions in this region are highly variable and exert strong effects on population dynamics. Grasslands have been subject to regular fire for millennia (Karp et al. 2021). Bison are native to this ecosystem and have grazed primary graminoids since the middle-Holocene (Widga et al., 2010). Bison reduce grass cover, allowing for increased forb cover and richness (Fahnestock and Knapp, 1994; Elson and Hartnett, 2017), and increase landscape heterogeneity (Knapp et al., 1999), as well as plant and animal diversity (Collins et al., 1998; Nickell et al., 2018; Ratajczak et al., 2022). Grasshoppers are abundant herbivores in grassland systems (Branson et al. 2006, Branson 2008) whose effects on total above ground plant biomass are comparable to, or even greater than, ungulate grazers (Onsager 2000, Meyer et al. 2002, Laws et al. 2018). Grasshoppers are often highly mobile and fairly generalist insect herbivores, and can benefit plants through cycling nutrients, especially through frass excretions (Belovsky and Slade 2018).

KPBS is ideally suited to test the effects of these four drivers on plant population dynamics. Beginning in 1977, KPBS initiated a large-scale burning experiment, with replicate watersheds subjected to fire return intervals (FRI) of 1-, 2-, 4-, or 20-years. In 1987, 30 adult bison (*Bison bison bison*) were introduced to a portion of KPBS. Later, in 1992, bison were introduced to additional experimental units ("watersheds") of KPBS. From 2013 to 2023 there have been, on average, 283 bison (Blair 2024) with year-round access to ten watersheds (~1,000 ha) of replicated FRI treatments. In this analysis, we use 2003-2020 KPBS climate, plant cover, and grasshopper abundance data collected in upland areas in 14 watersheds, including eight

ungrazed watersheds and six bison-grazed watersheds (see Appendix Table B.1 for specific watersheds), to test for effects of climatic and biotic drivers (grasshoppers and bison), as well as FRI, on plant population dynamics.

3.3.9 Datasets

Plant cover data: Plant cover data collection (Hartnett et al. 2020) was started in 1983 as part of the National Science Foundation's Long-Term Ecological Research (NSF LTER) program. In each of the 14 watersheds, four 50m long transects were established within three topographic positions; we only use upland topographic position in this analysis (Florence soil). Along each transect are five permanent 10 m^2 circular plots. Twice a year (late May to mid-June and August to early September), canopy cover for all vascular plants located within each plot are estimated using a modified Daubenmire percent cover scale with seven cover classes (0-1% cover; 2-5% cover; 5-25% cover; 25-50% cover; 50-75%; 75-95% cover; 95-100% cover). We use the midpoint percent values for each cover class in our analyses (i.e., 0.5%, 3.5%., etc.; hereafter, "cover"), and set the cover to zero if a species was not present in the plot. If a species was recorded in both seasons in a plot, we used the highest cover value for that year for analyses. We confine our analysis to native species and species that were present in >= 40 plot-year combinations.

Climate data: We used the Standardized Precipitation and Evaporation Index (SPEI) to represent annual climate variation (Vicente-Serrano et al. 2010). To calculate SPEI, we used long-term climate data from the KPBS headquarters weather station (Nippert 2024). We first used the Thornwaite method for calculating PET (Thornthwaite 1948) from the SPEI R package (version 1.8.1) (Santiago Beguería and Vincente-Serrano 2023). We then used the PET values to calculate the monthly climatic water balance (difference between monthly cumulative

precipitation and monthly PET). Twelve-month SPEI was then calculated using the *spei* function in the SPEI R package. We calculated year-specific SPEI, defining a year as June 1-June 1; in our analyses we regress SPEI over the previous year against changes in plant cover over that year (assuming all plant sampling is conducted June 1).

Grasshopper abundance data: Sampling is conducted in late July to early August by sweeping netting ten sets of 20 sweeps at two sites within a watershed (Joern 2023). Grasshoppers are then frozen and identified to species. In our analyses, we calculate watershed- and year-specific grasshopper abundance by summing the number of grasshoppers caught in a watershed per year and dividing by the number of sampling events to account for sampling effort, which can differ between years and watersheds (Welti et al. 2021).

3.3.10 Range size estimation

For all plant species, we delineate the geographic range (here defined as the extent of occurrence) using occurrence records from iDigBio and the Global Biodiversity Information Facility (GBIF) (accessed August 2024). Occurrence records were downloaded using the 'occ' function in the *spocc* package (Owens et al. 2024) (version 1.2.3). We then filtered records to those with latitude and longitude coordinates, and limited to 5000 records. We removed duplicated observations, those not occurring over terrestrial North and South America, or those that overlapped botanical garden locations using the *CoordinateCleaner* package in R (version 3.0.1) (Zizka et al. 2019). We estimated range size by constructing a minimum convex polygon around all occurrences excluding the outermost 1% records (to reduce the influence of outliers) by calculating the centroid of all occurrence points, removing the furthest 1% of points from the centroid, and finally making the convex polygon using the *chull* R function. Range size was then estimated as the terrestrial area within the polygon.

3.3.11 Analyses

Our analytical approach involved three steps: first, we estimated the effect sizes of biotic and climatic drivers for each species using a series of species-specific models of three demographic rates (colonization, a population growth rate corollary, and extirpation). Second, we used the (model-estimated) effect size of each driver to ask how the effect of each driver on these three demographic rates varied with range size. Finally, we repeated the second step for plant species known to be consumed by grasshoppers at KPBS. Below, we describe each step in detail.

To estimate the effect sizes of biotic and climatic drivers for a species, we fit species-specific models for three demographic rates: probability of colonization (i.e., if species cover was 0 in a plot in time *t-1*, but >0 in *t,* the next year), change in cover (i.e., $cover_t$ / $cover_{t-1}$, given cover was >0 in both years), and probability of plot level extinction (i.e., if species cover was >0 in a plot in time *t-1*, but 0 in *t*; we refer to this as "extirpation") using generalized linear models. All models included the following predictor variables: bison presence (yes/ no), SPEI, log-transformed grasshopper abundance in year *t*, FRI, and time since fire (TSF; FRI and TSF may exert distinct effects, Sutton et al. (2024)). We also included a term for log-transformed grasshopper abundance in *t-1* to account for any lagged effects. Additionally, to account for variation in effect size due to life span (Morris et al. 2008, Dalgleish et al. 2010, Mashau et al. 2021), we added an additional lifespan parameter (annual, biannual, or perennial) to our models. Response variable was binary for colonization and extirpation and normal for change in cover. If any regression had fewer than <40 data points or insufficient data to estimate a particular coefficient, we exclude that regression or the associated coefficient from downstream analyses.

We then used the results of these regressions to estimate how the effect of climatic and biotic drivers (bison presence, SPEI, grasshopper abundance in year *t* and *t-1*, TSF, and FRI) varied with range size. We extracted coefficient values for each of the parameters in the species-specific models for each demographic rate. We use coefficients to represent the effect size of a driver on the demographic rate for that species, as each coefficient quantifies how much a change in the driver affects demographic rates. Because we are interested in exploring the magnitude a driver, rather than the direction of influence for a driver, we use the absolute value of the regression coefficients. Hereafter, we call the log-transformed absolute values of SPEI, bison presence, grasshopper abundance in time *t,* and grasshopper abundance in *t-1* coefficients for a given demographic rate the "effect size" of climate, bison, grasshoppers, and lagged grasshoppers, respectively. We then asked whether effect sizes for each driver varied with species' range size. Namely, for each demographic rate and driver, we regressed effect sizes against range size using a linear model and used AICc to determine which effect sizes were related to range size .

Opler (1974) predicts that plant species with a large range will be consumed by a higher species richness of grasshopper herbivores. To test this hypothesis, we used independent data on grasshopper diets in the KPBS region (Mulkern 1969, Campbell et al. 1974, Welti et al. 2019) to fit a linear regression between plant range size (log transformed) and number of grasshopper species whose have been observed to consume that plant species (log transformed).

One complication to our analysis is that both herbivores in our system (bison and grasshoppers) are unlikely to consume all species included in our analysis. Thus, for some species included in our analysis, grasshoppers might have minimal effect on plant population dynamics simply because they are not herbivores for those species. To guard against this

problem, we used the same grasshopper diet data (Mulkern 1969, Campbell et al. 1974, Welti et al. 2019) to subset our regressions to only plant species known to be consumed by grasshopper species. Campbell et al. (1974) and Mulkern (1969) use microhistological methodologies on grasshopper gut contents while Welti et al. (2019) use DNA barcoding. We were unable to conduct similar analyses with bison diets, as we were unable to find a study with plant species included in bison diets identified to species taxonomic level and including more than one KPBS species. However, we approximated bison diet by filtering to only grass species, as bison primarily (~90% of diet in tallgrass prairies) consume grasses (Plumb and Dodd 1993). We use the same methods described above to create a linear regression using range size and AICc to determine if bison effect size varies with plant range size.

3.4 Results

Our dataset included 95 plant species and over 113,000 cover class transitions not including 0-0 transitions (over 400,000 when including 0-0) with a median of 673 transitions per species. The lowest number of observations was 42 for *Spartina pectinata*, with a high of 3997 transitions for *Andropogon gerardii*. Range sizes for plant species had a median value of 5.8×10^6 km^2, with a range of 1.2×10^6 km^2 (*Dalea multiflora)* to 3.4×10^7 km^2 (*Achillea millefolium)*. We found a weak, but significant, positive relationship between the number of grasshopper species found to consume a given plant species and the plant species' range size (Figure 3.2; range size coefficient (slope) of 0.22; AICc weight of 0.79; R^2 =0.04 and p-value of 0.03). Continuous driver values were highly variable; median grasshopper abundance per transect per watershed was 109 (range 9.5-564) and median SPEI was -0.46 (-1.83 - 1.30).

The relative importance of each driver was similar across all demographic rates across species, and species were highly variable in their responses to drivers (Figure 3.3). Effect sizes of

bison were highest for all demographic rates (median of untransformed absolute effect size for colonization: 1.34, change in cover: 0.68, and extirpation: 0.87), followed by FRI (0.40, 0.35, and 0.27 median effect size for colonization, change in cover, and extirpation respectively). For all demographic rates, effect sizes of grasshoppers (median effect sizes of 0.12, 0.24, and 0.13) and SPEI (median effect sizes of 0.09, 0.17, and 0.07) were lowest. Note that our measurement of effect sizes cannot fairly compare the effect sizes of categorical variables (i.e., bison and FRI) with continuous variables (i.e., grasshopper abundance or SPEI). Bison effect sizes were the most variable with a standard deviation of 4.72, over double that of the next most variable: FRI at 1.86.

Range size was related to effect size for multiple drivers and demographic rates; however, range size effects were not consistent across driver nor model type (Figure 3.4 and Appendix Figure B.1). The effect of grasshopper abundance on fluctuations in cover significantly increased with plant species range size (range size coefficient from linear model = 0.61; all other demographic rates did not vary with range size). The effects of SPEI on colonization significantly increased with plant species range size (0.28; Figure 3.4; ; all other demographic rates did not vary with range size). Effects of lagged grasshopper abundance, bison, FRI, or TSF did not vary with plant species range size for any demographic rate (Appendix Figure B.1).

When subsetting to the 57 plant species known to be consumed by grasshoppers, we found that the effect of both bison presence and grasshopper abundance on change in cover increased with plant range size (slopes of 0.57 and 0.66 respectively; Figure 3.5), with no change in bison or grasshopper effects on colonization or extirpation with range size. Climate, fire, and lagged grasshopper abundance effects on changes in plant cover, colonization, or extirpation all

did not vary with plant range size (Appendix Figure B.2). In Appendix B, we show results derived from only histological or only DNA-derived estimates of grasshopper diet.

When we confined our analyses to only species consumed by bison (i.e., all 17 grass species), we found that the effects of fire (TSF) on change in cover decreased with plant range size (coefficient value of -4.08), with no change in TSF effect with plant range size for colonization or extirpation. We found that the effect of SPEI on extirpation increased with plant range size (coefficient value of 1.42; Appendix Figure B.3). The effect of biotic drivers did not vary with plant range size for any demographic rate.

3.5 Discussion

In this study, we find no support for the niche breadth hypothesis but strong support for the Opler hypothesis. When considering change in cover class, response to environmental drivers (biotic or abiotic) never decreased with plant range size (Figure 3.4), contrary to the niche breadth hypothesis. We do find support for the Opler hypothesis: namely, the richness of grasshopper species consuming a given plant species increases with the plant species' range size (Figure 3.2) and that effect of grasshoppers on change in plant cover increases with plant range size (Figure 3.4). Also consistent with the Opler hypothesis, the effect of bison on plant cover does not change with range size (Figure 3.4) or increases less strongly than effects of grasshoppers (Figure 3.5). Environmental drivers' impacts on colonization and extinction probabilities do not change with range size (with the notable exception of effects of SPEI on colonization).

The niche breadth hypothesis predict species with smaller population growth responses to drivers should have a larger geographic range (Slatyer et al. 2013) due to larger fundamental niches (Sexton et al. 2017). When measured at the level of population growth, previous work has

supported the niche breadth hypothesis for climatic (abiotic) drivers (Pearce-Higgins et al. 2015). While work on population growth rate correlates suggest that the effect of biotic drivers on population growth rate should decrease only weakly or not at all with range size (Laube et al. 2013, Slatyer et al. 2013), we lack tests of the niche breadth hypothesis for biotic drivers at the level of population growth rate, let alone tests that adopt a standardized experimental approach that allows for fair comparison across diverse species. Louthan et al. (*in press*) used a meta-analysis approach to compare responses across a variety of species and found little support for the niche breadth hypothesis (though methods of quantifying effect size varied dramatically across species). Similarly, our results, using both a wide variety of species and a standardized approach to estimating effect size, do not find support for the niche breadth hypothesis. The one exception is grass species' response to time since fire (Appendix Figure B.3), which does support the niche breadth hypothesis (though SPEI shows the opposite pattern). Given the support for the niche breadth hypothesis at the level of population growth rate (Pearce-Higgins et al. 2015), perhaps previously observed patterns failing to support the niche breadth hypothesis are a symptom of variation in driver intensity across studies leading to spurious results (Louthan et al. *in press*) or bias towards publication of insignificant results (Pearce-Higgins et al. 2015).

Our results for changes in plant cover are consistent with the Opler hypothesis (1974). Opler's hypothesis posits that plant species with a large range tend to have ranges that intersect with a higher number of herbivore species' ranges. As a grasshopper species intersects the plant species' range, the grasshopper may begin to consume that plant species (either via making behavioral modifications or adaptation). Thus, plant species with larger ranges (whose ranges will intersect a higher number of grasshopper species' ranges), will host a higher species richness of grasshopper consumers than plant species with smaller ranges (Figure 3.2). Because higher

richness of grasshopper species that can consume a given host plant should result in larger effects of grasshoppers on population dynamics, we should see a larger effect of grasshopper herbivory on population growth rate in plant species with a larger range compared to those with a smaller range (Figure 3.4). Conversely, bison herbivory is effected by one species that is able to traverse longer distances than grasshoppers. As such, Opler's hypothesis predicts that we should not see an increase in bison effect size with increasing plant range size; we find results consistent with this prediction (Figure 3.4).

When only including species known to be consumed by grasshoppers, the effect of bison on change in percent cover increased with plant range size (inconsistent with Opler's hypothesis). Such an effect could occur due to diet preferences of individual bison that is somewhat similar to Opler's hypothesis; for example, if an individual bison encounters a plant species within the bison's home range, it may begin to preferentially consume that species; because a higher number of individual bison are likely to encounter a wide-ranging plant species, each wide-ranging plant species is likely to be consumed by a higher fraction of the bison population. Alternatively, if local population density increases with range size and bison prefer to consume locally dense species (Dumont et al. 2002), bison herbivory could be higher on large-ranged species. This result could also be attributed to an interactive effect between bison and grasshoppers on plant communities, which has been documented previously (Joern 2004, Jonas and Joern 2007, Welti et al. 2019, Varriano et al. 2020).

One limitation to our findings is that we cannot differentiate direct vs. indirect effects on herbivores. In addition to directly affecting plant populations via consumption or trampling, herbivores could indirectly influence plant populations through altering competitor, mutualist, or other consumer densities or behavior (Crawley 1989, Whiles and Charlton 2006, Maron and

Crone 2006). For example, bison consume dominant grasses, indirectly increasing population growth rate of sub-dominant species such as forbs (Knapp et al. 1999). In addition to positive indirect effects of herbivory, we might also see positive direct effects of herbivory if plants engage in compensatory regrowth (McNaughton 1983, Belsky 1986, Agrawal 2000). In future work, we plan to try to isolate the consumption effects from other indirect effects by conducting additional analyses on species that respond negatively to herbivore abundances (indicating the net effect of herbivory is negative).

All previous work testing the niche breadth hypothesis at the level of population growth rate has focused on population dynamics in already established populations, rather than colonization or extirpation probabilities. We found that most environmental drivers' impacts on colonization and extinction probabilities do not change with range size, expect for the effect of SPEI on colonization. We found a significant positive relationship between the effect of SPEI on colonization and plant range size, opposite of the negative relationship we would expect under the niche breadth hypothesis. These results suggest that as a plant species' range size increases, the effect of extreme weather conditions on colonization becomes stronger. Depending on the sign of this effect (i.e., positive vs. negative effects of hot and dry conditions), this finding could have major implications for species' range shifts with climate change. For example, if hot and dry conditions tend to increase colonization more substantially in plant species with a large range, we might expect that species with a large range will be better able to shift their ranges in a future climate.

Understanding how species respond to environmental drivers is important for management of native plant communities, especially in a changing climate, in the face of global and regional insect declines (Burkle et al. 2013, Hallmann et al. 2017, Welti et al. 2020), and the

widespread loss of large native mammalian herbivores from North America (Martin, 1967; Barnosky et al., 2004; Smith et al., 2018; Meltzer, 2020). Our results suggest that biotic drivers such as herbivory have important ecological roles, particularly for plant species with large geographic ranges, and should be accounted for when planning habitat management and conservation.

3.6 Data availability

All data used in this study is publicly available. Full datasets and detailed sampling protocols for KPBS can be accessed on the KPBS LTER website: http://lter.konza.ksu.edu/data (dataset codes: vegetation cover = PVC02, climate = AWE01, grasshopper abundance = CGR02). Grasshopper diet studies are cited in-text.

3.7 Figures

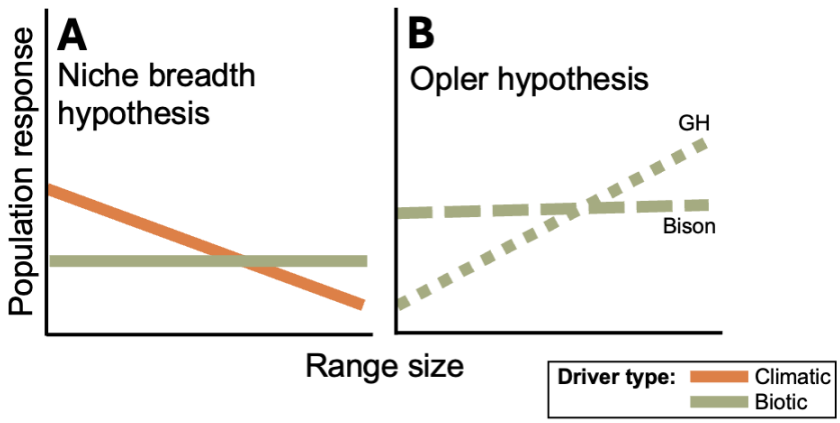

Figure 3.1: Expected population responses due to climatic (abiotic) drivers (orange lines) and biotic drivers (green lines) with increasing range size for two scenarios. Panel **A** shows the expected responses as predicted by the niche breadth hypothesis. Panel **B** shows the predictions of the Opler hypothesis for two biological drivers: grasshopper abundance (GH; green dotted line) and bison presence (green dashed line). We do not expect to see a change in population response to bison presence with increasing range size, however we do expect to see an increasing change in population due to grasshopper abundance due to higher diversity of insect consumers found on larger ranged plant species (Opler 1974).

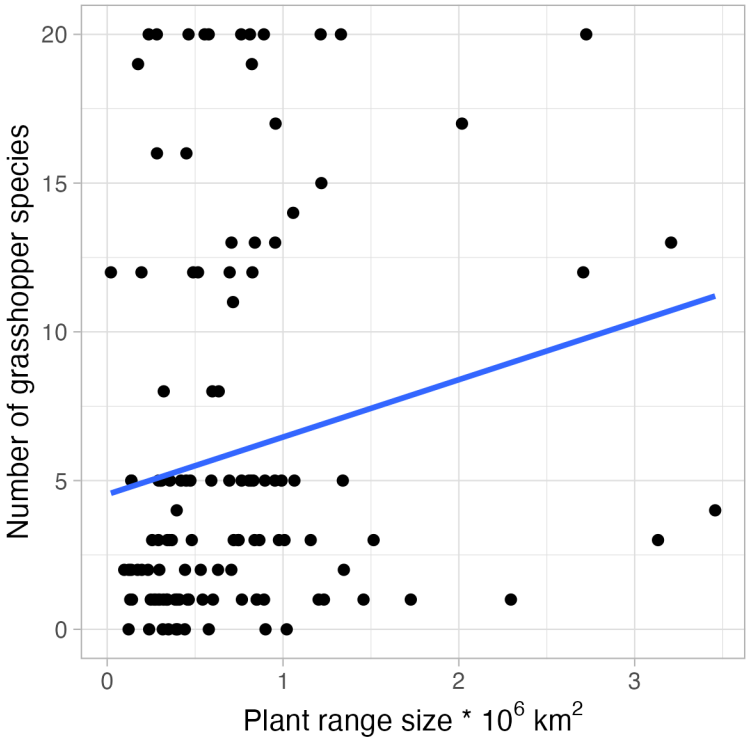

Figure 3.2: Number of grasshopper species documented consuming a plant species vs. plant species' range size at Konza Prairie Biological Station (KPBS). The number of grasshopper species consuming a given plant species (i.e., the y axis) was generated from a grasshopper-plant network constructed using DNA barcoding of grasshopper gut contents by Welti et al. (2019) for KPBS species; methods of data collection are described in that publication.

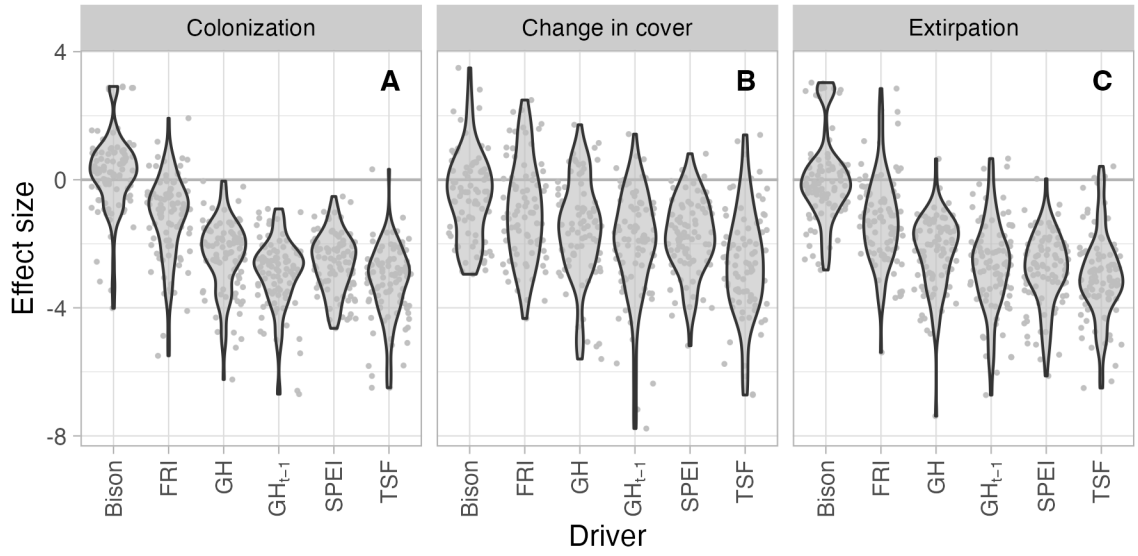

Figure 3.3: Distributions of effect sizes for each driver (bison, fire return interval (FRI), grasshopper (GH) abundance and in previous year (t-1), SPEI (standardized precipitation-evapotranspiration index; drought index), and time since fire (TSF) for three demographic rates (probability of colonization, change in percent cover, and probability of extirpation). Gray dots are effect sizes for each species, with violin plots showing the distribution of effect sizes for a given driver; points have been jittered horizontally to improve readability. We define effect sizes as the log-transformed absolute coefficients of the indicated driver for species-specific models for demographic rates.

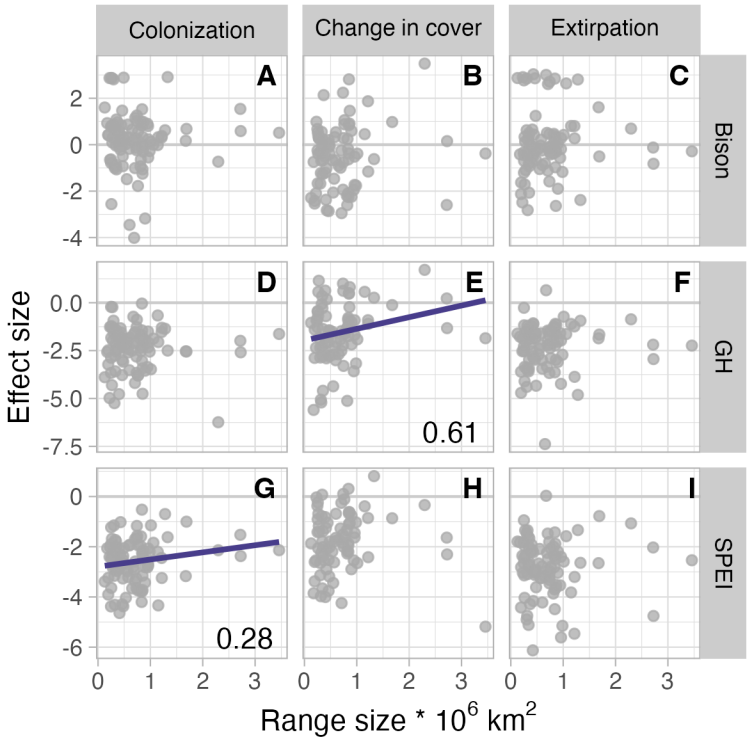

Figure 3.4: Effect sizes vs. plant range size when using all plant species. Columns are our three demographic rates: probability of colonization (panels A, D, and G), change in cover (B, E, and H), and probability of extirpation (C, F, and I). Rows are driver type: bison presence (A-C), grasshopper abundance (GH; D-F) and SPEI (standardized precipitation-evapotranspiration index; drought index; G-I) in the t-1 to t interval. Gray dots are species-specific effect sizes for the respective driver and demographic rate. Dark lines indicate a significant relationship between effect size and range size for a respective model and driver, as indicated by AICc results; text indicates the fitted coefficient values for the range size parameter. No line indicates a non-significant relationship. See **Appendix Figure B.1** for remaining driver results (FRI, lagged grasshoppers, and TSF).

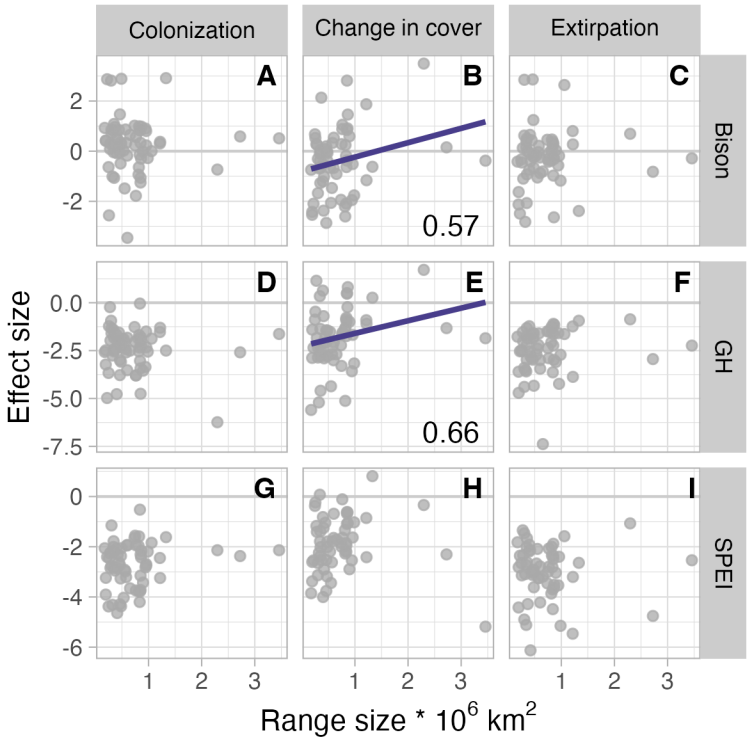

Figure 3.5: Effect sizes vs. plant range size when subsetting to plant species consumed by grasshoppers. Columns are our three demographic rates: probability of colonization (panels A, D, and G), change in cover (B, E, and H), and probability of extirpation (C, F, and I). Rows are driver type: bison presence (A-C), grasshopper abundance (GH; D-F) and SPEI (standardized precipitation-evapotranspiration index; drought index; G-I) in the t-1 to t interval. Gray dots are species-specific effect sizes for the respective driver and demographic rate. Dark lines indicate a significant relationship between effect size and range size for a respective model and driver, as indicated by AICc results; text indicates the fitted coefficient values for the range size parameter. No line indicates a non-significant relationship. See **Appendix Figure B.2** for remaining driver results (FRI, lagged grasshoppers, and TSF).

Chapter 4 Rarity and dispersal influence leading edge population movement in grassland forb species

4.1 Abstract

Understanding the combined effects of rarity and dispersal ability on plant species' responses to environmental drivers is crucial for conservation, especially under climate change. We investigated the population dynamics and potential range shifts of 15 North American grassland species, focusing on how different rarity types (combinations of range size, habitat specificity, and local population density) and dispersal traits influence speed of movement at the species' leading edges. Using density-structured models, we analyzed species' responses to climate, grazing, and fire, and combined these models with estimates of long-distance wind dispersal to run 50-year simulations to predict range shifts for each species. We found species generally exhibited weak responses to temporal variation in environmental drivers, though four species' population dynamics, across a variety of rarity types, differed in leading edge vs. central populations of the species' ranges. Dispersal traits varied among rarity types but did not predict probability of long-distance dispersal. However, probability of long-distance dispersal was the primary driver of range shift distance. Among rarity types, habitat specificity emerged as the most limiting factor in leading-edge movement. These results are robust to alternate climate scenarios. Our findings highlight the need for species-specific conservation strategies that prioritize species conservation based on both dispersal abilities and habitat requirements. These insights are critical for informing conservation efforts in grassland systems, where climate change and habitat loss may simultaneously limit range shifts.

4.2 Introduction

If rare species are to be conserved on our landscapes, we must understand how they respond to environmental drivers if we are to ensure their survival. Rare species have long been a focus of ecologists (Levins and Culver 1971, Myers et al. 2000, Bonn and Gaston 2005), and are of primary concern for conservation due to their higher likelihood of extinction (Harnik et al. 2012, Bland et al. 2017, Dudley et al. 2019, Chichorro et al. 2019, Staude et al. 2020). Despite this focus, there is no broadly accepted classification scheme defining rarity (Rabinowitz 1981, Kunin and Gaston 1993, Wilfahrt et al. 2021, Crisfield et al. 2024), however there is general consensus on the importance of range size, habitat specificity, and local population density as indicated by the broad use of the framework laid out by Rabinowitz (1981) (Crisfield et al. 2024). This framework described by Rabinowitz described seven possible rarity types (combinations of small range, habitat specialization, and small local populations) and one "common" type (large range, habitat generalist, and dense local populations).

As climate change continues to increase in severity, these at-risk species will face increasingly higher probabilities of decline and extinction. The long-term persistence of species is dependent on either adapting to changing environmental conditions at extant populations or shifting geographic location to track optimal climatic conditions, often to higher elevations or latitudes (Loarie et al. 2009, Dudley et al. 2019). The ability of a species to respond to changing environmental conditions is species specific and will depend on species phenological traits and ability to modify those traits (Parmesan 2006). If species are not able to adapt, their only option is to move to more suitable habitat, a non-trivial task for stationary species, such as plants.

For a species to move to a more suitable habitat it is essential 1) there still exists suitable habitat and 2) the propagules can reach the suitable habitat. As habitats become increasingly

fragmented, the distances between patches of suitable habitat increases, decreasing the probability of propagules reaching those habitats (Merel et al. 2004). The ability of a propagule to reach a suitable habitat is limited by a) its dispersal distance, which increases with seed size, height when seeds are released, and seed terminal velocities) (Katul et al. 2005, Thomson et al. 2011, Beckman et al. 2018), and b) the population size at the source population (Simberloff 2009) with larger populations producing more propagules, thus increasing the chances of a propagule reaching hospitable habitat. Recent work has emphasized the need to account for both population demographics and dispersal ability to fully understand species' potential response to climate change (Kot et al. 1996, Neubert and Caswell 2000, Hemrová et al. 2017, Barber et al. 2019, Wall et al. 2024), which is likely to vary by rarity type.

Population responses and dispersal ability are likely to be differentially impacted by the effects of climate change, which are likely to vary across a species' range. This is especially true for temperate species or large range species where climatic conditions at northern range limits could become more favorable (Thuiller et al. 2005, Evans and Jacquemyn 2022). Leading-edge populations, or those at the expanding edge of a species' range, may respond to climate change differently from more central populations: as climate warms, leading-edge populations are more likely to encounter suitable conditions for growth and expansion, enabling them to act as "pioneers" in colonizing new habitats (Safriel et al. 1994). Understanding the response of leading-edge populations is crucial, as they play a key role in facilitating range shifts and influencing the pace of species' responses to climate change.

Rarity type may provide insight into species' population dynamics and dispersal capabilities. Species with smaller ranges should exhibit larger responses in population growth rate in response to environmental drivers, particularly climatic drivers (i.e. niche breadth

hypothesis) (Sexton et al. 2017). Additionally, smaller range sizes have been linked to higher survival rates (Dickinson et al. 2007) and less investment in reproduction (Murray et al. 2002, Cofre et al. 2007), which could render such long-lived species less responsive to climate change (Morris et al. 2008). Similarly, habitat specialist species are more likely to outcross (Espeland and Emam 2011) and have shorter lifespans but lower colonization ability (Evju et al. 2015), likely increasing population growth rate change in response to drivers. Smaller local populations generally have slower life-histories (e.g., fewer but larger seeds) (Murray et al. 2002, Farnsworth 2007) and less variability in population growth rate than larger populations (Dickinson et al. 2007, Sritharan et al. 2022) making these species' population growth rates more stable, but producing fewer propagules lowering dispersal ability (Simberloff 2009). The impacts of multiple types of rarity is seldom examined, but these rarity combinations appear to result in distinct reproductive traits (Espeland and Emam 2011) and could mitigate some threat of extinction risk depending on the specific rarity combinations (Harnik et al. 2012).

Here, we examine the combined effects of rarity type and dispersal on potential leading edge range populations' ability to shift in response to climate change using 15 Great Plains grassland species. The Great Plains of the United States is a critically threatened ecosystem, with less than half of pre-European settlement native prairie remaining, and less than five percent of tallgrass prairies remaining (Scholtz and Twidwell 2022). Many species in the region are likely to be impacted by climate change, with regions of the Great Plains already experiencing more extreme weather variability than has been observed historically (Wuebbles et al. 2017). Much of the Great Plains has little topographical variation, as no major mountain ranges bisect the region. Thus, for species to track their climatic envelopes, they will have to move at a faster velocity than species that can retreat uphill (Loarie et al. 2009). Additionally, the grasslands of the Great

Plains have evolved under millennia of regular grazing by large mammalian herbivores and frequent burning (Samson et al. 2004, Widga et al. 2010), however, large native grazers (i.e. bison) have been functionally removed from nearly the entirety of North American grasslands (McHugh 1972) and replaced with domestic cattle (*Bos taurus*), and fire regimes have been drastically altered (Samson et al. 2004, Ratajczak et al. 2016). The direction and magnitude of fire and grazer effects on native plant populations is unclear, but previous work suggests little population response in rare native tallgrass prairie plants to fire (Novak et al. 2022). It is possible grazing of dominant plant species (here, grass species) by herbivores could increase population growth rate of sparse species by reducing competition by sparse species (McCain et al. 2010, MacDougall et al. 2013, Ratajczak et al. 2022). Understanding the patterns of native plant population responses will prove essential to their long-term persistence on the landscape.

This project aims to 1) quantify species-specific responses to environmental drivers (grazing, climate, and fire), 2) quantify dispersal abilities, and 3) predict possible leading edge position shifts under future climate predictions for 15 grassland forb species and how this varies across rarity types. We combined long-term plant cover data from the center of each species' range at Konza Prairie Biological Station (KPBS) in Kansas, USA and at the leading edge of each species range. We predict that species with small range, will respond more strongly than species with a large range to climatic drivers, but that all species will have weak responses to fire and grazing. We expect dispersal ability to vary by rarity type, but anticipate strong differences in species' leading-edge position change, particularly in habitat specialists due to restricted habitat availability.

4.3 Methods

4.3.12 Species selection and study sites

Much of the data used to parameterize our models (discussed below) was collected at Konza Prairie Biological Station (KPBS), a 3,500-ha untilled native tallgrass prairie in the Flint Hills of NE Kansas, USA. KPBS is one of the largest remaining fragments of the critically imperiled tallgrass prairie ecosystem (Sampson and Knopf 1994). KPBS has a mean annual precipitation of 850 mm and a mean annual temperature of 13° C (Nippert 2024). While perennial warm-season grasses including big bluestem (*Andropogon gerardii*), little bluestem (*Schizachyrium scoparium*), and Indian grass (*Sorghastrum nutans*) comprise most of the above-ground biomass in tallgrass prairies, forb species represent most of the diversity in the region (Towne 2002). Since 1977, KPBS has conducted a large-scale burning experiment, with replicate watersheds subjected to fire return intervals (FRIs) of 1, 2, 4, or 20 years. In 2010 and 2011, cattle were introduced into two sets of four watersheds. Three watersheds in each set are subject to patch-burn grazing, with one of three watersheds burned each year (resulting in an FRI of 3), and the remaining watershed subject to annual burning. Cattle are present from approximately May 1st to October 1st. Most data in our study (99% of 158985 observations) come from KPBS.

To measure how populations near the leading edge of their range (i.e., the Northern edge) respond to environmental drivers, we collected additional data on public and private lands in 11 sites closer to the leading edge than KPBS. These sites were located across the Black Hills of South Dakota (58 observations), the Prairie Coteau of South Dakota (40 observations), and the Wisconsin Pine Barrens (24 observations). The Black Hills are located on the border of Wyoming and South Dakota and are an anomalous unglaciated mountain range surrounded by mixed-grass prairies of the Great Plains. Our sites are generally located near Hot Springs and

Spearfish, South Dakota in grassland or open ponderosa pine forests. The Prairie Coteau of South Dakota is a glacial moraine region situated within the tallgrass prairies of the Great Plains and is one of the largest remaining tracts of untilled prairie in the northern Great Plains (Bauman et al. 2014). Our sites on the Prairie Coteau are situated near Clear Lake, South Dakota. Finally, the Wisconsin Pine Barrens is a region of sandy soils dominated by grasses, shrubs and few trees primarily located in the northwest region of Wisconsin (Curtis 1959).

Fire has historically been a key driver in maintaining plant communities in the lower elevation regions of the Blacks Hills (Brown and Sieg 1999), tallgrass prairies of the Prairie Coteau (and KPBS) (Changnon et al. 2002, Allen and Palmer 2011), and the Wisconsin Pine Barrens (Forman and Boerner 1981, Givnish 1981). We located populations of focal species using herbarium records (accessed through Integrated Digitized Biocollections - iDigBio [www.idigbio.org] and Global Biodiversity Information Facility – GBIF [www.gbif.org]) collected within the last 10 years.

KPBS plant cover data: We used plant cover data collected by KPBS from 2000-2023 in seven cattle-grazed watersheds and 15 ungrazed watersheds (Appendix Table C.1) both to categorize plant species into rarity classes, as well as to fit the population models that contribute to our simulations of range shifts. KPBS staff sample plant cover data along four 50m long transects in upland areas of each watershed. Along each transect are five permanently marked 10 m^2 circular plots. Twice in each growing season (late May to mid-June & August to early September), KPBS staff estimate canopy cover for all vascular plants within a plot using a modified Daubenmire percent cover scale with seven classes (1 - >0-1% cover; 2 - 2-5% cover; 3 - 5-25% cover; 4 - 25-50% cover; 5 - 50-75%; 6 - 75-95% cover; 7 - 95-100% cover). If a

species was recorded in both May/June and August/ September, we used the highest value for that year for analyses.

Selection of focal species: We used these KPBS cover data, paired with estimates of species' geographic range derived from herbarium records and state ranking of native habitat fidelity, to select 15 focal species that represented all combinations of large vs. small geographic range, habitat specialist vs. generalist, and locally dense vs. sparse. Given the importance of forbs for biodiversity in this system, the potential effect of latitudinal position within range on population dynamics, and the necessity of sufficient data to fit models, we only consider forb species for which 1) KPBS was not at the edge of its latitudinal range (between 10^{th} and 90^{th} percentiles of occurrence observations); and 2) the species was observed in at least 30 plot-year combinations and at least one plot had three years of contiguous presence.

To determine whether each species present in the KPBS cover data had large vs. small geographic range, we used occurrence records from iDigBio and the Global Biodiversity Information Facility (GBIF) (accessed August 2024) to delineate the geographic range (here defined as the extent of occurrence). Occurrence records were collected using the 'occ' function in the *spocc* package (Owens et al. 2024) (version 1.2.3), filtered to those with latitude and longitude coordinates, and limited to 5000 records. We removed observations not occurring over terrestrial North and South America, duplicated, or overlapping botanical garden locations using the CoordinateCleaner package in R to do so (version 3.0.1) (Zizka et al. 2019). We estimated range size by constructing a minimum convex polygon around all occurrence records excluding the outermost 1% records to reduce over-estimation of the polygon. We classified species with a range size larger than the 50th percentile as having a large geographic range, and those with a range size less than the 50th percentile as having a small range. We found range sizes exhibited

an exponential pattern, thus splitting range sizes by the 50th percentile maintains relatively small range sizes and has been used in previous work (Choe et al. 2019). Reducing this threshold to 25% does not change our results (Appendix Figure C.2).

To determine whether each species was a habitat specialist or a generalist, we used Kansas state coefficients of conservatism (CoC). CoC values are regionally specific (in our case, state specific) indicators of species' fidelity to native plant communities that have been developed by a team of experts (Freeman et al. 2002, Freeman 2012) and have been shown to be ecologically relevant (Matthews et al. 2015, Bauer et al. 2018) and a reasonable metric of habitat specificity in grasslands (Zinnen et al. 2021). High CoC values (i.e., 9-10) indicate that a particular species is nearly exclusively found in pristine native habitat under a natural disturbance regime, whereas lower values (0 or 1) indicate the species is almost exclusively found in non-pristine habitat. While CoC values cannot indicate all aspects of habitat specificity (e.g., a species with a high CoC value must occur in pristine habitat but could be further specialized to wetland areas within pristine habitat), CoC values do provide a metric of whether a species is specialized to a particular disturbance regime. Further, on the landscape scale, species with a higher CoC value will be "patchier" than those with a lower CoC value (particularly in the highly fragmented Great Plains region), as we would expect for a habitat specialist. We define species as habitat specialists if their CoC value is greater than five, defined as species not likely to establish in human disturbed systems (Freeman et al. 2002, Freeman 2012).

We used the KPBS plant cover dataset to determine whether each species was locally dense vs. locally sparse. For each species in the percent cover data, we calculated the median and maximum cover class observed at KPBS as an estimate of local density. When using median cover class, we found most species present at KPBS had a median cover class of 1 (i.e., >0-1%).

We found that species varied widely in the maximum cover class attained at KPBS, allowing us to classify species into locally sparse (i.e., a maximum cover class of 3 or less, or less than 25 percent cover) vs. locally dense (a maximum cover class of more than three). In all, we identified 15 focal species that both satisfied the rarity type requirements and for which we found sufficient leading-edge populations. Note that three of these species were in the "common" class (i.e., locally dense, large range, and habitat generalist). All species and their rarity classes are listed in Table 4.1.

Leading edge plant cover data: At each leading-edge population of the 15 focal species, we searched areas surrounding historical observations to locate all extant individuals of each focal species in 2021. When we found one or more individuals of a focal species, we placed a stake within one meter of the individual(s) to mark the center of a circular 10 m^2 plot (identical to KPBS protocols). If possible, we placed plots to maximize the number of individuals and focal species occurring in that plot. In 2021, we established 34 plots at these leading-edge populations, and we opportunistically added seven in 2022 and two in 2023 (see Appendix Table C.2 for plot locations). We estimated percent cover annually until 2024 using similar methods to those used at KPBS; we visited twice per growing season in mid-June and late July and estimated (binned) cover classes. Together, we have a median of 19 plant-years of data across species at the leading edge.

Environmental data: We aimed to estimate the effects of fire, cattle, and climate on our focal species' population dynamics. KPBS has kept records of grazing and burn histories for all watersheds on site since the inception of the Long-term Ecological Research Program in 1980. For our leading-edge populations, we obtained burn histories by contacting land managers when possible, or in the Black Hills, we used the Fire Burned Areas online map (Eidenshink et al.

2007), which includes 1984-2022 data from the U.S. Geological Survey and Forest Service's Monitoring Trends in Burn Severity program. Presence of cattle was either apparent in the field (presence of recent cattle feces or observing cattle) or confirmed with land managers for each site. To represent fire history, we defined plots as recently burned (<5 years) and historically burned (>=5 years), because multiple leading edge populations had no recorded burning in the last 30+ years under current management.

We used the Standardized Precipitation and Evaporation Index (SPEI) to represent annual climate variation (Vicente-Serrano et al. 2010). Large positive values of SPEI indicate wet and/or cool conditions and large negative values indicate drought conditions (dry and/or hot). SPEI values near zero indicate near average conditions. To calculate SPEI, we used climate data (precipitation and temperature) from the ClimateNA software package developed and maintained by the University of British Columbia (Wang et al. 2016, Mahony et al. 2022). ClimateNA downscales PRISM (Daly et al. 2008) monthly climate data, producing scale-free monthly climate variables for individual years between 1901 and 2100. To calculate SPEI, we first used the Thornwaite method for calculating PET (Thornthwaite 1948) from the SPEI R package (version 1.8.1) (Santiago Beguería and Vincente-Serrano 2023). We then used the PET values to calculate the monthly climatic water balance (difference between monthly precipitation and monthly PET). Twelve-month SPEI was then calculated using the *spei* function in the SPEI R package. We then averaged over growing season months (those where average temperature was < 0 C) to get a yearly SPEI value. We define a year as June 1-June 1.

4.3.13 Population models

We combined the percent cover data from KPBS and leading-edge populations to construct species-specific density structured population models that predicted plant percent cover

as a function of cattle presence, fire history, SPEI, and region within a species' range. These density structured models are similar to the commonly used population matrix models, but instead of predicting the probabilities of transitioning among size classes, they predict the probability of transitions among density classes (Freckleton et al. 2011, Queenborough et al. 2011, Goodsell et al. 2021). Following Sutton et al. (2024), we used a multinomial logistic regression to estimate the effects of cattle presence, FRI, and SPEI on transition probabilities among cover classes. We then used these density structured models to project future changes in cover class under different suites of environmental conditions and, in combination with estimates of dispersal, to project leading-edge position changes across a theoretical landscape. We describe each step in more detail below.

4.3.13.1 Density structured models

Density structured models require estimates of the multinomial probability of a plot transitioning from one (discrete) cover class to another. We used a multinomial logistic regression to estimate the effect of cattle presence, fire history, SPEI, and region (central—i.e., KPBS-- or leading edge) on these probabilities. For these regressions, due to the paucity of data available for these rare species, we combined data from all species into one regression and used species identity as a predictor variable; this approach allows us to estimate probabilities of a particular species' transitions by borrowing power from other species, while still allowing for species specific responses. We fit a multinomial logistic regression model that predicted the (multinomial) probability of transitioning into cover classes 0-5 (we excluded cover classes 6 and 7, because these species almost never attained cover classes of 6 and 7) as a function of initial cover class, species identity, fire history, grazing (cattle presence/ absence), SPEI, and region. We also included interactions between species identity and fire history, grazing, and

SPEI, between initial cover class and grazing, initiating cover class and fire history, and grazing and fire history. Models were fit using nnet package version 7.3-19 (Venables et al. 2002), in R.

We used the multinomial logistic regression to construct species-specific density structured models, which we used both to estimate driver impacts on population dynamics, as well as to simulate realistic shifts in species' ranges under climate change. To estimate the impacts of drivers on population dynamics, we constructed a density structured population model for all combinations of: cattle present/ absent, recently or historically burned, and high vs. low SPEI (reflecting drought vs. wet conditions). We then used each density structured model to calculate mean cover class by calculating the stable stage distribution (i.e., the dominant eigenvector, similar to population matrix models) and obtaining the modal cover class for each combination, which we then converted to the midpoint of the percent cover value of that cover class (e.g. for the 5- 25% cover class the midpoint is 15.5%). Finally, we calculated log response ratios (LRR) as a metric of driver effect on population dynamics:

$$LRR = log\left(\frac{Cover_{driver\ present}}{Cover_{driver\ absent}}\right)$$

Where $Cover_{driver\ present}$ indicates the percent cover when the driver is present (i.e., drought, cattle grazed, leading edge, or recent burn) and $Cover_{driver\ absent}$ indicates the percent cover when the driver is absent (average climate, ungrazed, central, or historic fire). LRRs have been used in similar previous studies (Morris et al. 2020, Sutton et al. 2024). To generate confidence intervals on driver impacts on population growth rate, we generated 500 iterations of parameter estimates based on the multivariate normal distribution of the multinomial logistic model coefficient estimates and recalculated each species' LRR for each set of coefficient estimates (Louthan et al. 2022). We assumed that a species' response to a driver differed significantly when the confidence interval on a species' LRR did not overlap zero.

4.3.14 Simulation approach

4.3.14.1 Dispersal

To project changes in population dynamics across a landscape, we combined the density structured models (which can predict location-specific percent cover) with estimates of dispersal distances (which predict movement of seeds -and thus potential colonization- among locations). Following the methods of Sullivan et al. (2018), we estimated wind seed dispersal distances for species using the Wald Analytical Long-distance Dispersal (WALD) model (Katul et al. 2005, 2018). The WALD model requires estimates of height at seed release, wind velocity, and seed terminal velocity. To estimate height at seed release, we located at least three fruiting individuals at KPBS. Samples were opportunistically sampled between May and December in 2022 through 2024. For each individual, we recorded the minimum and maximum height of seed release (distance between ground and natural height of inflorescence – i.e. not "stretched") and collected mature fruits. We dried fruits at 60° C for at least two weeks. Once fruits were dried, we removed all other tissues not relating to dispersal from seeds. To estimate wind velocity, we used the maximum windspeed measured at KPBS Headquarters' wind gauge (Nippert 2024) occurring over the range of dates seeds were collected. For example, if we collected seeds from August 1-September 15, we use the maximum windspeed observed over that period as our estimate of wind velocity. If seeds were collected in under a week, we used at least seven days of wind data centered around dates of seed collection.

Terminal velocity: To estimate seed terminal velocity, we used the same apparatus used by Sullivan et al. 2018: a 10.16 cm PVC tube equipped with light sensor arrays that detect seed presence through light disruptions. We dropped seeds from 1 m above the first light sensors, ensuring they reached terminal velocity. Ten species were measured with 20 trials using different

seeds, however for five species (*Comandra umbellata, Hieracium longipilum, Penstemon grandifloras, Ratibida columnifera,* and *Dalea purpurea*), we were only able to conduct 10-19 trials due to limited seeds. When possible, we dropped only one seed at a time. However, for particularly small seeds, the sensors were unable to consistently detect the seeds. Instead, we dropped seeds in multiples, attempting to drop as few seeds as possible; number dropped ranged from 2 to 20 seeds. We were unable to get data for *Artimisia ludoviciana* or *Achillea millefolium*, as such, we used the measured terminal velocities from Sullivan et al. (2018). We were unable to retrieve ripe seeds for *Asclepias viridiflora*, so we used an average of our other three *Asclepias* species' terminal velocities. Finally, fruit measurements for *Asclepias viridiflora* were collected in 2024, but as of this publication windspeed data were not yet available; we used 2023 wind speeds for the same dates instead. We used t-tests to examine if rarity type explained differences in dispersal traits (seed terminal velocity and seed release height), pooling data from all 15 species. In these t-tests, we only included species for which we collected seeds in the field (i.e., we did not use species data from Sullivan et al. 2018 for *Artemisia ludoviciana* or *Achillea millefolium*).

Dispersal: To estimate each species' dispersal ability we used the WALD model (Wald 1947, Katul et al. 2005, Teller et al. 2014), a simplified Langrangian stochastic model (Pope 2000) to estimate species specific dispersal kernels (probability distribution of propagule dispersal distance from parent plant). This model assumes wind flow has low turbulence, seeds reach terminal velocity instantaneously, and wind is acting only in the horizontal direction (i.e., no updrafts). We used the same parameters described in Sullivan et al. (2018): we assume a dense and uniform canopy by setting the scaling coefficient to 0.3, canopy height as 1.0 m (Soons et al. 2004a), and boundary conditions to be one-half the spatial and temporally averaged

wind velocity used to achieve low turbulence (Katul et al. 2005). Finally, we parameterized the model using the height at seed release and terminal velocity data. We report mean dispersal distance, and long-distance dispersal (LDD), defined as the distance travelled by the furthest 1% of seeds (Nathan 2006). Terminal velocity and dispersal kernels were calculated using R code provided in Sullivan et al. (2018). We simulated the WALD model across a large range of possible dispersal distances to create a fully realized probability dispersal function.

4.3.14.2 Simulations

We combined the density structured models, dispersal kernels derived from the WALD model results, and spatially and temporally explicit predictions of future climate conditions at the leading-edge to project changes leading-edge position change. Steps of our simulation include: 1) generate landscape, 2) assign initial populations for year one based on rarity class, 3) predict percent cover in extant populations in $t+1$ using density structured model, 4) dispersal, and 5) repeat steps 3 and 4 for 50 years. We repeated these simulations 500 times. Each step is described in more detail below.

Generate landscape: We used satellite imagery of real landscapes to create simulated landscapes in which we could measure range shifts of each of our species. We use two counties (Riley County, Kansas, where KPBS is located, and Burnett County, Wisconsin, where some of our leading-edge populations are located) as possible landscapes our focal species could encounter as they shift their ranges. These two counties provide two scenarios of grassland fragmentation: Riley County has relatively high levels of intact grassland compared to much of the remaining Great Plains, and Burnett County has very little grassland remaining and is more representative of most of the Great Plains grasslands at this point in time. We created

1000X1000 matrix corresponding to 30,00 km x 30,000 km landscape based off Riley County, Kansas or Burnett County, Wisconsin, National Land Cover Database (NLCD) grassland cover for 2021. Burnett county contains 3% of the grassland area of Riley county (24 ha average grassland patch for Riley versus 1 ha for Burnett respectively; values estimated using calculate_lsc function in the R package *landscapemetrics* by Hesselbarth (2019) on NLCD grassland cover maps). We used the high grassland cover landscape (Riley County) to represent distribution of grassland for habitat generalists, and the low grassland cover landscape (Burnett County) to represent distribution of grassland for habitat specialists. Note that using NLCD landcover data to estimate grassland cover is an optimistic approach, as these data are quite coarse and does not capture nuanced grassland variables such as community composition or management practices. Thus, the use of NLCD landscapes could over-estimate real-world realizations of species' movement across the landscape. Using these two real landscapes, we generated two sets of simulated landscapes using the same landscape metrics (number of patches, patch size, etc). Landscapes were created using *flsgen* R package version 1.2.2 (Justeau-Allaire et al. 2022). flsgen is a neutral landscape generator that allows for the creation of landscapes based on habitat patch structures (e.g. patch area, proportion of landscape, number of patches, etc.) of existing landscapes through a stochastic algorithm. We generated a unique landscape for each of our 500 simulations.

We additionally populated our landscape matrix with the same drivers included in our density structured models (cattle presence, fire history, SPEI, and region). For each simulation, cattle presence was randomly distributed across grassland habitat patches at 90% coverage, a realistic value for the Flint Hills region surrounding KPBS (With et al. 2008). We simulated a burn on 67% of grassland habitat patches annually, corresponding to observed values for the

region surrounding KPBS (With et al. 2008, but see Ratajczak et al. 2016). For each simulation, we initialized the landscape with a burn "history" using a mean TSF of 3 years, a standard deviation of 3, and a range of 0 to 20 years. We then added +1 to the TSF value for each cell of the landscape in each consecutive year of the simulation (up to +50), however TSF value was reset to zero if that cell was determined to burn in the corresponding year. To match our density structured models, we then converted values to two levels ("recent" burn, < 5 years since last burned, or "historic" burn, > 5 years since last burn).

To populate the landscape with climate, we used ClimateNA, as we did to parameterize our density structured models, however, instead of historic climate data, we used climate predictions estimated using general circulation models (GCMs) ensemble of eight models of the Coupled Models Intercomparison Project (CHIP6) (Eyring et al. 2016, Wang et al. 2016, Mahony et al. 2022) consistent with IPCC's "very likely" future climate sensitivity as estimated by (Mahony et al. 2022). Within this ensemble climate model we include multiple climate scenarios referred to as "Socioeconomic pathways" (SSPs): scenarios 1, 2, 3, and 5 (which will be referred to hereafter as SSP1, SSP2, SSP3, and SSP5). These SSPs correspond to varying levels of climate change mitigation strategies; SSP1 assumes largescale global decreases in CO_2 emissions and SSP5 assumes an increase in CO_2 emissions; SSPs 2 and 3 assume intermediate emissions.

We used these ClimateNA temperature and precipitation data to calculate 12-month SPEI at leading edge populations using the methods described above for 2023 through 2073. While we used precise location information to calculate SPEI for each when fitting models of population dynamics, for our simulations we averaged population-specific values of SPEI to generate regional climatic predictions for the leading edge (averaging across Black Hills, South Dakota,

Prairie Coteau, South Dakota, and Pine Barrens, Wisconsin). As our simulated landscapes are not expansive, we used a single SPEI value for every cell in our landscape matrix, with this value changing for each year of each iteration.

Assign initial populations: Populations were started by randomly sampling cover class values from a uniform distribution bounded on the lower end by 1; upper bound was determined by population density category, 5 for "dense" and 3 for "sparse"), for 5 rows of the matrix (equates to 30m x5 depth). This allowed us to start with a large "population" pool on the matrix and examine speed of movement across the matrix.

Population dynamics: We predicted population dynamics within each occupied cell of our matrix using our density structured model. As our density structured models include colonization, cover change, and extinction probabilities, all population dynamics are included within the model and are thus not estimated individually. Each cell in the matrix (i.e., a "patch") had a corresponding value of cover class at time *t*, climate (SPEI), grazing (cattle presence or absence), and fire history (recently or historically burned), which we used to estimate probabilities of change in cover class in the next time step. We then used these probabilities to conduct a weighted random draw to determine cover class value for the next time step (t+1). Thus, our population models include stochasticity in population dynamics at each cell.

Dispersal: We used a probabilistic approach when estimating dispersal to prevent large storage and memory overhead as would be needed to track each individual propagule (i.e., seed). For each occupied patch (cover class value > 0), we determined number of seeds by cover class using arbitrary values (4,000, 5,000, 10,000, 15,000, or 20,000 for cover class one though five respectively), and were held constant across species. Only 1% of these seeds would disperse outside of an occupied element (i.e., 4, 5, 10, 15, or 20, for cover class one though five

respectively). We used our species-specific dispersal kernels to estimate LDD events at a probability of one percent. If a cell was predicted to undergo an LDD, we used the species 99th percentile dispersal distance (Table 4.2) to establish how far each seed would travel and randomly selected a direction of travel. We used a probability of 0.1 that an occupied cell that did not undergo LDD dispersed into an adjacent cell to represent an individual on the edge of an occupied cell dispersing a short distance. We assumed if a seed landed in a grassland cell on the landscape it would establish in t+1 at a cover class of 1.

At the end of each iteration, we calculated the mean distance traveled across the landscape (number of cells away from starting rows) for each simulation for each species. We could then test for significant differences in distance traveled across rarity types using a t-test in each simulation (i.e., three t-tests for each simulation). We used a similar approach to conduct an ANOVA to test for differences in climate scenario. Significance was determined if the p-value was less than 0.05, adjusted using a Bonferroni correction for multiple tests. We then added up the number of significant results across iterations to assess differences in leading edge movement.

4.4 Results

For the rest of this paper, we reduce our rarity classes to three-character codes to improve readability in the form of XXX. The first character will always refer to range size ('L' for large or 'S' for small), followed by the middle character indicating habitat specificity ('B' for broad or 'S' for specific), and finally the third character being population density ('D' for dense or 'S' for sparse). For example, a common species will be designated as LBD (large range, broad habitat requirements, and dense populations) or the rarest species will be designated as SSS (**s**mall range size, **s**pecific habitat requirements, and **s**parse population density).

4.4.15 Population models

We found significant effects of region (leading edge or central) on population dynamics, as measured by LRR, across multiple species and rarity types, but found no significant effects of other drivers (Figure 4.1). Four species (*Cirsium undulatum* - LBD*, Comandra umbellata* -LSD*, Astragalus crassicarpus* –SSD and, *Baptisia australis* - SSS) exhibited higher percent cover in leading edge populations compared to central populations in the central region (Figure 4.1). Mean cover class and confidence intervals can be found in Appendix Table C.3. With only three species exhibiting significant responses to a driver, we were unable to test if rarity type influenced LRRs.

4.4.16 Dispersal

Species differed dramatically in their dispersal traits (Table 4.2). Mean seed release height ranged from 0.65 m (*Hieracium longipilum* - SBS) to 0.0025 m (*Astragalus crassicarpus* - SSD). Terminal velocity ranged from 3.77 m/s (*Astragalus crassicarpus*) to 0.16 m/s (*Asclepias verticillata* - LBD). We found a wide range of long-distance dispersal (LDD) distances ranging from 0.04 m (*Astragalus crassicarpus*) to 230 m (*Asclepias verticillata*) (Figure 4.2 and Table 4.2). The next largest LDD distance was much smaller than that of *Asclepias verticillata* at 114 m for *Asclepias viridiflora* - LSS. We found significant differences in mean seed release height among species with smaller release heights for large range species (mean of 0.41 m versus 0.52 m; $t = 2.65$, p-value = 0.01) and species with dense populations (0.37 m versus 0.48 m; $t = -3.13$, p-value = 0.003), but did not find any differences between habitat specificity types (0.44 for habitat generalist and 0.42 for specialists; $t = 0.77$, p-value = 0.44). We additionally found higher terminal velocity for large range species (mean terminal velocity of 1.49 m/s for large range species versus 1.03 m/s for small range species; $t = 2.34$, p-value = 0.02) and habitat specialists

(0.6 versus 1.95 m/s for generalists and specialists respectively; t = -10.42, p-value = < 0.001) but no differences between dense vs. sparse density species (1.11 versus 1.52 m/s for dense and sparse population densities respectively; t = -1.11, p-value = 0.27). In spite of the significant effects of rarity type on dispersal traits, we did not find any significant differences in LDD distances between rarity types (range size: mean LDD distance of 53.54 m for small range and 36.92 for large range species, t = 0.64, p-value = 0.53; habitat specificity: 51.12 m for generalists and 30.69 m for specialists; t = 0.58, p-value = 0.58; population density: 43.12 m for dense species and 37.65 m for sparse species; t = 0.15, p-value = 0.88).

4.4.17 Simulations

While we found species were able to successfully move across the landscape in 50 years, we found wide variation in distance moved across species and rarity type. All four of our included climate scenarios (SSPs 1, 2, 3, and 5) resulted in extremely similar movement distances, none of which were significantly different from one another (p-values > 0.9; Appendix Figure C.1). As such, for the remaining results, we only show and discuss results for one intermediate climate model (SSP 2).

We found drastic differences among the distances moved by species across a simulated landscape (Figure 4.3). *Asclepias* species were notably successful, with *Asclepias verticillata* - LBD far surpassing all other species with a mean distance moved of 5956 m (sd = 56), followed by *Hieracium longipilum* -SBS at 666 m (sd = 122). *Comandra umbellata* - LSD had the lowest mean distance at 106 m (sd = 72). When grouping results by rarity type, we find no significant effects of range size (large or small), habitat specificity (broad or specific), or population density (dense or sparse) on the mean distance moved (all p-values > 0.1). However, when we remove *Asclepias* species from the analyses, we find a significant effect of habitat specificity on the

mean distance moved for all 500 simulations, with habitat generalists moving farther than habitat specialists. We see no significant effect of large vs. small range size (all p-values > 0.1) or dense vs. sparse population density (all p-values > 0.1) on distance moved.

4.5 Discussion

Our findings underscore the importance of considering both rarity type and dispersal traits when predicting species' responses to environmental changes, particularly in the context of climate change. While we observed significant effects of region (leading edge or central) in four species, there was no clear pattern linking rarity type to species' responses to environmental drivers such as grazing, fire, or climate. These results suggest that rarity type is not always a reliable predictor of a species' response to environmental drivers. The significant variability in dispersal traits—particularly seed release height and terminal velocity—further emphasizes the role of dispersal in determining species' capacity to shift their ranges. Notably, species with smaller ranges and habitat specialists exhibited lower terminal velocity but species with smaller ranges and sparse populations had higher mean seed release height, but long-distance dispersal (LDD) was not significantly different across rarity types. Species leading-edge movement was largely dictated by habitat specificity and dispersal ability which has also been found in similar studies (Sullivan et al. 2021). These complex dynamics highlight the need for nuanced approaches to conservation that account for species-specific responses to environmental drivers.

Despite the expectation that climate, grazing, and fire would drive population dynamics, our results show no large effect of any one driver. It is somewhat surprising that we find no variation in effect of climate between large or small range sizes, as is expected under the niche breadth hypothesis (Sexton et al. 2017). However, recent work has found only weak support for the hypothesis (Louthan et al. *in press*). We anticipated some effects of grazing and fire on

population growth due to our focal species benefiting from reduction of dominant grassland species (i.e. grasses) which has been attributed to increases in non-dominant species presence in grassland systems at the community level (McCain et al. 2010, MacDougall et al. 2013, Ratajczak et al. 2022), however we found no significant effects which correspond to studies examining effects of fire (Sritharan et al. 2022, Novak et al. 2022) but not grazing (Strauss and Agrawal 1999, Rooney and Waller 2003, Heckel et al. 2010) at the population level. It is possible our categorizing fire into two categories (recently or historically burned) obscures nuanced fire effects. Sutton et al. (2024) also constructed density structured models at KPBS using similar data and found significant effects of fire and grazing for forb species at KPBS, however, their data utilized long-term bison (*Bison bison*)- grazed areas at KPBS. Bison have been shown to have larger impacts on plant communities than do domestic cattle in this system (Ratajczak et al. 2022). Additionally, differences in how Sutton et al. (2024) incorporated colonization/extinction and fire in their models could additionally be leading to these differences.

The face that our density structured model results indicated that four species (*Cirsium undulatum*- rarity type LBD*, Comandra umbellata*-LSD*, Astragalus crassicarpus*-SSD, and *Baptisia australis*-SSS) have higher mean cover in Northern populations was surprising. There do not appear to be any patterns regarding why these species, and not others, have such high cover values in Northern populations. These species span all rarity types (large and small ranges, broad and specific habitat requirements, and dense and sparse population densities) and belong to wide ranging taxonomic families (Asteraceae, Santalaceae, and Fabaceae). Although non-significant, we found all our other focal species to have negative LRR values (i.e. leading-edge populations have greater mean cover than central populations). While we have limited data in Northern population for our 15 focal species, our density structured models have been

parameterized using extensive, species-specific data from KPBS, making it unlikely that these are spurious findings are due to limited data. Unfortunately, we do not have enough data in this study to elucidate the potential mechanisms behind these findings, whether those mechanisms reflect leading-edge effects of climate change, unaccounted-for environmental drivers, or species-specific responses unrelated to rarity type.

While we did find differences in dispersal traits between rarity types, we did not find these differences resulted in significant variation in LDD between rarity types. While previous work has noted differences in dispersal traits between rarity types (Espeland and Emam 2011), we fail to find a connection between traits and LDD. This disconnect between dispersal related traits and resulting LDD emphasizes the need to not exclusively rely on single traits as a proxy for dispersal ability. While our terminal velocity and mean release seed height are similar to previous work in Great Plains grasslands by Sullivan et al. (2018) using some of the same species included in this study, we found much higher LDD values due to higher windspeed values. While the use of WALD models has been shown to accurately predict colonization in grasslands (Soons et al. 2004b, a, Skarpaas and Shea 2007, Sullivan et al. 2018), animal dispersal—which is not included in WALD models-- could play an important role in LDD for some of our species (e.g., *Comandra* and *Astragalus crassicarpus*). Unfortunately, the evidence for animal dispersal of our focal species is colloquial and little to no work has been done to quantify these effects (Piehl 1965, Stubbendieck et al. 1989, Boe and Johnson 2017). Additionally, quantifying animal dispersal is challenging and data intensive (Russo et al. 2006), and likely complicated by human disturbance and habitat loss (Markl et al. 2012). However, animal dispersal can be a key component of plant dispersal (Howe and Smallwood 1982, Godó et al. 2022). While it is likely our estimates of dispersal could be improved for some of our focal

species, this study provides an initial estimate of possible dispersal ability on rare grassland species.

Leading-edge position changes in our study suggest habitat specificity is the most limiting factor for species range shifts. The observed variability is largely driven by the quantity of suitable grassland in our landscape. , which, although based on realistic landscapes, may not fully capture the complexity of habitat quality and management practices. For example, our use of broad "grassland" landcover designations by the National Land Cover Database (NLCD) likely oversimplifies actual habitat suitability, leading to overly optimistic estimates of suitable patch quantity. Additionally, seeds landing in densely vegetated tallgrass prairie are unlikely to establish successfully, as we generously assumed in our model (Benson and Hartnett 2006), but is thought to be an important process in maintaining sub-dominant species (i.e. forbs) in this system (Platt 1975). Species with wind-dispersed seeds, such as *Asclepias, Cirsium,* and *Hieracium*, showed marginally (or extremely in the case of *Asclepias verticillata*) better performance than those without such adaptations. This result highlights how dispersal traits can outweigh rarity types in predicting range shifts. These dual effects of dispersal and rarity type (which impacts population dynamics) are consistent with other studies that emphasize the complex interplay between dispersal and population demographics in species range shifts (Barber et al. 2016, Hemrová et al. 2017).

Our study has several limitations that should be addressed in future work. First, the assumptions made in our simulations, while based on available data, are not intended to represent realistic conditions. These values are approximations and should be interpreted with caution. Additionally, while we focused on the roles of dispersal and population dynamics, there is a critical need to further examine how these processes interact (Hemrová et al. 2017). Trait-based

studies are essential for improving our understanding of species' responses to environmental changes, particularly in rare species, where data on life history and dispersal traits and mechanisms are often lacking (Murray et al. 2002, Lyons et al. 2005, Jain et al. 2014). Additionally, we do not include biotic drivers outside of large mammal herbivores. Competition, especially from dominant grasses, are likely to influence species' responses to environmental drivers and possible successful dispersal (Benson and Hartnett 2006, McCain et al. 2010).

Here, we use density-structured models, an under-utilized population modeling method with great promise for plant conservation, particularly when cover data is more readily available than individual demographic data, which is often scarce for rare species (Queenborough et al. 2011). We additionally find rarity type does not predict population responses to environmental drivers, nor dispersal ability. Species with good dispersal abilities will likely be the best off under climate change, but could be significantly limited by rarity type. However, there is already strong evidence that native species are not able to disperse fast enough to keep pace with climate change (Bradley et al. 2024), of which grassland species will experience the some of the highest temperature change velocities (Loarie et al. 2009). Additionally, the loss of large native herbivores across and the wholesale loss of untilled grasslands in North America exacerbate species' abilities to move across the landscape (Sampson and Knopf 1994, Godó et al. 2022, World Wildlife Fund 2024). Integrating both demographic traits and dispersal capabilities into conservation efforts will be essential for protecting rare species. Our results emphasize the urgency of managing habitats for species with limited dispersal abilities and limited habitat, as these factors are key to their long-term survival in the face of environmental changes.

4.6 Data availability

All data used in this study is publicly available. Full datasets and detailed sampling protocols for KPBS can be accessed on the KPBS LTER website: http://lter.konza.ksu.edu/data (dataset codes: vegetation cover = PVC02 and PBG01 and climate = AWE01).

4.7 Tables

Table 4.1: Species classifications into seven rarity classes and one common class (all combinations of small or large range size, broad or specific habitat specificity, and dense or sparse local population density).

Range size	Large		Small	
Habitat specificity	Broad	Specific	Broad	Specific
Dense population density	*Achillea millefolium* *Artemisia ludoviciana* *Cirsium undulatum*	*Comandra umbellata*	*Asclepias verticillata*	*Astragalus crassicarpus* *Dalea purpurea*
Sparse population density	*Brickellia eupatorioides* *Ratibida columnifera*	*Asclepias viridiflora*	*Hieracium longipilum*	*Asclepias stenophylla* *Baptisia australis* *Dalea candida* *Echinacea angustifolia*

Table 4.2: Dispersal traits measured in the field and lab and dispersal kernels calculated using WALD dispersal model. Terminal velocity mean and standard deviation (SD) were measured using terminal velocity tube. Wind speeds were collected from KPBS Headquarters weather station (Nippert 2024). Release height (mean and SD) was measured in the field at KPBS. Long distance dispersal (LDD; distance the furthest 1% of seeds can travel). *m* = meter and *s* = second. * Species (*Achillea millefolium* and *Artemisia ludoviciana*) which had seeds too small for the terminal velocity measurement device to measure. Here we are using values measured by Sullivan et al. 2018. † We were unable to find ripe fruits for *Asclepias viridiflora*. As such, here we use the mean terminal velocity values of our other Asclepias species. § We were only able to find one individual of *Astragalus crassicarpus* with fruits ripe and still attached, preventing us from calculating a standard deviation.

Species	Terminal velocity mean (m/s)	Terminal velocity SD (m/s)	Maximum wind speed (m/s)	Release height mean (m)	Release height SD (m)	Mode distance (m)	LDD (m)
Achillea millefolium	1.09*	0.41*	3.12	0.33	0.07	0.12	7.58
Artemisia ludoviciana	0.67*	0.09*	3.36	0.39	0.14	0.17	19.10
Asclepias stenophylla	0.24	0.05	4.02	0.41	0.08	0.19	111.38
Asclepias verticillata	0.16	0.03	4.42	0.46	0.09	0.24	229.79
Asclepias viridiflora	0.22 †	0.06 †	3.56	0.46	0.05	0.24	114.92
Astragalus crassicarpus	3.77	0.78	3.12	0.00	NA §	0.00	0.04
Baptisia australis	2.94	1.27	4.99	0.43	0.05	0.19	3.95
Brickellia eupatorioides	0.69	0.20	2.83	0.37	0.15	0.15	13.82
Cirsium undulatum	0.40	0.11	3.12	0.50	0.08	0.28	41.43
Comandra umbellata	2.55	1.17	3.12	0.10	0.02	0.01	1.14
Dalea candida	2.48	0.61	3.43	0.52	0.11	0.26	3.20
Dalea purpurea	2.21	0.67	3.43	0.39	0.03	0.16	3.30
Echinacea angustifolia	2.07	0.83	4.99	0.55	0.06	0.31	7.56
Hieracium longipilum	0.48	0.15	3.43	0.65	0.09	0.47	41.68

Ratibida columnifera	1.82	0.38	3.43	0.44	0.04	0.20	4.69

4.8 Figures

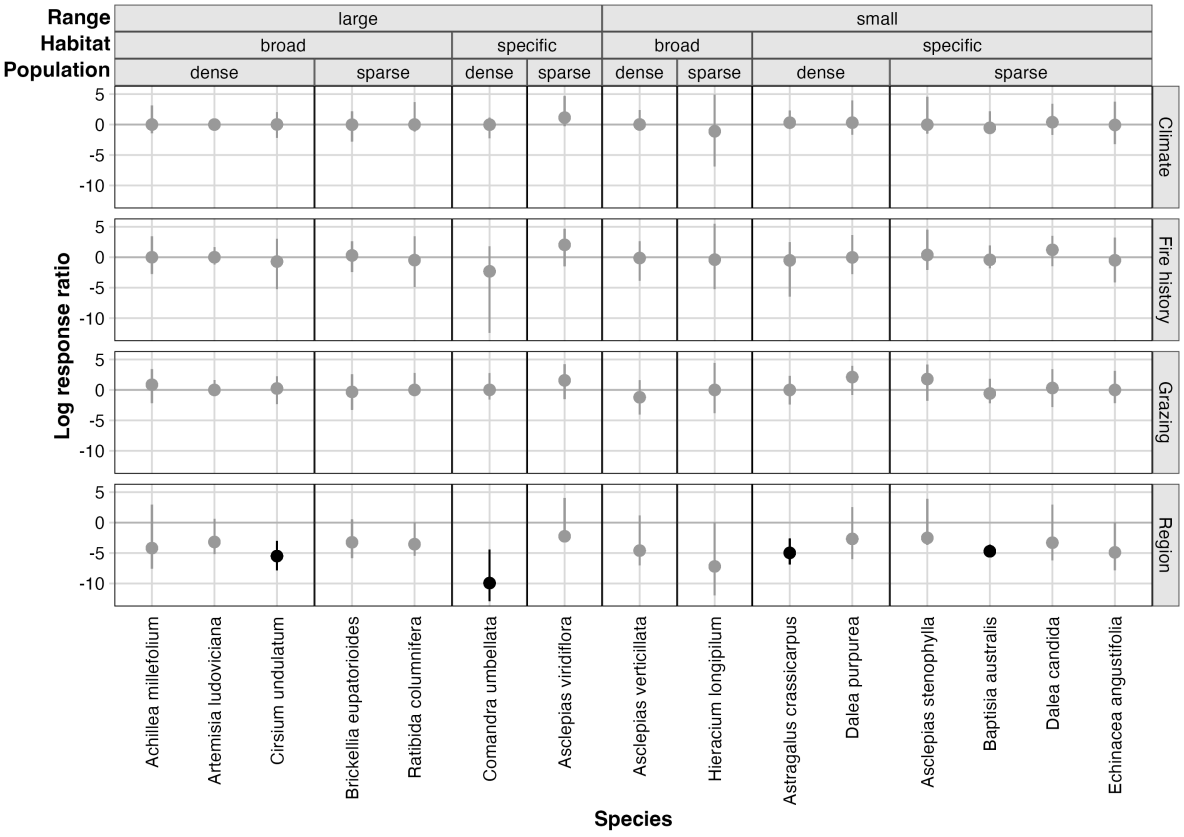

Figure 4.1: Log response ratio (LRR) of mean percent cover for each species across drivers (climate, fire history, grazing, and region) holding all other drivers constant. Rarity type is indicated labels above data with range size (large or small) indicated by top row of labels, habitat specificity (broad or specific) middle row, and local population density (dense or sparse) shown in the bottom row. Points indicate median effect size and vertical lines indicate 95% confidence interval estimated using parameter uncertainty. We considered a treatment significant if the confidence interval did not overlap zero. Positive LRR values indicate higher levels of a driver increase mean cover, while negative values indicate higher cover under baseline conditions of a driver (we considered baseline conditions as: average climate conditions, ungrazed, central region (KPBS), and recently burned). Grazing, region, and fire history are factors and as such cannot be directly compared to each other or to climate. Significant values zero are black while insignificant values are gray.

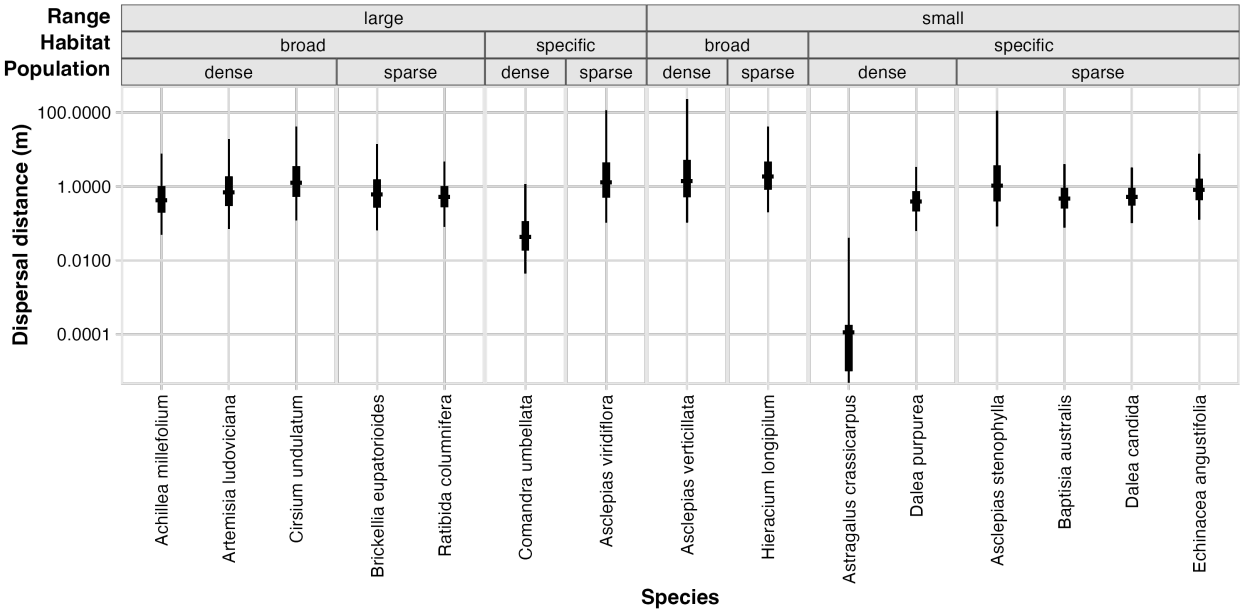

Figure 4.2: Dispersal distances derived from the WALD dispersal model kernels for 15 focal species. Rarity type is indicated labels above data with range size (large or small) indicated by top row of labels, habitat specificity (broad or specific) middle row, and local population density (dense or sparse) shown in the bottom row. Horizontal dash indicates 50th percentile dispersal distance, thick vertical lines indicate 25-75th percentile, and thin vertical lines show 1-99th percentile of dispersal distances. y-axis is log-transformed.

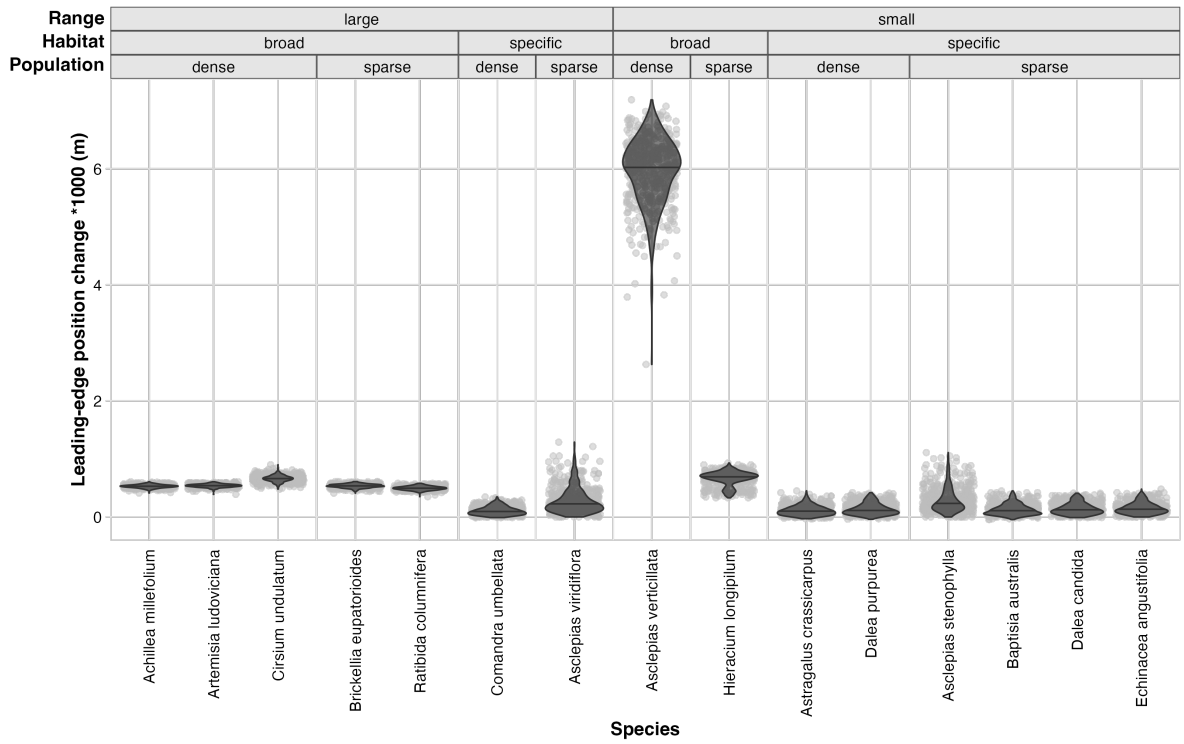

Figure 4.3: Leading edge position change (m) for 15 focal species across 500 simulation iterations. Rarity type is indicated labels above data with range size (large or small) indicated by top row of labels, habitat specificity (broad or specific) middle row, and local population density (dense or sparse) shown in the bottom row. Gray dots indicate change in position for each iteration, while dark gray violin plot displays spread of the gray dots. Horizontal line in violin plot indicates 50% percentile of observations.

Chapter 5 – Conclusions

This dissertation explores the complex interplay between biotic and climatic drivers on species' population dynamics, emphasizing how these interactions vary within species and across species, and in the context of species' range shifts in response to climate change. At the core of this dissertation lies the recognition that species and populations are not uniformly affected by environmental drivers. Instead, responses vary depending on the specific context of populations, species traits, and the types of environmental stressors they face. This variability has critical implications for predicting biodiversity patterns in a changing world, especially under the dual pressures of climate change and habitat loss.

In the first chapter of this dissertation, we investigate the within-species variation in population responses to environmental drivers, focusing on the interaction between biotic and climatic factors. One framework for predicting how the effects of drivers might vary across a species is the stress gradient hypothesis (SGH) (Bertness and Callaway 1994). The SGH predicts the effect of neighboring species (a biotic driver) should change in sign along abiotic gradients, with neighbors acting as competitors in less stressful conditions (e.g., warm or wet) but facilitators in more stressful conditions (e.g., cold/hot or dry). While this hypothesis predicts neighbor responses at the level of fitness (i.e., population growth rate), few studies test fitness but rather examine components of fitness (e.g., survival, reproduction, or spatial patterns in distributions) limiting how these effects vary within a species. Using a common alpine plant species, *Sedum lanceolatum*, we demonstrate neighbor effects on population growth rates vary substantially across populations. This variation in population growth rates was primarily driven by differences in population sensitivities to demographic rates, particularly reproductive rates, rather than variation in the effects of the neighbors themselves. These findings highlight the

importance of considering spatial variation in demographic sensitivities when predicting how populations will respond to environmental drivers. If a driver has a consistent effect on a particular demographic rate (e.g., survival or reproduction), the overall impact on population growth can vary by population.

The second chapter focuses on how species' responses to environmental drivers vary with species' range size. The niche breadth hypothesis predicts species with larger niches (i.e., larger ranged species) should experience weaker population responses to environmental drivers (Sexton et al. 2017). An alternative hypothesis, proposed by Opler (1974), proposes the opposite pattern (at least for biotic drivers): the effect of biotic drivers such as insect herbivores should increase with species' range size. We use long term plant cover data in an experimental grassland to examine the effects of abiotic (climate and fire) and biotic (bison and grasshoppers) drivers on demographic rates across nearly a hundred native plant species of varying range size. We found no relationship between fire and range size, but a positive relationship between range size and climate effects on colonization. We found mixed effects of herbivory across plant range size, with no relationship for large native herbivores (bison), but, found a positive relationship between grasshopper abundance and plant range size for changes in cover. These results are consistent with observations by Opler, but refute the niche breadth hypothesis. These results call into question the broad applicability of the niche breadth hypothesis, suggesting other factors, particularly biotic drivers, may play a more significant role than previously thought in shaping species' responses to environmental changes and should be included when considering range shifts and species distribution modeling.

The third chapter of this dissertation examined how species' rarity types and dispersal traits influence their potential for range shifts in response to climate change. Understanding the

ability of species to track shifting climatic conditions is essential for predicting future biodiversity patterns and informing conservation strategies, particularly for rare species that may be more vulnerable to extinction. Using long term plant cover data, we created density structured models for 15 North American grassland forb species of varying rarity type. Density structured models are an underutilized population growth model utilizing density classes (here we used cover classes) and are robust even without detailed data on individual performance (Queenborough et al. 2011), a common limitation for rare species. We use these models, in addition to dispersal estimates, to simulate shifts in species ranges at the leading edge. Our results indicate no significant impact of drivers (fire, climate, and cattle herbivory) on populations, regardless of rarity type. However, we did find significant differences in populations between northern and central populations, suggesting the ability to maintain or expand range leading edges may depend on localized responses to environmental changes. Habitat specificity emerged as the most significant limiting factor for species' ability to shift their ranges, as species with narrow habitat requirements failed to move across simulated landscapes as well as more generalist species. We found no differences in long-distance dispersal distances between rarity types; however, we did see species with particularly high dispersal ability were better at shifting leading-edge populations. This finding suggests while dispersal traits are important, they may not always be sufficient to overcome the challenges posed by fragmented habitats and habitat specialization.

This dissertation contributes to a growing body of literature highlighting the complex and context-dependent nature of species' population responses to environmental drivers. The findings underscore the need for conservation strategies that account for variability in demographic sensitivities, the role of biotic interactions, and the challenges posed by species

rarity. Global biodiversity loss threatens more than 25 percent of currently extant species with extinction (Díaz et al. 2019). Rare species face higher probability of extinction than more common species, but we know little about how rare species will respond to changes in climate. Rare species account for most of the biodiversity and functional richness in communities (Preston 1948, Brown 1984, Leitão et al. 2016, Enquist et al. 2019) and offer novel functional traits, providing distinct ecosystem services from common species (Cardinale et al. 2006) or can offer functional redundancy through providing similar function as common species (Tucker et al. 2011, Jain et al. 2014). However, not all rare species are the same: a "rare" species can have restricted range size, narrow habitat requirements, and/or low population densities (Rabinowitz 1981). Given that these three types of rarity have quite different implications for long-term population dynamics, it is imperative that we differentiate between these different types of "rare" species when predicting future population responses to climate change and shifts in distributions. Successful conservation will require species-specific strategies that consider the unique demographic, ecological, and dispersal characteristics of each species.

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Appendix A

Using a global model and likelihood ratio tests rather than model selection

In the main text, we present demographic rate models and IPMs derived from a model selection approach. Here, we show IPMs derived from the global model for each demographic rate (to allow for the full complement of neighbor effects, even if absent from the best-fit model). We also use a likelihood ratio test (LRT) to examine the significance of our demographic rate model coefficients. In LRTs, we used the R package 'car' (Fox and Weisberg, 2019) *Anova* function (package version 3.1-1) to obtain a type III sum of squares.

Population effects on demographic rates and population growth rates

Using the global demographic rate models vs. best fit models resulted in nearly identical results. In our main text results for demographic data, the best fit model for all demographic rates included log transformed plant size and population, except for variance in growth which only included population. For our model testing using LRT, we found the same pattern: all demographic rates, except for variance in growth, had log transformed plant size and population as significant (App. Table A.6). Our LRT results for variance in growth indicated population, but not plant size, was significant, the same pattern as our model selection results. Estimated demographic rates and population growth rates using global models were nearly identical to our model selection methods (App. Fig. A.6).

Neighbor effects on demographic rates and population growth rates

Using the global demographic rate models to build IPMs resulted in similar patterns to our model selection results for population growth rate, though an LRT supported somewhat different parameters. Using model selection methods, the best fit models for survival and growth included log plant size and treatment, whereas probability of fruiting and number of fruits had plant size and population (but not treatment) included. The only demographic rate containing a treatment x population interaction effect was variance in growth (App. Table A.7). By contrast, our LRT results indicate no support for a removal treatment x population term for any demographic rate. However, population was significant across all demographic rates (App. Table A.7, matching our model selection results in the main text). Population growth rates maintain the same pattern as when using model selection (App. Fig. A.7).

We show effects of LRT for the climate experiment in App. Table A.8; results are also similar.

Changes in results when using the same recruitment rates in neighbor removal treatments and control treatments

In the main text, we present results from projections that assume higher recruitment in neighbor removal treatments than in control treatments (A. Louthan, pers. ob.). Specifically, we multiplied seedlings per fruit values for removal treatments by two, resulting in a value of seedlings per fruit in neighbor removal treatments that is twice as high as in the unmanipulated control treatments. Using the same methods described in the manuscript, but using unmodified seedlings per fruit values (i.e., the same value of seedlings per fruit for control and for neighbor removal treatments), we show here that our main result is similar. Namely, the effect of neighbors on population growth rate varies (non-significantly) across populations, and this effect

is due to among-population variation in sensitivity to demographic rates, rather than differential effects of neighbors on demographic rates across populations. First, we find that the effect of neighbor on population growth rate varies across populations, with the largest effect size at our two high elevation populations (App. Fig. A.8). While these differences are not significant, there is substantial among-population variation in the effect of neighbors on population growth rate. All size-dependent demographic rates remain unchanged with modification of seedlings per fruit. As such, the effect of neighbors on demographic rates remains unchanged from the results described in text (see *Neighbor effects on demographic rates and population growth rate methods* section). Ultimately, these findings do not substantially differ from those described in the main text.

Changes in results when excluding neighbor-population interaction term in variance in growth demographic rate

In the main text, we present results derived from a model selection methodology, which included an interaction term between neighbor removal treatment and population in the best fit model for the variance in growth demographic rate. We wanted to examine whether the significant variation in sensitivities among populations was sufficient to generate among-population variance in neighbor effect on population growth rate. To do so, we reran all projections of population growth rate using the neighbor removal functions, but excluding an interaction effect from the variance in growth demographic rate. We found our main result is similar: the effect of neighbors on population growth rate varies across populations, with significant positive effects of neighbor removal at high elevations and non-significant effects of neighbors at low elevations (App. Figure A.1).

Citations

Fox, John, and Sanford Weisberg. *An R Companion to Applied Regression*. Third ed. Thousand Oaks, CA: Sage, 2019. Print.

Lüdecke et al., (2021). performance: An R Package for Assessment, Comparison and Testing of Statistical Models. Journal of Open Source Software, 6(60), 3139. https://doi.org/10.21105/joss.03139

Appendix Table A.1: Temperature data collected at each population from 2011-2015. Data were collected using iButtons (Maxim/Dallas Semiconductor Corp., USA) buried 5-10 cm underground at each population. June, July, and August data are missing for populations L1 and L2 for 2012. Standard deviation of average temperatures is in parentheses.

Population	Average temperature (°C)	Maximum temperature (°C)	Minimum temperature (°C)	Number of observations	Average temperature July-September (approximate snow free months)
L1	6.80 (9.95)	48	-14.5	23943	18.5 (6.97)
L2	7.29 (9.54)	47.5	-13.5	22264	18.0 (6.55)
H1	2.58 (9.84)	46.5	-19.5	16120	14.2 (7.13)

H2	3.23 (9.35)	39	-18	16120	14.8 (6.51)

Appendix Table A.2: Soil temperature and volumetric soil moisture resulting from heating and water addition experiments at Alpine-Treeline Warming Experiment (ATWE) at Niwot Ridge Long-Term Ecological Research Site. Treatments occurred during snow free months, ~June-September. Treatments were initiated in 2010 and continued through 2014. Here we show effects of heating and watering on soil temperature (C°) and volumetric soil moisture (m^3/m^3) over the entire treatment period and for the two years in which we collected our demography data, 2013 and 2014. More detail on the methods used for heating and watering treatments can be found in Jabis et al. (2020).

Treatment	Soil temperature (C°)			Volumetric soil moisture (m3/m3)		
	2010-2014	2013	2014	2012-2014	2013	2014
Heating	1.33 +/- 0.03	1.50 +/- 0.09	1.39 +/- 0.08	-0.012 +/- 0.001	-0.02 +/- 0.002	-0.02 +/- 0.002
Watering	-0.24 +/- 0.01	-0.08 +/- 0.03	-0.0 +/- 0.03	0.026 +/- 0.001	0.03 +/- 0.001	0.03 +/- 0.001

Appendix Table A.3: Coefficient estimates for the fixed effects component of the best fit demographic rate models derived from the demography data. Standard errors of the coefficients are in parentheses following the coefficient estimate. We show the AICc, AICc weights, and total number of observations (Num. obs.) of each best-fit model at the bottom of the table. We see very strong support for the best fit model for all demographic rates. Reference condition for the population coefficients is L1. We show conditional r-squared and marginal r-squared calculated using the r2_nakagawa function in the performance package (Lüdecke et al. 2021).

Coefficients	**Prob. of survival**	**Prob. of fruiting**	**Number of fruits**	**Mean growth**	**Variance in growth**
Intercept	1.24	-1.25	2.11	0.33	1.47
	(0.26)	(0.38)	(0.24)	(0.18)	(0.17)
Log(size)	0.59	0.93	0.46	0.73	
	(0.04)	(0.10)	(0.08)	(0.02)	
Population: L2	-0.09	0.33	0.27	-0.20	-0.33
	(0.18)	(0.27)	(0.18)	(0.09)	(0.24)
Population: H1	2.58	-0.18	-0.53	-0.66	-0.73
	(0.22)	(0.31)	(0.24)	(0.08)	(0.21)
Population: H2	2.37	-0.98	-1.12	-0.90	-0.89
	(0.22)	(0.42)	(0.36)	(0.09)	(0.22)
Model statistics					
AICc	1346.40	554.53	427.9	3111.4	5183.34
AICc weight	>0.99	0.94	0.99	>0.99	0.71
Conditional R2	0.468	0.571	0.397	0.718	0.013

Marginal R2	0.436	0.534	0.359	0.695	0.012
Num. obs.	1632	825	155	1090	1090

Appendix Table A.4: Coefficient estimates for the fixed effects components of the best fit demographic rate models derived from the neighbor removal data. Standard errors of the coefficients are in parentheses following the coefficient estimate. We show the AICc, AICc weight and total number of observations (Num. obs.) of each best-fit model at the bottom of the table; we see strong support for the best fit models. Reference conditions for categorical predictors are: L1 (population) and no neighbors (neighbor effect), such that coefficients indicate the effect of neighbors, relative to no neighbors, on performance. We show conditional r-squared and marginal r-squared calculated using the r2_nakagawa function in the performance package (Lüdecke et al. 2021) for all demographic rates besides variance in growth, which was fit with a linear model; adjusted r-squared was 0.027.

Coefficient	**Prob. of survival**	**Prob. of fruiting**	**Number of fruits**	**Growth**	**Variance in growth**
Intercept	1.14	-0.74	2.18	-0.04	2.01
	(0.24)	(0.39)	(0.22)	(0.20)	(0.51)
Log(size)	0.62	0.91	0.49	0.67	
	(0.06)	(0.10)	(0.07)	(0.02)	
Population: L2	0.23	0.34	0.36		-0.66
	(0.23)	(0.28)	(0.18)		(0.60)
Population: H1	2.09	-0.85	-0.33		-1.17
	(0.30)	(0.35)	(0.27)		(0.64)
Population: H2	2.47	-0.85	-0.72		-1.44
	(0.33)	(0.36)	(0.28)		(0.63)
Neighbor effect	0.38			-0.19	1.42
	(0.17)			(0.07)	(0.76)
Population L2 * Neighbor effect					-2.38
					(0.88)
Population H1 * Neighbor effect					-1.70
					(0.93)
Population H2 * Neighbor effect					-1.60
					(0.92)
Model Statistics					
AICc	920.53	765.82	803.25	3506.10	6335.71
AICc weight	0.75	0.69	0.74	0.50	0.95
Conditional R2	0.352	0.485	0.288	0.424	N/A
Marginal R2	0.335	0.444	0.270	0.386	N/A
Num. obs.	1348	839	277	1089	1089

Appendix Table A.5: Coefficient estimates for the fixed effects components of the best fit demographic rate models derived from the climate experiment data. Standard errors of the coefficients are in parentheses following the coefficient estimate. The reference condition for the climate manipulation is control, such that coefficients indicate the effect of the indicated manipulation on the demographic rate, relative to the unmanipulated control. We show the AICc, AICc weight, and total number of observations (Num. obs.) of each best-fit model at the bottom of the table. We show conditional r-squared and marginal r-squared calculated using the r2_nakagawa function in the performance package (Lüdecke et al. 2021) for all demographic rates besides survival, which was fit with a generalized linear model; McFadden's pseudo-r squared for this model was 0.281.

Coefficient	Prob. of survival	Prob. of fruiting	Number of fruits	Growth	Variance in growth
(Intercept)	4.02	-4.67	0.52	0.51	0.49
	(0.63)	(1.22)	(0.58)	(0.14)	(0.44)
Climate manipulation: heating	0.59	1.03		0.83	
	(0.13)	(0.33)		(0.03)	
Climate manipulation: watering	-0.95	1.57	1.87		1.20
	(0.48)	(1.03)	(0.65)		(0.69)
Model statistics					
AICc	118.01	78.56	69.64	451.34	825.56
AICc weight	0.31	0.29	0.36	0.5	0.39
Conditional R2	N/A	0.790	0.352	0.856	0.054
Marginal R2	N/A	0.697	0.321	0.836	0.027
Num. obs.	191	164	19	153	153

Appendix Table A.6: Likelihood ratio tests results for each of our five demographic rate models using our demography dataset. Test statistic results are followed by an indication of significance. Asterisks denote significance of coefficients: * p-value < 0.05, ** < 0.01, and *** < 0.001.

Coefficients	Df	Prob. of survival	Prob. of fruiting	Number of fruits	Mean growth	Variance in growth
Log(size)	1	202.88***	83.42***	29.60 ***	1804.40 ***	0.12
Population	3	219.21***	10.39 *	24.90 ***	125.82 ***	19.10 ***

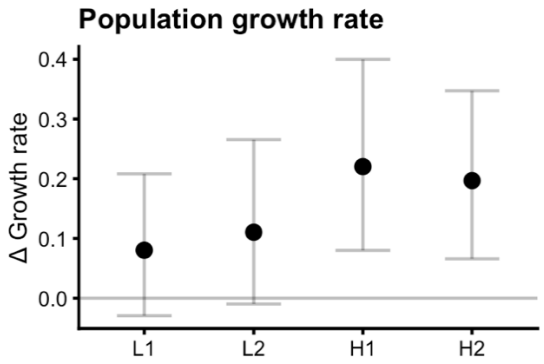
Appendix Table A.7: LRT results for each of our five demographic rate models using our neighbor removal experiment dataset. Test statistic results are followed by an indication of significance. Asterisks denote significance of coefficients: * p-value < 0.05, ** < 0.01, and *** < 0.001.

Coefficients	Df	Prob. of survival	Prob. of fruiting	Number of fruits	Mean growth	Variance in growth
Log(size)	1	193.43***	141.39 ***	37.84 ***	542.68***	1.52
Population	3	129.30***	32.95 ***	42.68 ***	19.62***	39.14***
Treatment	1	3.33	0.09	2.30	5.21*	0.009
Population x Treatment	3	1.28	0.81	0.91	0.495	7.77

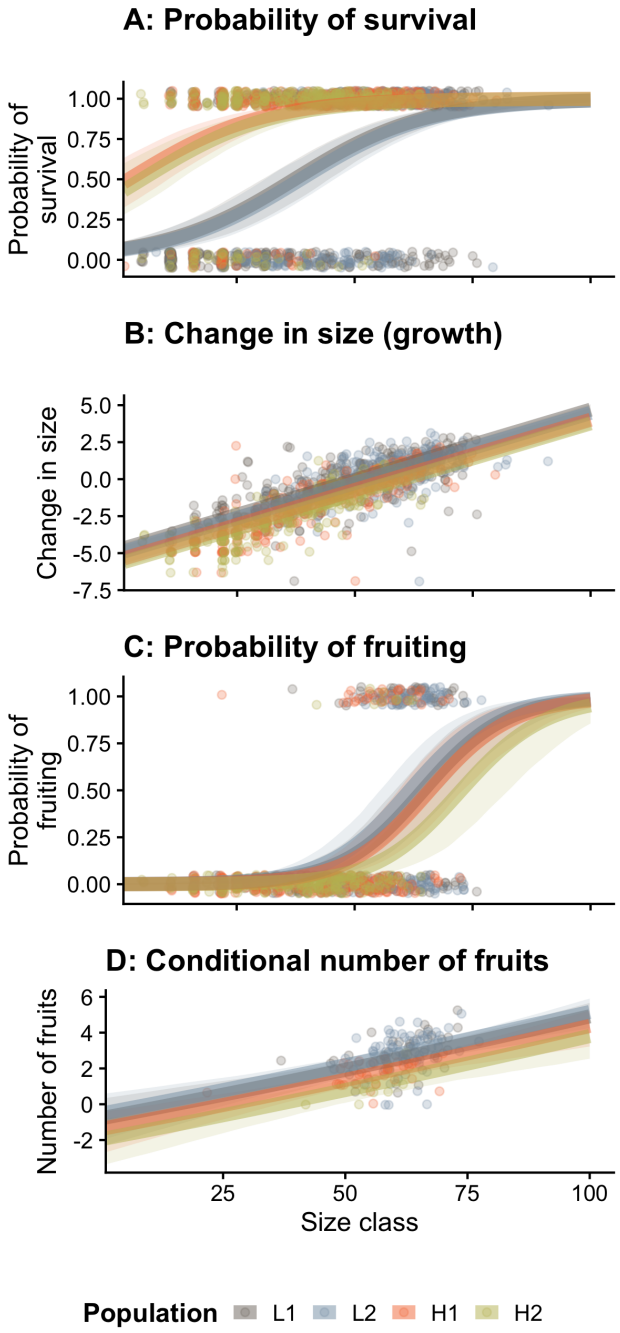
Appendix Table A.8: LRT results for each of our five demographic rate models using our climate manipulation experiment dataset. Test statistic results are followed by an indication of significance. Asterisks denote significance of coefficients: * p-value < 0.05, ** < 0.01, and *** < 0.001.

Coefficients	Df	Prob. of survival	Prob. of fruiting	Number of fruits	Mean growth	Variance in growth
Log(size)	1	19.52 ***	10.99 ***	1.44	669.28 ***	0.65
Watering	1	1.30	2.81	0.54	0.55	2.50
Heating	1	4.50	3.25	3.91 *	0.13	6.96E-05

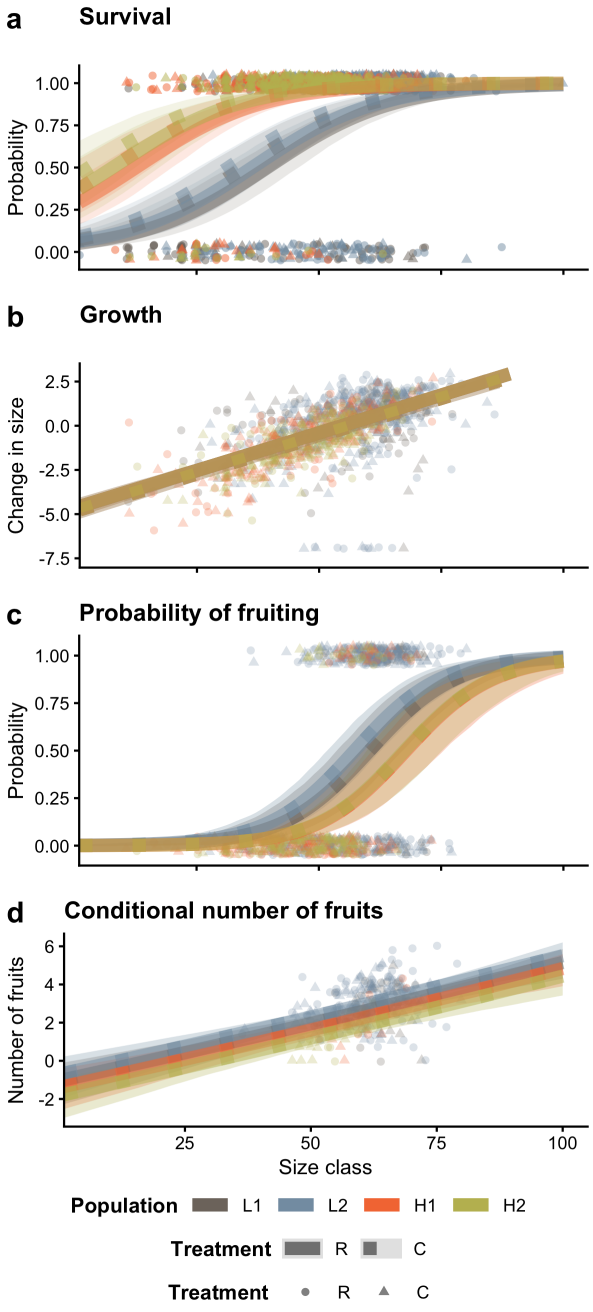
Supplementary Figures



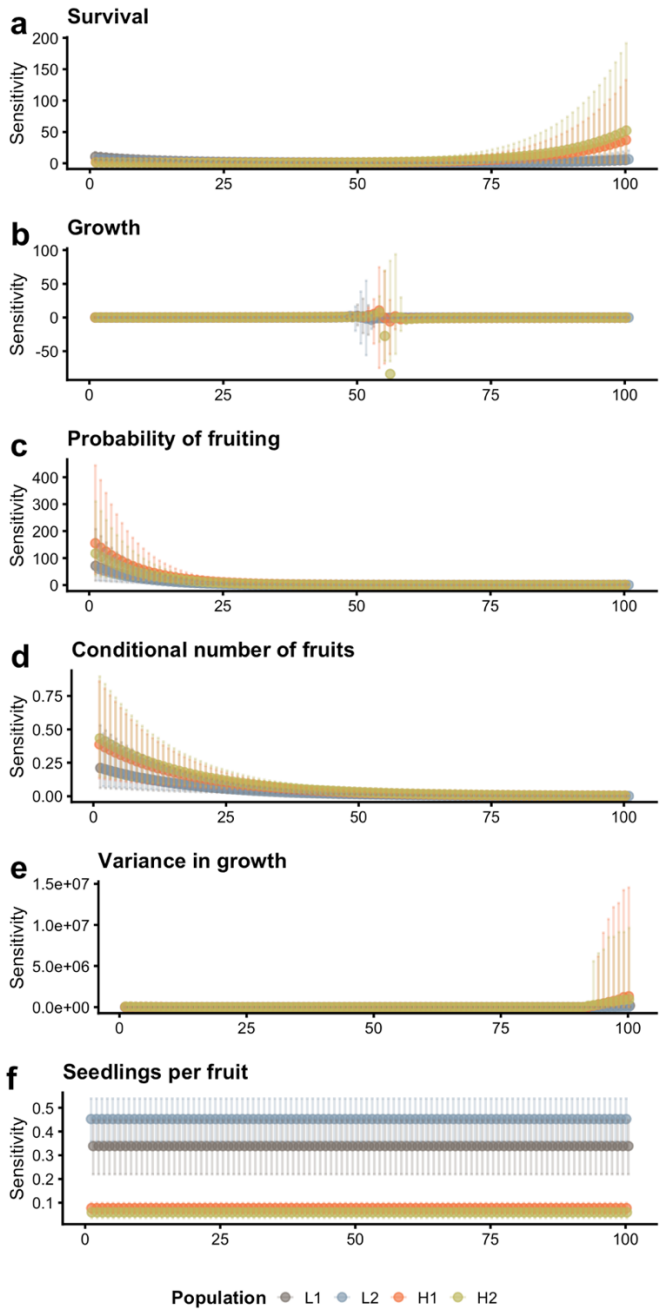
Appendix Figure A.1: Effects of neighbor removal treatment on population growth rate and demographic rates across populations with no neighbor treatment x population interaction in the variance in growth demographic rate. Δ denotes the difference between neighbor removal and control treatments (i.e., value without neighbors minus value with neighbors), such that positive values mean competition and negative values mean facilitation; a gray bar indicates 0, or no effect of neighbor removal treatments on population growth rate. Error bars are 95% confidence intervals derived from incorporating parameter uncertainty into the demographic rate functions used to construct the IPM. When calculating the 95% confidence intervals on the differences between neighbor effect among populations, as in the main text, we find that the effect of neighbors is significantly higher at H1 than at L1 and L2, and significantly higher at H2 than at L1 and L2.



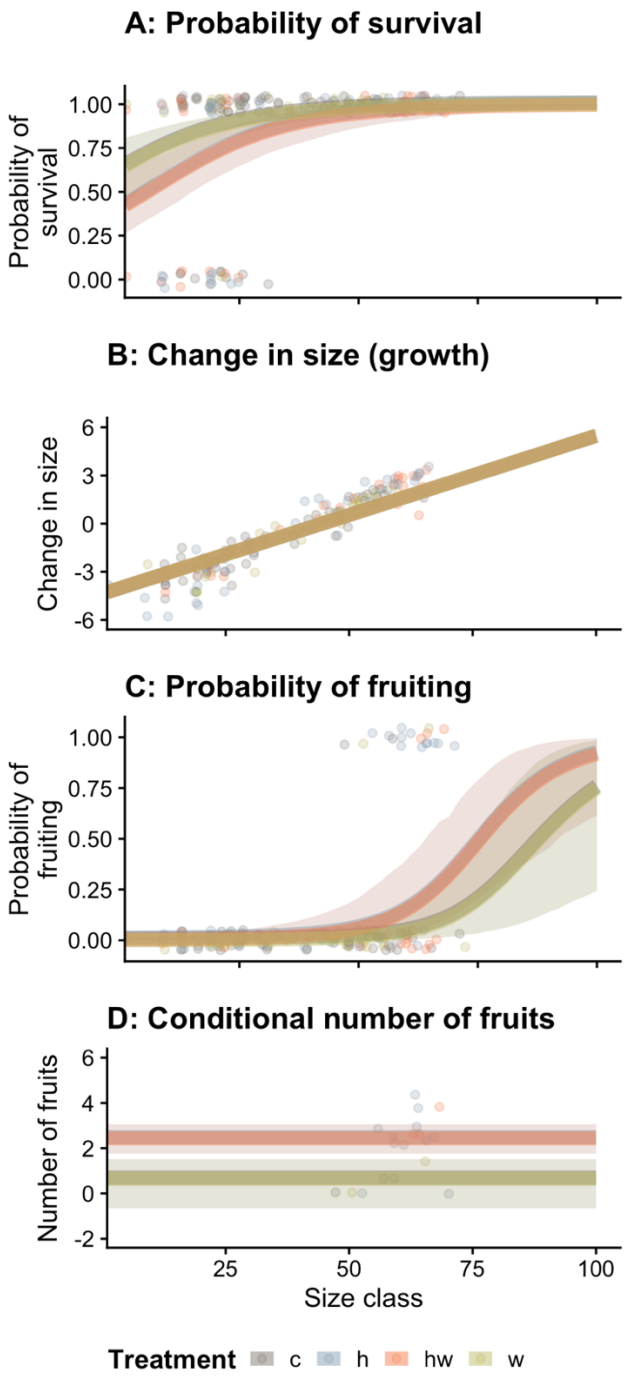
Appendix Figure A.2: Effects of population on demographic rates. Lines indicate the predicted demographic rate values across size classes using the best-fit models for each demographic rate (which we also used to construct the IPMs). Transparent polygons show the 95% confidence intervals on the fixed effect estimates. Points show the observed data. "Conditional" number of fruits indicates that the number of fruits was conditional on that plant producing >0 fruits.



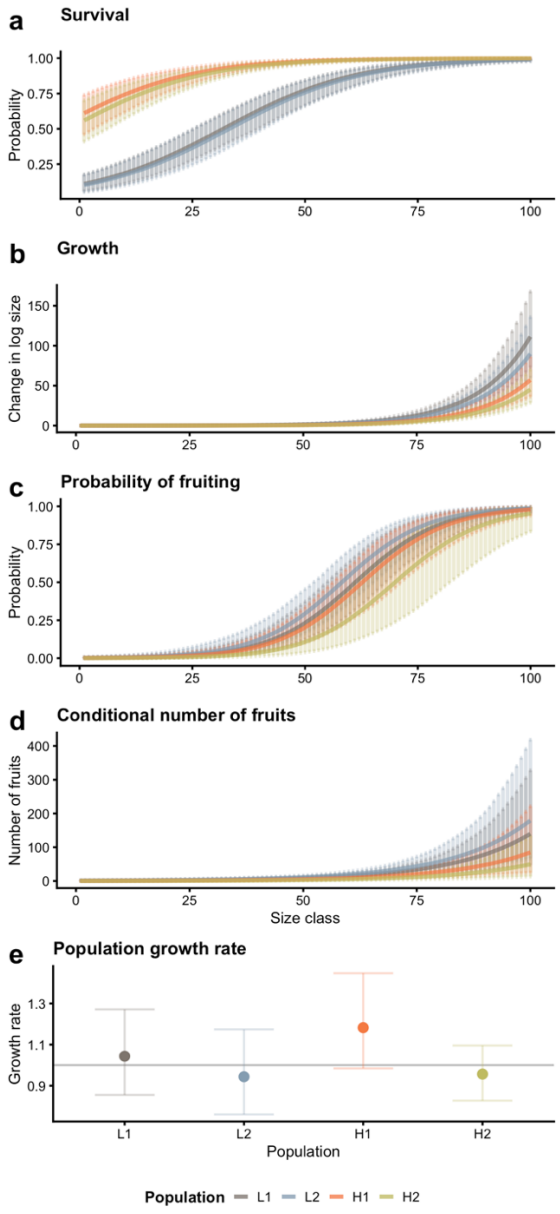
Appendix Figure A.3: Effects of population and removal treatment on demographic rates. In all panels, C represents the control treatment and R represents removal. Lines indicate the predicted demographic rate values across size classes using the best-fit models for each demographic rate (which we also used to construct the IPMs). Transparent polygons show the 95% confidence intervals on the fixed effect estimates. Points show the observed data. "Conditional" number of fruits indicates that the number of fruits was conditional on that plant producing >0 fruits.



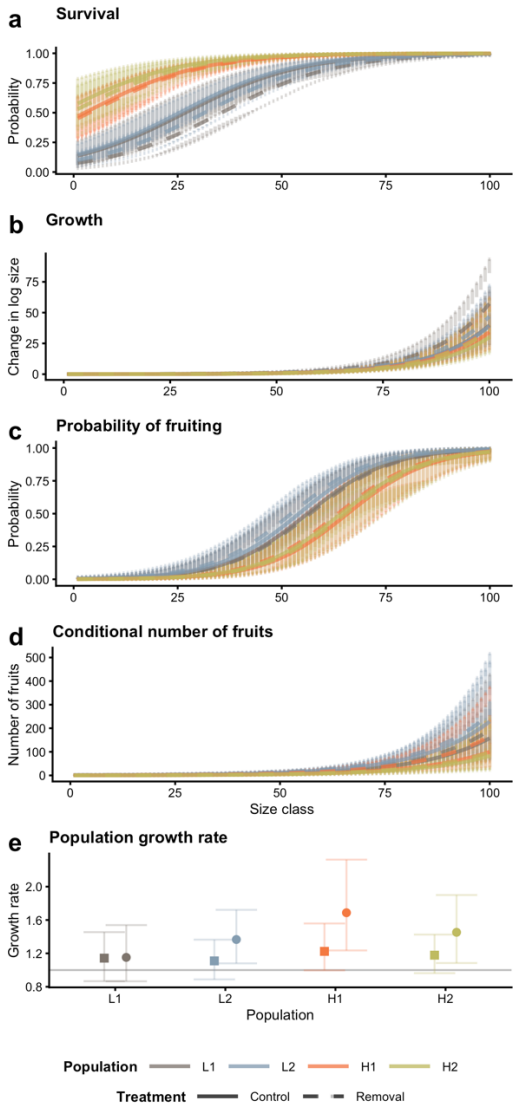
Appendix Figure A.4: Sensitivity of population growth rate across our four populations (L1, L2, H1, H2 – indicated by color; "L" suffix indicates low and "H" indicates high elevation) to demographic rates for all size classes. Error bars indicate 95% confidence intervals derived from incorporating parameter uncertainty into the demographic rate functions (using our global models) used to construct the IPM. Sensitivities were quantified using perturbation. "Conditional" number of fruits indicates that the number of fruits was conditional on that plant producing >0 fruits.



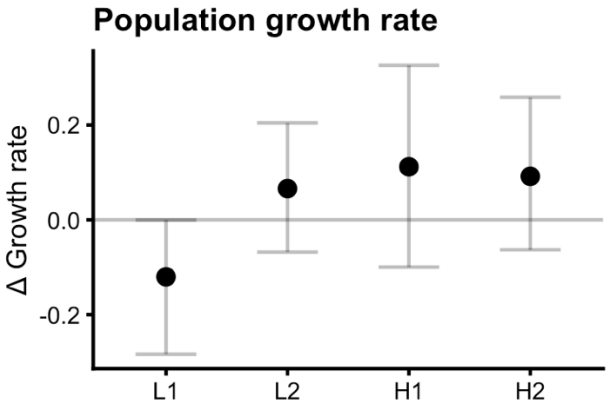
Appendix Figure A.5: Effects of four climate treatments on demographic rates. In all panels, c represents the control treatment, h = heating, w = watering, and hw = heating + watering. Lines indicate the predicted demographic rates values across size classes using the best-fit models for each demographic rate (which we also used to construct the IPMs). Transparent polygons show the 95% confidence intervals on the fixed effect estimates. Points show the observed data. "Conditional" number of fruits indicates that the number of fruits was conditional on that plant producing >0 fruits.



Appendix Figure A.6: Population effects on population growth rate and demographic rates using our global demographic rate models. Panels a-d show predicted demographic rates across size classes using the best fit models for each demographic rate (which we also used to construct the IPMs). Panel e shows predictions of deterministic growth rate from integral projection models (IPMs) constructed using demography data for each population. We show the critical value of one with a grey horizonal line. Error bars show 95% confidence intervals on the fixed effect estimates (a-d) or 95% confidence intervals derived from incorporating parameter uncertainty into the demographic rate functions used to construct the IPM (e). "Conditional" number of fruits indicates that the number of fruits was conditional on that plant producing >0 fruits.



Appendix Figure A.7: Effects of neighbor removal treatment on population growth rate and demographic rates (using global models with fixed effects of size, neighbor removal treatment, population, and their interaction) across populations (L1, L2, H1, H2 – indicated by color; "L" suffix indicates low and "H" indicates high elevation).. Panels a-d show the effect of neighbors on predicted demographic rates across size classes using the best-fit models for each demographic rate (which we also used to construct the IPMs). Panel e shows deterministic growth rates for neighbor removal vs. control treatment, predicted using integral projection models (IPMs) constructed from neighbor removal data. Error bars show 95% confidence intervals on the fixed effect estimates (a-d) or 95% confidence intervals derived from incorporating parameter uncertainty into the demographic rate functions used to construct the IPM (e). When calculating 95% confidence intervals on the differences in neighbor effect across populations (as in Fig. 3F), effect of neighbor removals is significantly positive at L2 and H1, but overlaps 0 at L1 and H2.

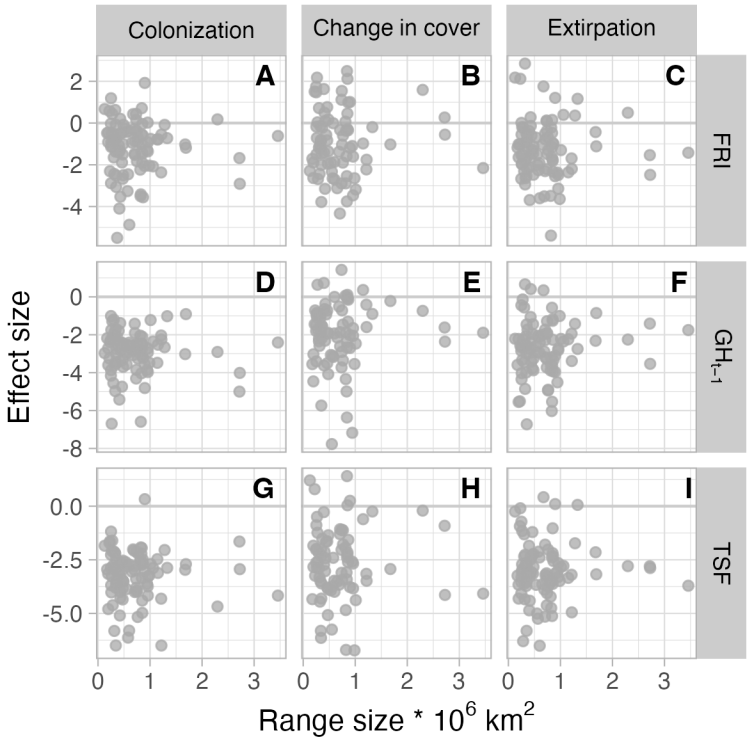


Appendix Figure A.8: Effects of neighbor removal treatment on population growth rate and demographic rates across populations assuming removal treatment does not affect seedlings per fruit (L1, L2, H1, H2; "L" suffix indicates low and "H" indicates high elevation). Δ denotes the difference between neighbor removal and control treatments (i.e., value without neighbors minus value with neighbors), such that positive values mean competition and negative values mean facilitation; a gray bar indicates 0, or no change between treatments. Error bars are 95% confidence intervals derived from incorporating parameter uncertainty into the demographic rate functions used to construct the IPM.

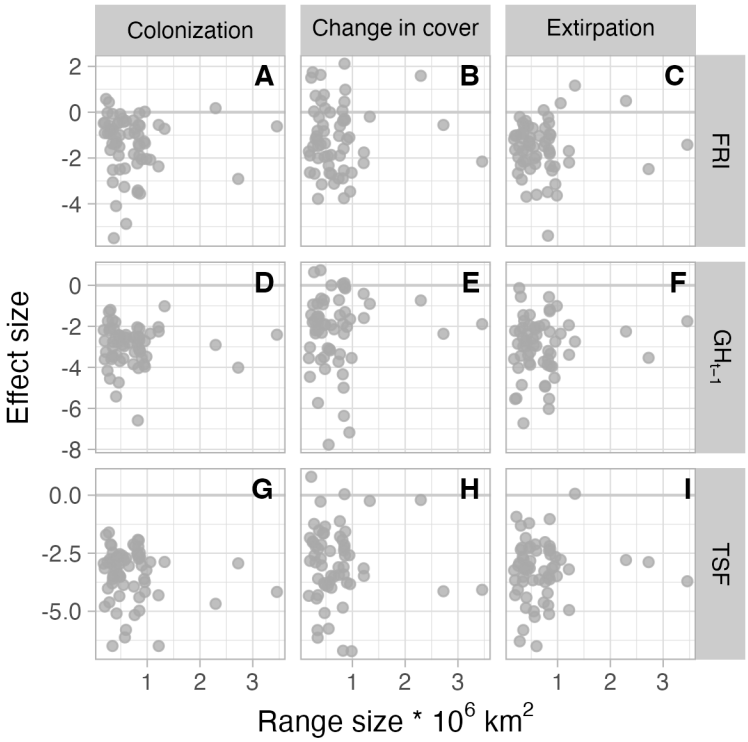
Appendix B

Appendix Table B.1: Treatment replicates (watersheds) at KPBS used in this study and their corresponding treatments. Watershed names are those used in KPBS LTER datasets. Fire return interval (FRI) indicates how often a watershed is burned in years (e.g., a value of 1 indicates a watershed is burned annually). Burning season indicates time of year a watershed is burned, and grazing indicates whether bison are present in the watershed.

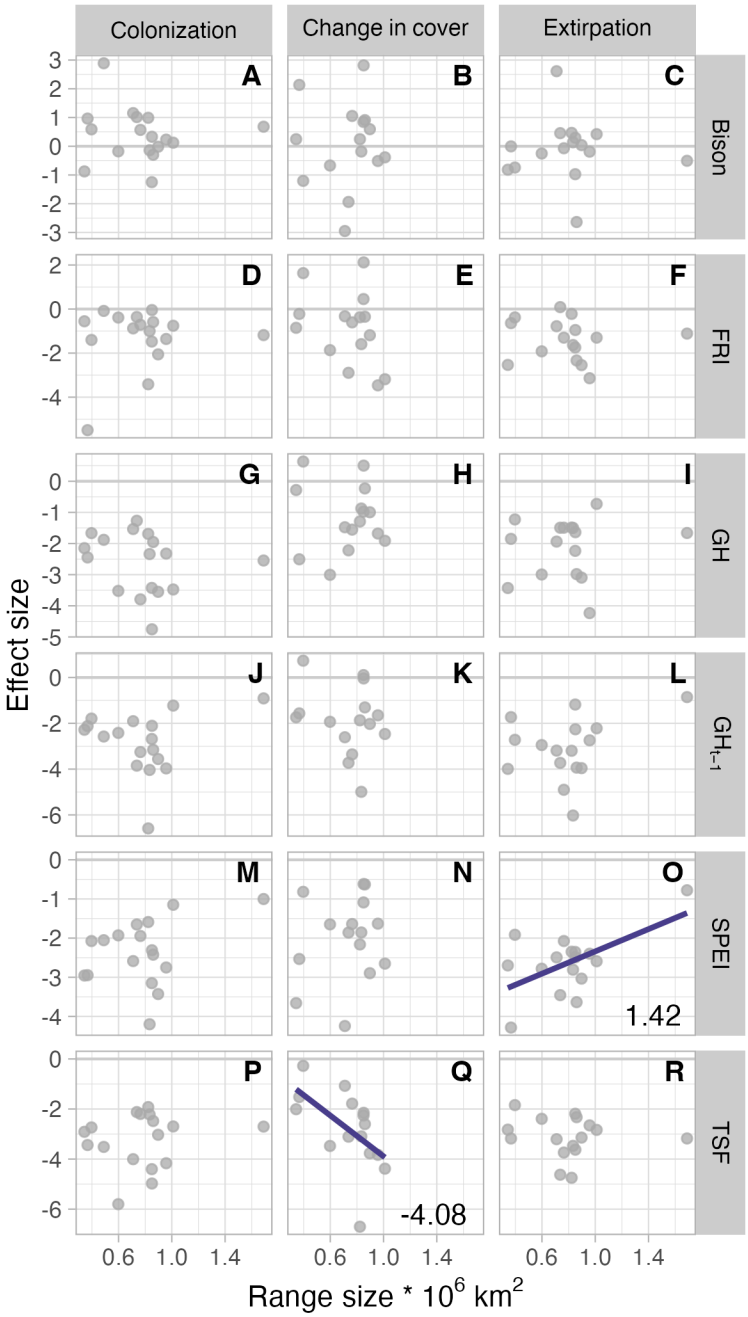
Watershed	*FRI*	*Burning season*	*Grazing*
1D	1	Fall	Ungrazed
20B	20	Fall	Ungrazed
2C	2	Fall	Ungrazed
2D	2	Fall	Ungrazed
4B	4	Fall	Ungrazed
4F	4	Fall	Ungrazed
N1A	1	Fall	Bison
N1B	1	Fall	Bison
N20A	20	Fall	Bison
N20B	20	Fall	Bison
N4A	4	Fall	Bison
N4D	4	Fall	Bison
SPB	1	Spring	Ungrazed
SUB	1	Summer	Ungrazed



Appendix Figure B.1: Effect sizes vs. plant range size. Columns are our three demographic rates: probability of colonization (panels A, D, and G), change in cover (B, E, and H), and probability of extirpation (C, F, and I). Rows are driver type: fire return interval (FRI; A-C), grasshopper abundance in the previous year (GH_{t-1}; D-F) and time since fire (TSF; G-I) in the t-1 to t interval. Gray dots are species-specific effect sizes for the respective driver and demographic rate. No line indicates a non-significant relationship. See **Figure 3.4** in main text for significant driver results.



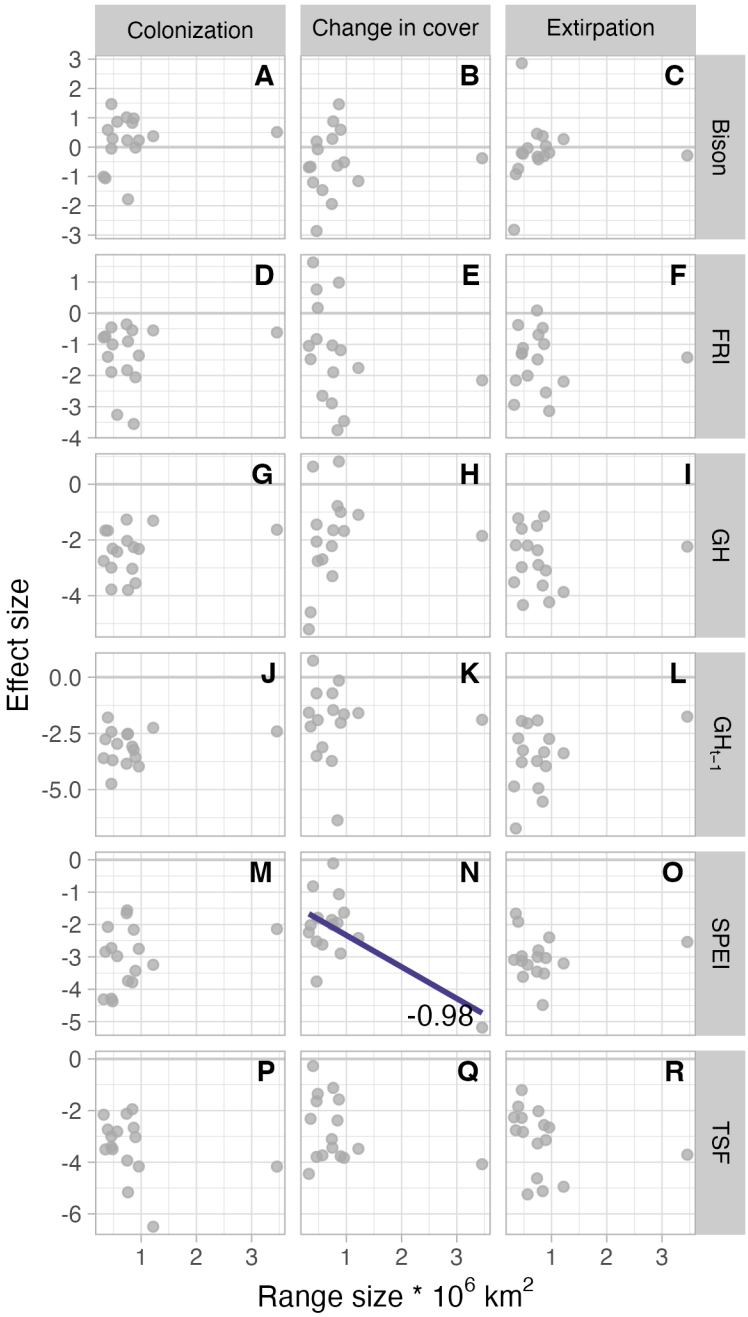
Appendix Figure B.2: Effect sizes vs. plant range size subset by species consumed by grasshoppers (Mulkern 1969, Campbell et al. 1974, Welti et al. 2019). Columns are our three demographic rates: probability of colonization (panels A, D, and G), change in cover (B, E, and H), and probability of extirpation (C, F, and I). Rows are driver type: fire return interval (FRI; A-C), grasshopper abundance in the previous year (GH_{t-1}; D-F) and time since fire (TSF; G-I) in the t-1 to t interval. Gray dots are species-specific effect sizes for the respective driver and demographic rate. See **Figure 3.5** in main text for significant driver results.



Appendix Figure B.3: Effect sizes vs. plant range size subset to grass species as an approximation of bison diet. Columns are our three demographic rates: probability of colonization (panels A, D, and G), change in cover (B, E, and H), and probability of extirpation (C, F, and I). Rows are driver type: bison presence (A-C), fire return interval (FRI; D-F), grasshopper abundance (GH; G-I), grasshopper abundance in the previous year (GH_{t-1}; J-L), SPEI (standardized precipitation-evapotranspiration index; drought index; M-O) ,and time since fire (TSF; P-R) in the t-1 to t interval. Gray dots are species-specific effect sizes for the respective driver and demographic rate. Dark lines indicate a significant relationship between effect size and range size for a respective model and driver, as indicated by AICc results; text

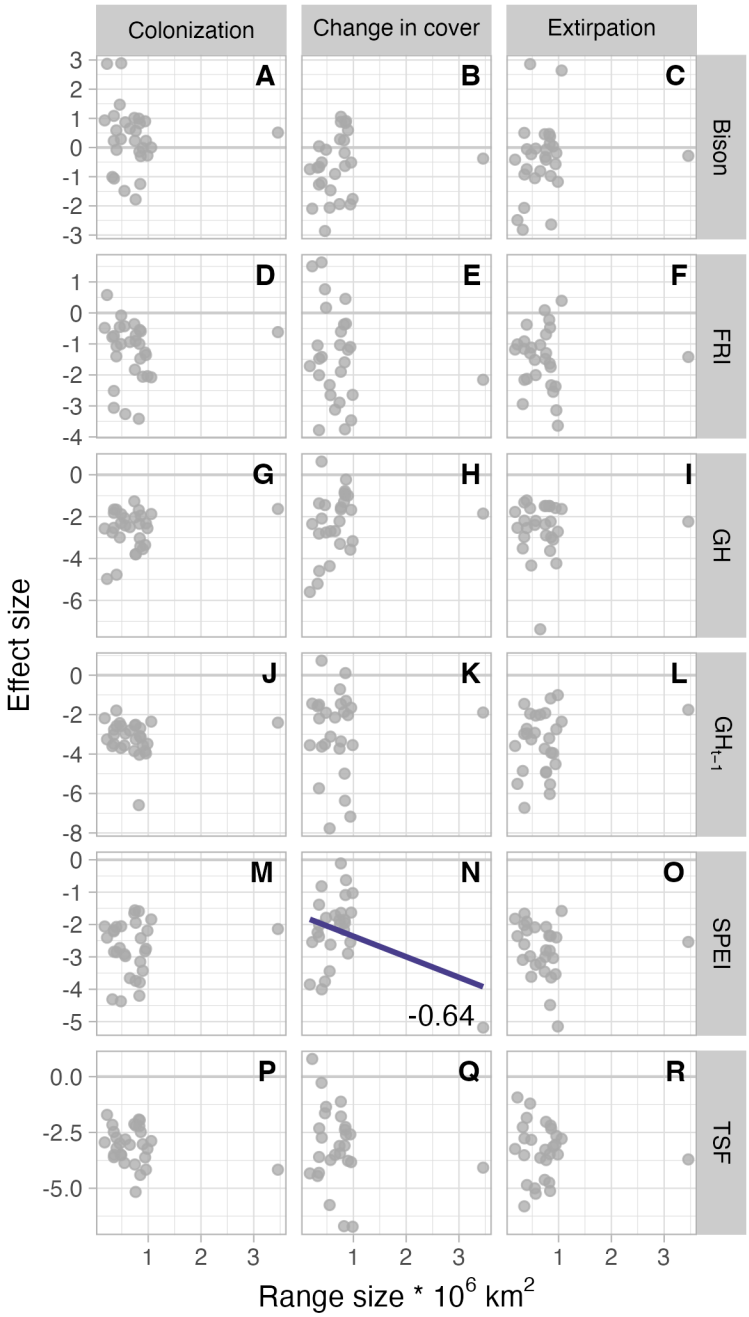
indicates the fitted coefficient values for the range size parameter. No line indicates a non-significant relationship.

Our smallest dataset was the Mulkern species list, which reduced our species to only 16. The resulting linear models indicated only one driver across all three model types showed a relationship with range size: probability of extirpation coefficients decreased with range size for TSF (range coefficient = -0.70, Appendix Figure B.4). The Campbell et al. species list resulted in 27-29 species included our models. Again, only one driver under one model type showed a relationship with range size, but this time it was bison presence and probability of extirpation (Appendix Figure B.5) with a notably large value of 1.05 compared to our other range size coefficients. Finally, using the Welti et al. species list, our dataset included 46-50 species for each model and driver type. Here, we found more significant relationships between drivers and range size across model types (Appendix Figure B.6). Whereas our results when using all species had two driver-model type pairs with significant relationships, using the Welti et al. dataset we found eight. We found a negative relationship (-0.36) between range size and FRI (fire return interval) coefficients for probability of extirpation, the only relationship we found for any driver in our extirpation models. Bison presence was significant and positive for both change in cover (0.76) and extirpation (0.41), as was grasshopper presence (0.69, 0.6) and SPEI (0.52, 0.51) for the same model types respectively. TSF also showed a significant relationship with range size for probability of extirpation (0.36).



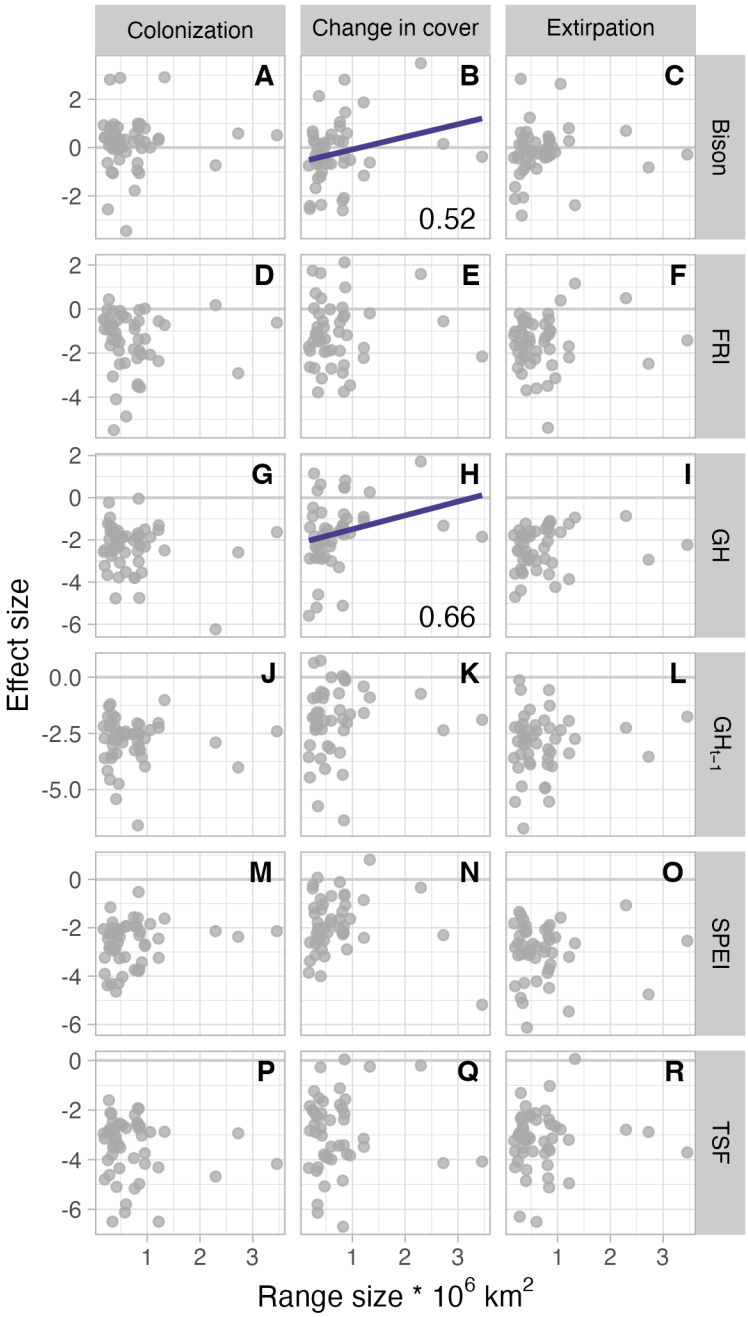
Appendix Figure B.4: Effect sizes vs. plant range size subset to plant species consumed by grasshopper species as described by **Mulkern** (1969). Columns are our three demographic rates: probability of colonization (panels A, D, and G), change in cover (B, E, and H), and probability of extirpation (C, F, and I). Rows are driver type: bison presence (A-C), fire return interval (FRI; D-F), grasshopper abundance (GH; G-I), grasshopper abundance in the previous year (GH_{t-1}; J-L), SPEI (standardized precipitation-evapotranspiration index; drought index; M-O) ,and time since fire (TSF; P-R) in the t-1 to t interval. Gray dots are species-specific effect sizes for the respective driver and demographic rate. Dark lines indicate a significant relationship between effect size and range size for a respective model and driver, as indicated by AICc results; text

indicates the fitted coefficient values for the range size parameter. No line indicates a non-significant relationship.



Appendix Figure B.5: Effect sizes vs. plant range size subset to plant species consumed by grasshopper species as described by **Campbell et al.** (1974). Columns are our three demographic rates: probability of colonization (panels A, D, and G), change in cover (B, E, and H), and probability of extirpation (C, F, and I). Rows are driver type: bison presence (A-C), fire return interval (FRI; D-F), grasshopper abundance (GH; G-I), grasshopper abundance in the previous year (GH_{t-1}; J-L), SPEI (standardized precipitation-evapotranspiration index; drought index; M-O) ,and time since fire (TSF; P-R) in the t-1 to t interval. Gray dots are species-specific effect sizes for the respective driver and demographic rate. Dark lines indicate a significant relationship between effect size and range size for a respective model and driver, as indicated by AICc

results; text indicates the fitted coefficient values for the range size parameter. No line indicates a non-significant relationship.



Appendix Figure B.6: Effect sizes vs. plant range size subset to plant species consumed by grasshopper species as described by **Welti et al.** (2018). Columns are our three demographic rates: probability of colonization (panels A, D, and G), change in cover (B, E, and H), and probability of extirpation (C, F, and I). Rows are driver type: bison presence (A-C), fire return interval (FRI; D-F), grasshopper abundance (GH; G-I), grasshopper abundance in the previous year (GH_{t-1}; J-L), SPEI (standardized precipitation-evapotranspiration index; drought index; M-O) ,and time since fire (TSF; P-R) in the t-1 to t interval. Gray dots are species-specific effect sizes for the respective driver and demographic rate. Dark lines indicate a significant relationship between effect size and range size for a respective model and driver, as indicated by AICc

results; text indicates the fitted coefficient values for the range size parameter. No line indicates a non-significant relationship.

Appendix C

Appendix Table C.1: KPBS watersheds (treatment units) used to classify species to density rarity class and parameterize our density structured models, along with their cattle grazing treatment (present or no grazers present) and fire return interval treatment in years.

Watershed	*Cattle present*	*Fire return interval*
1D	No	1
2C	No	2
2D	No	2
4A	No	4
4B	No	4
4F	No	4
FA	No	1
FB	No	1
WA	No	1
WB	No	1
20B	No	20
SpA	No	1
SpB	No	1
SuA	No	1
SuB	No	1
C1A	Yes	1
C3A	Yes	3
C3B	Yes	3
C3C	Yes	3
C1SB	Yes	1
C3SA	Yes	3
C3SC	v	3

Appendix Table C.2: Site and location information for northern population plots. Site is the name of the parcel of land or an approximate location. Plot is the number of plot within a site. Grazing indicates if cattle are or were at some point present. Year of last burn is the last recorded burn encompassing a plot; information was collected by contacting land managers or U.S. Geological Survey and Forest Service's Monitoring Trends in Burn Severity program data. Some sites had no recorded burn under current ownership or predated 1980; these sites are noted with NA. State is South Dakota (SD) or Wisconsin (WI).

Site	*Plot*	*Latitude*	*Longitude*	*Elevation (m)*	*Owner*	*Grazing*	*Year of last burn*	*State*	*County*
Altamont GPA	1	44.86	-96.72	574.55	SD State	cattle	2012	SD	Deuel
Altamont GPA	2	44.86	-96.72	574.24	SD State	cattle	2012	SD	Deuel
Altamont GPA	3	44.86	-96.72	580.03	SD State	cattle	2012	SD	Deuel
Altamont GPA	4	44.86	-96.72	577.90	SD State	cattle	2012	SD	Deuel
Altamont Prairie	1	44.89	-96.54	443.18	TNC	cattle	None	SD	Deuel
Angostura Reservoir	1	43.35	-103.43	957.38	SD State	cattle	None	SD	Fall River
Angostura Reservoir	2	43.35	-103.54	1169.21	SD State	ungrazed	2000	SD	Fall River
Angostura Reservoir	3	43.32	-103.46	1000.05	SD State	ungrazed	2000	SD	Fall River
Angostura Reservoir	4	43.35	-103.54	1130.20	SD State	ungrazed	2000	SD	Fall River
Brush Lake	1	44.31	-97.10	542.54	FWS	cattle	2010	SD	Deuel
Brush Lake	2	44.31	-97.10	544.98	FWS	cattle	2010	SD	Deuel
Brush Lake	3	44.31	-97.10	552.60	FWS	cattle	2010	SD	Deuel
Brush Lake	4	44.31	-97.10	559.31	FWS	cattle	2010	SD	Deuel
Brush Lake	5	44.31	-97.10	549.86	FWS	cattle	2010	SD	Deuel
Brush Lake	6	44.31	-97.10	546.51	FWS	cattle	2010	SD	Deuel
Brush Lake	7	44.31	-97.10	542.85	FWS	cattle	2010	SD	Deuel
Coteau Prairie	1	44.89	-96.71	545.59	FWS	cattle	2018	SD	Deuel
Coteau Prairie	2	44.89	-96.72	545.90	FWS	cattle	2018	SD	Deuel
Coteau Prairie	3	44.89	-96.72	546.20	FWS	cattle	2018	SD	Deuel
Coteau Prairie	4	44.89	-96.71	547.73	FWS	cattle	2018	SD	Deuel
Coteau Prairie	5	44.89	-96.71	547.73	FWS	cattle	2018	SD	Deuel
Coteau Prairie	6	44.89	-96.71	544.98	FWS	cattle	2018	SD	Deuel
Coteau Prairie	7	44.89	-96.72	544.37	FWS	cattle	2018	SD	Deuel

Coteau Prairie	8	44.89	-96.72	545.59	FWS	cattle	2018	SD	Deuel
Crex Meadows	1	45.89	-92.65	289.86	WI DNR	ungrazed	None	WI	Burnett
Crex Meadows	2	45.89	-92.65	288.65	WI DNR	ungrazed	None	WI	Burnett
Crex Meadows	3	45.89	-92.65	291.69	WI DNR	ungrazed	None	WI	Burnett
Fish Lake	1	45.71	-92.71	284.38	WI DNR	ungrazed	2022	WI	Burnett
Gary Gulch	1	NA	NA	NA	SD State	cattle	None	SD	Deuel
Gary Gulch	2	44.79	-96.47	480.67	SD State	cattle	None	SD	Deuel
Gary Gulch	3	44.79	-96.47	485.85	SD State	cattle	None	SD	Deuel
Gary Gulch	4	44.79	-96.47	486.16	SD State	cattle	None	SD	Deuel
Gary Gulch	5	44.79	-96.47	474.57	SD State	cattle	None	SD	Deuel
Gary Gulch	6	44.79	-96.47	484.02	SD State	cattle	None	SD	Deuel
Gary Gulch	7	44.79	-96.47	484.63	SD State	cattle	None	SD	Deuel
Hot Springs	1	43.43	-103.55	1189.33	SD State	cattle	None	SD	Fall River
Jacobson Fen	1	44.79	-96.63	527.61	TNC	ungrazed	None	SD	Deuel
Jacobson Fen	2	44.79	-96.63	527.91	TNC	ungrazed	None	SD	Deuel
Jacobson Fen	3	44.79	-96.63	530.66	TNC	ungrazed	None	SD	Deuel
Jacobson Fen	4	44.79	-96.63	535.84	TNC	ungrazed	None	SD	Deuel
Jacobson Fen	5	44.79	-96.63	532.18	TNC	ungrazed	None	SD	Deuel
Jacobson Fen	6	44.79	-96.63	530.05	TNC	ungrazed	None	SD	Deuel
Lookout Mountain	2	44.49	-103.83	1313.38	City of Spearfish	cattle	None	SD	Fall River
Lookout Mountain	22-4	44.49	-103.83	1313.38	City of Spearfish	cattle	None	SD	Fall River
Lookout Mountain	3	44.49	-103.83	1341.12	City of Spearfish	cattle	None	SD	Fall River
Lookout Mountain	4	44.49	-103.83	1309.73	City of Spearfish	cattle	None	SD	Fall River
Lookout Mountain	5	44.49	-103.83	1302.41	City of Spearfish	cattle	None	SD	Fall River
Mud Lake	1	44.78	-96.60	564.18	SD State	ungrazed	None	SD	Deuel
Reed Lake	1	45.91	-92.55	293.83	WI DNR	ungrazed	None	WI	Burnett
S Black Hills	1	43.60	-103.51	1394.76	Forest Service	cattle	2012	SD	Fall River
S Black Hills	10	44.14	-103.61	1641.35	Forest Service	cattle	None	SD	Fall River
S Black Hills	11	44.14	-103.61	1635.56	Forest Service	cattle	None	SD	Fall River
S Black Hills	12	43.60	-103.68	1490.17	Forest Service	cattle	None	SD	Fall River
S Black Hills	13	43.56	-103.65	1447.50	Forest Service	ungrazed	None	SD	Fall River

S Black Hills	14	43.56	-103.65	1449.02	Forest Service	ungrazed	None	SD	Fall River
S Black Hills	2	43.60	-103.51	1399.03	Forest Service	cattle	2012	SD	Fall River
S Black Hills	22-1	43.51	-103.56	1376.48	Forest Service	cattle	None	SD	Fall River
S Black Hills	22-2	43.51	-103.56	1399.34	Forest Service	cattle	None	SD	Fall River
S Black Hills	22-3	43.60	-103.51	1396.29	Forest Service	cattle	2012	SD	Fall River
S Black Hills	23-1	43.52	-103.66	1431.04	Forest Service	ungrazed	None	SD	Fall River
S Black Hills	23-2	43.56	-103.65	1448.41	Forest Service	ungrazed	None	SD	Fall River
S Black Hills	3	43.52	-103.66	1423.42	SD State	ungrazed	None	SD	Fall River
S Black Hills	4	43.47	-103.51	1238.10	Forest Service	ungrazed	None	SD	Fall River
S Black Hills	5	43.51	-103.56	1377.09	Forest Service	cattle	None	SD	Fall River
S Black Hills	6	43.51	-103.56	1381.35	Forest Service	cattle	None	SD	Fall River
S Black Hills	7	43.51	-103.56	1382.27	Forest Service	cattle	None	SD	Fall River
S Black Hills	8	43.51	-103.56	1402.99	Forest Service	cattle	None	SD	Fall River
S Black Hills	9	44.08	-103.64	1507.85	Forest Service	cattle	None	SD	Fall River
Sioux Prairie	1	44.03	-96.78	515.42	TNC	cattle	None	SD	Deuel
Sioux Prairie	2	44.03	-96.78	515.11	TNC	cattle	None	SD	Deuel

Appendix Table C.3: Mean percent cover and 95% confidence intervals as estimated by our density structured models for all focal species and drivers. Table is organized by species name. Values are percent cover derived from the midpoint value from cover class values estimated using density structured models. Grazing indicates presence of cattle (cattle grazed or ungrazed), fire history describes how long since plot was last burn as a two-level factor (recent or historic; recent are plots burned <5 years). SPEI is a drought index capturing climatic impacts on plants with three levels measured in this study: average climate was SPEI = 0, drought conditions (hot and dry) were minimum observed SPEI at -1.15, and wet was maximum overserved SPEI at 2.33.)

Species	*Grazing*	*Fire history*	*SPEI*	*Region*	*Median % cover*	*95% CI lower limit*	*95% CI upper limit*
Achillea millefolium	Ungrazed	Recent	Average	Central	1.43	0.83	38
Achillea millefolium	Cattle	Recent	Average	Central	2.88	1.5	33.37
Achillea millefolium	Ungrazed	Historic	Average	Central	2.17	0.78	38
Achillea millefolium	Cattle	Historic	Average	Central	4.3	0.6	38
Achillea millefolium	Ungrazed	Recent	Hot and dry	Central	4.91	0.74	38
Achillea millefolium	Cattle	Recent	Hot and dry	Central	7.57	1.25	62.41
Achillea millefolium	Ungrazed	Historic	Hot and dry	Central	14.08	0.78	63
Achillea millefolium	Cattle	Historic	Hot and dry	Central	38	0.65	63
Achillea millefolium	Ungrazed	Recent	Cool and wet	Central	1.34	0.83	38
Achillea millefolium	Cattle	Recent	Cool and wet	Central	2.12	1.64	10.54
Achillea millefolium	Ungrazed	Historic	Cool and wet	Central	1.78	0.8	38
Achillea millefolium	Cattle	Historic	Cool and wet	Central	2.33	0.62	38
Achillea millefolium	Ungrazed	Recent	Average	North	3.14	1.32	38
Achillea millefolium	Cattle	Recent	Average	North	9.03	2.81	38
Achillea millefolium	Ungrazed	Historic	Average	North	3.72	1.49	63
Achillea millefolium	Cattle	Historic	Average	North	4.16	1.16	63

Achillea millefolium	Ungrazed	Recent	Hot and dry	North	8.17	1.22	61.51
Achillea millefolium	Cattle	Recent	Hot and dry	North	16.2	2.65	63
Achillea millefolium	Ungrazed	Historic	Hot and dry	North	12.08	1.53	63
Achillea millefolium	Cattle	Historic	Hot and dry	North	16.42	1.26	63
Achillea millefolium	Ungrazed	Recent	Cool and wet	North	2.96	1.41	38
Achillea millefolium	Cattle	Recent	Cool and wet	North	5.96	2.81	38
Achillea millefolium	Ungrazed	Historic	Cool and wet	North	2.96	1.47	38
Achillea millefolium	Cattle	Historic	Cool and wet	North	2.88	1.31	38
Artemisia ludoviciana	Ungrazed	Recent	Average	Central	9.67	6.26	35.97
Artemisia ludoviciana	Cattle	Recent	Average	Central	14.05	4.82	37.06
Artemisia ludoviciana	Ungrazed	Historic	Average	Central	18.94	4.74	55.53
Artemisia ludoviciana	Cattle	Historic	Average	Central	25.63	1.86	63
Artemisia ludoviciana	Ungrazed	Recent	Hot and dry	Central	16.13	6.41	49.58
Artemisia ludoviciana	Cattle	Recent	Hot and dry	Central	22.85	4.59	55.89
Artemisia ludoviciana	Ungrazed	Historic	Hot and dry	Central	26.76	4.72	60.61
Artemisia ludoviciana	Cattle	Historic	Hot and dry	Central	31.62	1.58	63
Artemisia ludoviciana	Ungrazed	Recent	Cool and wet	Central	7.25	5.55	26.06
Artemisia ludoviciana	Cattle	Recent	Cool and wet	Central	7.94	5.39	11.31
Artemisia ludoviciana	Ungrazed	Historic	Cool and wet	Central	9.85	5.11	45.07
Artemisia ludoviciana	Cattle	Historic	Cool and wet	Central	17.26	1.92	62.44
Artemisia ludoviciana	Ungrazed	Recent	Average	North	26.44	4.11	63
Artemisia ludoviciana	Cattle	Recent	Average	North	28.71	4.37	63
Artemisia ludoviciana	Ungrazed	Historic	Average	North	22.05	4.99	63

Artemisia ludoviciana	Cattle	Historic	Average	North	22.68	4.64	63
Artemisia ludoviciana	Ungrazed	Recent	Hot and dry	North	32.24	3.92	63
Artemisia ludoviciana	Cattle	Recent	Hot and dry	North	34.48	4.09	63
Artemisia ludoviciana	Ungrazed	Historic	Hot and dry	North	26.02	4.67	63
Artemisia ludoviciana	Cattle	Historic	Hot and dry	North	26.8	4.15	63
Artemisia ludoviciana	Ungrazed	Recent	Cool and wet	North	16.62	4.61	63
Artemisia ludoviciana	Cattle	Recent	Cool and wet	North	18.87	4.95	63
Artemisia ludoviciana	Ungrazed	Historic	Cool and wet	North	18.68	5.61	63
Artemisia ludoviciana	Cattle	Historic	Cool and wet	North	17.43	5.76	63
Asclepias stenophylla	Ungrazed	Recent	Average	Central	0.5	0.5	15.5
Asclepias stenophylla	Cattle	Recent	Average	Central	3.5	0.5	15.5
Asclepias stenophylla	Ungrazed	Historic	Average	Central	1.39	0.53	38
Asclepias stenophylla	Cattle	Historic	Average	Central	3.5	0.5	38
Asclepias stenophylla	Ungrazed	Recent	Hot and dry	Central	0.5	0.5	37.27
Asclepias stenophylla	Cattle	Recent	Hot and dry	Central	3.5	0.5	20.5
Asclepias stenophylla	Ungrazed	Historic	Hot and dry	Central	15.5	0.5	63
Asclepias stenophylla	Cattle	Historic	Hot and dry	Central	15.5	1.66	63
Asclepias stenophylla	Ungrazed	Recent	Cool and wet	Central	0.53	0.5	0.73
Asclepias stenophylla	Cattle	Recent	Cool and wet	Central	0.5	0.5	3.5
Asclepias stenophylla	Ungrazed	Historic	Cool and wet	Central	2.96	0.75	15.5
Asclepias stenophylla	Cattle	Historic	Cool and wet	Central	3.05	0.5	15.74
Asclepias stenophylla	Ungrazed	Recent	Average	North	0.53	0.5	15.62
Asclepias stenophylla	Cattle	Recent	Average	North	3.5	0.5	38

Asclepias stenophylla	Ungrazed	Historic	Average	North	2.22	0.74	63
Asclepias stenophylla	Cattle	Historic	Average	North	3.5	0.5	63
Asclepias stenophylla	Ungrazed	Recent	Hot and dry	North	1.06	0.5	38
Asclepias stenophylla	Cattle	Recent	Hot and dry	North	15.5	0.5	63
Asclepias stenophylla	Ungrazed	Historic	Hot and dry	North	15.5	0.53	63
Asclepias stenophylla	Cattle	Historic	Hot and dry	North	15.5	0.5	63
Asclepias stenophylla	Ungrazed	Recent	Cool and wet	North	0.68	0.53	1.94
Asclepias stenophylla	Cattle	Recent	Cool and wet	North	0.5	0.5	3.5
Asclepias stenophylla	Ungrazed	Historic	Cool and wet	North	3.35	1.46	15.5
Asclepias stenophylla	Cattle	Historic	Cool and wet	North	3.17	0.5	15.5
Asclepias verticillata	Ungrazed	Recent	Average	Central	16.81	4.38	54.79
Asclepias verticillata	Cattle	Recent	Average	Central	1.57	0.59	63
Asclepias verticillata	Ungrazed	Historic	Average	Central	38	0.62	63
Asclepias verticillata	Cattle	Historic	Average	Central	7.86	0.5	63
Asclepias verticillata	Ungrazed	Recent	Hot and dry	Central	56.49	4.02	63
Asclepias verticillata	Cattle	Recent	Hot and dry	Central	11.99	0.68	63
Asclepias verticillata	Ungrazed	Historic	Hot and dry	Central	38	0.98	63
Asclepias verticillata	Cattle	Historic	Hot and dry	Central	25.67	0.53	63
Asclepias verticillata	Ungrazed	Recent	Cool and wet	Central	15.67	2.77	29.52
Asclepias verticillata	Cattle	Recent	Cool and wet	Central	0.59	0.53	38
Asclepias verticillata	Ungrazed	Historic	Cool and wet	Central	37.77	0.53	63
Asclepias verticillata	Cattle	Historic	Cool and wet	Central	0.53	0.5	48.09
Asclepias verticillata	Ungrazed	Recent	Average	North	25.9	3.9	63

Asclepias verticillata	Cattle	Recent	Average	North	2.5	0.89	62.16
Asclepias verticillata	Ungrazed	Historic	Average	North	12.9	1.28	63
Asclepias verticillata	Cattle	Historic	Average	North	6.31	0.53	63
Asclepias verticillata	Ungrazed	Recent	Hot and dry	North	35.31	4.01	63
Asclepias verticillata	Cattle	Recent	Hot and dry	North	4.4	1.23	63
Asclepias verticillata	Ungrazed	Historic	Hot and dry	North	15.57	1.79	63
Asclepias verticillata	Cattle	Historic	Hot and dry	North	15.43	0.56	63
Asclepias verticillata	Ungrazed	Recent	Cool and wet	North	19.7	2.54	63
Asclepias verticillata	Cattle	Recent	Cool and wet	North	1.32	0.59	38
Asclepias verticillata	Ungrazed	Historic	Cool and wet	North	11.13	0.65	63
Asclepias verticillata	Cattle	Historic	Cool and wet	North	1.08	0.51	63
Asclepias viridiflora	Ungrazed	Recent	Average	Central	0.53	0.5	15.5
Asclepias viridiflora	Cattle	Recent	Average	Central	0.5	0.5	15.5
Asclepias viridiflora	Ungrazed	Historic	Average	Central	3.47	0.5	38
Asclepias viridiflora	Cattle	Historic	Average	Central	3.9	0.5	38
Asclepias viridiflora	Ungrazed	Recent	Hot and dry	Central	0.62	0.5	37.82
Asclepias viridiflora	Cattle	Recent	Hot and dry	Central	3.5	0.5	18.65
Asclepias viridiflora	Ungrazed	Historic	Hot and dry	Central	15.5	0.5	62.75
Asclepias viridiflora	Cattle	Historic	Hot and dry	Central	15.5	0.5	63
Asclepias viridiflora	Ungrazed	Recent	Cool and wet	Central	0.5	0.5	0.56
Asclepias viridiflora	Cattle	Recent	Cool and wet	Central	0.5	0.5	3.5
Asclepias viridiflora	Ungrazed	Historic	Cool and wet	Central	0.5	0.5	3.5
Asclepias viridiflora	Cattle	Historic	Cool and wet	Central	0.5	0.5	38

Asclepias viridiflora	Ungrazed	Recent	Average	North	0.62	0.53	15.5
Asclepias viridiflora	Cattle	Recent	Average	North	3.47	0.5	38
Asclepias viridiflora	Ungrazed	Historic	Average	North	3.5	0.5	63
Asclepias viridiflora	Cattle	Historic	Average	North	4.24	0.5	63
Asclepias viridiflora	Ungrazed	Recent	Hot and dry	North	1.67	0.53	38
Asclepias viridiflora	Cattle	Recent	Hot and dry	North	15.5	0.5	63
Asclepias viridiflora	Ungrazed	Historic	Hot and dry	North	15.5	0.5	63
Asclepias viridiflora	Cattle	Historic	Hot and dry	North	15.5	0.5	63
Asclepias viridiflora	Ungrazed	Recent	Cool and wet	North	0.53	0.5	0.97
Asclepias viridiflora	Cattle	Recent	Cool and wet	North	0.5	0.5	3.5
Asclepias viridiflora	Ungrazed	Historic	Cool and wet	North	0.5	0.5	3.5
Asclepias viridiflora	Cattle	Historic	Cool and wet	North	0.5	0.5	3.5
Astragalus crassicarpus	Ungrazed	Recent	Average	Central	7.22	5.22	11.09
Astragalus crassicarpus	Cattle	Recent	Average	Central	5.12	3.18	38
Astragalus crassicarpus	Ungrazed	Historic	Average	Central	13.63	0.8	38
Astragalus crassicarpus	Cattle	Historic	Average	Central	8.47	0.5	38
Astragalus crassicarpus	Ungrazed	Recent	Hot and dry	Central	15.25	6.82	31.06
Astragalus crassicarpus	Cattle	Recent	Hot and dry	Central	7.41	3.35	38
Astragalus crassicarpus	Ungrazed	Historic	Hot and dry	Central	28.2	1.07	61.51
Astragalus crassicarpus	Cattle	Historic	Hot and dry	Central	38	1.23	63
Astragalus crassicarpus	Ungrazed	Recent	Cool and wet	Central	5.12	3.57	8.91
Astragalus crassicarpus	Cattle	Recent	Cool and wet	Central	3.64	2.32	38
Astragalus crassicarpus	Ungrazed	Historic	Cool and wet	Central	8.72	0.53	38

Astragalus crassicarpus	Cattle	Historic	Cool and wet	Central	4.09	0.5	38
Astragalus crassicarpus	Ungrazed	Recent	Average	North	13.2	4.26	38
Astragalus crassicarpus	Cattle	Recent	Average	North	10.1	3.56	38
Astragalus crassicarpus	Ungrazed	Historic	Average	North	14.05	2.42	38
Astragalus crassicarpus	Cattle	Historic	Average	North	13.51	0.65	63
Astragalus crassicarpus	Ungrazed	Recent	Hot and dry	North	14.91	4.33	38
Astragalus crassicarpus	Cattle	Recent	Hot and dry	North	13.93	3.59	63
Astragalus crassicarpus	Ungrazed	Historic	Hot and dry	North	27.63	3.48	63
Astragalus crassicarpus	Cattle	Historic	Hot and dry	North	38	0.85	63
Astragalus crassicarpus	Ungrazed	Recent	Cool and wet	North	10.63	3.84	38
Astragalus crassicarpus	Cattle	Recent	Cool and wet	North	7.67	3.12	38
Astragalus crassicarpus	Ungrazed	Historic	Cool and wet	North	10.55	0.94	38
Astragalus crassicarpus	Cattle	Historic	Cool and wet	North	5.81	0.53	38
Baptisia australis	Ungrazed	Recent	Average	Central	2.6	2.15	5.24
Baptisia australis	Cattle	Recent	Average	Central	3.11	2.75	15.5
Baptisia australis	Ungrazed	Historic	Average	Central	2.72	1.61	38
Baptisia australis	Cattle	Historic	Average	Central	2.98	1.25	38
Baptisia australis	Ungrazed	Recent	Hot and dry	Central	2.24	1.6	38
Baptisia australis	Cattle	Recent	Hot and dry	Central	3.05	2.51	25.39
Baptisia australis	Ungrazed	Historic	Hot and dry	Central	12.54	1.44	62.47
Baptisia australis	Cattle	Historic	Hot and dry	Central	38	1.76	63
Baptisia australis	Ungrazed	Recent	Cool and wet	Central	3.92	2.87	7.25
Baptisia australis	Cattle	Recent	Cool and wet	Central	3.23	3	15.5

Baptisia australis	Ungrazed	Historic	Cool and wet	Central	2.93	2.03	15.5
Baptisia australis	Cattle	Historic	Cool and wet	Central	2.9	1.64	15.5
Baptisia australis	Ungrazed	Recent	Average	North	4.29	2.84	13.73
Baptisia australis	Cattle	Recent	Average	North	3.41	3.11	36.11
Baptisia australis	Ungrazed	Historic	Average	North	3.35	2.33	58.73
Baptisia australis	Cattle	Historic	Average	North	3.32	2.34	63
Baptisia australis	Ungrazed	Recent	Hot and dry	North	3.89	2.45	38
Baptisia australis	Cattle	Recent	Hot and dry	North	6.05	3.02	63
Baptisia australis	Ungrazed	Historic	Hot and dry	North	12.26	2.13	63
Baptisia australis	Cattle	Historic	Hot and dry	North	15.54	2.37	63
Baptisia australis	Ungrazed	Recent	Cool and wet	North	6.62	3.48	14.27
Baptisia australis	Cattle	Recent	Cool and wet	North	3.44	3.26	15.5
Baptisia australis	Ungrazed	Historic	Cool and wet	North	3.38	2.7	15.5
Baptisia australis	Cattle	Historic	Cool and wet	North	3.32	2.64	15.5
Brickellia eupatorioides	Ungrazed	Recent	Average	Central	1.7	1.44	38
Brickellia eupatorioides	Cattle	Recent	Average	Central	0.86	0.71	38
Brickellia eupatorioides	Ungrazed	Historic	Average	Central	2.45	1.78	38
Brickellia eupatorioides	Cattle	Historic	Average	Central	1.01	0.56	38
Brickellia eupatorioides	Ungrazed	Recent	Hot and dry	Central	1.91	1.55	38
Brickellia eupatorioides	Cattle	Recent	Hot and dry	Central	1.01	0.71	38
Brickellia eupatorioides	Ungrazed	Historic	Hot and dry	Central	2.99	1.89	63
Brickellia eupatorioides	Cattle	Historic	Hot and dry	Central	38	0.59	63
Brickellia eupatorioides	Ungrazed	Recent	Cool and wet	Central	1.4	1.11	38

Brickellia eupatorioides	Cattle	Recent	Cool and wet	Central	0.8	0.65	38
Brickellia eupatorioides	Ungrazed	Historic	Cool and wet	Central	2.62	1.49	38
Brickellia eupatorioides	Cattle	Historic	Cool and wet	Central	37.43	0.56	38
Brickellia eupatorioides	Ungrazed	Recent	Average	North	3.32	2.29	38
Brickellia eupatorioides	Cattle	Recent	Average	North	2.85	1.26	38
Brickellia eupatorioides	Ungrazed	Historic	Average	North	5.43	3.03	48.51
Brickellia eupatorioides	Cattle	Historic	Average	North	3.27	1.07	63
Brickellia eupatorioides	Ungrazed	Recent	Hot and dry	North	3.38	2.39	38
Brickellia eupatorioides	Cattle	Recent	Hot and dry	North	3.44	1.37	63
Brickellia eupatorioides	Ungrazed	Historic	Hot and dry	North	7.33	3.17	63
Brickellia eupatorioides	Cattle	Historic	Hot and dry	North	14.27	1.19	63
Brickellia eupatorioides	Ungrazed	Recent	Cool and wet	North	3.46	2.03	38
Brickellia eupatorioides	Cattle	Recent	Cool and wet	North	3.53	1.13	38
Brickellia eupatorioides	Ungrazed	Historic	Cool and wet	North	7.24	2.95	38
Brickellia eupatorioides	Cattle	Historic	Cool and wet	North	36.16	1.28	38
Cirsium undulatum	Ungrazed	Recent	Average	Central	3.26	1.85	32.06
Cirsium undulatum	Cattle	Recent	Average	Central	3.98	2.49	38
Cirsium undulatum	Ungrazed	Historic	Average	Central	15.5	1.35	38
Cirsium undulatum	Cattle	Historic	Average	Central	2.66	0.62	38
Cirsium undulatum	Ungrazed	Recent	Hot and dry	Central	4.95	1.91	37.77
Cirsium undulatum	Cattle	Recent	Hot and dry	Central	6.14	2.4	38
Cirsium undulatum	Ungrazed	Historic	Hot and dry	Central	15.5	1.44	63
Cirsium undulatum	Cattle	Historic	Hot and dry	Central	35.48	1.28	63

Cirsium undulatum	Ungrazed	Recent	Cool and wet	Central	3.13	1.37	37.17
Cirsium undulatum	Cattle	Recent	Cool and wet	Central	2.66	2.02	38
Cirsium undulatum	Ungrazed	Historic	Cool and wet	Central	15.5	1.31	38
Cirsium undulatum	Cattle	Historic	Cool and wet	Central	2.63	0.59	38
Cirsium undulatum	Ungrazed	Recent	Average	North	8.93	2.85	38
Cirsium undulatum	Cattle	Recent	Average	North	8.72	3.44	38
Cirsium undulatum	Ungrazed	Historic	Average	North	15.5	2.16	57.26
Cirsium undulatum	Cattle	Historic	Average	North	3.29	1.29	63
Cirsium undulatum	Ungrazed	Recent	Hot and dry	North	11.36	3.13	38
Cirsium undulatum	Cattle	Recent	Hot and dry	North	12.2	3.56	63
Cirsium undulatum	Ungrazed	Historic	Hot and dry	North	15.5	2.22	63
Cirsium undulatum	Cattle	Historic	Hot and dry	North	15.5	1.4	63
Cirsium undulatum	Ungrazed	Recent	Cool and wet	North	7.06	2.36	38
Cirsium undulatum	Cattle	Recent	Cool and wet	North	5.64	2.88	38
Cirsium undulatum	Ungrazed	Historic	Cool and wet	North	15.5	2.24	38
Cirsium undulatum	Cattle	Historic	Cool and wet	North	3.05	1.2	37.65
Comandra umbellata	Ungrazed	Recent	Average	Central	10.91	4.47	29.57
Comandra umbellata	Cattle	Recent	Average	Central	11.47	4.98	57.79
Comandra umbellata	Ungrazed	Historic	Average	Central	13.32	2.34	38
Comandra umbellata	Cattle	Historic	Average	Central	37.69	1.75	63
Comandra umbellata	Ungrazed	Recent	Hot and dry	Central	11.17	3.96	31.51
Comandra umbellata	Cattle	Recent	Hot and dry	Central	12.27	3.77	61.96
Comandra umbellata	Ungrazed	Historic	Hot and dry	Central	13.05	2.39	38

Comandra umbellata	Cattle	Historic	Hot and dry	Central	34.47	1.81	63
Comandra umbellata	Ungrazed	Recent	Cool and wet	Central	17.64	3.69	37.06
Comandra umbellata	Cattle	Recent	Cool and wet	Central	27.35	6.13	60
Comandra umbellata	Ungrazed	Historic	Cool and wet	Central	15.64	1.39	46.48
Comandra umbellata	Cattle	Historic	Cool and wet	Central	38	1.22	63
Comandra umbellata	Ungrazed	Recent	Average	North	14.97	4.41	62.3
Comandra umbellata	Cattle	Recent	Average	North	19.2	4.63	63
Comandra umbellata	Ungrazed	Historic	Average	North	10.89	3.71	63
Comandra umbellata	Cattle	Historic	Average	North	27.41	2.84	63
Comandra umbellata	Ungrazed	Recent	Hot and dry	North	14.9	4.16	61.85
Comandra umbellata	Cattle	Recent	Hot and dry	North	16.21	4.18	63
Comandra umbellata	Ungrazed	Historic	Hot and dry	North	12.11	3.56	63
Comandra umbellata	Cattle	Historic	Hot and dry	North	23.19	3.15	63
Comandra umbellata	Ungrazed	Recent	Cool and wet	North	15.38	3.65	63
Comandra umbellata	Cattle	Recent	Cool and wet	North	32.91	4.18	63
Comandra umbellata	Ungrazed	Historic	Cool and wet	North	10.9	3.18	63
Comandra umbellata	Cattle	Historic	Cool and wet	North	35.55	2	63
Dalea candida	Ungrazed	Recent	Average	Central	1.13	0.79	38
Dalea candida	Cattle	Recent	Average	Central	1.16	0.8	38
Dalea candida	Ungrazed	Historic	Average	Central	12.49	1.59	38
Dalea candida	Cattle	Historic	Average	Central	32.88	0.75	38
Dalea candida	Ungrazed	Recent	Hot and dry	Central	2.23	0.83	38
Dalea candida	Cattle	Recent	Hot and dry	Central	2.67	0.81	38

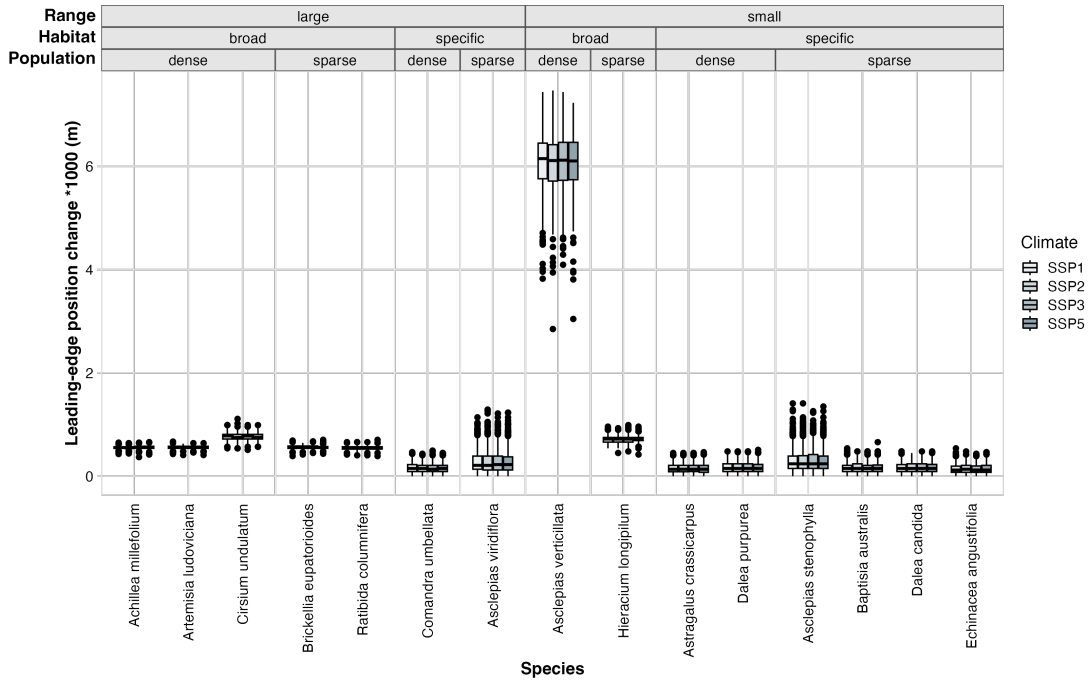
Dalea candida	Ungrazed	Historic	Hot and dry	Central	26.71	2.64	62.38
Dalea candida	Cattle	Historic	Hot and dry	Central	38	3.15	63
Dalea candida	Ungrazed	Recent	Cool and wet	Central	0.83	0.68	38
Dalea candida	Cattle	Recent	Cool and wet	Central	0.86	0.71	38
Dalea candida	Ungrazed	Historic	Cool and wet	Central	4.98	0.77	38
Dalea candida	Cattle	Historic	Cool and wet	Central	2.6	0.56	38
Dalea candida	Ungrazed	Recent	Average	North	4.07	1.46	38
Dalea candida	Cattle	Recent	Average	North	4.35	1.67	38
Dalea candida	Ungrazed	Historic	Average	North	14.49	4.37	38
Dalea candida	Cattle	Historic	Average	North	24.24	3.55	58.21
Dalea candida	Ungrazed	Recent	Hot and dry	North	8.08	1.79	38
Dalea candida	Cattle	Recent	Hot and dry	North	11.65	1.89	63
Dalea candida	Ungrazed	Historic	Hot and dry	North	31.23	5.73	63
Dalea candida	Cattle	Historic	Hot and dry	North	38	3.99	63
Dalea candida	Ungrazed	Recent	Cool and wet	North	2.43	1.17	38
Dalea candida	Cattle	Recent	Cool and wet	North	2.52	1.16	38
Dalea candida	Ungrazed	Historic	Cool and wet	North	8.54	1.8	38
Dalea candida	Cattle	Historic	Cool and wet	North	3.49	0.89	38
Dalea purpurea	Ungrazed	Recent	Average	Central	0.95	0.83	38
Dalea purpurea	Cattle	Recent	Average	Central	61.12	3.01	63
Dalea purpurea	Ungrazed	Historic	Average	Central	1.88	0.65	63
Dalea purpurea	Cattle	Historic	Average	Central	36.96	0.84	63
Dalea purpurea	Ungrazed	Recent	Hot and dry	Central	11.28	0.88	63

Dalea purpurea	Cattle	Recent	Hot and dry	Central	63	3.81	63
Dalea purpurea	Ungrazed	Historic	Hot and dry	Central	11.06	0.7	63
Dalea purpurea	Cattle	Historic	Hot and dry	Central	51.49	1.74	63
Dalea purpurea	Ungrazed	Recent	Cool and wet	Central	0.86	0.74	38
Dalea purpurea	Cattle	Recent	Cool and wet	Central	2.57	1.67	63
Dalea purpurea	Ungrazed	Historic	Cool and wet	Central	1.27	0.59	63
Dalea purpurea	Cattle	Historic	Cool and wet	Central	9.45	0.59	63
Dalea purpurea	Ungrazed	Recent	Average	North	3.05	1.54	63
Dalea purpurea	Cattle	Recent	Average	North	38	3.42	63
Dalea purpurea	Ungrazed	Historic	Average	North	3.63	1.44	63
Dalea purpurea	Cattle	Historic	Average	North	13.33	3	63
Dalea purpurea	Ungrazed	Recent	Hot and dry	North	5.04	1.72	63
Dalea purpurea	Cattle	Recent	Hot and dry	North	54.18	3.66	63
Dalea purpurea	Ungrazed	Historic	Hot and dry	North	5.42	1.66	63
Dalea purpurea	Cattle	Historic	Hot and dry	North	36.82	3.2	63
Dalea purpurea	Ungrazed	Recent	Cool and wet	North	2.54	1.26	63
Dalea purpurea	Cattle	Recent	Cool and wet	North	9.82	3.15	63
Dalea purpurea	Ungrazed	Historic	Cool and wet	North	2.98	1.21	63
Dalea purpurea	Cattle	Historic	Cool and wet	North	9.35	2.01	63
Echinacea angustifolia	Ungrazed	Recent	Average	Central	1.76	0.65	26.93
Echinacea angustifolia	Cattle	Recent	Average	Central	2.93	1.79	15.5
Echinacea angustifolia	Ungrazed	Historic	Average	Central	0.77	0.53	38
Echinacea angustifolia	Cattle	Historic	Average	Central	4.28	0.53	38

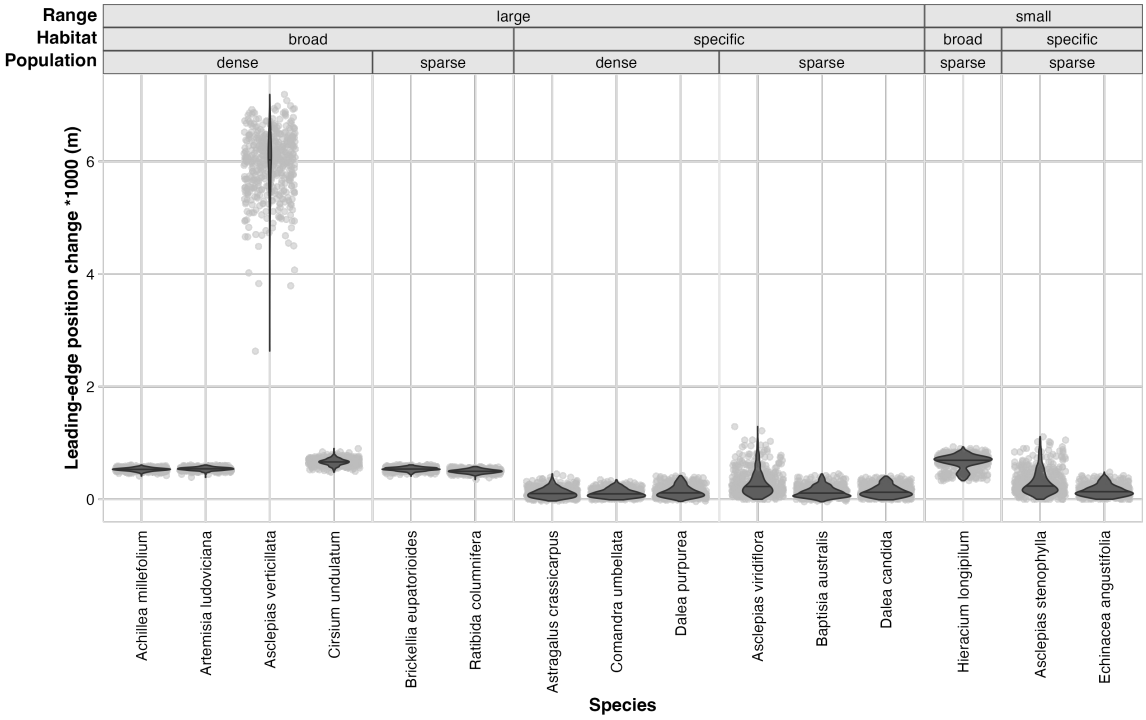
Echinacea angustifolia	Ungrazed	Recent	Hot and dry	Central	2.03	0.53	38
Echinacea angustifolia	Cattle	Recent	Hot and dry	Central	3.08	1.04	33.56
Echinacea angustifolia	Ungrazed	Historic	Hot and dry	Central	3	0.53	63
Echinacea angustifolia	Cattle	Historic	Hot and dry	Central	38	0.66	63
Echinacea angustifolia	Ungrazed	Recent	Cool and wet	Central	2.33	1.02	15.5
Echinacea angustifolia	Cattle	Recent	Cool and wet	Central	3.17	2.51	15.5
Echinacea angustifolia	Ungrazed	Historic	Cool and wet	Central	1.16	0.56	14.62
Echinacea angustifolia	Cattle	Historic	Cool and wet	Central	2.09	0.56	14.57
Echinacea angustifolia	Ungrazed	Recent	Average	North	2.79	1.01	24.12
Echinacea angustifolia	Cattle	Recent	Average	North	3.38	2.61	34.32
Echinacea angustifolia	Ungrazed	Historic	Average	North	1.82	0.77	62.77
Echinacea angustifolia	Cattle	Historic	Average	North	5.43	1.3	63
Echinacea angustifolia	Ungrazed	Recent	Hot and dry	North	3.08	0.68	38
Echinacea angustifolia	Cattle	Recent	Hot and dry	North	14.96	2.07	63
Echinacea angustifolia	Ungrazed	Historic	Hot and dry	North	4.48	0.65	63
Echinacea angustifolia	Cattle	Historic	Hot and dry	North	28.75	1.07	63
Echinacea angustifolia	Ungrazed	Recent	Cool and wet	North	3.12	1.82	15.5
Echinacea angustifolia	Cattle	Recent	Cool and wet	North	3.41	3.06	15.5
Echinacea angustifolia	Ungrazed	Historic	Cool and wet	North	2.42	0.83	15.04
Echinacea angustifolia	Cattle	Historic	Cool and wet	North	3.44	1.16	14.57
Hieracium longipilum	Ungrazed	Recent	Average	Central	0.74	0.5	22.08
Hieracium longipilum	Cattle	Recent	Average	Central	0.68	0.5	15.5
Hieracium longipilum	Ungrazed	Historic	Average	Central	0.59	0.5	38

Hieracium longipilum	Cattle	Historic	Average	Central	1.28	0.5	38
Hieracium longipilum	Ungrazed	Recent	Hot and dry	Central	0.56	0.5	38
Hieracium longipilum	Cattle	Recent	Hot and dry	Central	0.59	0.5	29.85
Hieracium longipilum	Ungrazed	Historic	Hot and dry	Central	1.56	0.5	63
Hieracium longipilum	Cattle	Historic	Hot and dry	Central	38	0.5	63
Hieracium longipilum	Ungrazed	Recent	Cool and wet	Central	2.92	0.53	15.5
Hieracium longipilum	Cattle	Recent	Cool and wet	Central	2.6	0.68	15.5
Hieracium longipilum	Ungrazed	Historic	Cool and wet	Central	14.99	0.81	15.5
Hieracium longipilum	Cattle	Historic	Cool and wet	Central	15.08	0.53	15.5
Hieracium longipilum	Ungrazed	Recent	Average	North	1.55	0.53	36.54
Hieracium longipilum	Cattle	Recent	Average	North	1.88	0.53	38
Hieracium longipilum	Ungrazed	Historic	Average	North	0.92	0.53	63
Hieracium longipilum	Cattle	Historic	Average	North	1.74	0.5	63
Hieracium longipilum	Ungrazed	Recent	Hot and dry	North	1.04	0.5	38
Hieracium longipilum	Cattle	Recent	Hot and dry	North	8.18	0.5	63
Hieracium longipilum	Ungrazed	Historic	Hot and dry	North	1.75	0.5	63
Hieracium longipilum	Cattle	Historic	Hot and dry	North	17.66	0.5	63
Hieracium longipilum	Ungrazed	Recent	Cool and wet	North	3.35	0.66	15.5
Hieracium longipilum	Cattle	Recent	Cool and wet	North	3.29	1.31	15.5
Hieracium longipilum	Ungrazed	Historic	Cool and wet	North	15.38	2.11	15.5
Hieracium longipilum	Cattle	Historic	Cool and wet	North	15.38	0.59	15.5
Ratibida columnifera	Ungrazed	Recent	Average	Central	0.89	0.63	15.5
Ratibida columnifera	Cattle	Recent	Average	Central	0.62	0.53	15.5

Ratibida columnifera	Ungrazed	Historic	Average	Central	3.08	0.83	38
Ratibida columnifera	Cattle	Historic	Average	Central	1.48	0.53	38
Ratibida columnifera	Ungrazed	Recent	Hot and dry	Central	1.43	0.65	38
Ratibida columnifera	Cattle	Recent	Hot and dry	Central	0.77	0.53	31.33
Ratibida columnifera	Ungrazed	Historic	Hot and dry	Central	10.56	1.14	63
Ratibida columnifera	Cattle	Historic	Hot and dry	Central	38	0.56	63
Ratibida columnifera	Ungrazed	Recent	Cool and wet	Central	0.74	0.56	15.5
Ratibida columnifera	Cattle	Recent	Cool and wet	Central	0.56	0.53	15.5
Ratibida columnifera	Ungrazed	Historic	Cool and wet	Central	2.12	0.57	15.44
Ratibida columnifera	Cattle	Historic	Cool and wet	Central	0.59	0.5	14.57
Ratibida columnifera	Ungrazed	Recent	Average	North	2.24	0.9	15.5
Ratibida columnifera	Cattle	Recent	Average	North	1.55	0.65	17.35
Ratibida columnifera	Ungrazed	Historic	Average	North	4.56	1.8	60.48
Ratibida columnifera	Cattle	Historic	Average	North	2.5	0.68	63
Ratibida columnifera	Ungrazed	Recent	Hot and dry	North	2.92	0.96	38
Ratibida columnifera	Cattle	Recent	Hot and dry	North	11.89	0.68	63
Ratibida columnifera	Ungrazed	Historic	Hot and dry	North	10.34	2.04	63
Ratibida columnifera	Cattle	Historic	Hot and dry	North	32.79	0.8	63
Ratibida columnifera	Ungrazed	Recent	Cool and wet	North	1.85	0.68	15.5
Ratibida columnifera	Cattle	Recent	Cool and wet	North	1.13	0.59	15.5
Ratibida columnifera	Ungrazed	Historic	Cool and wet	North	3.37	0.95	15.38
Ratibida columnifera	Cattle	Historic	Cool and wet	North	1.13	0.56	13.15



Appendix Figure C.1: Leading edge position change (m) for each of our 15 focal species and four climate scenarios corresponding to possible CO2 emission possibilities "socioeconomic pathways" (SSPs) and are indicated by color: SSP1 = global warming of approximately 3.5 degrees C (lightest gray), SSP2 and SSP3 = 4 degrees C, SSP5 = 5 degrees C (darkest gray). Rarity type is indicated labels above data with range size (large or small) indicated by top row of labels, habitat specificity (broad or specific) middle row, and local population density (dense or sparse) shown in the bottom row. Center of each box plot indicates 50th percentile of observed movement across 500 iterations with upper and lower bounds of boxplots show 25th and 75th percentiles with points indicating outliers.



Appendix Figure C.2: Leading edge position change (m) for 15 focal species across 500 simulation iterations. Rarity type is indicated labels above data with range size (large or small) indicated by top row of labels, habitat specificity (broad or specific) middle row, and local population density (dense or sparse) shown in the bottom row. Gray dots indicate change in position for each iteration, while dark gray violin plot displays spread of the gray dots. Horizontal line in violin plot indicates 50% percentile of observations. Compare to Figure 4.3 in the main text.