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KING OF THE HILL? HOW BIOTIC INTERACTIONS AFFECT BIOGEOGRAPHICAL PATTERN AND SPECIES RESPONSES TO CLIMATE CHANGE

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KING OF THE HILL? HOW BIOTIC INTERACTIONS AFFECT BIOGEOGRAPHICAL PATTERN AND SPECIES RESPONSES TO CLIMATE CHANGE

by

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Bachelor of Science, Syracuse University, 2013

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ABSTRACT

As climate has warmed, many species have moved up mountains as physiological limits to their distributions have ameliorated. These distribution shifts are creating novel communities, begging the question: What happens to species at the tops of mountains as potential antagonists encroach upwards? Theory predicts that upward migrations will cause range contractions for high-elevation species because of novel interactions with encroaching antagonists. My dissertation work is one of the most comprehensive tests of this question to date, using a combination of ecological niche modeling (ENM), experiments, and demographic and trait-based modeling approaches. I created novel ENMs that suggest context-dependency of biotic interactions, where predictions of biotic interactions change from positive to negative over environmental gradients, is common over elevation gradients. Additionally, ENMs suggested the current focus on plant-plant interactions in niche modeling targets the most important biotic interaction for many species. I then constructed space-for-time experiments that transplanted alpine species into novel low elevation plant and mammal communities expected to encroach upwards, as well as into their native high elevation communities. Plant competition was manipulated by vegetation removals and mammals were excluded in a separate factorial experiment using below- and aboveground fencing. In both experiments, low elevation plant and mammal communities suppressed growth of alpine species to a greater extent than those antagonists found in their home range. However, demographic models suggested that environmental factors (e.g. temperature) other than novel plant and mammal communities are more consequential for determining population fate. The experiments validated a novel trait-based model of competitive interactions that can be broadly applied to other systems and conservation needs. My dissertation work found that alpine plants are unlikely to remain “king of the hill” under climate change, in part due to the upward encroachment of novel competitors and intensification of herbivore pressure.

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Chapter 1: Context-dependent biotic interactions predict plant abundance across steep environmental gradients

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Abstract

Diverse biotic interactions can influence community structure, yet pairwise competitive interactions have been the focus of most distribution modeling efforts for plants. Furthermore, many biotic interactions are context-dependent with abiotic stress, e.g., plant-plant interactions can grade from competition to facilitation over temperature gradients. With a hierarchical Bayesian framework, we tested hypotheses about changes in the direction and strength of six biotic interactions (i.e., their context-dependency) over abiotic stress gradients used to predict the abundance of 12 plant species across a mountain landscape. We modeled plant abundance with abiotic gradient data on soil depth, nutrients, moisture, and climate interacting with field-based estimates of biotic interactions: foliar herbivory, pathogen damage, fungal root colonization, fossorial mammal disturbance, and both plant cover and plant diversity to represent competition. All biotic interactions were significantly context-dependent along gradients of temperature that tracked elevation. Additionally, models predicting abundance using plant cover as a proxy for plant-plant interactions were superior to models of other biotic interactions for half of the species, suggesting that a focus on plant-plant interactions is often justified. Observations supported stress gradient theory for context-dependency, where a biotic interaction (e.g., competition) switched from suppressing to promoting plant abundance along a gradient from low to high stress (e.g., warmer to colder temperature). As anticipated, the ability to detect context-dependency was stronger when the full elevation range of a species was sampled than when a subset of a species' elevation range was sampled. Explicitly incorporating the context-dependency of biotic interactions generated novel hypotheses about drivers of plant abundance across abiotic gradients and may improve the accuracy of niche models.

Introduction

Species distributions have traditionally been studied over abiotic gradients (e.g., temperature, precipitation). For example, classic work by Whittaker (1956, 1960) showed that soil moisture and soil substrate gradients predicted tree species abundance. This practice set the stage for ecological niche models, which predict species occurrence and/or abundance over environmental and spatial gradients (Guisan and Thuiller 2005; Elith and Leathwick 2009; Araújo and Peterson 2012; Merow et al. 2014; Authier, Saraux, and Péron 2017).

Modelers have increased predictive power by including variables that capture biotic interactions (Leathwick and Austin 2001; Heikkinen et al. 2007; Meier et al. 2010, 2011; Pellissier et al. 2010; McQuillan and Rice 2015), emphasizing the importance of species interactions for predicting species distributions, especially under climate change (Blois et al. 2013). However, prior studies of plants have largely focused on competition and/or facilitation -- interactions within the same trophic level -- with few exceptions (Araújo and Luoto 2007; le Roux et al. 2013). For example, most studies use a plant species' distribution as a function of another plant species' distribution to represent competition/facilitation (e.g. Leathwick and Austin 2001, Meier et al. 2010, 2011, Pellissier et al. 2010, le Roux et al. 2012, le Roux et al. 2014, Mod et al. 2016). The few examples that included trophic interactions improved model predictive ability (but see le Roux et al. 2013), such as models of butterfly distributions where models including both climate and host plant distribution were superior to models including only one of the predictor sets (Araújo and Luoto 2007). Given evidence that interactions other than competition and facilitation are important for plants, the inclusion of more types of species interactions, such as predation and mutualism, could improve species distribution modeling efforts.

Prior work has used the stress-gradient hypothesis (SGH; Bertness and Callaway 1994) to establish expectations for how biotic interactions influence species distributions. The SGH proposed that competition is more frequent in benign abiotic environments, but interactions switch to facilitation as stress intensifies (Bertness and Callaway 1994; Maestre et al. 2009; Bronstein 2009). Here, we follow the original conception of “stress” as an aspect of the abiotic environment that reduces primary production (Grime 1977). The SGH has garnered substantial experimental support (Callaway et al. 2002; Dangles, Herrera, and Anthelme 2013; He, Bertness, and Altieri 2013; Graff and Aguiar 2017; Klanderud et al. 2017). For instance, Callaway et al. (2002) found that removals of neighbor plants decreased absolute plant fitness (facilitation) at high-elevation sites where stress was high and plant productivity was low, but increased absolute fitness (competition) at less stressful and more productive low-elevation sites.

In studies of biogeographic gradients, the SGH can be combined with an older hypothesis proposed by Dobzhansky (1950) and MacArthur (1972), which states that physiologically harsh abiotic environments limit a species’ presence toward high altitude/latitude, while intensified antagonistic species interactions limit a species towards low altitude/latitude (the DMH, or "Dobzhansky-MacArthur hypothesis"; Brown 1995, Louthan et al. 2015). Although the DMH did not incorporate beneficial species interactions, it parallels the SGH in hypothesizing that antagonisms will dominate towards less stressful, low altitude/latitude range limits, and abiotic stress will dominate towards more stressful, high altitude/latitude range limits. Thus, the DMH can be merged with the SGH to predict *where* biotic interactions will influence species abundance. However, Godsoe et al. (2017b) identified where SGH and DMH predictions may not align because of the distribution of important non-focal species across a stress gradient. For instance, if competitors were more abundant at the middle of a stress gradient, competition could drive the exclusion of a focal species, where it would otherwise establish (Godsoe et al. 2017).

The DMH prediction of abiotic constraints on species' upper range limits (high altitude/latitude) have been supported (e.g. Hobbie and Chapin 1998, Sunday et al. 2011, 2012). For example, alpine plants transplanted above their elevation range limit had low survival because of an inability to tolerate lower temperatures (Klimeš and Doležal 2010). The prediction that antagonisms determine low-elevation range limits has received less experimental attention than abiotic constraints on high-elevation limits (but see Connell 1961, Hairston 1980). For example, plants transplanted below their low-elevation range limits and competed against the low-elevation plant community had lower fitness relative to competitors originating from the plants' resident elevations (Alexander, Diez, and Levine 2015).

Tests of the SGH using ecological niche models could explicitly examine how the direction or strength of a biotic interaction changes as a function of abiotic stress. Some modeling techniques (e.g., generalized additive models) allow for complexity in the relationship between biotic interactions and other variables (Merow et al. 2014).

However, these techniques alone cannot evaluate how the direction and strength of the biotic interaction varies with abiotic stress, that is, evaluate context-dependency. For example, Meier et al. (2011) found that co-occurrence between European beech and competitor tree species decreased towards less stressful sites with longer growing seasons and greater precipitation, but they did not investigate whether the effect of competitors on beech shifted along these abiotic stress gradients.

SGH context-dependency in biotic interactions can be represented in niche models via a statistical interaction between a biotic predictor and an abiotic stressor (e.g. Leathwick and Austin 2001, leRoux et al. 2012, Mod et al. 2014, Lany et al. 2017). Shifts in the direction of the biotic predictor's correlation with focal species abundance (specifically, from a negative relationship at low abiotic stress to positive at high abiotic stress) would provide observational support for the SGH. For instance, the fecundity of 14 plant species varied with the amount of cover of a dominant shrub in the tundra of Northern Finland, but the correlation between fecundity and shrub cover ranged from competitive (negative) to facilitative (positive), depending on soil moisture and geomorphological disturbance (Mod, le Roux, and Luoto 2014). In contrast, there was little evidence of context dependency in predation by sea stars when predicting mussel and barnacle abundances over stress gradients in dynamic species distribution models (Lany et al. 2017). Incorporating SGH context-dependency will be most important for biotic interactions that easily switch from positive to negative effects, such as plant-plant interactions, which span facilitation to competition (Bertness and Callaway 1994; Callaway et al. 2002). However, ample evidence suggests that other interactions, such as microbial symbioses and even herbivory, exhibit context-dependency (Chamberlain, Bronstein, and Rudgers 2014).

We developed a novel model to evaluate the DMH and SGH for 12 Rocky Mountain plant species. Mountain ecosystems exhibit high rates of turnover in abiotic conditions (Körner 2007) and allow for independent replication of gradients within manageable spatial scales. We use "biotic interaction" as a catch-all for several interaction types (e.g. plant-fungi, plant-herbivore) and "biotic predictor" to denote the metric we used to quantify a biotic interaction (e.g. root colonization by fungi, leaf damage by herbivores). For biotic predictors, we examined aboveground plant cover to represent competition for light or facilitation of stress, plant species diversity, foliar herbivory, foliar pathogen damage, disturbance by fossorial mammals, and arbuscular mycorrhizal fungal colonization of roots. We developed new hierarchical Bayesian models to evaluate specific DMH and SGH expectations (Table 1). Specifically, how are biotic predictors correlated to abiotic stress gradients? And how does the direction/magnitude of a biotic predictor's relationship to abundance change over stress gradients? For example, we used plant cover to evaluate whether patterns are consistent with the DMH and SGH: In accordance with the DMH, we expected that plant cover should decrease with greater abiotic stress (e.g., less plant biomass at colder temperatures; Table 1). We expect a negative relationship between plant cover and focal species abundance (competition) at less stressful sites and a positive relationship (facilitation) at more stressful sites (Table 1). Our model identified context-dependency when the biotic predictor's relationship to focal plant abundance (the beta posteriors) changed in sign and/or magnitude along an abiotic gradient. Additionally, we used Bayesian model selection procedures to ask: Which biotic interactions had the greatest ability to predict species abundance? This question aimed to elucidate the value of incorporating biotic predictors other than competition/facilitation into distribution modeling efforts.

Methods

Study area and site selection

We collected data in the Upper Gunnison Basin of the Colorado Rocky Mountains, USA (Figure 1). In 2014, we surveyed six independent peak-to-valley gradients spanning ~1300 m (2700 m to 4000 m a.s.l.; Figure 1). Sites started at the peaks of mountains, then established every 100 m down in elevation. This method produced 67 sites, ~11 randomly chosen sites per gradient. To bolster data for alpine species, in 2016, we surveyed an additional 2-3 sites on five gradients (3462-3960 m a.s.l.), resulting in 79 total sites (Figure 1). Sites were dominated by perennial plants (> 95% of species) with low year-to-year variance in plant abundance.

Study species and abundance estimates

We focused on native, dominant grass species. Grass species abundance was estimated along three parallel 20 m transects placed perpendicular to the mountain slope and spaced 10 m apart. The focal taxa were bunch grasses (with the exception of *Poa pratensis*) with a maximum diameter of ~0.5 m at the ground, therefore, 20 m transects were sufficiently long to capture species abundance across a site. To estimate abundance, we counted the number of grass individuals of each species that touched the transect. Abundance estimates were summed across transects for a site. This process resulted in abundance estimates for a total of 16 grass species, although four had insufficient occurrence across sites to be modeled (four or fewer occurrences).

Context-dependency will depend on the environmental context sampled. For example, patterns of plant-plant interactions may range from facilitation to competition when the whole stress gradient a species occupies is sampled, but this pattern may be obscured when only part of the species range is sampled. Therefore, species were grouped by what part of their elevation distribution was sampled: the whole elevation range (*Elymus trachycaulus*, *F. rubra*, *F. saximontana*, *P. stenantha*, *Trisetum spicatum*), only the high-elevation range (*Achnatherum lettermanii, A. nelsonii*, *Festuca thurberi*, *Poa pratensis*), or only the low-elevation range (*E. scribneri*, *F. brachyphylla*, *P. alpina*). Species were divided into the three groups by visualizing their distributions over the elevation gradients and assessing what part of their range was sampled. Summary statistics for each species can be found in Supplementary material 1.

Abiotic environment predictors

Abiotic variables were chosen to assess our hypotheses in Table 1. At each site, two 20 m transects were placed perpendicularly, with one transect horizontal to the prevailing slope. We estimated soil volumetric water content (VWC) and soil depth every 5 m along transects (10 estimates per site). Soil VWC was measured using a Fieldscout TDR (10 cm probes; Spectrum Technologies, Aurora, IL, USA) at two time points over the growing season (12-24 July, 23 Sept-8 Oct, 2014), then averaged within a site and over sampling dates. We estimated soil depth with a 1.5 m tile probe (AMS, inc., American Falls, ID, USA) inserted until it met bedrock (average of 10 estimates per site). At the end of each transect, we deployed four sets of Plant Root Simulator (PRS) Probes (Western Ag Innovations, Saskatoon, SK, Canada) for ~10 weeks (12 July - 30 Sept, 2014) that measured plant available nitrate, ammonium, and phosphorus and were analyzed together for a single measure per site. We also collected soil from each transect end, pooled the four collections, and measured soil pH (Hanna Instruments HI 9813-6 Portable; Woonsocket, RI, USA). We used regional climate interpolation to predict climate for each site using methods described in Lynn et al. (2018). Due to high collinearity between climate variables, we only used mean annual temperature (MAT) in our analysis. A schematic diagram of measurements (including plant sampling) at each site can be found in Supplementary material 2.

Biotic interaction predictors

We briefly describe methods for estimating biotic interaction predictors here (more detail in Supplementary material 2). Estimates of plant cover and community diversity were assessed with vegetation surveys. Shannon diversity (hereafter, diversity) was selected because it was most correlated with all other diversity indices. Herbivory and pathogen damage were visually estimated as percentage leaf area damaged on 10 individuals per focal species per site. To enable modeling of consumptive interactions when an individual was not present, we calculated grass community weighted means of herbivory and pathogen damage to represent the herbivory and pathogen "pressure" for each site. Similar community weighted means were applied to arbuscular mycorrhizal fungi (AMF) colonization of roots, which was assessed for all grasses at a site following Ranelli et al. (2015). Finally, gopher disturbance was assessed using methods described in Lynn et al. (2018).

Species distribution models

All data analyses were performed in R (R Core Team 2017). Prior to analysis, variables were standardized to a mean of zero and standard deviation of 0.5. This enabled the direct comparison of regression coefficients (beta posteriors): larger absolute values of beta posteriors indicate stronger correlation between biotic predictors and focal species abundance. Soil available nutrients (nitrogen, phosphorus), soil depth, herbivory, and pathogen damage were natural log-transformed prior to standardization to improve normality.

Bayesian models (described below) were implemented using JAGS (Plummer 2003) (*R2jags* package; Su and Masanao Yajima 2015). All models were run with three Markov chains, thinned every five iterations, and had a minimum of 50,000 iterations, or until the effective samples size for each parameter reached 3000 and had a potential scale reduction factor close to one (*Rhat*<1.01; Gelman and Rubin 1992). The first 25,000 iterations were used as burn-in. Traceplots of each variable were analyzed to ensure good mixing. Autocorrelation plots were inspected to ensure accurate posterior estimates. For cases of missing data (e.g. soil N for the 2016 sites), we stochastically imputed data using a prior distribution with a mean of 0 and standard deviation of 0.5. Code can be found in Supplementary material 2.

How are biotic predictors correlated to abiotic stress gradients? How does the direction/magnitude of a biotic predictor's relationship to abundance change over stress gradients?

First, we constructed hierarchical Bayesian models to investigate the SGH and DMH (Table 1). The model was specified as:

1. $y_i \sim NegBinom(\lambda_i, \kappa)$
2. $\log(\lambda_i) = \alpha_0 + \beta_j bio_i + \beta_{j+1} bio_i abio_{i,k} + \cdots$
3. $bio_i \sim N(\mu_i, \sigma^2)$
4. $\mu_i = \beta_k abio_{i,k}$
5. $\alpha_0 \sim N(\mu_0, {\sigma^2}_0)$
6. $\beta_j \sim N(\mu_j, {\sigma^2}_j)$

7. $\beta_k \sim N(\mu_k, \sigma^2{}_k)$

Where in (1), y_i is abundance of a species at a site with mean λ_i and κ, the dispersion parameter of the negative binomial distribution (*NegBinom*). Mean abundance at a site (λ_i) is modeled with a log-link function and is predicted by an intercept term, α_0, and the relationship, β_j, with a given biotic predictor, bio_i. All "betas" (β) are hereafter referred to as "beta posteriors." Context-dependency in biotic predictors is represented by the statistical interaction between that biotic predictor and abiotic variables, $abio_{i,k}$, expected to moderate the effect, β_{j+1}, of the biotic variable according to the SGH (Table 1). For example, we expect plant cover will have competitive effects (negative beta posteriors) in warmer areas of a species range but will switch to facilitation (positive beta posteriors) towards the colder, more physiologically stressful end of the species range. The change in direction of beta posteriors is dependent on the stress gradient. We assessed the DMH by modeling the relationship, β_k, between abiotic gradients, $abio_{i,k}$, and the biotic variable, $bio_{i,}$. This equation (4) has an intercept constrained to zero. In this form, each biotic interaction is treated as a random variable modeled by a linear combination of abiotic variables, allowing for propagation of uncertainty in biotic interactions into models of plant abundance (Hobbs and Hooten 2015). Equations (5-7) are uninformative priors on the intercept and beta posterior-slope terms. Models were constructed for each of the 12 species, and each biotic predictor was investigated individually to compare their predictive abilities.

To evaluate model fit, we performed two posterior predictive checks: 1) visualizations of model fit to real data versus data simulated by the model (Elderd and Miller 2015), and 2) calculation of "Bayesian *P*-values". For 1), model fit is adequate when real data deviate from the model predictions to a similar extent as data simulated from the model. We compared the sum of squared residuals (SSQ) between observed and simulated abundance data for each model and present the visualizations in Supplementary material 3. The Bayesian *P*-value quantifies the frequency that the discrepancy (here, SSQ) is greater for simulated than observed data- models fit well when values were close to 0.5 (Gelman, Meng, and Stern 1996). We suspected that model fit was related to the number of occurrences for species. We used linear mixed effects models to examine if model fit (across all models) improved with number of occurrences, including plant species identity as a random effect. Absolute distance from optimal model fit as determined by the Bayesian *P*-value (0.5) decreased with the number of occurrences (likelihood $R^2 = 0.72$; Supplementary material 2).

We utilized two functions in our model selection procedure: Wantanabe-Akaike information criterion (WAIC) and leave-one-out cross-validation (LOO-CV). WAIC is a fully Bayesian information criterion that is valid in hierarchical models, unlike the deviance information criterion (Hooten and Hobbs 2015). LOO-CV is based on leaving out a single data point at a time and summing the log posterior predictive densities across each model with a different datum held out (Gelman, Hwang, and Vehtari 2014). As with other model selection criteria, smaller values of WAIC and LOO-CV indicate greater within sample model predictive ability.

Lastly, we took a meta-analytic approach to summarize context-dependency across the 12-plant species. In the *metafor* package (Viechtbauer 2010), we took the absolute value of beta posterior medians for the biotic predictors from the above described models, then weighted the estimates by their inverse standard deviation, thereby using the standardized beta posteriors as effect size metrics. We first examined which environmental gradient had the largest absolute effect size for the interaction with biotic predictors. We then investigated which biotic predictor exhibited the most context-dependency (largest interaction effect size for each biotic predictor). Finally, we used the three bins of elevation ranges (whole range, high-elevation range, or low-elevation range) to ask if the magnitude of context-dependency for each biotic predictor depended on the sampled elevation range of the species.

Results

Meta-analysis of context-dependency across plant species

Context-dependency, given by effect sizes, in model predictions of abundance was significant for every abiotic gradient and biotic predictor (Table 2). Across plant species and types of biotic predictors, temperature was associated with the most context-dependency in biotic predictors, followed by soil pH, which specifically influenced root colonization by arbuscular mycorrhizal fungi ($p < 0.001$ for all factors; Table 2). Soil phosphorus was involved in the least context-dependency.

Among the biotic predictors, pathogen damage and plant cover were the most context-dependent (largest effect size; Table 2), although all biotic predictor terms were significantly context-dependent. Herbivory had the least context-dependency. We found little evidence that the sampled portion of a species’ elevation range affected the magnitude of context-dependency in biotic predictors (Table 2). The only such case was for plant cover, where we found less context-dependency in species for which we sampled only high- or low-elevations limits ($p = 0.004$ and 0.064, respectively; Table 2).

Which biotic predictor was most predictive of grass abundance?

Of the six biotic predictors investigated, plant cover best predicted grass species abundance (best model by WAIC and LOO-CV of 6/12 species; Table 3). However, each other examined biotic predictor was most predictive of grass species' abundance at least once. Some of the best models were not very different from the next best models, as determined by both WAIC and LOO-CV. For instance, the top three models predicting *A. nelsonii* abundance (pathogen, herbivory, and plant cover -- in order) were less than 2 WAIC and 3.1 LOO-CV different from each other, suggesting that no single model had greater within sample predictive ability than the others (Supplementary material 4). Additionally, the top two models for *P. alpina* abundance differed by only 0.5 WAIC, but the difference in LOO-CV was greater (3.8). Across models, posterior predictive checks indicated sufficient model fits (Supplementary material 3 and 4). Bayesian *P*-values generally fell within +/- 0.2 of 0.5, and were often >0.5, consistent with adequate model fit (Table 3; Supplementary material 4). Every parameter estimated in our models can be found in Supplementary material 4.

How are biotic predictors correlated to abiotic stress gradients?

Biotic predictors often varied with abiotic gradients: as abiotic conditions were less stressful (e.g., warmer sites), a given biotic predictor increased in magnitude. Plant cover increased with higher MAT, phosphorus, and soil depth. Insect herbivory increased with higher MAT. Gopher disturbance increased with higher MAT and deeper soils. Finally, AMF colonization increased with higher soil pH, which in our system ranged from acidic (4.6) to neutral (7.7). However, plant diversity and leaf pathogen damage were not reliably predicted by any hypothesized abiotic gradient, although there was weak evidence that plant diversity increased with deeper soil depth, and leaf pathogen damage increased with greater soil phosphorus. Full results can be found in Supplementary material 4.

Context-dependency in plant-plant interactions: temperature and nitrogen shifted interactions along the competition-facilitation continuum

The two metrics of plant-plant interactions displayed context-dependency over temperature and nitrogen gradients. Plant cover was predicted to increase abundance of two species, *P. stenantha* and *F. rubra*, in cold environments (low MAT), but this relationship became negative (competitive) at warm sites, based on beta posteriors (Figure 2a). The abundance of two species sampled at their low-elevation range (*P. alpina* and *E. scribneri*) decreased with more plant cover, but the negative relationship suggestive of competition weakened at less stressful, warmer sites of their low-elevation limit. In contrast, abundance of *P. alpina* declined with greater plant diversity in sites that were less stressful with greater soil nitrogen. Plant abundance increased with plant diversity for species sampled across their entire range (e.g., *F. saximontana*). For two species sampled only at their high-elevation range (*A. nelsonii*, *F. thurberi*), plant diversity positively correlated with abundance only in less stressful, high nitrogen sites (Figure 2b).

Context-dependency in foliar herbivory and pathogen damage: associated with temperature in a species-specific manner

Herbivory was context-dependent with temperature in a third of species (4/12). Herbivory's relationship with plant abundance ranged from positive to negative among plant species. For plants that we captured the low-elevation range, abundance declined with high herbivore pressure, and for plants that we captured their high range, abundance increased with greater herbivore pressure, based on beta posteriors. Three of these high range limit species (*A. lettermanii*, *F. thurberi*, and *P. pratensis*) increased in abundance with higher herbivore pressure at cold sites but decreased with greater herbivore pressure at warm sites (Figure 2c). The opposite pattern occurred in one case where we captured only the low-elevation range. *Poa alpina* abundance declined with herbivore pressure, but this decline weakened in less stressful, warmer sites.

The abundance of two species sampled at their low-elevation range, *P. alpina* and *F. brachyphylla*, decreased with high pathogen damage; all other beta posteriors overlapped zero. As with other biotic predictors, for pathogen damage, the most common stress gradient associated with context-dependency was temperature (Figure 2d; 6/12 species). Four plant species were predicted to decline in abundance more with pathogen damage at warmer sites than at cooler sites. Two species sampled at their low-elevation range had opposite patterns: *E. scribneri* abundance decreased more with high pathogen loads in warmer sites than cooler sites, while *P. alpina* increased in abundance with high pathogen loads in warmer sites.

Context-dependency in belowground interactions: AMF more parasitic in high pH and gopher disturbance decreases plant abundance in warmer temperature

Belowground interactions diverged in their context-dependency. Abundance of *A. lettermanii*, *E. trachycaulus*, and *F. saximontana* all increased with greater AMF colonization in low pH soils, but as pH increased and became less stressful, abundance declined with more AMF colonization, suggesting AMF became more parasitic (Figure 2f). Gopher disturbance decreased abundance more towards warmer sites for species which we captured the entire and high end of their elevation range (i.e. *A. lettermanii*, *F. rubra*, *F. thurberi*, *P. pratensis*, and *P. stenantha*). However, the alpine restricted *F. brachyphylla* presented the opposite pattern (Figure 2e).

Discussion

We found strong evidence that biotic predictors of species abundance exhibit context-dependency over abiotic gradients. Across all plant species, every biotic predictor had significant context-dependency, with the greatest context-dependency occurring in plant cover and pathogen damage. Additionally, every investigated abiotic stress gradient was associated with significant context-dependency, although temperature was the most important, as expected for mountain ecosystems. We suggest that incorporating context-dependency of biotic interactions can improve the realism of niche models (see other approaches in Mod et al. 2014, Lany et al. 2017). Adding context-dependency into species distribution models may aid in explaining underlying variation in complex model fitting procedures (Merow et al. 2014) by explicitly representing how stress gradients alter predictions of biotic interaction relationships with species' distributions.

Hierarchical models, multiple biotic interactions, and biogeographic hypotheses

Plant-plant interactions.

Plant cover was the best biotic predictor for half the species. Plant cover ranged from patterns suggestive of facilitation to competition dependent on focal species identity. This result suggests that past work focusing on the role of plant-plant interactions in modeling efforts (e.g. Meier et al. 2011, leRoux et al. 2012) has captured the most predictive biotic interaction for many plant species. Species sampled at their low-elevation range declined in abundance at sites with more plant cover, while species sampled at their high-elevation range had patterns suggesting facilitation at sites with more plant cover (e.g. Figure 2a). Together these patterns support the DMH in that the low end of a species range is limited by biotic interactions while the high end of a species range is limited by harsher abiotic environments (Brown 1995), where facilitative interactions are more frequent (SGH; Bertness and Callaway 1994). This result is also consistent with experimental work showing that low-elevation ranges are restricted by competitive interactions (Alexander, Diez, and Levine 2015), while the high end of a species' distribution experiences more facilitation (Callaway et al. 2002). In addition, the effect of plant cover for two species (*P. stenantha* and *F. rubra*) was predicted to become more competitive towards warmer sites. Combined with the evidence that plant cover increased at warmer sites, this supports both the SGH and DMH expectation that plant-plant interactions become more competitive in less abiotically stressful sites. This evidence is compelling because we sampled the entire elevation distribution of these two species. However, predicted facilitative effects of plant cover increased in warmer sites for two species with their low-elevation range sampled (i.e. *P. alpina* and *E. scribneri*), which is surprising in a growing season-limited system (Euskirchen et al. 2006), where in other grassland systems warmer temperatures increased competition (Fridley et al. 2016). This contrast may be due to precipitation seasonality in the region, where snow melts earlier at low-elevation sites causing a mid-summer drought before the late summer monsoons. Growing season length may be less limiting than the mid-summer drought stress, which may be minimized if high plant cover soils at warmer sites retain more water.

We originally hypothesized that increased plant diversity would decrease plant abundance given the probability of encountering a strong competitor should increase with diversity (Dobzhansky 1950; Louthan, Doak, and Angert 2015), but found diversity often associated with increased grass abundance (e.g. Figure 2b). There are three compelling alternative hypotheses: a) few strong competitors exclude other plants, leading to low diversity and low probability of a focal species being present; b) high diversity sites are more likely to hold a strong facilitator; and c) high diversity sites are more likely to possess a focal species by virtue of holding a greater portion of the regional species pool. Experiments are required to determine which of these hypotheses is at work.

Soil available nitrogen, a key production limiting nutrient in temperate systems (LeBauer and Treseder 2008), was involved in context dependency with plant diversity often. For two species that we sampled at their high-elevation range (*A. nelsonii*, *F. thurberi*), abundance increased with diversity more at sites with greater soil nitrogen, although the alpine restricted *P. alpina* had the opposite pattern. *Achnatherum nelsonii* and *F. thurberi* are large, productive bunchgrasses while *P. alpina* is a small stress-tolerant plant (Shaw 2008). This pattern may reflect that plant species with competitive life histories benefit from nitrogen fixing plant species, which are more likely to occur in more diverse plant communities (Wright et al. 2017), while the slow growing/stress tolerating *P. alpina* cannot compete in higher resource environments. These results support hypotheses in Table 1, that greater nitrogen/less stress will increase competition.

Plant-consumer interactions

The DMH proposes increased herbivory with warmer temperatures along biogeographical gradients (Anstett et al. 2016), and our results predicted greater negative effects of herbivory in the warmer, less thermally harsh environments, aligning with past experimental work (Bruelheide and Scheidel 1999). This pattern held for three species sampled at their high-elevation range (Figure 2c, Supplementary material 4), but was not the case for *P. alpina*, which was sampled at its low-elevation range. For *P. alpina*, this may be a case of apparent competition, where negative competitive interactions between species are mediated by herbivores – and thus by a different trophic level (Holt 1977; Underwood, Inouye, and Hambäck 2014). At warmer sites, competitors of *P. alpina* may decline from increased herbivory, allowing *P. alpina* to increase abundance. This mechanism of apparent competition is common (e.g. Rand 2003, Orrock and Witter 2010, Bhattarai et al. 2017), but experimentation is required to establish causality in our system. We found modest evidence that plant abundance would decline more with pathogen damage at warmer sites, consistent with past work finding that pathogen fitness across host populations is dependent on temperature (Laine 2008).

Belowground interactions

Grass abundance generally decreases in soils disturbed by pocket gophers in the region (Sherrod, Seastedt, and Walker 2005), consistent with our general results. Surprisingly, *F. brachyphylla* abundance increased more with greater gopher disturbance in warmer sites than in cooler sites. Given that competition tends to increase in warm relative to cool sites in mountain ecosystems (Alexander, Diez, and Levine 2015), higher amounts of gopher-caused disturbance towards the warm end of *F. brachyphylla*'s range may increase plant diversity (Sherrod, Seastedt, and Walker 2005) and allow *F. brachyphylla* to persist in communities where it would otherwise be competitively excluded (Grime 1973; Grime 1973; Huston 2014).

Root colonization by AMF was not the best predictor of plant abundance for most species but was particularly important for *E. trachycaulus*. *Elymus trachycaulus* abundance increased with greater root colonization (Figure 2f). Past work has found that *E. trachycaulus* has high levels of AMF colonization in this system (Ranelli et al. 2015), and it may be more reliant on this symbiosis than other species we surveyed. AMF colonization was context-dependent across multiple environmental gradients, including temperature, N and pH. AMF colonization in high N and pH soils was associated with lower plant abundance, which supports the SGH in that these environments are less stressful, potentially causing AMF to become parasitic (Johnson, Graham, and Smith 1997). Past work in glasshouses have shown that plant production can be suppressed by AMF in high nitrogen environments (Reynolds et al. 2005). Soil pH is recognized as a driver of AMF community composition (e.g. Hazard et al. 2013) and global distributions of AMF taxa (e.g. Kivlin et al. 2011), and so our results may reflect turnover in fungal communities that differentially effect plant performance. There is a growing appreciation of how symbionts can alter a species' niche dimensions across geographic scales (e.g. Brown and Vellend 2014, Afkhami et al. 2014) and may be valuable for species distribution modeling (Pellissier et al. 2013). Our results highlight that work aimed at explicitly linking symbiont and host abundances biogeographically is an exciting area for future models.

Caveats and model limitations

Our model is aimed at utilizing observational data for the development of hypotheses on how context-dependent interactions can shape a species distribution. As with all observational statistical models (Araújo and Luoto 2007), the model should ultimately be paired with experimental manipulations to link observed patterns with processes of context-dependency in biotic interaction strength. Recent work suggests that models of spatial cooccurrence as a measure of competitive interactions can do a poor job of recapitulating experimental results (Barner et al. 2018). Indeed, simulation work calls into question whether the fitness consequences of biotic interactions can be inferred from distribution models (Godsoe, Franklin, and Blanchet 2017). It is possible that results reflect unmeasured variables that co-vary with our set of predictors, rather than indicating a direct effect of a given biotic predictor. This may explain mismatches between past experimental and modeling work in other systems (Barner et al. 2018). Our selection of variables was based on knowledge of plant physiology and natural history to reduce this issue. Additionally, we constrained model complexity to better fit our a priori hypotheses (Merow et al. 2014) that make linear predictions. It is possible that results from our model selection procedure may have been different if we had utilized other types of models, such as generalized additive models (GAMs), which utilize smoothing functions to relate independent to dependent variables (e.g. Meier et al. 2011). Finally, our data are limited in space, time, and sample size. Our model appears to be "data hungry," because model fit (by Bayesian *P*-value) scaled with number of occurrences for species (Supplementary material 2). Given our objective to collect original, fine-scale data on a large suite of interactions and environmental variables, the spatial extent of the dataset is necessarily limited by the detailed nature of the data collected. Future work will replicate the study temporally to test model predictions with climate changes, given recent evidence of pronounced change in the region and in mountain ecosystems (Pepin and Losleben 2002; Rangwala and Miller 2012).

Conclusions

We developed a novel statistical modeling approach to address predictions of the stress gradient and Dobzhansky-MacArthur hypotheses and found general support for each across a set of 12 native grass species. Context-dependency of the relationship between biotic predictors and focal plant abundance over environmental gradients was common, suggesting it is the rule, rather than exception. Support may depend on how much, or which part, of a species range is sampled, suggesting that range-wide sampling may be crucial for accurate assessments. Finally, although half of our species were best predicted by plant cover, biotic predictors not often employed in niche modeling were better predictors for the other half, suggesting that interactions beyond plant-plant (e.g. plant-symbiont) have predictive utility.

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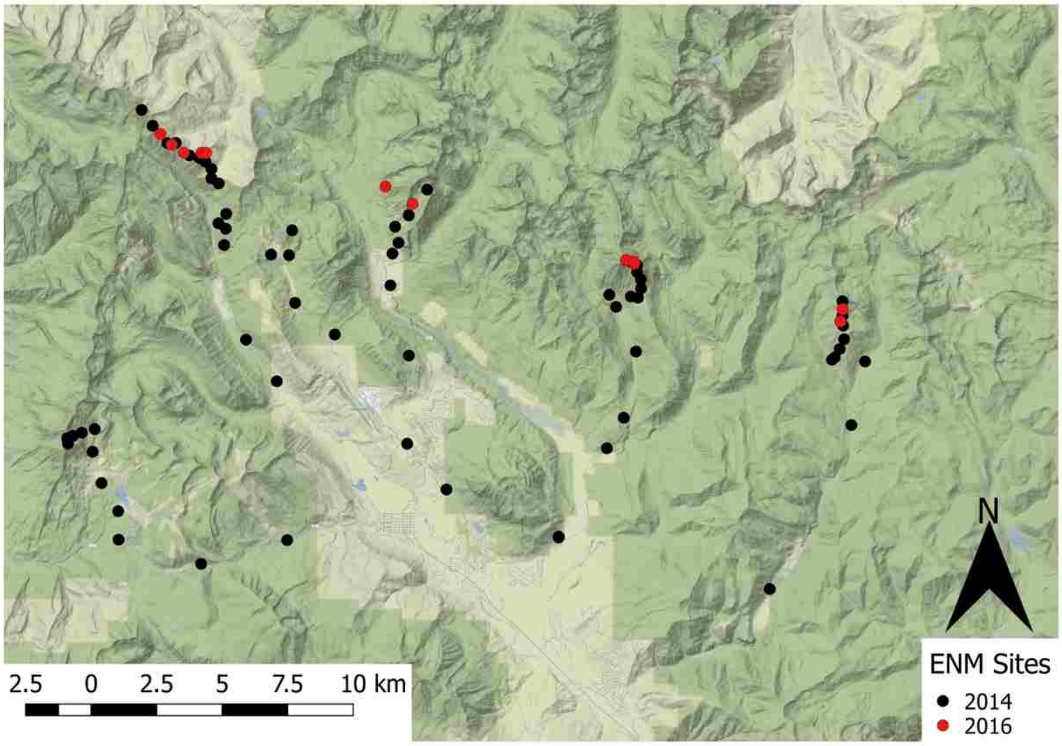
Figures

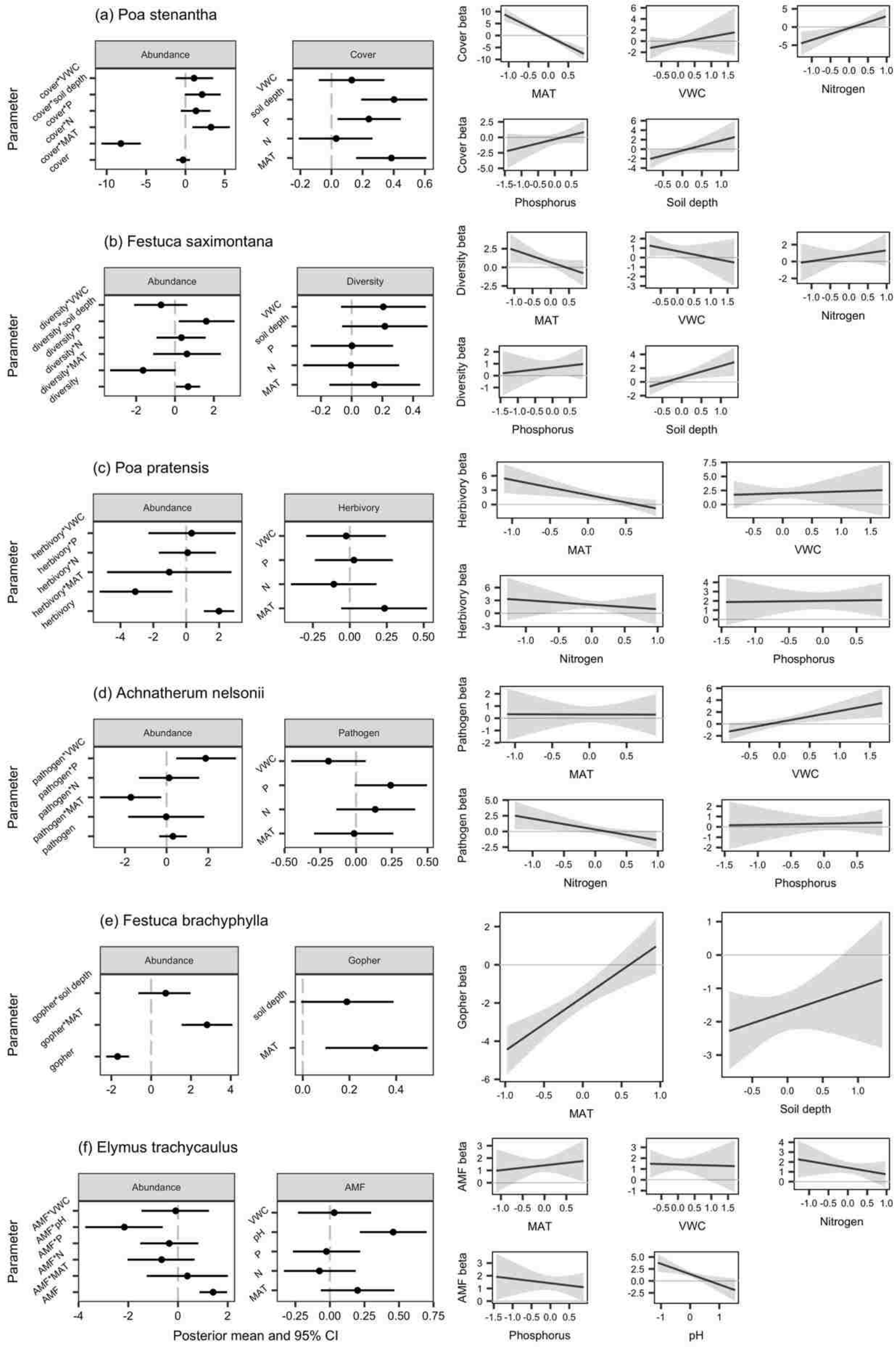
Chapter 1 Figure 1. Map of sites within the West Elk Mountains and Gunnison National Forest near Crested Butte, Colorado, USA. Green shaded areas are U.S. National Forest Service land. Colored points refer to the year in which the site was sampled.

Chapter 1 Figure 2. Beta posteriors and 95% credibility intervals and visualizations of how beta for a given biotic predictor varies with stress gradients. Each panel (a, b, etc.) represents one species and contains figures presenting beta posteriors for the abundance and biotic predictor model levels. To the right of these panels are visualizations of how the predicted effect of a biotic predictor varies over a given stress gradient. We present graphs for selected species and biotic predictors, but a full table of parameter estimates can be found in Supplementary material 4.

Chapter 1 Figure 1.



Chapter 1 Figure 2.



Tables

Chapter 1 Table 1. Hypotheses for how a given biotic interaction relates to species abundance and how the biotic interaction relates to environmental stress gradients. Down arrows denote hypothesized negative relationships, and up arrows indicate positive linear relationship. Columns with both up and down arrows have evidence for both relationships dependent on abiotic stress gradient. Absence of an arrow represents cases with no *a priori* hypotheses. “T” stands for temperature, "N" for plant available nitrogen, and "P" for plant-available phosphorus. Evidence comes from observational, experimental, and synthesis studies, summarized in the reference column. References: 1. Kraft et al. 2014, 2. Harpole et al. 2016, 3. Callaway et al. 2002, 4. Michalet et al. 2014, 5. Belcher et al. 1995, 6. Fridley et al. 2016, 7. Clark et al. 2007, 8. Hautier et al. 2009, 9. Wright et al. 2014, 10. Dobzhansky 1950, 11. MacArthur 1972, 12. Hawkins et al. 2003, 13. Gaston 2000, 14. Dornbush and Wilsey 2010, 15. Anderson et al. 2007, 16. Baer et al. 2003, 17. Bobbink et al. 2010, 18. Wassen et al. 2005, 19. Le Bagousse-Pinguet et al. 2014, 20. Maron and Crone 2006, 21. Stein et al. 2010, 22. Garibaldi et al. 2011, 23. Rasmann et al. 2014, 24. Gilliam 2006, 25. Brenes-Arguedas et al. 2009, 26. Tao and Hunter 2012, 27. Parker and Gilbert 2007, 28. Laine 2008, 29. Lambert 1986, 30. Jactel et al. 2012, 31. Pehkonen and Tolvanen 2008, 32. Sherrod et al. 2005, 33. Lynn et al. 2018, 34. Reichman and Seabloom 2002, 35. Hoeksema et al. 2010, 36. Compant et al. 2010, 37. Wilson et al. 2016, 38. Soudzilovskaia et al. 2015, 39. Gerz et al. 2016, 40. Yang et al. 2014, 41. Propster and Johnson 2015, 42. Postma et al. 2007.

Chapter 1 Table 2. Results from meta-analytic analysis of context-dependency from abiotic stress gradients (A), biotic predictors (B), and if the portion sampled of a species range effected our ability to detect context-dependency (C). In (C), estimates for the low and high biotic predictors are deviations from estimates for the broad predictor (i.e., do predictions for low and high differ from those for the broad species?). We took the absolute value of each variable analyzed and weighted the median beta posterior by its inverse standard deviation.

Chapter 1 Table 3. Best models predicting focal species abundance based on lowest WAIC and LOO-CV as a measure of model within sample predictive ability. ΔWAIC-NMB and ΔLOO-CV-NMB refer to the difference in either value to the "next best model" (NMB) in the model set. "*P*-values" are Bayesian *P*-values, where values close to 0.5 support a well-fitting model. Full selection results can be found in Supplementary material 4.

Chapter 1 Table 1.

		Environmental Stress Gradient						
Predictor	Focal plant abundance	T	Soil depth	Soil moisture	Soil N	Soil P	Soil pH	References
Plant cover (light competition/facilitation)	↓ ↑	↑	↑	↑	↑	↑		1, 2, 3, 4, 5, 6, 7, 8, 9
Plant diversity/richness	↓ ↑	↑	↑	↓	↓	↑ ↓		10, 11, 12, 13, 14, 15, 16, 17, 18, 19
Damage by insect herbivores	↓	↑		↑	↑	↓		20, 21, 22, 23, 24, 25, 26
Damage by foliar pathogens	↓	↑		↓	↑	↓		27, 28, 29, 30, 31
Soil disturbance by small mammals	↓	↑	↑					32, 33, 34
AM fungi colonization of roots	↑ ↓	↑ ↓		↓	↑ ↓	↓	↓ ↑	35, 36, 37, 38, 39, 40, 41, 42

Chapter 1 Table 2.

A. Abiotic Stress Gradient			
Parameter	*Eff. size*	*Std. err.*	*p-value*
MAT	1.720	0.1470	<0.0001
Soil pH	1.232	0.312	<0.0001
Soil N	1.025	0.157	<0.0001
Soil depth	0.864	0.197	<0.0001
Soil VWC	0.860	0.161	<0.0001
Soil P	0.698	0.1689	<0.0001
B. Biotic Predictor			
Pathogen	1.376	0.170	<0.0001
Cover	1.172	0.163	<0.0001
Gopher	1.082	0.247	<0.0001
AMF	1.027	0.163	<0.0001
Diversity	1.025	0.162	<0.0001
Herbivory	0.960	0.172	<0.0001
C. Sampled Elevation Range and Biotic Predictor Context-Dependency			
Broad:Cover	1.701	0.281	<0.0001
Broad:Pathogen	1.185	0.293	<0.0001
Broad:Gopher	1.036	0.434	0.0171
Broad:AMF	0.834	0.279	0.0028
Broad:Diversity	0.802	0.281	0.0043
Broad:Herbivory	0.714	0.292	0.0144
Low:AMF	0.340	0.389	0.3825
Low: Herbivory	0.305	0.455	0.5018
High:Pathogen	0.303	0.488	0.5353
High:AMF	0.239	0.413	0.5632
Low:Diversity	0.170	0.442	0.7012
High:Diversity	-0.108	0.473	0.8201
Low:Gopher	-0.130	0.628	0.8360
High:Herbivory	-0.251	0.504	0.6182
Low:Pathogen	-0.266	0.459	0.5624
High:Gopher	-0.345	0.672	0.6074
High:Cover	-0.886	0.477	0.0635
Low:Cover	-1.271	0.444	0.0042

Chapter 1 Table 3.

Species	Best model	WAIC	∆WAIC-NBM	LOO-CV	∆LOO-CV-NMB	*P*-value
Achnatherum lettermanii	Herbivory	487.0	4.1	487.4	5.7	0.5846
Achnatherum nelsonii	Pathogen	302.3	0.7	305.9	1.1	0.9207
Elymus scribneri	Cover	404.2	14.2	413.3	11.1	0.7014
Elymus trachycaulus	AMF	487.8	20.4	488.7	18.1	0.3593
Festuca brachyphylla	Gopher	402.3	18.9	406.7	20.9	0.7952
Festuca rubra	Cover	325.9	11.0	327.6	11.7	0.8572
Festuca saximontana	Diversity	291.0	6.1	292.4	5.7	0.8902
Festuca thurberi	Cover	512.7	10.9	513.9	10.5	0.2883
Poa alpina	Cover	376.3	0.5	385.6	3.8	0.5888
Poa pratensis	Herbivory	467.9	4.5	469.0	4.0	0.6136
Poa stenantha	Cover	480.2	15.2	480.5	16.1	0.7773
Trisetum spicatum	Cover	383.7	6.3	384.3	6.8	0.5656

Chapter 1 Supplementary Material

Chapter 1 Supplementary material 1. Information on the number of sites present, mean and standard deviation, median, minimum, and maximum elevation of sites where a species was present. Species are ordered according to their elevation rank, where the lowest mean elevation species is ranked first. m.a.s.l. is meter above sea level.

Species	*Elev. Rank*	*Numb. sites*	*Mean (m.a.s.l.)*	*Std. Dev.*	*Median (m.a.s.l.)*	*Min. (m.a.s.l.)*	*Max. (m.a.s.l.)*
Achnatherum nelsonii	1	16	2886.99	120.45	2846.04	2747.44	3157.28
Poa pratensis	2	28	3020.50	236.35	2976.98	2710.25	3633.25
Achnatherum lettermanii	3	39	3103.79	258.58	3054.50	2710.50	3667.31
Festuca thurberi	4	34	3114.54	285.44	3097.17	2710.50	3667.31
Festuca rubra	5	11	3192.71	180.73	3197.25	2867.89	3454.79
Elymus trachycaulus	6	50	3241.34	317.44	3198.25	2747.44	3878.89
Poa stenantha	7	31	3338.77	204.20	3347.44	2971.83	3771.50
Festuca saximontana	8	18	3399.05	283.54	3423.97	2798.68	3814.50
Trisetum spicatum	9	41	3493.00	271.09	3521.00	2932.03	4023.25
Festuca brachyphylla	10	30	3711.93	149.97	3712.64	3418.25	4023.25
Poa alpina	11	23	3712.46	187.97	3726.00	3197.25	4023.25
Elymus scribneri	12	17	3736.44	93.45	3726.00	3539.00	3878.89

Chapter 1 Supplementary material 2.

Biotic interaction predictors

Competition/facilitation.

We assessed plant community composition using visual cover estimates. We placed a 0.2 m x 0.2 m quadrat every 2.5 m along four 20 m transects per site. In each quadrat, we visually estimated percentage cover of every plant species or bare ground to total 100% (33 plant cover estimates per site). Specimens were collected and identified using Shaw (2008) for grasses and Weber and Wittmann (2012) for non-grasses. We corrected for current taxonomy using the USDA PLANTS Database (USDA and NRCS 2017). Unidentified species (e.g., non-flowering sedges) were morphotyped, assigned unique species codes, and matched to unknowns at other sites. Plant cover for a site was represented by the summed percentage cover estimate across the 33 quadrats (maximum of 3300 if site was 100% vegetated). We used the *vegan* package in R to calculate plant species diversity indices (Oksanen et al. 2017). Because diversity metrics were highly colinear, we used Shannon diversity (hereafter diversity) in all subsequent analyses, as it had the highest correlation with other diversity metrics.

Potential antagonisms.

We assessed insect herbivory and leaf pathogens via calibrated visual estimates of percentage leaf damage for 10 randomly selected individuals per focal grass species per site, with a minimum distance of two m between individuals. Insect herbivory and pathogen damage present a dilemma for niche modeling: how can one estimate a biotic interaction when a species is not present at a site? Therefore, we created a site-level metric of herbivore/pathogen pressure by calculating community weighted mean damage over all grass species present at a site. This metric estimated the expected damage that a grass individual would experience if it were present at the site.

We measured pocket gopher (*Thomomys talpoides*) disturbance to soil at each site along three 40 m long belt transects (methods in Lynn et al. 2018). Briefly, each belt transect was 1 m wide and each characteristic sign of gopher disturbance (e.g., mounds, eskers) were summed across the transects.

Potential mutualisms.

We assessed percentage fungal colonization of roots by pooling equal amounts of root tissue by volume from six plant individuals per species per site (methods in Ranelli et al. 2015). We scored colonization of roots by arbuscular mycorrhizal fungi (AMF; aseptate hyphae with vesicles and/or arbuscules; Glomeromycotina). We estimated site-level root colonization with community weighted means over all grass species present at a site.

References

Lynn, Joshua S., Samuel Canfield, Ross R. Conover, Jeremy Keene, and Jennifer A. Rudgers. 2018. "Pocket Gopher (*Thomomys talpoides*) Soil Disturbance Peaks at Mid-Elevation and Is Associated with Air Temperature, Forb Cover, and Plant Diversity." *Arctic, Antarctic, and Alpine Research* 50 (1): e1487659.

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Ranelli, Luciana B., Will Q. Hendricks, Joshua S. Lynn, Stephanie N. Kivlin, and Jennifer A. Rudgers. 2015. "Biotic and Abiotic Predictors of Fungal Colonization in Grasses of the Colorado Rockies." *Diversity and Distributions* 21 (8): 962–76.

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Code

Below we provide code to fit the model for one species, *Poa stenantha,* or POST, for one biotic factor, plant cover. Additionally, we provide the procedure for our variable standardization. All other models differed only in species and biotic factors analyzed. We constructed models for each different biotic factor according to Table 1 and Figure 2 in the manuscript.

```
# Context-dependent biotic interactions predict plant abundance across steep
environmental
# gradients


# Models for POST

# Clear R
rm(list=ls(all=TRUE))

#required packages
require(rjags)
require(R2jags)

# load data
setwd("")
dat <- read.csv("ENMdat.csv")
head(dat)
levels(dat$spp)

datpost <- dat[dat$spp=="POST",]
attach(datpost)

# 1. scale all variables

standard <- function(x) (x - mean(x, na.rm=T)) / (2* (sd(x, na.rm=T)))

vwc <- as.numeric(standard(vwc))
soildepth <- standard(log(AVG_Soil_Depth))
ph <- as.numeric(standard(pH))
```

```
nit <- as.numeric(standard(log(tot_N)))
phos <- as.numeric(standard(log(datpost$phos+1)))# plus one for zeros
mat <-as.numeric(standard(p1MAT))
wherb <- as.numeric(standard(log(w_herb)))
wpath <- as.numeric(standard(log(w_fung)))
amf <- as.numeric(standard(AVG_amf))
cover <- as.numeric(standard(cov))
gop <- as.numeric(standard(goph))
Hdiversity <- as.numeric(standard(Hdiv))

# add 1 to abundance for log transformation in JAGS code
abund <- as.numeric(datpost$abund+1)

### 2. Model for investigation of cover

## data for Jags
jags.data <- list("abund","cover","mat","vwc","nit","phos","soildepth")

# parameters to be measured
jags.param <- c("a","b1","b2","b3","b4","b5","g1","g2","g3","g4","prec1","r")

abun.mod <- function(){
  for(i in 1:67){

## model of context dependency/SGH

    abund[i]~dnegbin(p[i],r)
    log(mu[i]) <- a +
    b1*cover[i]+
    b2*cover[i]*mat[i]+
    b3*cover[i]*vwc[i]+
    b4*cover[i]*nit[i]+
    b5*cover[i]*phos[i]+
    b6*cover[i]*soildepth[i]

    p[i] <- r/(r+mu[i])

## DMH multilevel model

    cover[i]~dnorm(mu1[i],prec1)
    mu1[i] <- g1*mat[i]+g2*nit[i]+g3*phos[i]+g4*vwc[i]+g5*soildepth[i]

  }

# Priors
 r~ dunif(0,50)
 a~ dnorm(0,1.0E-6)
 b1~dnorm(0,1.0E-6)
```

```
 b2~dnorm(0,1.0E-6)
 b3~dnorm(0,1.0E-6)
 b4~dnorm(0,1.0E-6)
 b5~dnorm(0,1.0E-6)
 b6~dnorm(0,1.0E-6)
 g1~dnorm(0,1.0E-6)
 g2~dnorm(0,1.0E-6)
 g3~dnorm(0,1.0E-6)
 g4~dnorm(0,1.0E-6)
 g5~dnorm(0,1.0E-6)
 prec1~dgamma(0.001,0.001)
}

jagspostcover <- jags(data=jags.data,inits=NULL, parameters.to.save=jags.param,
                n.iter=50000 ,model.file=abun.mod, n.thin=5)

jagspostcover


detach(datpost)

### end code
```

Figure S1. Layout of a sampling site. Objects not to scale. Meter marks on transects describe what was measured at that point. Vegetation surveys occurred on each transect every 2.5 m, without duplicates at intersections. Abundance counts of focal species occurred along each horizontal transect. Dashed lines were used for vegetation and abundance surveys, only. "VWC" is volumetric water content and "SD" is soil depth. See methods section for further details.

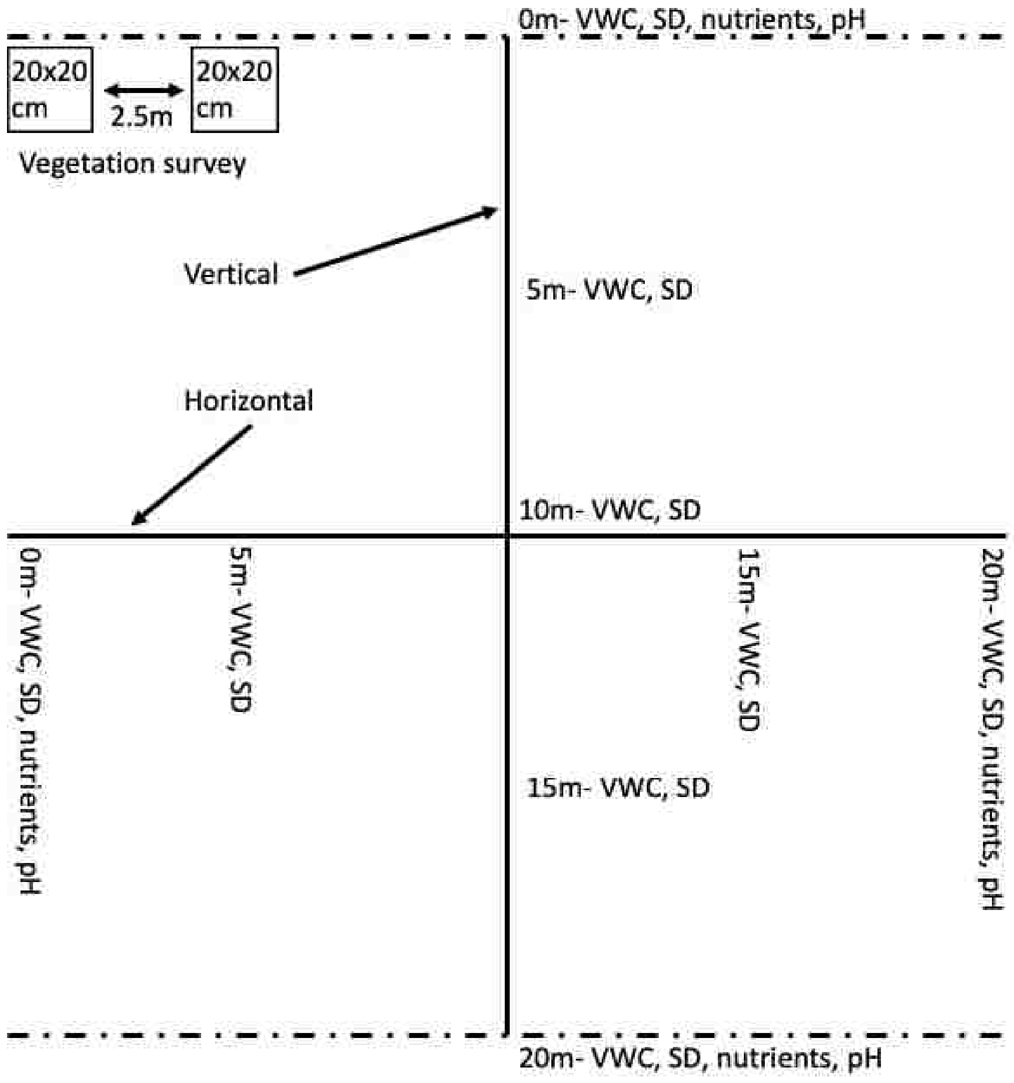
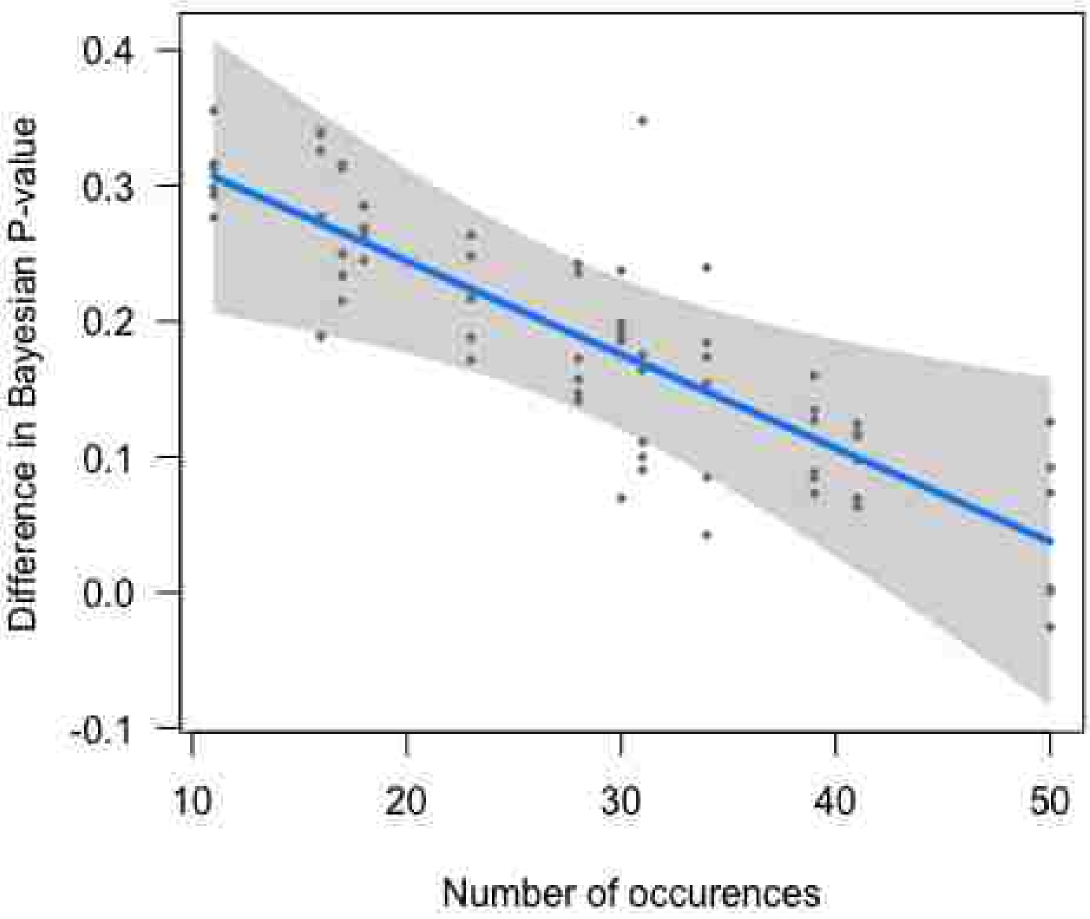
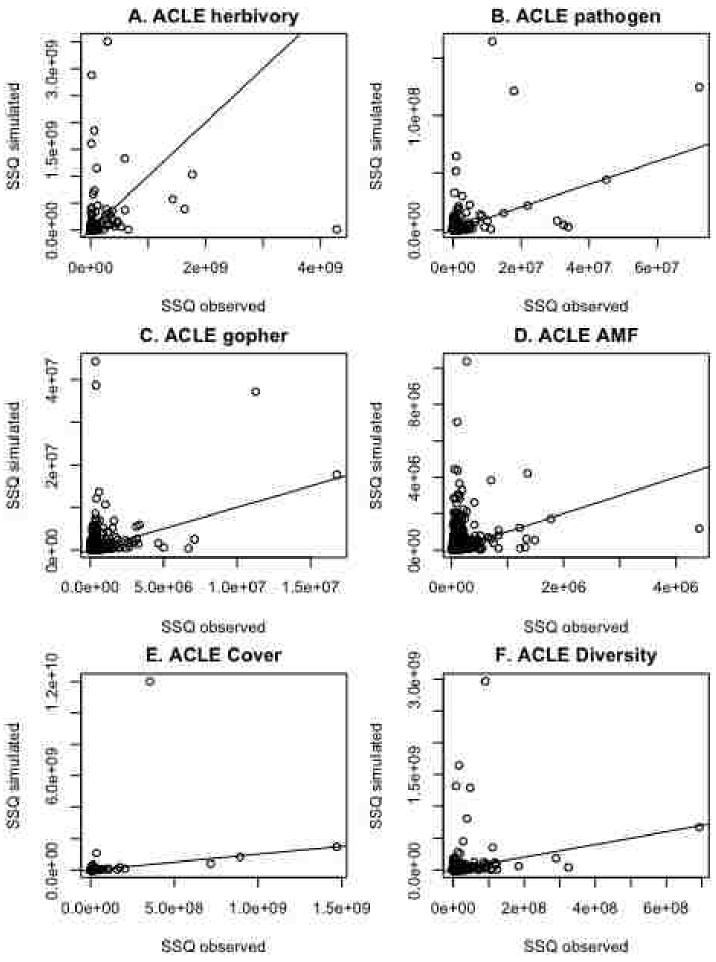


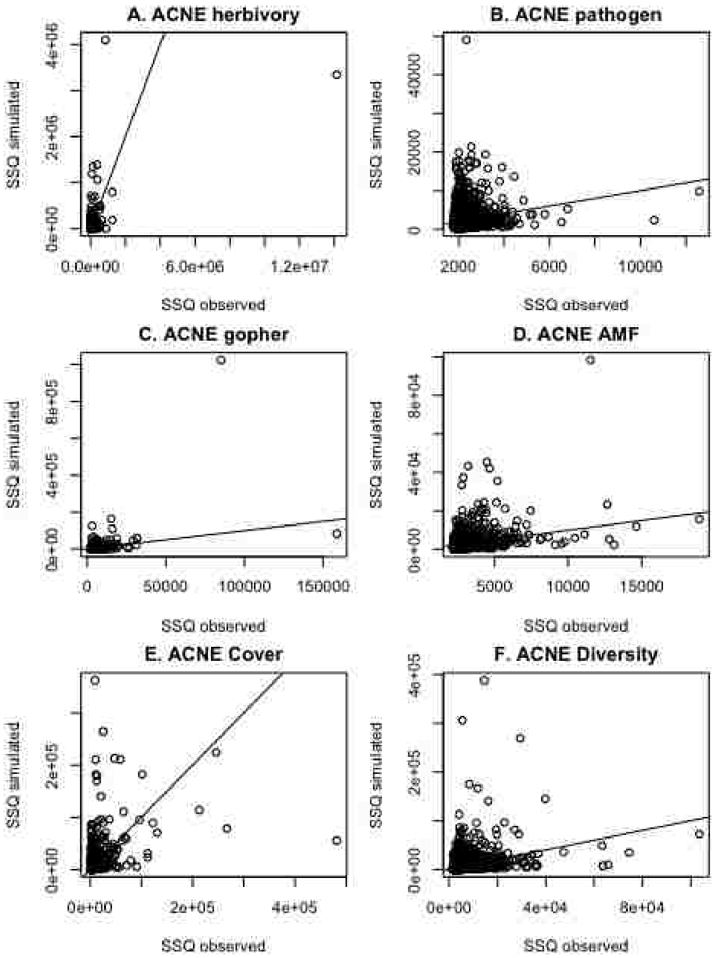
Figure S2. The difference in observed Bayesian *P*-value from optimal fit (0.5) decreased with number of occurrences for a species. The y-axis is the absolute value of the difference between the observed Bayesian *P*-value and an optimal fitting model at 0.5. The data points take into account random effects attributed to differences among species, given by a linear mixed effects model fit with maximum likelihood estimation.

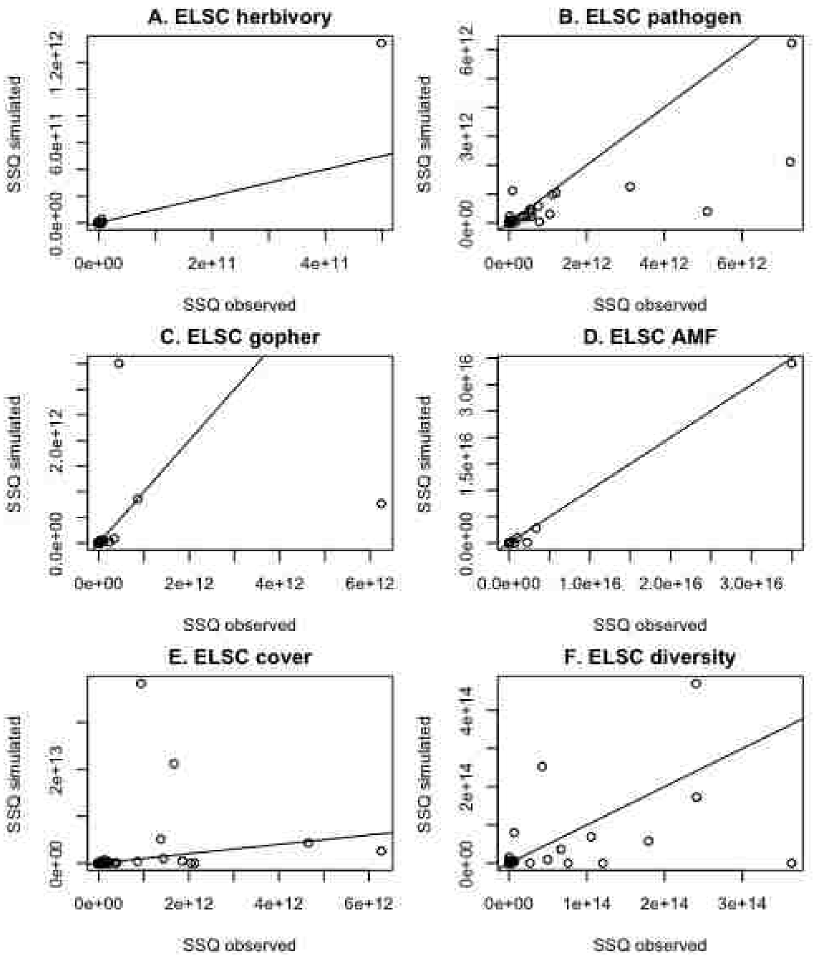


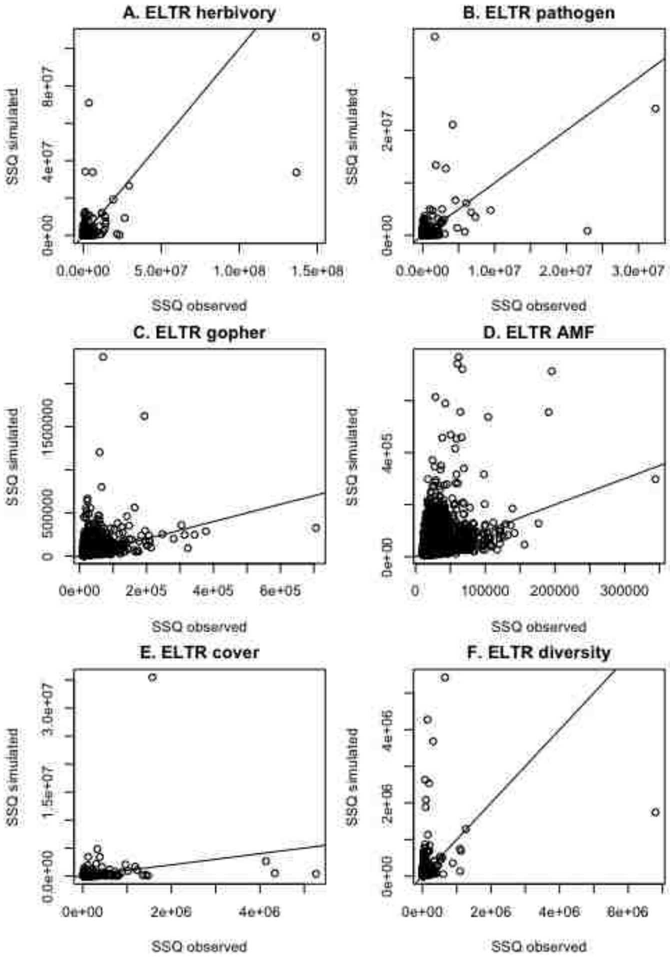
Chapter 1 Supplementary material 3.

Posterior predictive checks (PPC) use a standard discrepancy metric to compare observed data and data simulated by the model. Model fit is adequate when observed and simulated data deviate from model predictions to a similar extent. Discrepancy was measured using the sum of squared residuals (SSQ) for observed and simulated data. PPCs were assessed for each species and each biotic predictor. Figures are organized by species below. Models fit is sufficient when points center along the 1:1 line. This was generally true for all models, with a few outlier points.




A. ACNE herbivory
B. ACNE pathogen
C. ACNE gopher
D. ACNE AMF
E. ACNE Cover
F. ACNE Diversity
SSQ simulated
SSQ observed
0.0e+00
6.0e+06
1.2e+07
0e+00
2e+06
4e+06
2000
6000
10000
0
20000
40000
0
50000
100000
150000
4e+05
8e+05
5000
15000
4e+04
8e+04
2e+05
4e+05


A. ELSC herbivory
SSQ simulated
0.0e+00
6.0e+11
1.2e+12
0e+00
2e+11
4e+11
SSQ observed
B. ELSC pathogen
SSQ simulated
0e+00
3e+12
6e+12
0e+00
2e+12
4e+12
6e+12
SSQ observed
C. ELSC gopher
SSQ simulated
0.0e+00
2.0e+12
0e+00
2e+12
4e+12
6e+12
SSQ observed
D. ELSC AMF
SSQ simulated
0.0e+00
1.5e+16
3.0e+16
0.0e+00
1.0e+16
2.0e+16
3.0e+16
SSQ observed
E. ELSC cover
SSQ simulated
0e+00
2e+13
0e+00
2e+12
4e+12
6e+12
SSQ observed
F. ELSC diversity
SSQ simulated
0e+00
2e+14
4e+14
0e+00
1e+14
2e+14
3e+14
SSQ observed


A. ELTR herbivory
B. ELTR pathogen
C. ELTR gopher
D. ELTR AMF
E. ELTR cover
F. ELTR diversity
SSQ simulated
SSQ observed
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4e+07
8e+07
0.0e+00
5.0e+07
1.0e+08
1.5e+08
2e+07
1.0e+07
2.0e+07
3.0e+07
0
500000
1500000
2e+05
4e+05
6e+05
4e+05
100000
200000
300000
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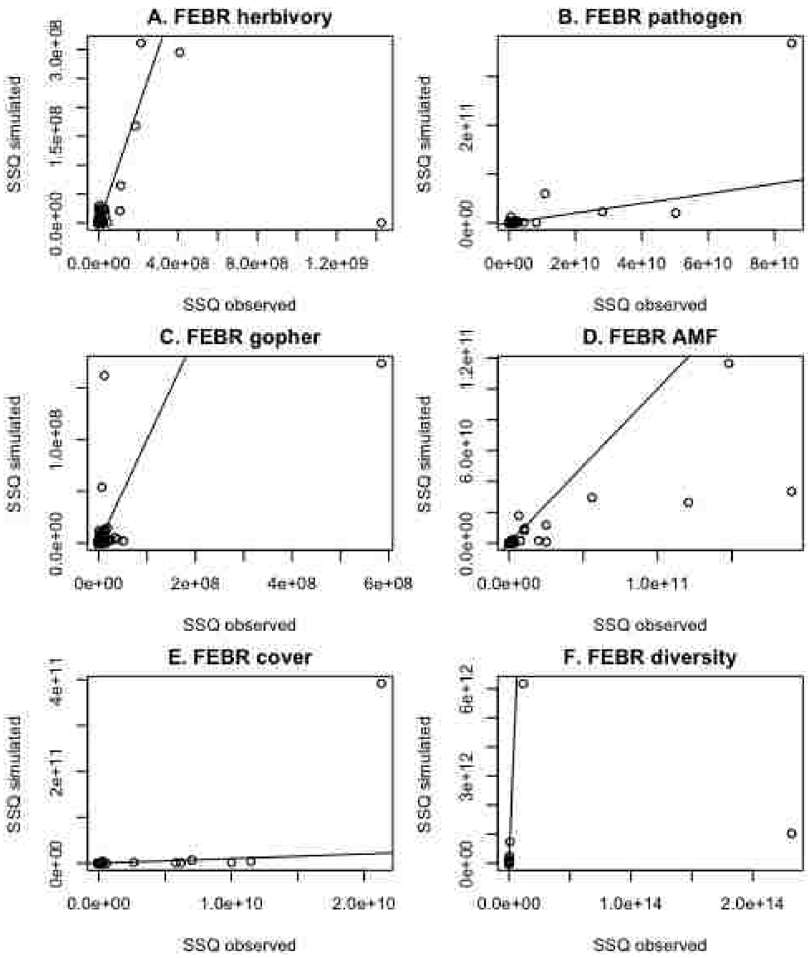
4e+06
6e+06


A. FEBR herbivory
SSQ simulated
SSQ observed
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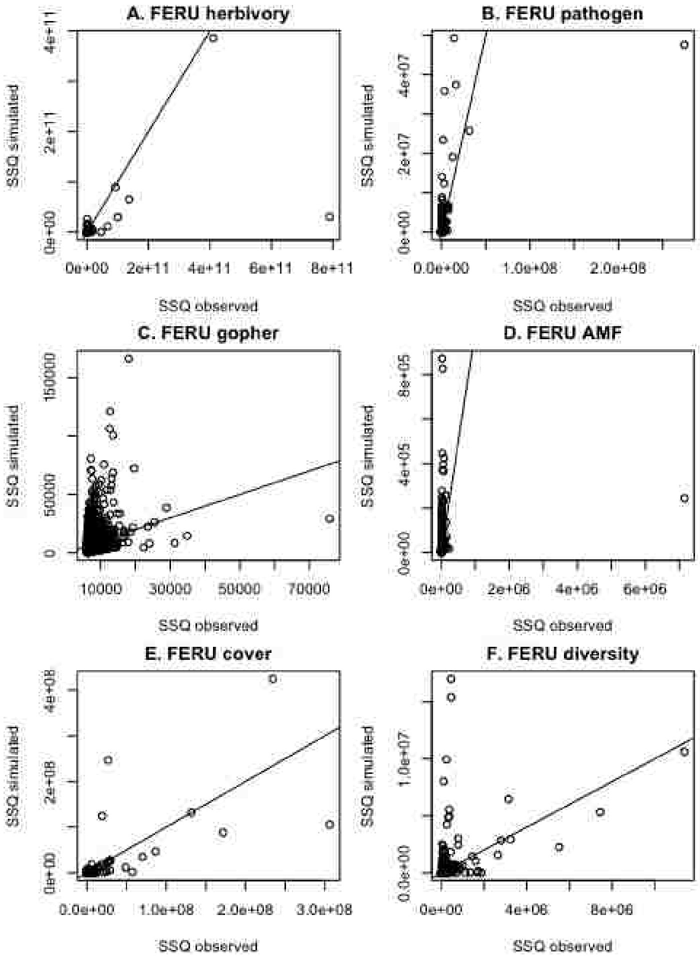
0.0e+00
4.0e+08
8.0e+08
1.2e+09
B. FEBR pathogen
SSQ simulated
SSQ observed
0e+00
2e+11
0e+00
2e+10
4e+10
6e+10
8e+10
C. FEBR gopher
SSQ simulated
SSQ observed
0.0e+00
1.0e+08
0e+00
2e+08
4e+08
6e+08
D. FEBR AMF
SSQ simulated
SSQ observed
0.0e+00
6.0e+10
1.2e+11
0.0e+00
1.0e+11
E. FEBR cover
SSQ simulated
SSQ observed
0e+00
2e+11
4e+11
0.0e+00
1.0e+10
2.0e+10
F. FEBR diversity
SSQ simulated
SSQ observed
0e+00
3e+12
6e+12
0.0e+00
1.0e+14
2.0e+14



A. FERU herbivory

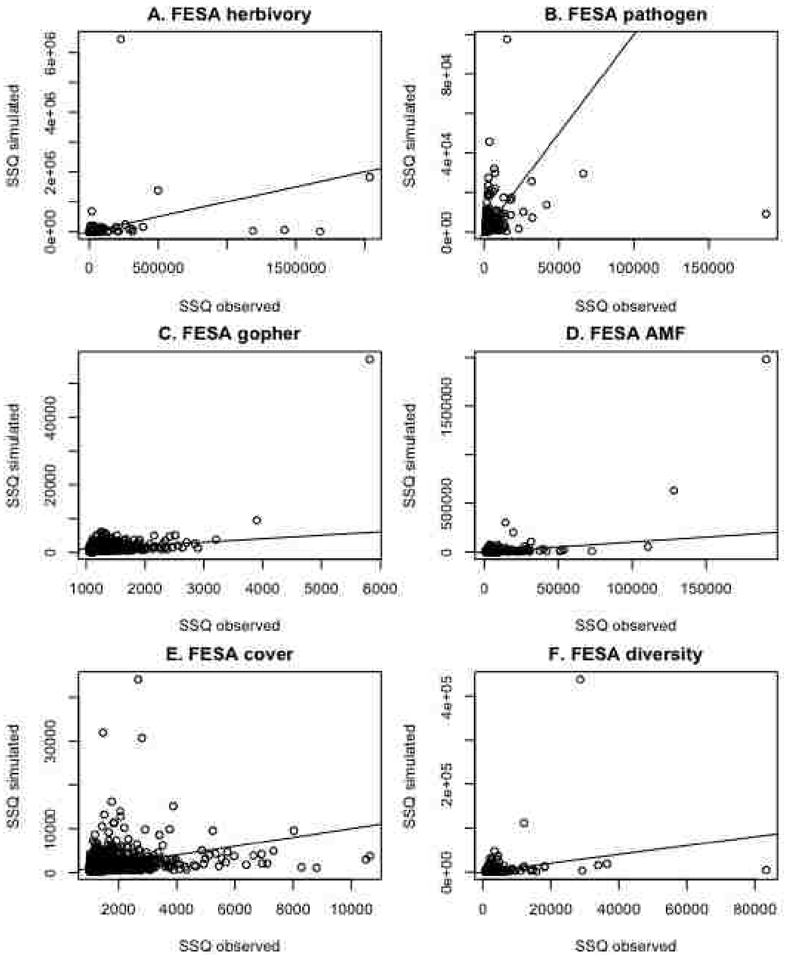
B. FERU pathogen

C. FERU gopher

D. FERU AMF

E. FERU cover

F. FERU diversity


A. FESA herbivory
SSQ simulated
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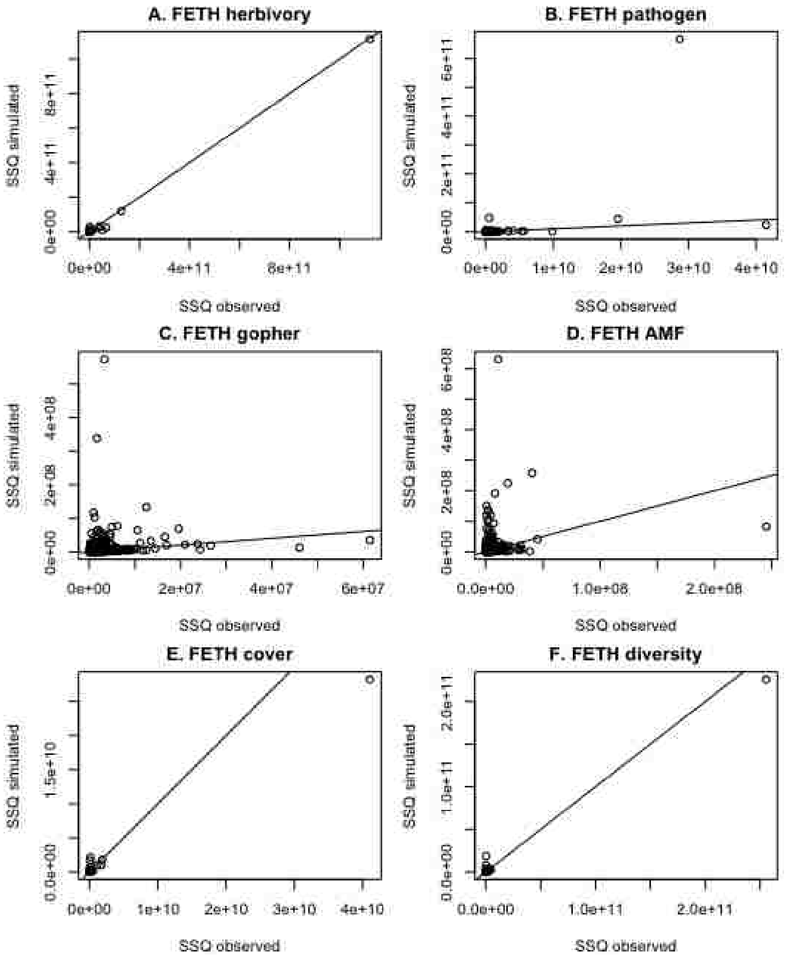
4e+06
6e+06
0
500000
1500000
SSQ observed
B. FESA pathogen
SSQ simulated
0e+00
4e+04
8e+04
0
50000
100000
150000
SSQ observed
C. FESA gopher
SSQ simulated
0
20000
40000
1000
2000
3000
4000
5000
6000
SSQ observed
D. FESA AMF
SSQ simulated
0
500000
1500000
0
50000
100000
150000
SSQ observed
E. FESA cover
SSQ simulated
0
10000
30000
2000
4000
6000
8000
10000
SSQ observed
F. FESA diversity
SSQ simulated
0e+00
2e+05
4e+05
0
20000
40000
60000
80000
SSQ observed


A. FETH herbivory
SSQ simulated
SSQ observed
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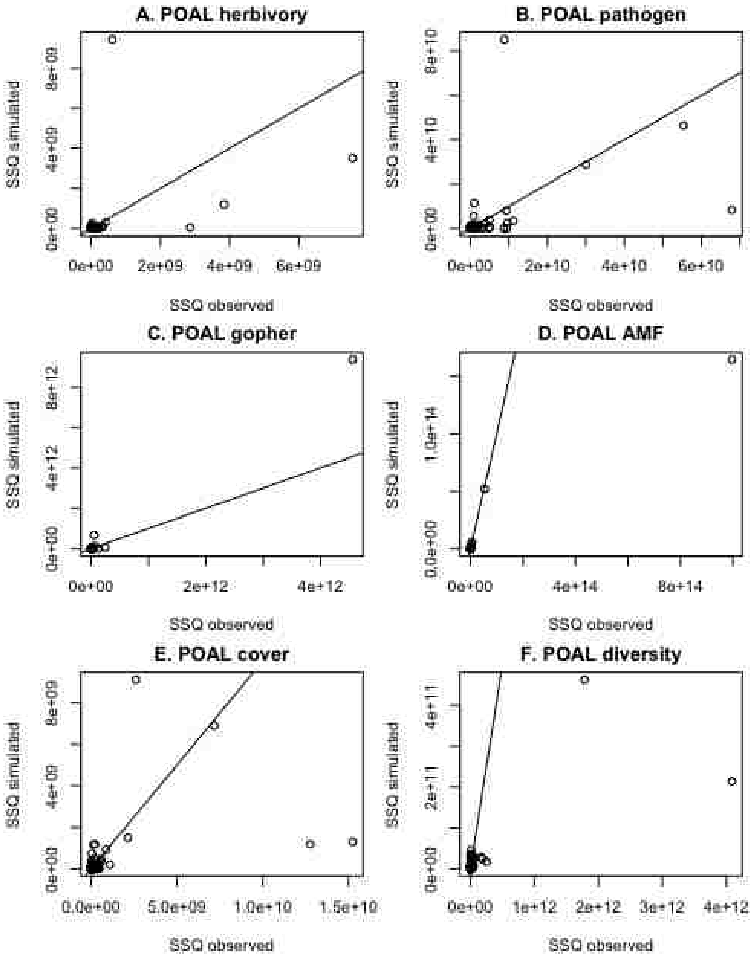
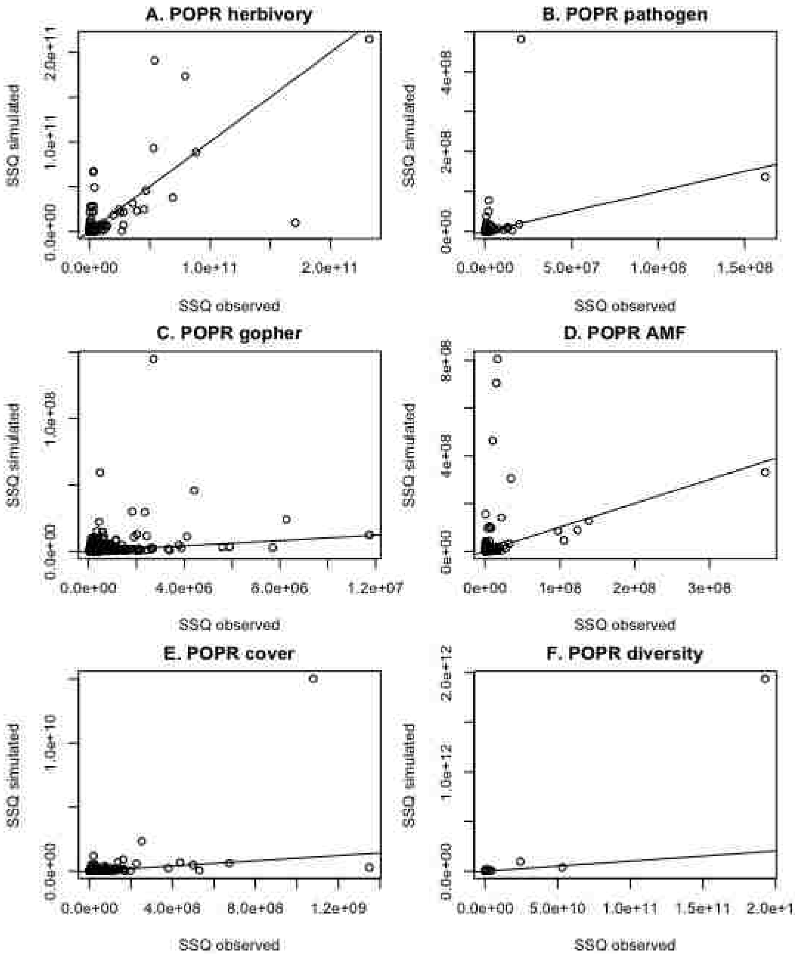
4e+11
8e+11
B. FETH pathogen
SSQ simulated
SSQ observed
0e+00
2e+11
4e+11
6e+11
1e+10
2e+10
3e+10
4e+10
C. FETH gopher
SSQ simulated
SSQ observed
0e+00
2e+08
4e+08
2e+07
4e+07
6e+07
D. FETH AMF
SSQ simulated
SSQ observed
0e+00
2e+08
4e+08
6e+08
0.0e+00
1.0e+08
2.0e+08
E. FETH cover
SSQ simulated
SSQ observed
0.0e+00
1.5e+10
0e+00
1e+10
2e+10
3e+10
4e+10
F. FETH diversity
SSQ simulated
SSQ observed
0.0e+00
1.0e+11
2.0e+11


A. POAL herbivory
B. POAL pathogen
C. POAL gopher
D. POAL AMF
E. POAL cover
F. POAL diversity
SSQ simulated
SSQ observed
0e+00
4e+09
8e+09
2e+09
6e+09
4e+10
8e+10
2e+10
6e+10
4e+12
8e+12
2e+12
0.0e+00
1.0e+14
4e+14
8e+14
5.0e+09
1.0e+10
1.5e+10
2e+11
4e+11
1e+12
3e+12


A. POPR herbivory
SSQ simulated
SSQ observed
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1.0e+11
2.0e+11
B. POPR pathogen
0e+00
2e+08
4e+08
0.0e+00
5.0e+07
1.0e+08
1.5e+08
C. POPR gopher
0.0e+00
1.0e+08
4.0e+06
8.0e+06
1.2e+07
D. POPR AMF
0e+00
4e+08
8e+08
1e+08
2e+08
3e+08
E. POPR cover
0.0e+00
1.0e+10
4.0e+08
8.0e+08
1.2e+09
F. POPR diversity
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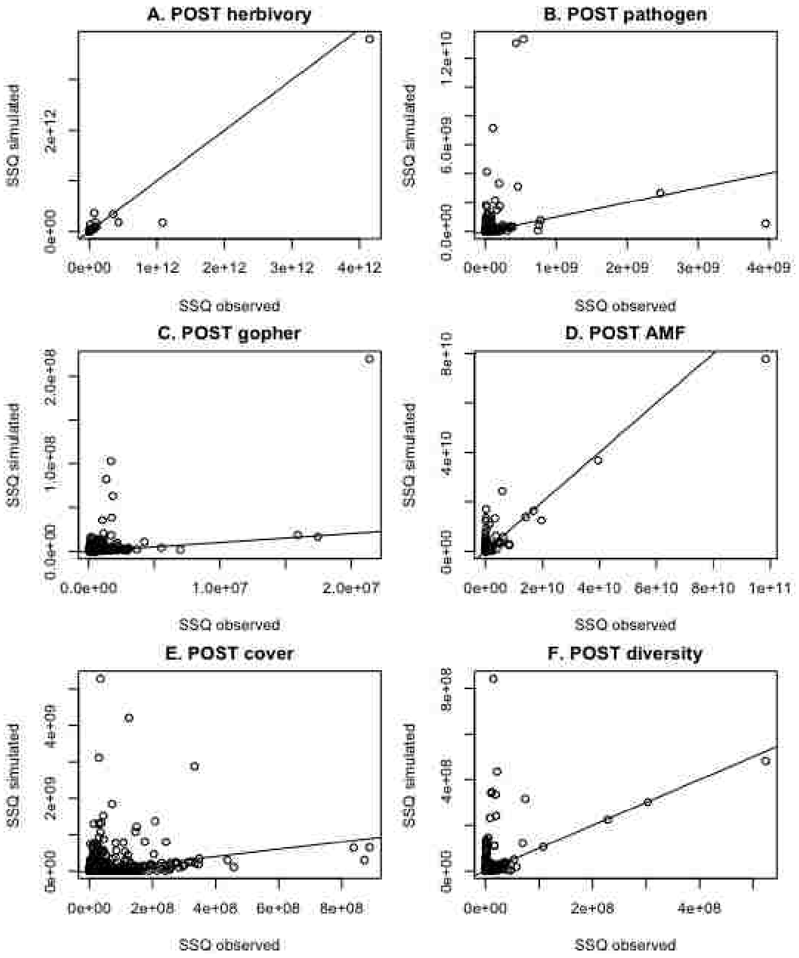
1.0e+12
2.0e+12
5.0e+10
1.0e+11
1.5e+11
2.0e+1


A. POST herbivory
SSQ simulated
0e+00
2e+12
SSQ observed
0e+00
1e+12
2e+12
3e+12
4e+12
B. POST pathogen
SSQ simulated
0.0e+00
6.0e+09
12e+10
SSQ observed
0e+00
1e+09
2e+09
3e+09
4e+09
C. POST gopher
SSQ simulated
0.0e+00
1.0e+08
2.0e+08
SSQ observed
0.0e+00
1.0e+07
2.0e+07
D. POST AMF
SSQ simulated
0e+00
4e+10
8e+10
SSQ observed
0e+00
2e+10
4e+10
6e+10
8e+10
1e+11
E. POST cover
SSQ simulated
0e+00
2e+09
4e+09
SSQ observed
0e+00
2e+08
4e+08
6e+08
8e+08
F. POST diversity
SSQ simulated
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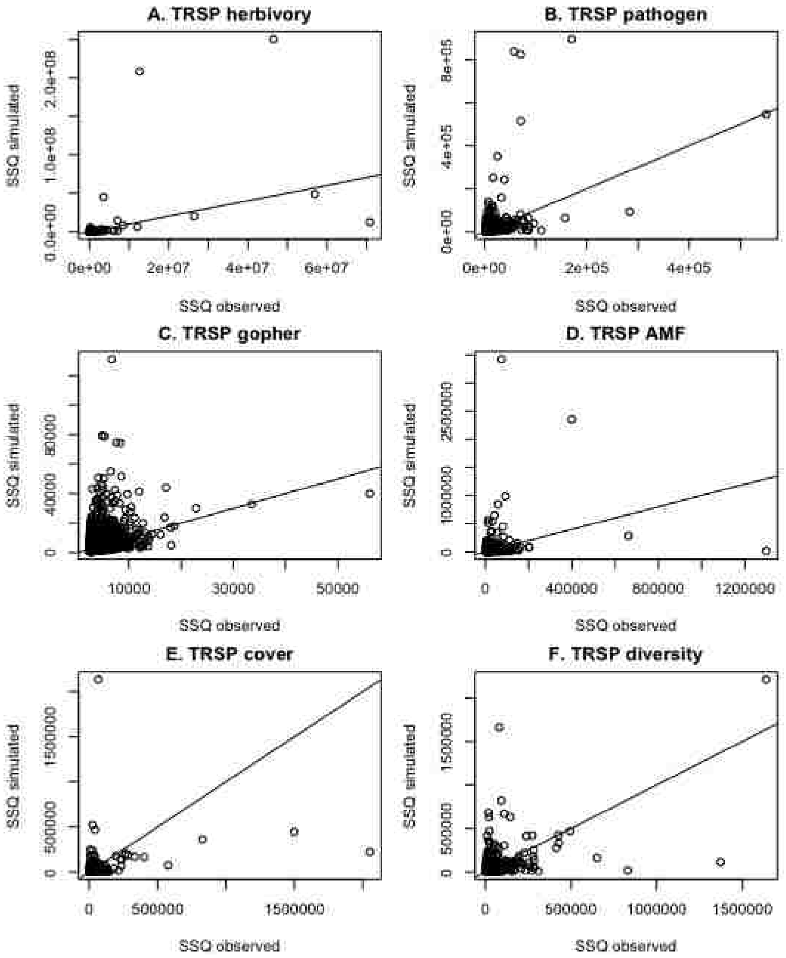
8e+08
SSQ observed
0e+00
2e+08
4e+08


A. TRSP herbivory
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1.0e+08
2.0e+08
0e+00
2e+07
4e+07
6e+07
SSQ observed
B. TRSP pathogen
SSQ simulated
0e+00
4e+05
8e+05
0e+00
2e+05
4e+05
SSQ observed
C. TRSP gopher
SSQ simulated
0
40000
80000
10000
30000
50000
SSQ observed
D. TRSP AMF
SSQ simulated
0
1000000
2500000
0
400000
800000
1200000
SSQ observed
E. TRSP cover
SSQ simulated
0
500000
1500000
0
500000
1500000
SSQ observed
F. TRSP diversity
SSQ simulated
0
500000
1500000
0
500000
1000000
1500000
SSQ observed

Chapter 1 Supplementary material 4.

The following link contains a full table of parameter estimates and model selection with informative table legends.

https://docs.google.com/spreadsheets/d/1Ptv0Cy2OYxrmX9p6GBvUn6tTn_dN4Z89PmISFVNpj7Q/edit?usp=sharing

Chapter 2: Mammalian herbivores restrict the altitudinal range limits of alpine grasses

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Abstract

Species geographic ranges are shifting upward in elevation under ongoing climate change. As these shifts occur, the trailing edges of species ranges may become vulnerable to novel interactions with upwardly encroaching species. The Dobzhansky-MacArthur hypothesis proposed that species' low elevation (or latitude) range limits are constrained primarily by antagonistic species interactions because these environments are less abiotically stressful than the high elevation limits of a species' range, which may be cold, windy, and resource-limited. We tested this theory for three alpine-restricted grass species by planting them below (novel), at (limit), or in the center (core) of their current elevational range and factorially excluding interactions with above- and belowground mammalian herbivores using fences. We monitored plant damage by mammal and insect herbivores as well as plant survival, biomass, and reproduction for three years, then parameterized demographic models to project herbivore effects on plant population growth. The probability and amount of herbivory were greater below range limits and smaller within the core of plants' current ranges, suggesting herbivory could be a factor limiting the focal species range. Plant survival generally increased when aboveground herbivores were excluded. Plants grew largest at novel sites below their current range limits, but only when above- and belowground herbivores were excluded. Reproduction declined at range limits, and the decline intensified with exposure to mammals,

suggesting that herbivory limits seed production available for plant range expansion into low elevation habitat. Our results suggest that if herbivores move upslope in future climates, increased herbivore pressure may cause population declines in alpine plants, potentially triggering local extinction for species that occupy the very peaks of mountains.

Introduction

Antagonistic species interactions have long been hypothesized to limit species distributions (Dobzhansky 1950; MacArthur 1972; Brown 1995; Louthan, Doak, and Angert 2015), but experimental investigations have generally been rare. Dobzhansky (1950) and MacArthur (1972) separately proposed that a species' high elevation/latitude range limit is determined by harsh abiotic conditions, while its low elevation/latitude range limit is set by strong antagonistic species interactions. This hypothesis was designated the "Dobzhansky-MacArthur Hypothesis" or DMH by Brown (1995). The high elevation/latitude prediction of the DMH has garnered broad support (Hobbie and Chapin 1998; J. M. Sunday, Bates, and Dulvy 2011; Jennifer M. Sunday, Bates, and Dulvy 2012; Hargreaves, Samis, and Eckert 2014). For example, plants planted above their elevation limits had greater mortality than plants planted within their range (Klimeš and Doležal 2010). Additionally, plants moved below their elevation range limit and competed against a novel, low elevation plant community often had lower survival, biomass, and reproduction than plants competing against their home range community transplanted into the same low elevation environment (Alexander, Diez, and Levine 2015). However, other antagonisms, such as plant-herbivore interactions, have received less attention than competition as potential mechanisms that restrict range limits in plants.

Understanding the causes of species range limits has become more important as the climate changes and causes species range shifts (Lenoir et al. 2008; Kelly and Goulden 2008; Gottfried et al. 2012; Lenoir and Svenning 2015), creating novel communities. Climate change can directly cause population decline via physiological stress (Cahill et al. 2012) or can alter species interaction outcomes (Tylianakis et al. 2008; Angert, LaDeau, and Ostfeld 2013; Fridley et al. 2016). Less studied is how range shifts associated with climate change create novel communities as species from previously disparate geographic locales come into contact (Alexander et al. 2016). Experimentally forcing species to interact in novel communities can help to predict community dynamics under future climates (Hargreaves, Samis, and Eckert 2014; Alexander et al. 2016).

Plant-herbivore interactions have the potential to restrict the geographic range limits of plants. To do so, the following conditions must be met: (1) Herbivory (plant biomass removed by herbivores) must increase from inside a species' range outward towards its range limit and reach the highest levels at novel sites beyond the range limit. According to the DMH, this pattern in herbivory tracks abiotic stress, such that harsh, low productivity abiotic environments (e.g. short growing-season) have less herbivory than abiotically benign, high productivity environments (e.g. long growing-season; Brown 1995; Louthan *et al.* 2015). Some data support this condition. For example, *Arnica montana* had 75% of leaf area consumed by slugs when transplanted below their elevation range limits, compared to <1% herbivory in their home range (Bruelheide and Scheidel 1999). However, ungulate herbivory was highest at high elevation sites for *Trillium erecta* on a mountain in Quebec, Canada (Rivest and Vellend 2018). Additionally, plant populations from high elevations may be more palatable than those from lower elevations (Pellissier et al. 2014), suggesting that plant species moved below their elevation range limit will be consumed at higher rates by low elevation herbivore communities.

The second criterion is: (2) Exclusion of herbivores increases plant fitness (Louda and Potvin 1995), and this benefit of exclusion increases along the gradient from within, at, and beyond the species range limit. Herbivory generally decreases plant fitness (Maron 1998; Maron and Crone 2006; Agrawal et al. 2012; Lehndal and Ågren 2015). However, the fitness effects of mammalian herbivores (and insects) on plants moved beyond their range have not been investigated, to our knowledge. In the experiments that have been performed, fitness effects of herbivores are difficult to parse because the cross-range transplants have not been pared with manipulations of the herbivore community and/or measurement of plant fitness metrics (e.g. Bruelheide & Scheidel 1999; Rivest & Vellend 2018).

Finally, criterion (3) is that herbivore exclusion should increase plant population growth rates, and at sites beyond the range limit, populations should be inviable ($\lambda < 1$) except when herbivores are excluded. Perhaps the closest example, for any herbivore, supporting this criterion was that large mammalian herbivores reduced population growth of *Hibiscus meyeri* more strongly in arid than mesic sites *within* the species distribution (Louthan et al. 2018). Additionally, insect herbivory on tree cholla cactus decreased with elevation, and the experimental removal of herbivory across an elevation gradient increased population growth rates more so in low than mid or high elevation populations (Miller et al. 2009). Across gradients of productivity and deer grazing, population growth rates of *Vaccinium myrtillus* decreased in more productive and deer-dense habitats, with the lowest population growth in sites with both high productivity and high deer density

(Hegland, Jongejans, and Rydgren 2010). This result suggests that a combination of intense herbivory and high productivity can exclude populations from establishing or persisting across range boundaries. However, ungulate herbivory and disturbance can have the opposite effect. For example, the invasive mustard, *Alliaria petiolata*, had higher population growth rates in the presence (because deer find it inedible) than absence of deer and was predicted to go locally extinct when deer were excluded (Kalisz, Spigler, and Horvitz 2014).

Here, we experimentally manipulated both above- and belowground mammalian herbivores using fencing to limit ungulate and/or fossorial pocket gopher access to alpine plants that were planted within, at, or below their elevational range limits in the West Elk Mountains, Colorado, USA. Alpine-restricted species are interesting case studies for climate change research. As the climate warms, these species cannot move further upslope to escape the heat or novel biotic interactions. Therefore, if altered climate or biotic interactions drive population declines, alpine populations may become locally extinct. We focused on three plant species (*Poa alpina*, *Festuca brachyphylla*, *Elymus scribneri*) that dominate alpine meadows. Prior niche models built with observational data showed decreases in abundance of all three species with increasing gopher disturbance and herbivory (Lynn et al. *Accepted*). We asked: 1) Does mammal and insect herbivory increase from the core habitat towards the range limit and peak at novel sites below species' elevational range limits? 2) Does ungulate or fossorial mammal herbivory reduce plant survival, growth, or reproduction to a greater extent in novel sites beyond the range limit than at the range limit or in the core of the range? 3) Does population growth increase more with than without herbivore exclusion in novel sites versus limit and core range sites?

Methods

Study species

We focused on three native, alpine-restricted grass species: *Poa alpina*, *Festuca brachyphylla*, and *Elymus scribneri.* All three species are caespitose and occur commonly in alpine meadows in the Rocky Mountains (Shaw 2008). Our system includes diverse native ungulate herbivores, including moose (*Alces alces shirasi*), elk (*Cervus elaphus nelsoni*), deer (*Odocoileus hemionus hemionus*), mountain goat (*Oreamnos americanus*), and mountain sheep (*Ovis canadensis canadensis*), as well as cattle, which move up valley seasonally in late August for a brief grazing period. In addition, the northern pocket gopher (*Thomomys talpoides*) creates substantial soil disturbance via mounding and underground tunneling; its disturbance effects peak at ~3200 m a.s.l. (Lynn et al. 2018).

Study sites

We performed experiments in the West Elk Mountains, in which temperature, atmospheric pressure, and plant available N and P decline with elevation, while precipitation increases (Kittel et al. 2002; Dunne, Harte, and Taylor 2003). The regional lapse rate is ~1°C decrease in temperature with ~140 m increase in elevation (Pepin and Losleben 2002). We used previous vegetation surveys (Lynn et al. *Accepted*) to locate experimental sites (sites) in (a) the core range (core), (b) at the range limit (limit), or (c) below the range limit (novel). Novel sites reflected ~2-3°C greater mean annual temperature than the range edge of each plant species, consistent with predicted climate warming for the region (Pepin and Losleben 2002; Rangwala and Miller 2012). The three site types (core, limit, novel) were replicated on three independent mountains for a total of nine sites. Geographic coordinates and elevation of each site can be found in Supplementary material 2 Table S1.

Experimental design

Greenhouse rearing. Focal species were grown from seed in the greenhouse at ~20°C for ~12 weeks at the University of New Mexico. Seeds were collected in 2015 from each core site population. In February 2016, we germinated seeds in flats using Metro-Mix 360 potting soil (sun gro Horticulture, Agawam, MA, USA). Once individuals were 2-6 leaves in size, we transferred them to ~150 ml root trainer pots (Stuewe and Sons, Inc., Tangen, Oregon, USA), in Metro-Mix 360, where they grew until planted into the field experiment. Each pot was top fertilized with ~15 ml of Osmocote Plus 15:9:12 N:P:K pellets (Scotts Miracle-Gro Company, Marysville, OH, USA) and watered three times daily with overhead sprayers (~50 mm per pot). Plants were transported to the Rocky Mountain Biological Laboratory in May 2016 and hardened off in their pots for ~20 d within a fenced area.

Experimental implementation. We used a 2x2 factorial design to allow/exclude aboveground ungulates and allow/exclude belowground fossorial rodents using fencing. The four exclosure treatments were control, aboveground, belowground, and both. Gophers were excluded by trenching and inserting wire mesh ~20 cm into the ground around a plot. Photographic evidence suggested this method of exclosure was successful, as gopher disturbances would abut but not enter the plots. Ungulates were excluded using 40 cm x 40 cm fences of 20-gauge chicken wire that was 30 cm tall. At each site, we marked 20 plots (30 cm x 30 cm) and randomly planted one individual of each species into an equilateral triangle at 15 cm spacing between individual plants. All vegetation was removed prior to planting and weeded monthly during the growing season until harvest. Herbivory treatments were randomly assigned to plots within a site. Each of the four herbivory treatments was replicated in five plots per site. Experimental set-up occurred during 22 June - 20 July 2016.

Repeated measures responses. Beginning in August 2016, we took monthly measurements of plant size and foliar damage by ungulate and insect herbivores. We included insects, although they were not manipulated, to capture all aboveground herbivory. Plant size was determined by counting the number of vegetative tillers and measuring the maximum vegetative height of each plant to the nearest mm. Additionally, we counted the number of inflorescences to estimate reproduction, but we collected them prior to anther dehiscence to limit gene transfer at novel sites. We took visual percentage estimates of the amount of damage present on each plant. Small, light-colored pockmarks were classified as damage by haustellate insects (aphids, leafhoppers, etc.). Chewed individual leaves were classified as mandibulate insect damage. Grazing by ungulates was identified by even clipping across the top of the plant. Gopher disturbance/ herbivory was recorded when characteristic mounding, eskers, or tunneling was observed (Lynn et al. 2018).

Harvest responses. We harvested plants from 14 – 27 August 2018. Immediately prior to harvest, all plants were assessed for size and damage as described in *Repeated measures* in order to provide allometric equations to estimate biomass in prior sampling periods. Plant aboveground biomass was cut at the meristem just below the soil surface, placed in a labeled paper bag, and transported to the lab. Plant material was immediately separated into litter and live biomass in the lab. All biomass was dried for 48 h at 60°C prior to weighing to the nearest 0.001 g on a mass balance (Mettler-Toledo MS104S and PL303, Columbus, OH, USA).

Demographic data

In 2015, we set up five 1 m x 5 m permanent plots in natural populations of the focal species' core range. We marked every individual with a metal tag and measured height (nearest mm), tiller number, and inflorescence number in August during 2015 - 2018. Survival was determined for marked individuals in each year. New recruits within the plots were identified and marked each year. In 2015, we sampled an additional 30 individuals of each focal species outside the permanent plots to estimate average seed production per inflorescence for each species without affecting recruitment potential.

Statistical analysis

All analyses were performed in the R programming language (R Core Team 2018).

Does mammal and insect herbivory increase from the core habitat towards the range limit and peak at novel sites below species' elevational range limits?

We used a model selection approach (Anderson 2008) to analyze the effects of fencing treatments and elevation on the presence and amount of herbivory across species. We compared eight models using model selection procedures (Tables S2 & S3): 1) null with random effects only (described below); 2) full model with interactions between above- and belowground exclosures and site; 3) interaction between aboveground exclosure and site; 4) interaction between belowground exclosure and site; 5) interaction between above- and belowground exclosure; 6) aboveground main effect only; 7) belowground main effect only; and 8) site main effect only. Models with interactions of variables are full factorial and also include the main effects of the interacting variables.

We first investigated how treatments affected the presence of herbivory, then removed cases of no damage and investigated how damage amount by insect, mammal, or both damage classes varied with treatments. The "all damage types" models can be interpreted as the combined insect and mammal damage categories, weighted by the higher frequency, but lower intensity, insect damage (551 records of insect damage versus 118 records of mammal damage). We analyzed all observations together with a species random effect, and then for each species separately. We used observation periods (July, August, and September, by year) as a random effect along with mountain identity. Additionally, for models of damage presence, we used plant individual as a random effect to account for repeated measures. However, in many instances, individuals were damaged only once, so models of damage amount could not accommodate an individual random effect. We only observed characteristic mammal damage to plants with aboveground exclosure in six of 118 damage estimates across all species, therefore aboveground exclosure was not used in models of mammal damage. Model selection procedures for mammal damage only included models 1, 4, 7, and 8. The hierarchical random effects structure for the models was individual nested in mountain identity.

Generalized linear mixed effects models were fit with maximum likelihood estimation using “glmer” in the *lme4* package (Bates et al. 2015). The presence/absence of damage used a binomial distribution and logit link function, while damage amount was Poisson distributed with a natural log-link function. Best models from a candidate set were chosen based on within-sample predictive error, scored by *AICc* values derived from the *MuMIn* package (Bartoń 2018). We used *AICc* to derive model weights, which can be interpreted as probabilities that a model is the best representation of reality, given the candidate model set. Finally, we calculated marginal (fixed effects) and conditional (fixed and random effects) likelihood R^2 values for each model using the “rsquared” function in the *piecewiseSEM* package (Lefcheck 2016).

Does ungulate or fossorial mammal herbivory reduce plant survival, growth, or reproduction to a greater extent in novel sites beyond the range limit than at the range limit or in the core of the range?

If ungulate and fossorial mammal herbivory depress plant fitness, then individuals in exclosures will have higher survival, biomass, and/or reproduction than controls without exclosures. We analyzed individual survival, biomass, and inflorescence number (for reproduction) using the same model selection procedures described for question 1, and the following modifications. We analyzed survival at harvest (0/1 - did the individual survive until the end of the experiment?) with a binomial distribution and logit-link function. Models of survival included mountain identity as the random effect, and also included a species random effect when all focal plant species were analyzed together. Inflorescence number was summed within a year to obtain total reproduction per individual by year and was Poisson distributed. Models for inflorescence number included mountain identity and sample period random effects, but not individual plant because only a single cumulative measure was used per individual per year.

To estimate biomass for individuals throughout the experiment, we constructed allometric equations using tiller number and maximum height to predict live biomass at final harvest using the base package "lm" function. Four models to predict plant biomass were compared based on *AICc*: i) interaction between height and tiller number; ii) additive model of height + tiller number; iii) height only; iv) tiller number only. Best models varied by species: *E. scribneri* and *F. brachyphylla* were best predicted by model (i) (R^2=0.68 and 0.80, respectively), and *P. alpina* by the additive model (ii) (R^2=0.64). Models of treatment effects on repeated estimates of biomass included date as a fixed effect and included random effects for mountain identity and individual plant to account for temporal autocorrelation in plant size.

Does population growth increase more with than without herbivore exclusion in novel sites versus limit and core range sites?

We briefly describe the population models but provide full details in Supplementary material 1. The vital rate and matrix projection model (MPM) methodology closely followed Compagnoni *et al.* (2016) and Elderd & Miller (2015). We fit models for five vital rates: survival, growth, flowering probability, number of inflorescences produced, and recruitment. All vital rates were size dependent, except for recruitment which was predicted using inflorescence numbers and the estimated average seed produced within a plot. Tiller number was our size metric and is a discrete size class, justifying the use of size class MPMs. Size-dependent vital rates were fit as linear models with intercept and slope terms relating the rate to tiller number. Vital rates were parameterized for natural populations separately from experimental populations, where all size-dependent vital rates were fit for each treatment combination except for the full factorial (site x above + site x below = 9 treatments), while recruitment was assumed to be the same as in natural populations because allowing recruitment to occur in experiments that moved plants outside their natural range would be unethical. Biotic limitations on recruitment at range limit or novel sites (e.g., herbivory on seedlings) make our models conservative.

All vital rate calculations were parameterized with Bayesian estimation in JAGS (Plummer 2003) with “R2jags” (Su and Masanao Yajima 2015). We used the MPMs to estimate deterministic population growth rates (λ) for the natural populations and experimentally manipulated plants with either aboveground fences or belowground fences. We estimated λ (via the dominant eigenvalue of the matrix) by taking 1000 random draws from the 90% credible posterior distributions of vital rate parameters, thereby fully leveraging the power of Bayesian posteriors (Hobbs and Hooten 2015).

The population models should be interpreted cautiously for two reasons: 1) Data for vital rates in experimental treatments were limited, given the maximum number of individuals for any one of the 9 treatments was 30, creating a large amount of uncertainty in parameter estimates. 2) The full range of focal plant size in nature was not reflected in experimental populations. Importantly, experimental individuals were, on average, larger than naturally occurring plants, and the experiments did not include seedlings, reducing the accuracy of interpolations of our results to natural populations.

Results

Does mammal and insect herbivory increase from the core habitat towards the range limit and peak at novel sites below species' elevational range limits?

Herbivory increased from within the focal species core range down towards limit then novel sites (Figure 1, criterion 1). Percentage damage strongly increased for all herbivore classes from the core, limit, then novel sites. For instance, across all damage classes and species, individuals below their range experienced 142% more damage than plants grown in core sites and 68% more damage than plants at range limit sites (Fig 1a). Generally, insect damage was highest at novel sites, while range limit sites had less damage than core sites across all species, especially in *E. scribneri* (Figure 1b). Consistently, mammalian damage was lowest in core sites, increased at the range limit (by ~65%), and was greatest at novel sites, which had 154% more damage than at core sites (Figure 1c). Mammal damage was >560% greater than insect damage (Figure 1b,c). Across all species, mammalian damage in control, novel sites was >800% greater than insect damage in control, novel sites. In control treatments (no exclosures), the probability an individual was consumed was lowest in the core sites and generally increased towards novel sites (Figure 1d).

All species. Fencing treatments altered the amount of damage experienced by an individual, but in opposite directions depending on what category of damage was analyzed (by model selection; Supplementary material 2 Table S2; Figure 2). For all damage types, damage increased from core to limit and novel sites and was 30% greater for plants without exclosures than with aboveground exclosure (R^2=0.89; all reported R^2 are conditional; Figure 2a). Insect damage was 53% greater for individuals with aboveground exclosures of mammals than in controls (R^2=0.8 Figure 2b). Finally, mammalian damage increased from core sites towards limit and novel sites and aboveground damage in belowground exclosures was 12% and 39% greater than controls in novel and limit sites, respectively (R^2=0.91; Figure 2c).

Elymus scribneri. Fencing treatments generally reduced damage as expected, except for insect damage, and interestingly, belowground fencing increased, rather than decreased, aboveground damage. Across all damage types, aboveground fencing reduced damage by 14% in *E. scribneri* (R^2=0.89; Figure 2a). Insect damage on *E. scribneri* in aboveground exclosures was 38% higher than without exclosures, and this effect was greatest at novel sites (R^2=0.81; Figure 2b). Belowground exclosures increased mammal damage to leaves by 41% compared to individuals without belowground exclosures, and this effect was greatest in novel sites (R^2=0.82; Figure 2c).

Festuca brachyphylla. Fencing treatment effects on *F. brachyphylla* damage were idiosyncratic. Across all damage types, individuals of *F. brachyphylla* with aboveground exclosures had reduced damage compared with fenced individuals, and this effect was largest (94% greater) at novel sites (*R^2*=0.94; Figure 2a). Additionally, at the core sites for all damage types, plants with both or control treatments had reduced damage compared to those with aboveground or belowground fences, due to insect damage. Insect damage was lowest at the range limit sites and was highest with aboveground fencing on *F. brachyphylla*, except at core sites, where belowground fences had the highest insect damage followed by aboveground fences (*R^2*=0.84; Figure 2b). Mammal damage on *F. brachyphylla* increased from core to range limit sites and was highest at novel sites (*R^2*=0.97; Figure 2c).

Poa alpina. Damage on *P. alpina* increased from core towards limit then novel sites, and both fencing treatments tended to reduce damage. For all damage types on *P. alpina*, damage increased from core towards range then novel sites, and fencing treatments had little effect on damage amount at the core and novel sites, but at the range limit sites, plants with aboveground exclosures experienced 232% less damage than those without (*R^2*=0.93; Figure 2a). Insect damage on *P. alpina* decreased from novel to limit to core sites. Additionally, insect damage was 95% higher with aboveground exclosures than without (*R^2*=0.83; Figure 2b). For *P. alpina*, damage by mammals was lowest in core sites, followed by novel sites, and damage peaked at the range limit (*R^2*=0.96; Figure 2c). Additionally, novel and core sites experience less damage with belowground exclosures than without, while range limit sites experience more damage with belowground exclosures than without (Figure 2c).

Does ungulate or fossorial mammal herbivory reduce plant survival, growth, or reproduction to a greater extent in novel sites beyond the range limit than at the range limit or in the core of the range?

Herbivory effects on survival, biomass, and reproduction generally followed expectations from criterion 2, in that excluding herbivores increased fitness estimates the most in novel sites and the least in core sites (full model results provided in Supplementary material 2 Table S3).

All species. The probability an individual survived was highest at core sites with aboveground exclosures (98.8 versus 95.7% without), followed by range limit sites with aboveground exclosures (98.7 versus 96.3% without), then novel sites had higher survival without aboveground exclosures (97.6 versus 96.9% with; R^2=0.24; Figure 3a), though these differences seem only marginally biologically significant. Additionally, the reduction in biomass from exposure to all herbivores versus having all herbivores fenced out was greatest in novel and limit sites compared to core sites (40%, 63%, and 28%, respectively; (R^2=0.63; Figure 4a). Across species, inflorescence production was lowest at range limit sites and the effect of fencing was small within sites (R^2=0.95; Figure 5a).

Elymus scribneri. In the presence of herbivores, survival probability of *E. scribneri* was highest in their core range with aboveground exclosures (90 versus 79% without), lowest at the range limit without aboveground fencing (50 versus 86% with), then novel sites flipping the effect of having aboveground fences (54 versus 76% without; R^2=0.2; Figure 3b). Reductions in *E. scribneri* biomass when aboveground herbivores were allowed access was greatest at range limit and novel sites (74 and 39%, respectively) versus core site, which had a 20% reduction (R^2=0.5; Figure 4c). *Elymus scribneri* inflorescence number was lowest at range limit sites, followed by novel sites (R^2=0.6; Figure 5b). There was high variance around inflorescence production for *E. scribneri*, but at the novel and core sites, individuals grown without aboveground exclosures had the lowest inflorescence production compared to other treatments, while both exclosures generally increased inflorescence number across sites (Figure 5b).

Festuca brachyphylla. Survival of *F. brachyphylla* was higher with above- or belowground exclosure than without (R^2=0.25; Figure 3c), and these models were indistinguishable based on *AICc* (Supplementary material 2 Table S3). The greatest reductions in biomass with belowground herbivore access occurred at range limit (46%) and novel sites (23%) versus in their core range (18%; R^2=0.43; Figure 4d). Every exclosure treatment had higher inflorescence production than control plants in novel and limit sites for *F. brachyphylla*, while this pattern was reversed at core sites where control and belowground exclosure plots had higher inflorescence production than the two treatments with aboveground fencing (R^2=0.87; Figure 5c). Inflorescence production was on average lowest in limit sites and highest in cores sites (Figure 5)c.

Poa alpina. Survival of *P. alpina* was highest with aboveground exclosures, and no other treatment explained variation in survival (R^2=0.27; Figure 3d). As with the other species, *P. alpina* had the greatest biomass on average in the novel sites, and herbivore access of all types decreased biomass by 36%, 35%, and 27% from novel to limit to core sites (R^2=0.39; Figure 4b). Again, inflorescence production was lowest on average at range limit sites for *P. alpina*, followed by core then novel sites, and across sites, control individuals produced the fewest inflorescences (R^2=0.72; Figure 5d).

Does population growth increase more with than without herbivore exclusion in novel sites versus limit and core range sites?

Surprisingly, population model results did not support our criteria or match individual fitness responses. We again caution that this may be due to data limitations (see methods), particularly because all estimates of λ were not only lower than those for natural populations but also less than 1. For instance, *E. scribneri* λ was lowest in novel habitats with aboveground exclosures while it was highest in the core of its range with aboveground exclosures (Figure 6a). Predicted population growth was highest across all the fencing treatments in the core of *E. scribneri*'s range, followed by the limit then novel sites. *Festuca brachyphylla* and *P. alpina* had the highest λ in novel sites without exclosures, exactly contrary to our criteria (Figure 6b,c). Both of these species also had their lowest λ in the core of their range, where aboveground exclosure increased λ compared to control and belowground populations at the core sites (Figure 6).

Discussion

We provide experimental evidence that herbivory can contribute to low elevation range limits of alpine-restricted grass species. In line with our first criterion, herbivore damage increased from the core of the species' range towards its' limit and beyond. Thus, observations on natural herbivory support the DMH prediction that individuals occupying lower elevation environments experience greater intensity of biotic interactions. Second, our experiments confirmed criterion 2, whereby mammal herbivores depressed plant fitness more in the novel and limit sites than in the core of their range, suggesting individuals would have higher survival, growth, and/or fecundity in these habitats in the absence of mammal herbivory. This work supports a growing body of evidence that species interactions can affect range dynamics under a changing climate (Alexander, Diez, and Levine 2015; Louthan et al. 2018).

Herbivory increased from within to outside of species' ranges

As in our study, damage by herbivores often increases with warm temperature associated with elevational (Bruelheide and Scheidel 1999; Pellissier et al. 2014; Moreira et al. 2018) and latitudinal gradients (Pennings & Silliman 2005; Baskett & Schemske 2018; but see Moles *et al.* 2011; Lynn & Fridley 2019). Favorable conditions for herbivores at low elevation can increase their abundance (Descombes et al. 2017), which acts as a selective force for lower palatability of plants towards low elevation. Our alpine plants moved below their range limits are not likely adapted to high herbivory environments (Grime 2006), and may be more palatable than resident plants at low elevations. Past work has shown that plant palatability increases and defense decreases with elevation for both plant populations (Pellissier et al. 2014, 2016) and communities (Descombes et al. 2017; Callis-Duehl et al. 2017). Additionally, direct temperature effects on increasing development and metabolic rates of insect herbivores (Irlich et al. 2009; Barrio, Bueno, and Hik 2016) and temperature effects on mammal foraging (Aublet et al. 2009) could lead to higher consumption at low elevation. Other possibilities include longer exposure of plants to herbivores, as there are more snow-free days towards lower elevations (Dunne, Harte, and Taylor 2003). To our knowledge, this is the first study to find that plants planted below their elevation range limits experienced greater mammalian herbivory than individuals in their core elevation range. Also, mammal herbivory showed stronger increases from core to limit and novel sites than insect herbivory, owing to the larger magnitude of damage caused by mammal herbivory. In contrast to our finding, tall forb species transplanted towards their high elevation range margin experienced more herbivory than those moved to their low elevation range margin (Kaarlejärvi and Olofsson 2014).

A side-effect of our fencing treatments was that insect herbivory increased under mammal exclosures. Excluding belowground herbivory also often promoted aboveground herbivory, suggesting plants undamaged belowground may be more attractive to aboveground herbivores. There are a few hypotheses to explain these results. First, insects may prefer plants that are unperturbed by mammal herbivores. For instance, excluding reindeer in willow patches increased the density of common insect herbivores in Finland (Den Herder, Virtanen, and Roininen 2004). Additionally, insect folivory (Lind et al. 2012) and abundance (Huntzinger, Karban, and Cushman 2008) can be depressed by natural browsing. Second, exclosures may limit bird predation of insects, creating islands of resources free of predation for insects (Bernays and Graham 1988). For example, leaf damage and insect abundance increased on sugar maple when bird predators were excluded (Strong, Sherry, and Holmes 2000), and white oak saplings had higher insectivorous leaf damage and lower growth when birds predators were excluded (Marquis and Whelan 1994). However, increased insect herbivory in aboveground exclosure plots is unlikely to affect our results, given the low amount of insect damage relative to mammalian damage (~10% versus 40% of leaf area, respectively) and evidence that aboveground exclosure generally increased survival, growth, and reproduction of our focal species. Another interesting finding was that aboveground herbivory increased with belowground exclosures, suggesting that aboveground and belowground herbivores may compete, possibly by inducing defenses (van Dam and Heil 2011).

Herbivore exclusion increased plant fitness

When mammalian herbivores were excluded, all species produced more biomass below their range than in their core range. This result is in line with past theory (Dobzhansky 1950; MacArthur 1972; Brown 1995; Louthan, Doak, and Angert 2015) predicting that the abiotic conditions at low elevations (e.g. longer growing season) are more conducive to growth in the absence of antagonistic species interactions, such as herbivory. However, increased herbivory towards range limits and beyond reduces plant fitness more so than in the core range. It is not uncommon to find greater biomass in plant populations and communities with ungulate exclusion (e.g. Maron and Pearson 2011, Clark et al. 2012, Evans et al. 2015), but the increased growth of individuals planted below their range under mammal exclusion is a novel finding. Additionally, low biomass at *F. brachyphylla's* low elevation range limit suggested depressed fitness near the range margin that could depress its expansion to yet lower elevation sites (Hargreaves, Samis, and Eckert 2014). Interestingly, gopher density was near its peak around elevations of *F. brachyphylla*'s range limit (Lynn et al. 2018), and past work suggests grasses are more negatively affected by gopher disturbance than forbs (Sherrod, Seastedt, and Walker 2005), pointing to gophers as key in limiting alpine grass distributions in this system.

Survival across species did not conform to criterion 2, in that survival was not lowest in novel habitats when exposed to herbivores. In fact, for *E. scribneri* survival at novel sites was lower with aboveground fences than in controls. This depressed survival with aboveground exclosures in *E. scribneri*'s novel range may be due to greater insect herbivory in this treatment relative to the belowground fences or controls (Figure 2b). But this relationship flipped at range limits sites for *E. scribneri*, where access to aboveground herbivores greatly decreased survival, which in part supports our second criterion. That mammalian herbivores had the greatest effect on survival at the range limit again suggests that reduced fitness at range margins may be a key factor in limiting species' elevation distribution. The two other species survival did not change across sites but did survive better without herbivores. As noted above, grasses are particularly vulnerable to gopher disturbance (Sherrod, Seastedt, and Walker 2005).

Surprisingly, inflorescence production for every species was lowest at range limits sites, which suggested that environmental constraints at the species' range limit may reduce focal species fecundity, and lower inflorescence production at the limit was exacerbated with mammal access to individuals. Mammal herbivory often reduces plant reproduction (Knight 2003; Gómez 2005; Pringle et al. 2014). Additionally, plants growing at their low elevation/latitude range limits can have lower reproductive output than interior populations (Levin and Clay 1984; Stinson 2005; Bontrager and Angert 2016). Herbivore imposed declines on inflorescence production was greatest at limit and novel sites, suggesting fitness limitations imposed by the abiotic and biotic environments at the range limit can act synergistically with dispersal limitations by restricting the number of dispersal units (seeds) most likely to expand a species range (Angert et al. 2018). Further experimentation that considers how reproductive output interacts with propagule pressure and recruitment at range limits is required to assess this hypothesis fully.

Treatment effects on population growth did not reinforce other results

We found little evidence that mammal herbivore exclusions influenced plant population growth rates, but these results are tenuous. Sample size limitations made accurate estimates of vital rate parameters difficult for the experimental plants. For instance, estimates of vital rate transitions (e.g. growth and survival to the next year) may have been highly inaccurate because of undue influence of a few plants. We also had an unrealistic size range of focal individuals, which skewed towards larger plants than those found in nature. This could affect size based vital rates by not providing accurate estimates of the intercept, which would be most influenced by plants towards the low size range. As a check, we would expect population growth rates from the core of the species range without exclosures to be close to estimates from natural populations, which was not the case. Given these caveats, population models did not reinforce results from the other analyses. For instance, *F. brachyphylla* and *P. alpina* populations without exclosures in novel elevations were predicted to have the highest population growth rates of any site-exclosure treatment combination, although these populations usually had the lowest biomass, survival, and inflorescence number. An exception was that in congruence with survival results, *E. scribneri* population growth was lowest in novel sites with aboveground exclosure, which had the highest rates of herbivory. Though our approach to demography had data limitations, we suggest that an exciting area of future research will involve creating experimental populations across species' geographic ranges to mimic altered abiotic or biotic interactions that would be expected under future climates.

Conclusions

Mammal herbivory generally satisfied the conditions expected for a species interaction to limit a species range. Mammal herbivory increased from sites at the core of species' ranges to their range limits and was greatest on individuals moved outside their natural range. Mammal exclosures increased plant fitness the most in sites beyond their range edges. Our population modeling exercise, however, was inconclusive given data limitations. Taken together, if mammals shift their foraging activity upslope with climate change (Büntgen et al. 2017), we expect focal alpine plant species to have reduced fitness and potentially face local extinctions as a result of this intensified herbivory and the lack of land available for migration.

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Figures

Chapter 2 Figure 1. Amount (% leaf area) and presence (% of individuals) of damage by herbivores in control (no exclosures) plots across core, limit, and novel sites (predicted mean and s.e.). Estimates were derived from best models determined by model selection (full results, Supplementary material 2 Table S2). Blue color refers to species analyzed all together with a species identity random effect. Species were "E. s."= *E. scribneri*, "F. b."= *F. brachyphylla*, or "P. a."= *P. alpina*. (a) The all damage panel is insect and mammal damage together. (b) Insect damage only, (c) Mammalian aboveground damage, (d) Presence of any damage (% individuals damaged).

Chapter 2 Figure 2. Treatment effects on herbivore damage amount (% leaf area) by type of herbivory (predicted mean and s.e.). "all"= all species modeled together with plant species as a random effect, "E. s."= *E. scribneri*, "F. b."= *F. brachyphylla*, and "P. a."= *P. alpina*. (a) "All damage types" is insect and aboveground mammal damage combined, "control" lacked exclosures, "below" had belowground exclosures, "above" had aboveground exclosures, and "both" had both. (b) "Insect damage" only; the treatment legend in (a) applies to panel b. In panel (c) "Mammal damage" the "all", "E. s.", and "P. a." included belowground exclosures in the best model, while "F. b." did not (indicated by black symbols). Estimates for mean and s.e. were derived from best models determined by model selection (full results in Supplementary material 2 Table S2).

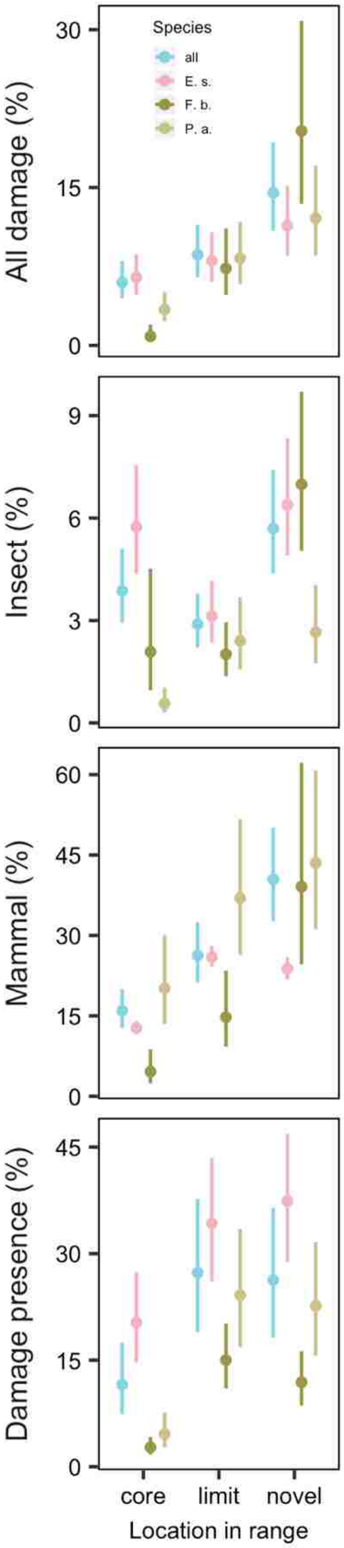
Chapter 2 Figure 3. Treatment effects on probability an individual survived to the end of the experiment varied among the grass species. Panels (a) and (b) share a legend for aboveground ("Above") exclosures, where "no" lacked exclosures and "yes" had exclosures. Estimates of the predicted mean and s.e. were derived from best models determined by model selection (full results, Supplementary material 2 Table S3) and the best models differed for each focal species. (a) Best model results for all species together with the random effect of species identity. (b) Results for *E. scribneri*. (c) Results for *F. brachyphylla* had two best models each with just the main effect of above- or belowground exclosure. (d) Results for *P. alpina* only had aboveground exclosures.

Chapter 2 Figure 4. Treatment effects on biomass production of species over the experiment's length (predicted mean and s.e.). The legend in panel (b) applies to panel (a), and "control" lacked all exclosures, "below" had belowground exclosures, "above" had aboveground exclosures, and "both" had both. Panels (a)-(d) represent results for all species analyzed together and the different focal species. Estimates were derived from best models determined by model selection (full results Supplementary material 2 Table S3) and were different for each focal species.

Chapter 2 Figure 5. Treatment effects on total inflorescence number (predicted mean and s.e.). The legend in "all" applies to each panel. In the legend, "control" lacked any exclosures, "below" had belowground exclosures, "above" had aboveground exclosures, and "both" had both. Panels (a)-(d) represent results for all species analyzed together and the different focal species. Estimates were derived from best models determined by model selection (full results Supplementary material 2 Table S3). "all"= all species modeled together with group effect, "E. s."= *E. scribneri*, "F. b."= *F. brachyphylla*, and "P. a."= *P. alpina*.

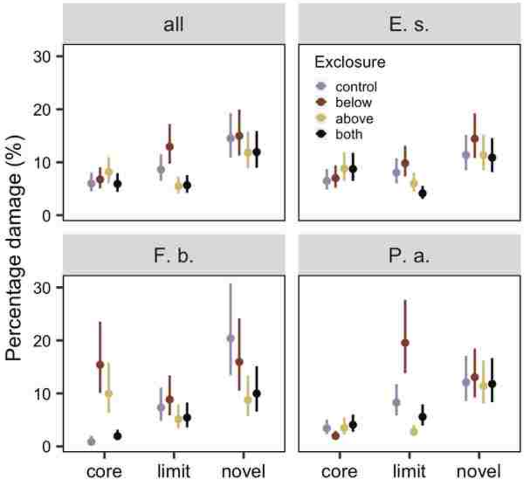
Chapter 2 Figure 6. Population growth rates of natural and experimental populations. Estimates are of mean and standard deviation of 1000 draws thinned to the 75% posterior credibility interval of lambda (λ). In the legend, “control” lacked any exclosures, “below” had belowground exclosures, and “above” had aboveground exclosures. (a)-(c) represent differ species.

Chapter 2 Figure 1.

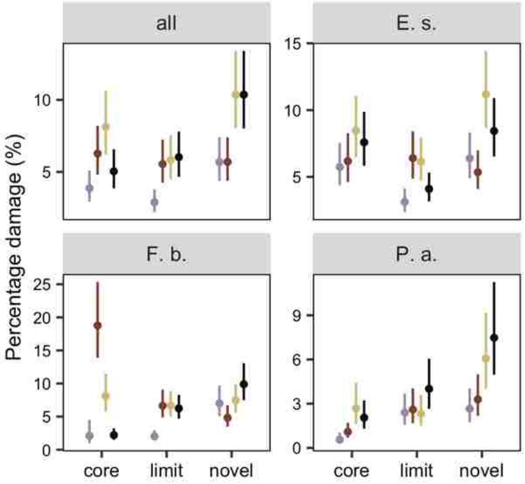


Chapter 2 Figure 2.

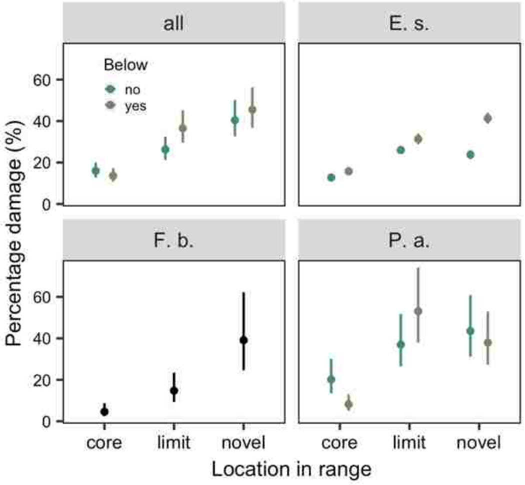
(a) All damage types



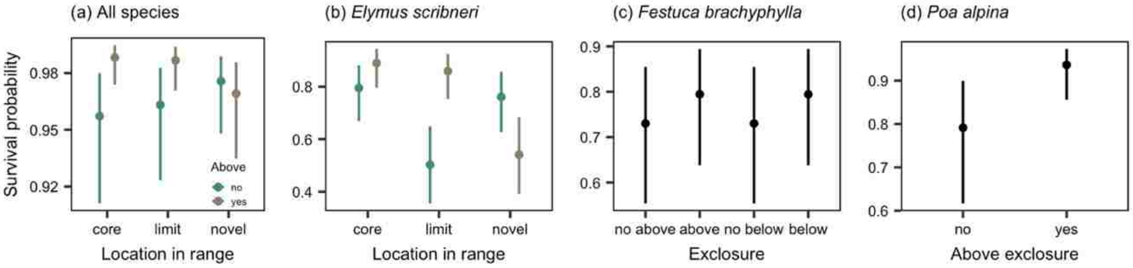
(b) Insect damage



(c) Mammal damage

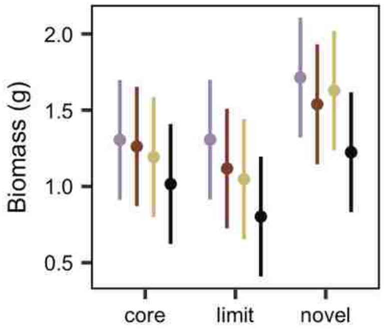


Chapter 2 Figure 3.

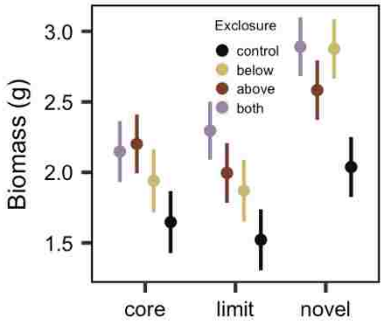


Chapter 2 Figure 4.

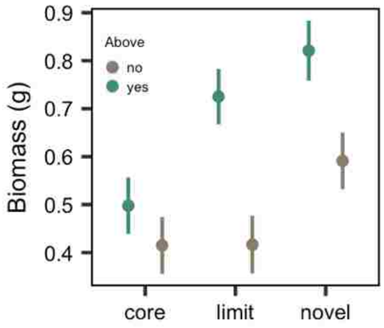
(a) All species



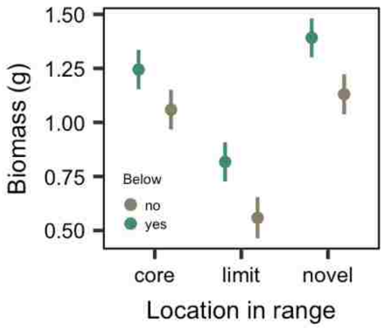
(b) *Poa alpina*



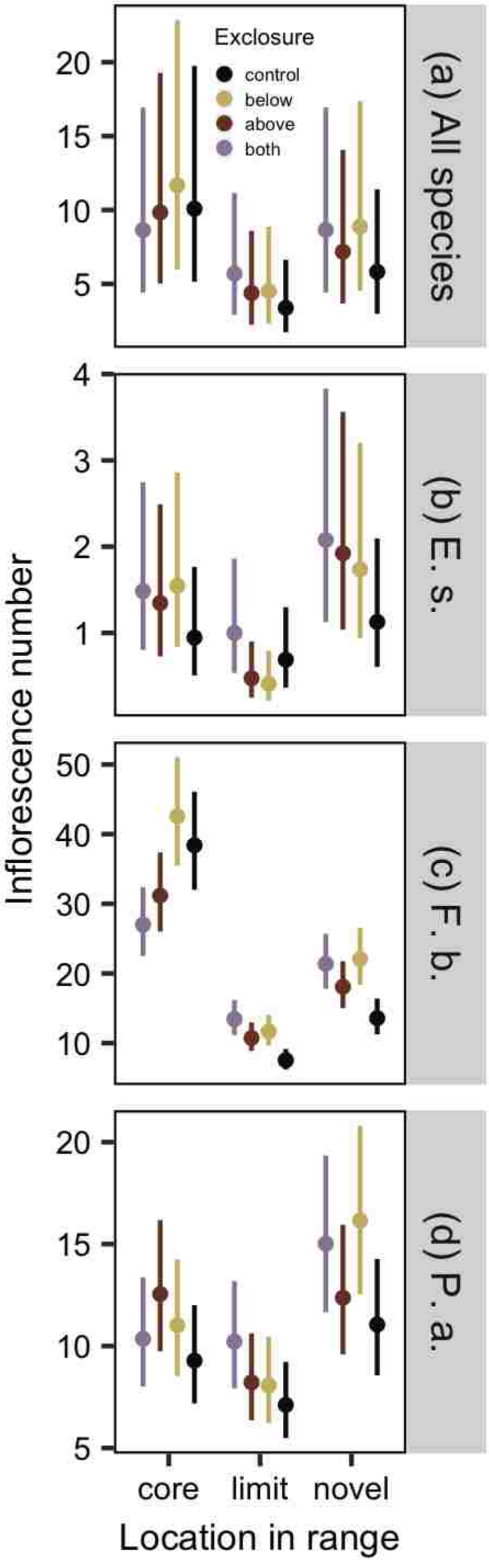
(c) *Elymus scribneri*



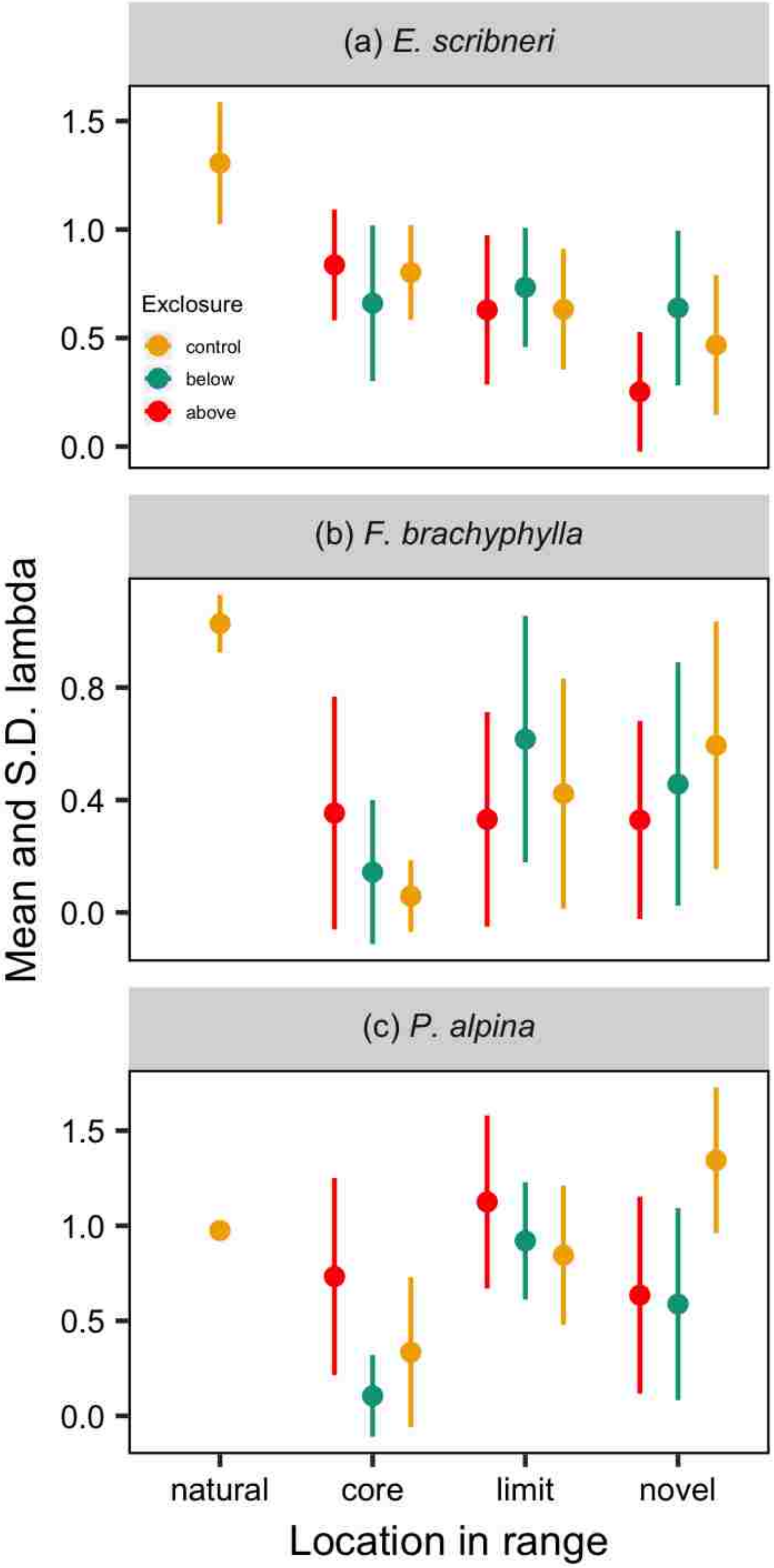
(d) *Festuca brachyphylla*



Chapter 2 Figure 5.



Chapter 2 Figure 6.



Chapter 2 Supplementary material

Chapter 2 Supplementary material 1.

Vital rate models

We fit demographic vital rate models of natural and experimental plants, separately. Natural populations had data from 2015-2018 (three transitions) and experimental populations had data from 2016-2018 (two transitions). We followed methods described in Elderd and Miller (2015) and Compagnoni et al. (2016) for our model fitting procedures. All models were fit using Bayesian estimation with *JAGS* (Plummer 2003) and *R2jags* (Su and Masanao Yajima 2015) in R (R Core Team 2018). Each model was run with three chains and a minimum 50,000 iteration Markov Chain Monte Carlo simulations with a 25000 burn-in. Parameter convergence was obtained when the potential scale reduction factor was close to one ($\hat{R}$<1.01; Gelman and Rubin 1992). Models were run for more iterations when the above failed to adequately converge. Trace- and autocorrelation plots were examined to ensure proper mixing and accurate posterior estimates. All priors were uninformative (“flat”).

Each vital rate model was assessed for model performance with two posterior predictive checks (PPCs; Elderd and Miller 2015; Compagnoni et al. 2016). The first plots the sum of squared residuals (SSQ) of observed data with data simulated/predicted from the fitted model. If the model fits well, observed and simulated SSQ create a cloud of points centered on a 1:1 line. Second, we calculated Bayesian p-values, which take a discrepancy measure (here, SSQ) and asks if the discrepancy is biased towards observed or simulated data (Gelman, Meng, and Stern 1996). Bayesian p-values of 0.5 indicate good model fit. All vital rate calculations passed these checks. Additionally, we fit group level effects of year for natural populations, and year and/or mountain transect for experimental populations, when they improved model fit according to PPCs. Table SM2 indicates when these effects were used.

Survival

Survival was modeled as a Bernoulli process (0/1) predicted in year t+1 (S_{t+1}) by size in the previous year t (x_t):

$$S_{t+1} \sim Bernoulli(\hat{S}) \quad \text{(S1a)}$$

$$logit(\hat{S}) = \alpha_{S_n} + \beta_{S_n} log_e(x_t) \quad \text{(S1b)}$$

$$logit(\hat{S}) = \alpha_{S_m} + \beta_{S_m} log_e(x_t) \quad \text{(S1c)}$$

$$\alpha_{S_m} \sim Normal(\mu_m, \sigma^2{}_m) \quad \text{(S1d)}$$

$$\beta_{S_m} \sim Normal(\mu_m, \sigma^2{}_m) \quad \text{(S1e)}$$

Where $\hat{S}$ is survival probability modeled as a linear function of size in S1b and S1c. S1b is the model for the natural populations, n, while S1c represents the experimentally manipulated populations, m. S1c had a different slope (β_{S_m}) and intercept (α_{S_m}) terms fit for experimental treatments, each with their own mean (μ_m) and variance ($\sigma^2{}_m$). Treatment effects were fit for the interaction of site*above and site*below without the three-way interaction because evidence from question 2 suggested the three-way interaction had limited importance and the sample size was limited for this treatment.

Growth

Plant size in year t+1 (G_t+1) was modeled as a function of plant size in the previous year, t. Our size metric for grasses is tiller number, which is an integer measure necessitating a negative binomial distribution. Growth was modeled as:

$$G_{t+1} \sim NegBin(\hat{G}, \theta_G) \qquad \text{(S2a)}$$

$$\log(\hat{G}) = \alpha_{G_n} + \beta_{G_n} log_e(x_t) \qquad \text{(S2b)}$$

$$\log(\hat{G}) = \alpha_{G_m} + \beta_{G_m} log_e(x_t) \qquad \text{(S2c)}$$

$$\alpha_{G_m} \sim Normal(\mu_m, \sigma^2{}_m) \qquad \text{(S2d)}$$

$$\beta_{G_m} \sim Normal(\mu_m, \sigma^2{}_m) \qquad \text{(S2e)}$$

Where $\hat{G}$ is the expected future size and θ_G is the dispersion parameter. Other notation and treatments follow that of Eq. S1.

Flowering

Whether or not an individual was flowering in year *t* (P_t) was modeled as Bernoulli process and as a function of its' size in *t*:

$$P_t \sim Bernoulli(\hat{P}) \qquad \text{(S3a)}$$

$$logit(\hat{P}) = \alpha_{P_n} + \beta_{P_n} log_e(x_t) \qquad \text{(S3b)}$$

$$logit(\hat{P}) = \alpha_{P_m} + \beta_{P_m} log_e(x_t) \qquad \text{(S3c)}$$

$$\alpha_{P_m} \sim Normal(\mu_m, \sigma^2{}_m) \qquad \text{(S3d)}$$

$$\beta_{P_m} \sim Normal(\mu_m, \sigma^2{}_m) \qquad \text{(S3e)}$$

Where $\hat{P}$ is the is the mean probability of flowering. Other notation and treatments follow that of Eq. S1. For experimental populations, flowering for all species was rare the year of transplantation, therefore, data from only 2017 and 2018 were used.

Fertility

Inflorescence number in year t (F_t) was modeled with a negative binomial distribution as a function of individual size in year t, given the individual was flowering:

$$F_t \sim NegBin(\hat{F}, \theta_F) \qquad \text{(S4a)}$$

$$\log(\hat{F}) = \alpha_{F_n} + \beta_{F_n} log_e(x_t) \qquad \text{(S4b)}$$

$$\log(\hat{F}) = \alpha_{F_m} + \beta_{F_m} log_e(x_t) \qquad \text{(S4c)}$$

$$\alpha_{F_m} \sim Normal(\mu_m, \sigma^2{}_m) \qquad \text{(S4d)}$$

$$\beta_{F_m} \sim Normal(\mu_m, \sigma^2{}_m) \qquad \text{(S4e)}$$

Where $\hat{F}$ is the is the mean number of inflorescences produced by an individual and θ_F is the dispersion parameter. Other notation and treatments follow that of Eq. S1. Again, data from only 2017 and 2018 were used for experimental populations.

Recruitment

The seed recruitment probability was modeled based on the seeds produced in year t turning into the number of recruits in year t+1. Recruitment was measured over an entire plot in the natural populations. We were not able to assess recruitment in the experimental plots, therefore we substituted recruitment models from the natural populations into experimental population models. A binomial model was used to estimate the probability of seeds-to-recruits transitions:

$$R_{t+1} \sim Binomial(\hat{R}, D_t) \qquad \text{(S5a)}$$

$$logit(\hat{R}) = \alpha_{R_n} \qquad \text{(S5b)}$$

D_t is the number of seeds produced in a plot, which was estimated by determining the mean number of seeds produced per inflorescence (*Elymus scribneri*= 11.0, *Festuca brachyphylla*= 9.8, and *Poa alpina*= 26.3) and multiplying by the number of inflorescences in the plot from the previous year.

Matrix population models

We used the above vital rate models to populate matrix population models (MPMs). MPMs are appropriate, given the discrete size classes of grass tiller number. MPMs were fit separately for natural and each experimental treatment combination based on parameter estimates from Eqs S1-5. Experimental plant size distributions were greater than natural populations, requiring different size transitions between the two sets. The natural populations of *P. alpina* were limited maximum of the 99th percentile of size because a single large plant had undue influence over vital rate calculations.

MPMs were constructed by combining individual survival and growth probabilities with fertility. Growth and survival contributions to populations dynamics predict the number of *y*-sized individuals in *t*+1 with fertility adding new individuals to the population with:

$$n_{y_{t+1_{n,m}}} = \sum_{x=1}^{x=U} S(x;\alpha_{S_{n,m}},\beta_{S_{n,m}})G(y,x;\ \alpha_{G_{n,m}},\beta_{G_{n,m}})n_{x_t} + P(x;\alpha_{P_{n,m}},\beta_{P_{n,m}})F(x;\alpha_{F_{n,m}},\beta_{F_{n,m}})\chi R(\alpha_{R_n})n_{x_t} \qquad \text{(S6)}$$

n_y is the y$^{\text{th}}$ element of vector **n**. Equation S6 portrays the survival *x* sized plants and their growth to size *y*, given natural or experimental specific vital rate parameters (e.g. $\alpha_{S_{n,m}}$), summed over all *x* sizes. Per-capita seedling production for a maternal plant of size *x* is the product of the probability a plant flowers (*P*), the number of inflorescences produced

(F), number of seeds per inflorescence (χ), and the probability a recruit establishes (R). Equation S6 takes specific vital rate parameters (e.g. $\alpha_{P_{n,m}}$) for natural or manipulated (n,m) populations. Note that probability a recruit establishes, R, was estimated for the natural population and applied to experimental populations because this data was unavailable. Methods for χ estimation are found in the main text. We made a simplifying assumption that seed production per inflorescence does not vary through time and does not respond to treatment effects.

Deterministic population growth rates (λ) were determined by taking the dominant eigenvalue of the above matrix. We estimated a unique λ for each natural and experimental population. Additionally, each estimate represents an independent draw from the posterior distributions of vital rates, thereby leveraging the full power of Bayesian analysis to quantify and propagate parameter uncertainty (Elderd and Miller 2015; Hobbs and Hooten 2015).

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Chapter 2 Supplementary material 2.

Table S1. Coordinates for experimental sites.

Peak	*Site*	*Elevation (m)*	*Latitude (°)*	*Longitude (°)*
Avery	Core	3655	38.98407	-106.97021
Avery	Limit	3455	38.92741	-106.97823
Avery	Novel	3192	38.97142	-106.98428
Cinnamon	Core	3726	38.99495	-107.07043
Cinnamon	Limit	3578	38.99356	-107.06754
Cinnamon	Novel	3366	38.97018	-107.02955
Treasury	Core	3598	39.00000	-107.08065
Treasury	Limit	3418	38.98793	-107.06498
Treasury	Novel	3197	38.97073	-107.05871

Table S2. Model selection table for herbivory analysis. The predictor variables were analyzed as interactions and appear in the “Formula” column, where “site”, “above”, and “below” refer to the three variables manipulated in the experiment. “*” refers to interactions among independent variables and include main effects. Lowest *AICc* models are the best representation of the data given the candidate model set. *ΔAICc* represents the difference between a given model and the best model. *Weights* is the *AICc* based likelihood and can be interpreted as the probability a given model is the true representation of the data out of the candidate model sets. Marginal (*Mar.* R^2) and conditional (*Cond.* R^2) are likelihood coefficients of determination for just fixed (marginal) and fixed with random effects (conditional).

Response	*Species*	*Formula*	*AICc*	*ΔAICc*	*Weights*	*Mar.* R^2	*Cond.* R^2	*df*
Presence	All	Site*above	2922.10	0.00	0.40	0.04	0.18	3143
		Site	2922.40	0.30	0.35	0.04	0.18	3146
		Site*above*below	2923.59	1.49	0.19	0.04	0.19	3137
		Site*below	2925.83	3.73	0.06	0.04	0.18	3143
		Above	3001.39	79.29	0.00	0.00	0.18	3147
		Above*below	3002.81	80.72	0.00	0.00	0.18	3145
		Null	3006.25	84.15	0.00	NA	NA	3148
		Below	3007.43	85.33	0.00	0.00	0.18	3147
	Poa alpina	Site*below	998.23	0.00	0.52	0.08	0.20	1078
		Site	999.42	1.19	0.29	0.06	0.18	1081
		Site*above*below	1000.92	2.69	0.14	0.08	0.20	1072
		Site*above	1002.61	4.38	0.06	0.06	0.18	1078
		Above*below	1032.73	34.50	0.00	0.01	0.18	1080
		Below	1034.69	36.45	0.00	0.00	0.17	1082
		Above	1035.16	36.93	0.00	0.00	0.18	1082
		Null	1036.10	37.87	0.00	NA	NA	1083
	Festuca brachyphylla	Site	683.32	0.00	0.75	0.06	0.16	998
		Site*below	686.44	3.12	0.16	0.07	0.16	995
		Site*above	687.64	4.31	0.09	0.06	0.16	995
		Site*above*below	695.93	12.60	0.00	0.08	0.17	989
		Above	712.38	29.06	0.00	0.00	0.14	999
		Null	712.48	29.16	0.00	NA	NA	1000
		Below	714.40	31.07	0.00	0.00	0.14	999
		Above*below	716.33	33.01	0.00	0.00	0.14	997
	Elymus scribneri	Site	1181.56	0.00	0.78	0.03	0.17	1056
		Site*above	1185.35	3.79	0.06	0.03	0.18	1053
		Site*below	1186.61	5.05	0.12	0.03	0.18	1053
		Site*above*below	1187.72	6.16	0.04	0.04	0.19	1047
		Null	1201.74	20.18	0.00	NA	NA	1058
		Above	1202.10	20.54	0.00	0.00	0.17	1057
		Below	1203.45	21.89	0.00	0.00	0.17	1057
		Above*below	1205.67	24.11	0.00	0.00	0.17	1055
All damage	All	Site*above*below	9980.74	0.00	1.00	0.21	0.89	659
		Site*above	10057.27	76.53	0.00	0.20	0.88	665
		Site*below	10327.58	346.85	0.00	0.14	0.88	665
		Site	10356.59	375.85	0.00	0.13	0.87	668

		Above*below	10658.57	677.83	0.00	0.07	0.86	667
		Above	10714.76	734.02	0.00	0.06	0.86	669
		Below	10921.83	941.09	0.00	0.01	0.85	669
		Null	10942.83	962.09	0.00	NA	NA	670
	Poa alpina	Site*above*below	3485.74	0.00	1.00	0.34	0.93	213
		Site*above	3614.99	129.25	0.00	0.29	0.92	219
		Site*below	3745.84	260.10	0.00	0.23	0.93	219
		Site	3792.81	307.07	0.00	0.20	0.92	222
		Above*below	3968.25	482.51	0.00	0.05	0.91	221
		Above	4004.51	518.77	0.00	0.04	0.90	223
		Below	4057.25	571.51	0.00	0.01	0.91	223
		Null	4074.60	588.86	0.00	NA	NA	224
	Festuca brachy-phylla	Site*above*below	1898.87	0.00	1.00	0.25	0.94	111
		Site*above	1958.28	59.41	0.00	0.20	0.92	117
		Site*below	2084.59	185.72	0.00	0.16	0.90	117
		Site	2089.13	190.26	0.00	0.16	0.90	120
		Above	2119.13	220.26	0.00	0.10	0.90	121
		Above*below	2123.42	224.55	0.00	0.10	0.90	119
		Null	2247.88	349.02	0.00	NA	NA	122
		Below	2249.99	351.13	0.00	0.00	0.86	121
	Elymus scribneri	Site*above*below	3893.52	0.00	1.00	0.17	0.89	308
		Site*above	3915.45	21.93	0.00	0.15	0.88	314
		Site*below	4000.75	107.24	0.00	0.10	0.88	314
		Site	4004.11	110.59	0.00	0.10	0.88	317
		Above*below	4131.36	237.84	0.00	0.04	0.88	316
		Above	4174.60	281.08	0.00	0.03	0.87	318
		Below	4211.12	317.60	0.00	0.01	0.88	318
		Null	4221.53	328.01	0.00	NA	NA	319
Insect	All	Site*above*below	4720.39	0.00	1.00	0.19	0.80	532
		Site*above	4765.16	44.77	0.00	0.15	0.78	538
		Site*below	4912.45	192.06	0.00	0.09	0.80	538
		Site	4919.52	199.12	0.00	0.08	0.79	541
		Above*below	4926.67	206.28	0.00	0.10	0.78	540
		Above	4949.79	229.40	0.00	0.08	0.78	542
		Below	5075.00	354.61	0.00	0.00	0.78	542
		Null	5077.15	356.76	0.00	NA	NA	543
	Poa alpina	Site*above*below	1196.97	0.00	0.97	0.22	0.83	180
		Site*above	1203.94	6.96	0.03	0.19	0.83	186
		Site*below	1299.22	102.25	0.00	0.18	0.83	186
		Site	1316.33	119.35	0.00	0.15	0.83	189
		Above	1333.51	136.54	0.00	0.11	0.83	190
		Above*below	1335.99	139.01	0.00	0.12	0.83	188
		Below	1448.94	251.97	0.00	0.01	0.80	190
		Null	1454.43	257.45	0.00	NA	NA	191
	Festuca brachy-phylla	Site*above*below	961.52	0.00	1.00	0.33	0.84	76
		Site*above	997.58	36.05	0.00	0.19	0.81	82
		Above*below	1046.23	84.71	0.00	0.11	0.79	84
		Site	1056.90	95.37	0.00	0.05	0.81	85
		Site*below	1058.15	96.62	0.00	0.06	0.81	82
		Below	1062.47	100.94	0.00	0.02	0.78	86
		Null	1068.56	107.04	0.00	NA	NA	87
		Above	1069.27	107.74	0.00	0.01	0.76	86
	Elymus scribneri	Site*above*below	1991.66	0.00	1.00	0.18	0.81	249
		Site*above	2021.39	29.73	0.00	0.13	0.78	255
		Site*below	2055.65	63.99	0.00	0.10	0.79	255
		Site	2064.76	73.09	0.00	0.09	0.79	258
		Above*below	2085.63	93.96	0.00	0.06	0.78	257
		Above	2106.20	114.54	0.00	0.05	0.76	259
		Below	2130.85	139.19	0.00	0.01	0.78	259
		Null	2136.56	144.90	0.00	NA	NA	260
Mammal	All	Site*below	2238.17	0.00	1.00	0.42	0.91	116
		Site	2282.36	44.19	0.00	0.38	0.91	119
		Below	2502.56	264.39	0.00	0.09	0.85	120
		Null	2564.13	325.96	0.00	NA	NA	121
	Poa	Site*below	422.62	0.00	1.00	0.22	0.96	25

alpina	Site	435.65	13.03	0.00	0.12	0.96	28
	Null	474.98	52.36	0.00	NA	NA	30
	Below	475.02	52.40	0.00	0.00	0.97	29
Festuca brachyphylla	Site	572.30	0.00	0.75	0.25	0.97	29
	Site*below	574.47	2.16	0.25	0.25	0.98	27
	Null	725.63	153.32	0.00	NA	NA	31
	Below	728.09	155.78	0.00	0.00	0.88	30
Elymus scribneri	Site*below	988.68	0.00	1.00	0.78	0.82	50
	Site	1034.59	45.91	0.00	0.66	0.81	53
	Below	1109.40	120.72	0.00	0.39	0.70	54
	Null	1180.58	191.90	0.00	NA	NA	55

Table S3. Model selection table for plant fitness analysis. The predictor variables were analyzed as interactions and appear in the "Formula" column, where "site", "above", and "below" refer to the three variables manipulated in the experiment. "*" refers to interactions among independent variables and include main effects. Lowest *AICc* models are the best representation of the data given the candidate model set. *ΔAICc* represents the difference between a given model and the best model. *Weights* is the *AICc* based likelihood and can be interpreted as the probability a given model is the true representation of the data out of the candidate model sets. Marginal (*Mar.* R^2) and conditional (*Cond.* R^2) are likelihood coefficients of determination for just fixed (marginal) and fixed with random effects (conditional). *Poa alpina* survival models with the full interaction set did not converge and were left out of selection.

Response	*Species*	*Formula*	*AICc*	*ΔAICc*	*Weights*	*Mar.* R^2	*Cond.* R^2	*df*
Survival	all	Site*above	525.70	0.00	0.97	0.05	0.24	532
		Site*above*below	534.28	8.58	0.01	0.06	0.25	526
		Above	534.71	9.01	0.01	0.01	0.20	536
		Above*below	538.34	12.64	0.00	0.02	0.20	534
		Site	539.76	14.06	0.00	0.01	0.20	535
		Null	540.66	14.96	0.00	NA	NA	537
		Below	542.64	16.94	0.00	0.00	0.18	536
		Site*below	545.14	19.44	0.00	0.01	0.20	532
	Poa alpina	Above	143.24	0.00	0.61	0.05	0.27	177
		Site*above	145.15	1.91	0.24	0.09	0.32	173
		Above*below	146.59	3.35	0.12	0.06	0.28	175
		Null	150.34	7.10	0.02	NA	NA	178
		Below	152.23	8.98	0.01	0.00	0.21	177
		Site	153.67	10.43	0.00	0.00	0.21	176
		Site*below	158.77	15.53	0.00	0.01	0.20	173
		Site*above*below	NA	NA	NA	NA	NA	NA
	Festuca brachyphylla	Null	184.27	0.00	0.34	NA	NA	178
		Above	185.45	1.18	0.19	0.00	0.25	177
		Below	185.45	1.18	0.19	0.00	0.25	177
		Site	185.77	1.50	0.16	0.02	0.26	176
		Site*above	187.65	3.38	0.06	0.05	0.30	173
		Above*below	188.39	4.12	0.04	0.01	0.26	175
		Site*below	190.85	6.58	0.01	0.02	0.27	173
		Site*above*below	198.92	14.65	0.00	0.06	0.31	167
	Elymus scribneri	Site*above	203.77	0.00	0.92	0.10	0.20	173
		Site	209.99	6.22	0.04	0.04	0.13	176
		Null	212.13	8.36	0.01	NA	NA	178
		Above	212.77	8.99	0.01	0.01	0.10	177
		Below	213.47	9.70	0.01	0.00	0.10	177
		Site*above*below	214.66	10.89	0.00	0.13	0.23	167
		Site*below	215.64	11.87	0.00	0.04	0.14	173
		Above*below	216.18	12.41	0.00	0.01	0.11	175
Biomass	all	Site*above*below	6905.72	0.00	1.00	0.06	0.63	3116

		Site*above	6917.33	11.61	0.00	0.04	0.63	3122
		Site*below	6919.12	13.39	0.00	0.04	0.63	3122
		Site	6933.48	27.76	0.00	0.03	0.63	3125
		Above*below	6956.64	50.91	0.00	0.02	0.63	3124
		Above	6971.46	65.74	0.00	0.01	0.63	3126
		Below	6972.75	67.03	0.00	0.01	0.63	3126
		Null	6987.13	81.41	0.00	NA	NA	3127
	Poa alpina	Site*above*below	3106.99	0.00	0.75	0.15	0.39	1063
		Site*below	3110.36	3.36	0.14	0.12	0.39	1069
		Site*above	3111.03	4.03	0.10	0.11	0.39	1069
		Site	3116.82	9.83	0.01	0.09	0.39	1072
		Above*below	3126.25	19.25	0.00	0.07	0.39	1071
		Above	3132.62	25.63	0.00	0.05	0.39	1073
		Below	3133.57	26.57	0.00	0.04	0.39	1073
		Null	3139.72	32.73	0.00	NA	NA	1074
	Festuca brachyphylla	Site*below	1729.93	0.00	0.96	0.16	0.43	987
		Site	1737.11	7.17	0.03	0.13	0.43	990
		Site*above*below	1739.78	9.85	0.01	0.17	0.43	981
		Site*above	1742.35	12.41	0.00	0.13	0.43	987
		Below	1772.66	42.73	0.00	0.03	0.43	991
		Above*below	1775.18	45.25	0.00	0.03	0.43	989
		Null	1779.68	49.74	0.00	NA	NA	992
		Above	1780.90	50.97	0.00	0.00	0.43	991
	Elymus scribneri	Site*above	942.06	0.00	0.99	0.12	0.50	1047
		Site*above*below	951.02	8.96	0.01	0.13	0.50	1041
		Above	954.42	12.36	0.00	0.06	0.50	1051
		Site	957.22	15.16	0.00	0.06	0.50	1050
		Above*below	957.33	15.26	0.00	0.06	0.50	1049
		Site*below	961.76	19.70	0.00	0.06	0.50	1047
		Null	967.57	25.51	0.00	NA	NA	1052
		Below	968.44	26.38	0.00	0.02	0.50	1051
Inflorescence	all	Site*above*below	8792.44	0.00	1.00	0.09	0.95	819
		Site*below	8877.59	8351.89	0.00	0.08	0.95	825
		Site*above	8928.41	8402.71	0.00	0.08	0.95	825
		Site	8988.31	8462.61	0.00	0.07	0.95	828
		Above*below	9848.11	9322.41	0.00	0.01	0.95	827
		Below	9873.55	9347.85	0.00	0.00	0.95	829
		Null	9938.17	9412.47	0.00	NA	NA	830
		Above	9939.85	9414.15	0.00	0.00	0.95	829
	Poa alpina	Site*above*below	2617.87	0.00	1.00	0.18	0.72	281
		Site*below	2631.49	2488.25	0.00	0.16	0.71	287
		Site*above	2657.92	2514.68	0.00	0.15	0.71	287
		Site	2665.36	2522.12	0.00	0.13	0.70	290
		Above*below	2765.16	2621.91	0.00	0.04	0.68	289
		Below	2774.74	2631.49	0.00	0.02	0.67	291
		Above	2793.87	2650.63	0.00	0.01	0.67	291
		Null	2796.84	2653.60	0.00	NA	NA	292
	Festuca brachyphylla	Site*above*below	4413.70	0.00	1.00	0.70	0.87	250
		Site*above	4492.14	4307.87	0.00	0.68	0.86	256
		Site*below	4527.97	4343.70	0.00	0.66	0.87	256
		Site	4590.61	4406.34	0.00	0.64	0.86	259
		Above*below	5734.87	5550.60	0.00	0.06	0.68	258
		Below	5755.78	5571.51	0.00	0.03	0.67	260
		Above	5778.14	5593.87	0.00	0.01	0.65	260
		Null	5780.43	5596.16	0.00	NA	NA	261
	Elymus scribneri	Site*above*below	1089.24	0.00	0.95	0.13	0.60	261
		Site*below	1096.62	892.85	0.02	0.10	0.58	267
		Site*above	1096.68	892.90	0.02	0.10	0.59	267
		Site	1099.16	895.39	0.01	0.09	0.58	270
		Above*below	1154.52	950.75	0.00	0.02	0.58	269
		Below	1155.45	951.68	0.00	0.01	0.57	271
		Above	1161.22	957.45	0.00	0.01	0.57	271
		Null	1164.37	960.60	0.00	NA	NA	272

Chapter 3: Predicting outcomes of climate induced novel competitive interactions

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Abstract

Climate change may be causing the upward migration of plant species in elevation (Lenoir et al. 2008; Gottfried et al. 2012), introducing novel competitors into communities. Past theory on the constraints on species geographic ranges correctly predicted this upward expansion (Brown 1995; MacArthur 1972; Dobzhansky 1950), but hypotheses on how novel competitive interactions will influence a species trailing range edge have received less and mixed support (Alexander, Diez, and Levine 2015; Stinson 2005). Further, we are lacking models to predict the consequences of novel competitor encroachment. We used experimental plant populations to construct population and functional trait-based models (Kunstler et al. 2012) comparing the effects of competition on population growth and fitness in current and novel environments expected with climate change. Though novel competitors suppressed the population growth of focal species, the novel environment generally caused greater reductions in population growth rates over competitive effects- a conclusion that was only apparent when integrating life history events into population models. Trait-based models revealed that competitive effects increased when competitors were more resource acquisitive (e.g. taller), and that encroaching low-elevation communities had a higher frequency of resource acquisitive trait strategies than focal species current competitors. Our modeling approach suggests that direct changes to the environment are a greater threat to alpine plant populations than

intensified competitive interactions, which should be kept in mind when predicting extinction risk (Urban 2015; Urban, Tewksbury, and Sheldon 2012).

Main Body

Climate change shifts species geographic ranges tracking their physiological tolerances (Lenoir et al. 2008; Gottfried et al. 2012), creating novel competitive communities. Past work shows competitive shifts in species' dominance when the climate is altered *in situ* (Suttle, Thomsen, and Power 2007; Fridley et al. 2016). However, competitive outcomes are difficult to forecast when novel competitors arise from species' range shifts (Urban, Tewksbury, and Sheldon 2012), necessitating experiments that create the expected novel communities caused by climate changes (Alexander et al. 2016). Few such studies exist: One reported depressed fitness of individuals with novel competitors in a novel climate (Alexander, Diez, and Levine 2015), and another found depressed fitness due to an inhospitable abiotic environment (Stinson 2005). However, attempts to generalize results with predictive models is lacking.

Demographic models can inform when the abiotic and/or biotic context of a population suggests a risk of local extinction because they integrate across all vital life history events of a population. A species range is limited in space where its population growth rates are below replacement (Louthan, Doak, and Angert 2015), suggesting that some aspect of the abiotic and/or biotic environment makes the population inviable at that location. For instance, the experimental reduction of competition at a species range limit increased population growth rates, suggesting expansion beyond the range is limited in part by competition (Louthan et al. 2018). However, such studies cannot rule out dispersal limitation as the cause of the range limit, therefore, experimental populations must be moved beyond range limits in combination with manipulations of competition to assess drivers of range limits.

In the Colorado Rocky Mountains, USA, we planted alpine-restricted grasses into the center of their elevation range (core habitat) as well as 430 m below their elevation range limit (novel habitat) to simulate their current abiotic/biotic environment as well as the novel environment predicted under 2-3°C climate warming (Rangwala and Miller 2012) and upward migration of low elevation communities. The focal species (*Elymus scribneri*, *Festuca brachyphylla*, *Poa alpina*) occupy the peaks of mountains; thus, future range contractions could cause local extinctions. We manipulated the competitive environment of focal individuals by removing all vegetation in 0.3 x 0.3 m plots; control (competition) plots retained existing vegetation. Treatments were replicated in core and novel habitats on three independent mountains. We tracked focal individual growth, survival, and reproduction, for four growing seasons (2015-2018) and germination for two (2017-2018), and populated matrix projection models (MPMs) to Bayesian fits of population vital rates to predict the population finite rate of increase (λ), which created posteriors (probability distributions describing a value) of λ predicated on vital rate parameters.

Models predicted the extinction of populations exposed to the novel, warmer climates, and competition with novel plant communities increased the probability of extinction (Figure 1). Mean posteriors of λ for each species in the novel environment were below or very close to replacement ($\lambda<1$), suggesting inhospitable environmental conditions below the species range limit restrict the alpine species distribution. Competitors in the novel habitat drove decreases in population growth rates up to 23% compared to competitor removals (Figure 1, *P. alpina*). However, the effects of competition were inferior to the influence of elevation. Mean population growth rates in novel habitats without competitors were 79%, 47%, and 33% lower than in core habitats with competition for *E. scribneri*, *F. brachyphylla*, and *P. alpina*, respectively. Thus, the climate and edaphic conditions found below the species range (Stinson 2005) were more important than novel competitors (Alexander, Diez, and Levine 2015) in restricting species' range limits.

The conclusion that novel environments were more important than novel competitors in limiting species distributions was only possible with demographic modeling (Louthan, Doak, and Angert 2015). Past work found that novel competitors suppressed survival, biomass, or the probability of flowering of species moved below their range edge (Alexander, Diez, and Levine 2015), and we found similar patterns (Supplementary material Figure S1a, 1b, 1c). However, key life history events, such as seedling recruitment, can greatly influence population viability. Experiments that focus on single response variables may make misleading predictions about species responses to climate change that will be accounted for with a demographic approach (e.g. Louthan et al. 2018; Doak and Morris 2010).

Climate change will threaten a large number of species (Urban 2015) for which we lack necessary demographic data, and demographic models cannot readily be generalized beyond focal species populations. Thus, we need approaches that can scale from individuals to predict change in communities and ecosystems (Webb et al. 2010). Plant trait approaches are generalizable across most plant species, easily measured, and provide a mechanistic foundation for understanding ecological processes (Díaz et al. 2016; Mcgill et al. 2006). Competition among plants has successfully been modeled with traits using the competitive trait hierarchy hypothesis (Funk and Wolf 2016; Kraft et al.

2014; Kunstler et al. 2012, 2016), which proposes that differences in trait values between competing individuals predict their performance. Plants with similar traits access resources similarly while large trait differences connote a competitive advantage for one of the individuals. Traits vary predictably along environmental gradients (Díaz et al. 2016; Wright et al. 2004), suggesting that the model will have greater predictive utility if it can incorporate environmental effects on traits and better capture the environmental context in which a suite of traits will dominate.

We collected trait and abiotic environment data and predicted focal plant responses to competition. We measured two functional traits (vegetative plant height: H_{max}; and specific leaf area: SLA) on both the focal species (18 populations of 3 species) and 60 populations of 43 species comprising the top 90% of vegetative cover at our six experimental sites. We chose traits based on the leaf:height:seed schema (Westoby 1998), which captures the main axes of variation in plant life history strategies (Díaz et al. 2016; Grime 2006). We used traits to parameterize Bayesian hierarchical models that determine how the environment influences trait distributions of both the focal species and competing community (community-weighted mean traits) and models plant performance (survival, biomass, and reproduction) using the competitive trait hierarchy hypothesis. We expected that trait differences predict lower performance when competitors had more resource acquisitive traits (e.g. tall H_{max}, high SLA), and those resource acquisitive traits would occur more commonly in low than high elevation habitats due to the warmer temperatures (though drier) at low elevations. We did not allow trait difference predictions of individual performance to vary with habitat (i.e. different slopes and intercepts for novel and core habitats) because we are interested in the generality of trait differences to predict plant performance irrespective of context.

Across 43 species, competitors with more resource acquisitive traits (i.e. taller with thinner leaves) suppressed focal plants more than competitors with similar traits (Figure 2). Focal plants had greater survival and biomass when they had higher SLA than their competitors, suggesting that lower carbon investment per area light capture was advantageous (Figure 2a,c). SLA of competitors increased with higher temperature and soil moisture (Figure 3a,c), again suggesting the resource-acquisitive traits dominating in low elevation communities represent more competitive life history strategies. Focal species SLA increased weakly with higher soil moisture and temperature (except *F. brachyphyalla*; Figure 3e,f), showing intraspecific patterns of SLA over environmental gradients follow community patterns. Survival decreased sharply as competitors exceeded focal individual height by >30 cm (Figure 2b), and competitors were taller in warmer habitats while focal species (except *P. alpina*) decreased in height with higher temperatures (Figure 3d,h). Community and focal species height decreased with soil moisture (Figure 3c,g). Though biomass also increased as focal individuals were taller than their competitors, this effect was weaker than SLA (Figure 2d). The probability a focal individual flowered was poorly predicted by trait differences (Figure 2e,f), though trends suggest focal species have a lower probability of flowering with taller, higher SLA competitors.

We find complementary predictions from two modeling frameworks. The low elevation range limit of these alpine species appears determined by the abiotic environment, evidenced by the depressed population growth rates in novel environments, which rejects the previous theory on the role of biotic interactions in determining low elevation range limits (Brown 1995; MacArthur 1972; Dobzhansky 1950; Louthan, Doak, and Angert 2015). However, in both the population and trait modeling frameworks, competitors tended to lower population growth/individual performance. If climate is driving these declines, we expect that populations may be threatened with extinction as snow melts earlier, temperatures warm (Doak and Morris 2010), and aridity increases (Louthan et al. 2018). This decline will be exacerbated as low elevation restricted species encroach upward and take up more resources (e.g. light from taller plants), supporting theory on plant life history strategies (Grime 2006) and trait-mediated competition (Kunstler et al. 2012; Funk and Wolf 2016; Kraft et al. 2014; Kunstler et al. 2016). Our results highlight the need for rigorous experiments and modeling frameworks to make quantitative predictions on how a changing climatic and biotic environment will impact extinction risk and biodiversity management (Urban 2015; Doak and Morris 2010; Dawson et al. 2011). Though past work suggests biotic interactions may be important for determining geographic range shifts with climates change (Alexander, Diez, and Levine 2015; Louthan et al. 2018), alpine species in our system are likely to be pushed off the top of the mountain by global change.

Methods

Site selection, focal species, and transplant experiment. Experiments were performed in the West Elk Mountains, Gunnison National Forest, Colorado, USA. The regional lapse rate is ~1°C decrease in temperature with ~140m increase in altitude (Pepin and Losleben 2002) and the region is expected to experience ~2-3°C increase in temperature with ongoing climate change (Rangwala and Miller 2012). Using previous vegetation surveys and distribution models, we found sites on/near the peaks of three independent mountains that contained our focal species to serve as "core" habitats. We then picked sites ~420m below the core habitats to serve as “novel” habitats in climatic and biotic characteristics (site coordinates in Supplementary material S1).

We collected seed from three core habitat populations of our three focal species (*Elymus scribneri*, *Festuca brachyphylla*, and *Poa alpina*) in September 2014. Focal species from each population were grown from seed in a University of New Mexico (UNM) greenhouse (~20°C for ~8 weeks) starting in March 2015. Seeds were sown in germination flats with Metro-Mix 360 potting soil (sun gro Horticulture, Agawam, MA, USA). When seedlings reached 2-6 leaves in size, we repotted the individuals into ~150ml root trainer pots (Stuewe and Sons, Inc., Tangen, Oregon, USA), in Metro-Mix 360. We split individuals into 2 and raised them in their own pots once plants were ~15-20 tillers in size. This allowed for replication of genotypes in core and novel treatments. Pots were top fertilized with ~15ml of Osmocote Plus 15:9:12 N:P:K pellets (Scotts Miracle-Gro Company, Marysville, OH, USA) and watered three times a day with overhead sprayers (~50mm per pot). Plants were transported to the Rocky Mountain Biological Laboratory (RMBL) in June of 2015 and hardened off for ~15 days outside in their pots before being transplanted into experimental sites.

We used prior vegetation surveys to identify the dominant species within each of the six sites and marked out 72 30x30cm plots at each site that contained a high percentage cover (~75%) of dominants in 2015. We recorded percentage cover by species of each plot then randomly selected 36 plots as vegetation removal-no competition-plots. Each focal species was assigned to 24 plots per site, 12 with competition and 12 without. Additionally, half of the plots for a species were transplanted with three individuals to create an intraspecific competition treatment, but the effect of intraspecific competition was weak and left out of main analyses. When individuals died, we replaced them with greenhouse grown plants in 2016 and 2017 to increase sample size. Fossorial mammal disturbance in the region is high (Lynn et al. 2018), therefore, to avoid losing plots to disturbance, we trenched in wire mesh fences around plots ~20cm deep. Photographic evidence shows this is a successful method of mammal deterrence (Supplementary material Figure S2). Experiments were implemented in June and July of 2015.

We surveyed plants for size, survival, and reproduction every month of the peak growing season (July, August, September) starting September 2015. We measured plant height (cm) and the number of vegetative tillers as size metrics and counted inflorescence number. Inflorescences were collected each month to limit gene transfer of experimental populations to surrounding vegetation. We performed a final survey of size, survival, and reproduction in August of 2018 and harvested focal individuals by cutting at the meristem just below the soil surface. Biomass was placed in prelabeled paper bags and transported back to the laboratory where live and litter biomass was separated and immediately dried at 60°C for 48 hours. Biomass was then transported back to UNM from RMBL and weighed to the nearest 0.001g on a mass balance (Mettler-Toledo MS104S and PL303, Columbus, OH, USA).

Environmental data. We began monitoring soil volumetric water content (Fieldscout TDR, 5cm probes; Spectrum Technologies, Aurora, IL, USA) in every plot weekly-post snow-melt beginning in 2017. Additionally, in 2018, we deployed iButton temperature and humidity sensors (DS1923; Maxim Integrated, San Jose, CA, USA) and measured temperature and humidity at one-hour intervals beginning post snowmelt at a site and ending in mid-September 2018. Three iButtons were placed equidistant from each other within the sites, each accounting for temperature and humidity for 1/3 of the plots within a site.

Plant trait collection. We took detailed data on flowering phenology in 2017 to inform trait collection in 2018. All traits were collected during peak flowering of target plant communities (Pérez-Harguindeguy et al. 2013). We used prior vegetation surveys to determine which species made up 90% of the vegetative cover within plots (60 populations of 43 species), then collected leaf material and height (H_{max}) data within experimental plots, whenever possible. If target sample sizes (following recommendations of Pérez-Harguindeguy et al. (2013) for leaf material and H_{max} were not acquired within the plots, we further sampled by walking a 40m long transect and haphazardly selected target individuals for trait sampling at least 5m apart from each other. H_{max} was measured to the nearest 0.1 cm from the ground to the highest vegetative point on 25 individuals. Four leaves per ten individuals were directly placed in prelabelled plastic bags with small amounts of DI water and then kept in a cooler/refrigerator until lab processing (within 36 hours). Focal experimental individuals were randomly selected for sampling within competition plots, only, unless minimum sample sizes could not be obtained, then individuals in removal plots were sampled.

Leaves were pat-dried with a paper towel and weighed for fresh mass (nearest 0.0001g) estimation on a Mettler-Toledo XSR Analytical Balance (Columbus, OH, USA). We then scanned leaves with a CanoScan LiDE 210 (Canon, Tokyo, Japan). Leaves were then dried at 60°C for at least 48 hours or until a constant mass was reached. We then weighed dry leaf material (nearest 0.0001g) with a Mettler-Toledo MS104S (Columbus, OH, USA). We obtained single-sided leaf areas (cm^2) using image J software (Schneider, Rasband, and Eliceiri 2012). We calculated specific leaf area (SLA) as the one-sided area of a leaf divided by its dry mass (cm^2/g).

Demographic modeling. We used hierarchical Bayesian estimation to fit vital rate models of key focal species life history transitions (Compagnoni et al. 2016; Elderd and Miller 2015). Vital rate model parameters were then used in Matrix Projection Models (MPMs) to estimate deterministic population growth rates, λ. Five vital rate transitions were used in the MPM construction: survival, growth, flowering probability, inflorescence number, and recruitment. We used tiller number as our size metric.

Survival was modeled as a Bernoulli process (0/1) in year t+1 (S_{t+1}) as a linear function of size in the previous year t (x_t):

$$S_{t+1} \sim Bernoulli(\hat{S}) \quad \text{(S1a)}$$

$$logit(\hat{S}) = \alpha_{S_m} + \beta_{S_m} log_e(x_t) \quad \text{(S1b)}$$

$$\alpha_{S_m} \sim Normal(\mu_m, \sigma^2{}_m) \quad \text{(S1c)}$$

$$\beta_{S_m} \sim Normal(\mu_m, \sigma^2{}_m) \quad \text{(S1d)}$$

$\hat{S}$ is survival probability predicted by size with a specific slope (β_{S_m}) and intercept (α_{S_m}) based on treatment effects, m (core sites with and without competition and novel habitats with and without competition: four treatments per species). Each vital rate parameter is normally distributed with its own mean and variance (S1c,d).

Growth, in tiller number, in year t+1 (G_{t+1}) was a function of the previous year, t, plant size. Tiller number is a positive integer requiring a negative binomial distribution.

$$G_{t+1} \sim NegBin(\hat{G}, \theta_G) \quad \text{(S2a)}$$

$$\log(\hat{G}) = \alpha_{G_m} + \beta_{G_m} log_e(x_t) \quad \text{(S2b)}$$

$$\alpha_{G_m} \sim Normal(\mu_m, \sigma^2{}_m) \quad \text{(S2c)}$$

$$\beta_{G_m} \sim Normal(\mu_m, \sigma^2{}_m) \quad \text{(S2d)}$$

$\hat{G}$ is expected future size with dispersion parameter θ_G (with a flat gamma prior). Other notation follows Eq. S1.

The probability an individual flowered in year *t* (P_t) was modeled as a Bernoulli process dependent on plant size in year *t*:

$$P_t \sim Bernoulli(\hat{P}) \qquad \text{(S3a)}$$

$$logit(\hat{P}) = \alpha_{P_m} + \beta_{P_m} log_e(x_t) \qquad \text{(S3b)}$$

$$\alpha_{P_m} \sim Normal(\mu_m, \sigma^2{}_m) \qquad \text{(S3c)}$$

$$\beta_{P_m} \sim Normal(\mu_m, \sigma^2{}_m) \qquad \text{(S3d)}$$

$\hat{P}$ is the mean probability of flowering and other notation follows that of Eq. S1. Note, flowering was rare when the experiment was set up in 2015, therefore, we excluded flowering data for this year.

Inflorescences produced by an individual in year *t* (F_t) was modeled with a negative binomial distribution as a function of size in year *t* if the individual flowered.

$$F_t \sim NegBin(\hat{F}, \theta_F) \qquad \text{(S4a)}$$

$$\log(\hat{F}) = \alpha_{F_m} + \beta_{F_m} log_e(x_t) \qquad \text{(S4b)}$$

$$\alpha_{F_m} \sim Normal(\mu_m, \sigma^2{}_m) \qquad \text{(S4c)}$$

$$\beta_{F_m} \sim Normal(\mu_m, \sigma^2{}_m) \qquad \text{(S4d)}$$

$\hat{F}$ is mean inflorescences produced by an individual and θ_F is the dispersion parameter. Other notation follows Eq. S1 and, again, only data post-2015 was used for this vital rate.

In 2017, we conducted a recruitment experiment to determine treatment effects on this important life history event. We collected seed from the three previously described source populations for the focal species in 2016 and used water-soluble glue (School Glue, Elmer's Products Inc., High Point, NC, USA) to attach them to plastic toothpicks.

We placed out 100 seeds divided evenly among four plots per treatment per site (25 seeds x 4 plots x 2 competition treatments x 6 sites). We tracked new recruits in 2017 and 2018 per number of toothpicks recovered. We counted recruitment events once so that a recruit in 2017 was not counted again as a recruit in 2018. For the vital rate, recruitment probability was modeled based on the number of seeds placed out (*D_t*; toothpicks recovered) in year *t* becoming a recruit in year *t*+1 (R_{t+1}).

$$R_{t+1} \sim Binomial(\hat{R}, D_t) \qquad \text{(S5a)}$$

$$logit(\hat{R}) = \alpha_{R_m} \qquad \text{(S5b)}$$

$$\alpha_{R_m} \sim Normal(\mu_m, {\sigma^2}_m) \qquad \text{(S5c)}$$

$\hat{R}$ is the mean recruitment probability and α_{R_m} is the mean recruitment probability for each treatment.

All models were fit with data from years 2015-2018 except where noted. Each model included group-level variance effects (“random effect”) for mountain transect. In addition, recruitment models for *P. alpina* had year and *F. brachyphylla* had year and plot group-level variance effects to improve model fit. Vital rate models were fit in *JAGS* (Plummer 2003) using *R2JAGS* (Su and Masanao Yajima 2015) in R (R Core Team 2018). We used “flat”, uninformative priors. Models were run with at least 50,000 iterations across three chains and a 25,000 iteration burn-in. Trace plots were examined to ensure proper mixing and posterior estimates. Potential scale reduction factors were analyzed to check parameter convergence ($\hat{R}$<1.01) (Gelman and Rubin 1992). Vital rate model performance was assessed with two posterior predictive checks (PPCs) (Compagnoni et al. 2016; Elderd and Miller 2015). The first plots a discrepancy metric (here, the sum of squared residuals; SSQ) calculated for iterations of a model fit and observed data against data simulated using model predictions. When a model is properly fitting, SSQ for observed and simulated data create a cloud of points centered on a 1:1 line. Second, we calculated Bayesian *p*-values, which asks if there is bias in a discrepancy metric (SSQ) such that simulated data has much poorer or much greater fit compared to observed data. Bayesian *p*-values close to 0.5 indicate good model fit (Gelman, Meng, and Stern 1996). All models presented reasonable fit by these PPC.

Vital rate parameters were used to populate MPMs. New MPMs were fit for each of the four treatment levels (core competition, core removal, novel competition, novel removal). MPMs were specified as:

$$n_{y_{t+1_m}} = \sum_{x=1}^{x=U} S(x; \alpha_{S_m}, \beta_{S_m}) G\big(y, x;\ \alpha_{G_m}, \beta_{G_m}\big) n_{x_t} + P\big(x; \alpha_{P_m}, \beta_{P_m}\big) F(x; \alpha_{F_m}, \beta_{F_m}) \chi R(\alpha_{R_m}) n_{x_t} \tag{S6}$$

n_y is the y$^{\text{th}}$ element of vector $\mathbf{n}$. Equation S6 portrays the survival of *x* sized plants and their growth to size *y*, given experimental specific vital rate parameters, *m* (e.g. α_{S_m}), summed over all *x* sizes. Per-capita seedling production for a maternal plant of size *x* is the product of the probability a plant flowers (*P*), the inflorescence number (*F*), seeds produced per inflorescence (χ; *Elymus scribneri*= 11.0, *Festuca brachyphylla*= 9.8, and *Poa alpina*= 26.3), and the probability a recruit establishes (*R*). The number of plants in a given size class *x* (n_{x_t}, or the x$^{\text{th}}$ element of $\boldsymbol{n}_t$) is multiplied by the per capita rate of seedling production and summed across the size classes. χ was estimated by collecting inflorescence from individuals with a large range in body size in natural populations of the focal species (30 individuals, 1-34 flowers per individual). We made a simplifying assumption that seed production per inflorescence does not vary through time and does not respond to treatment effects.

We took the dominant eigenvalue of the above matrix to obtain deterministic λ (Caswell 2008). We estimated a unique λ for each experimental population. Additionally, each estimate represents an independent draw from the posterior distributions of vital rates, thereby leveraging the full power of Bayesian analysis to quantify and propagate parameter uncertainty (Elderd and Miller 2015; Hobbs and Hooten 2015).

Competitive trait hierarchy model. We constructed hierarchical Bayesian models of the competitive trait hierarchy hypothesis (CTHH):

$$P_i = \alpha_p + \beta_j\left(T_{j,i} - T_{j,c}\right) + \epsilon_{k,l} \qquad \text{(S7a)}$$

$$T_{j,i} = \alpha_{j,i} + \beta_{n,j,i} ENV_n + \gamma_k \qquad \text{(S7b)}$$

$$T_{j,c} = \alpha_{j,c} + \beta_{n,j,c} ENV_n + \delta_k \qquad \text{(S7c)}$$

P_i is a fitness metric (i.e. biomass, survival, flowering probability) of the focal species individual *i*. P_i is predicted by the difference between traits, *j*, of the focal species individual, $T_{j,i}$, and the competing community found in the associated plot, $T_{j,c}$, with a slope term, β_j. We used community weighted means (i.e. average trait value for a community weighted by the abundance of individual species members) to represent the traits of competitors. α_p is an intercept term for a performance metric, *p*, in Eq. S7a. The method created a gradient of microcosm communities that competed with a given focal species individual in a plot because each plot had a different composition of competitors. $T_{j,i}$ and $T_{j,c}$ are additionally predicted by environmental variables, ENV_n, where *n* is a given environmental variable (i.e. VWC, temperature). Each trait, *j*, for the focal individual, *i,* and competing community, *c*, has an intercept ($\alpha_{j,i}$ and $\alpha_{j,c}$). Traits have a predicted relationship with the environment, represented by $\beta_{n,j,i}$ or $_c$, which is the estimated slope, n, for a given trait, j, of either the focal species, i, or its competing community, c. $\varepsilon_{k,l}$, γ_k, and δ_k are all equation specific group level effects representing the replicated mountains, k, and year the individual was transplanted, l. Relationships of traits to the environment have been neglected in the past work on the CTHH (Kraft et al. 2014; Kunstler et al. 2012, 2016), even though the outcomes of competition are dependent on how the environment filters species and their traits. Traits for focal species in Eq. S7a were drawn from posterior means by site and species. We used raw trait data from experimental plots for Eq. S7b. Traits for the community-weighted means in Eq. S7a and S7c used posterior trait means by species and sites from the community, which were then multiplied by the percent abundance in a given plot by the site.

Eq. 7a-c remained the same for each performance metric with necessary link functions and likelihood functions:

$$S_i \sim Bernoulli(\hat{S}) \qquad \text{(S8a)}$$

$$F_i \sim Bernoulli(\hat{F}) \qquad \text{(S8b)}$$

$$B_i \sim Normal(\mu, \sigma^2) \qquad \text{(S8c)}$$

Individual i survival (until end of the experiment; S_i) and flowering probability (F_i) was modeled as a Bernoulli process with logit link functions. Individual i biomass was normally distributed with a respective mean, μ, and variance, σ^2. Group-level variance effects for survival models were implemented for species (all included in the same model), mountain peak, and year of transplanting (three transplant times). Flowering probability was assessed for every year except for 2015 and included species, year, and mountain peak group-level variance effects. We constructed allometric equations that used tiller number and height of species to predict live biomass at final harvest. We investigated models including the factorial interaction, just interaction, and main effects tiller number and height in *base* R (R Core Team 2018) lm regression and best models were determined by *AICc* model selection (lowest *AICc* model has greatest within sample predictive accuracy). Allometric equations fit as follows: *E. scribneri* R^2=0.79, *F. brachyphylla* R^2=0.81, *P. alpina* R^2=0.75.

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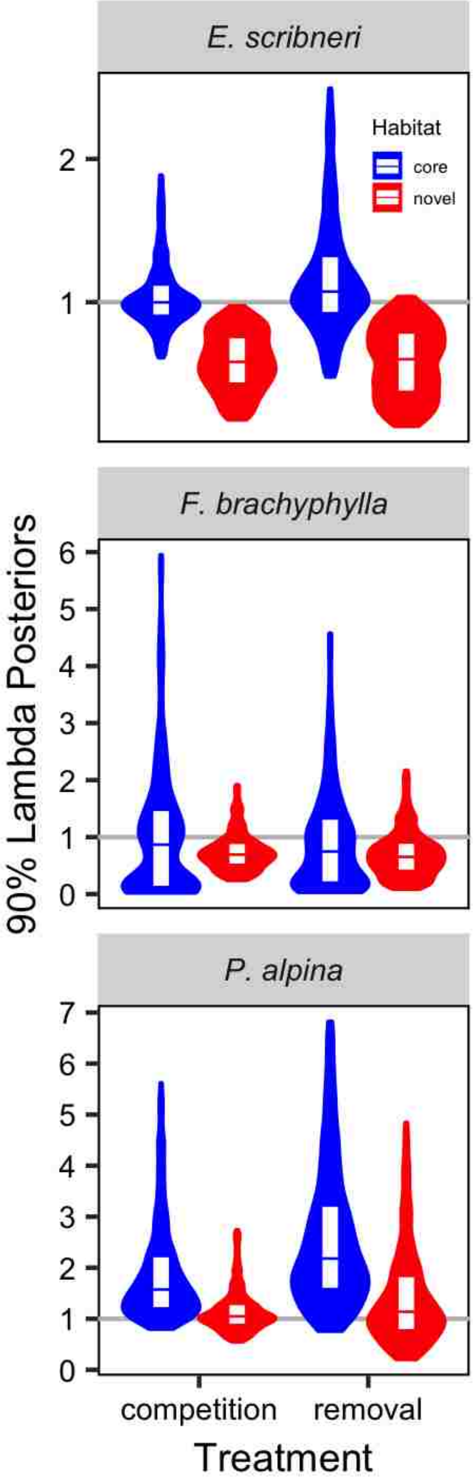
Figures

Chapter 3 Figure 1. Posterior distributions of lambda for experimental populations by competition treatment, location in range (“habitat”), and species. Violins represent the full 90% posterior while embedded boxplots show the mean (middle line) and 50% range of the posterior. Gray intercepts mark where lambda is equal to 1, where population growth is at replacement. Lambda was estimated via matrix projection models (see Methods).

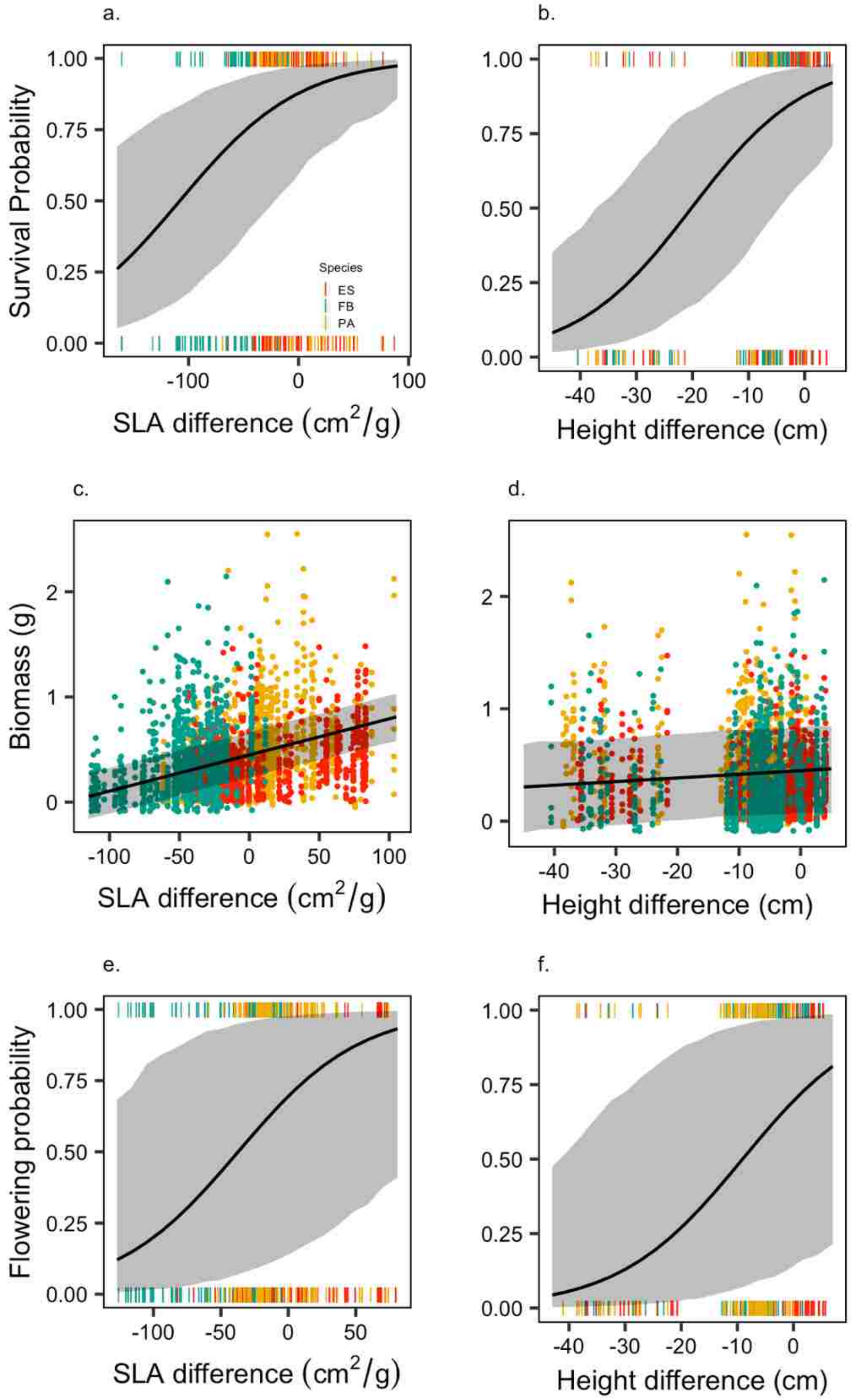
Chapter 3 Figure 2. Trait differences predict survival (a-b), biomass (c-d), and the flowering probability (e-f) of focal species. Data points are colored by focal species and follow the legend in panel a. Black lines are the mean relationship between trait difference and a given performance metric and the shaded gray areas represent 85% credibility intervals around the mean.

Chapter 3 Figure 3. Relationship of traits to environmental gradients. Panels (a-d) are the community-weighted mean traits of the competing community and use the legend that appears (d). Panels (e-h) show intraspecific variation in traits of the focal species and use the legend that appears in (e). Lines show the predicted relationships of traits and environmental variables scaled to have a mean of zero and divided by two s.d. Points represent raw data and confidence intervals are 95% posterior credibility intervals.

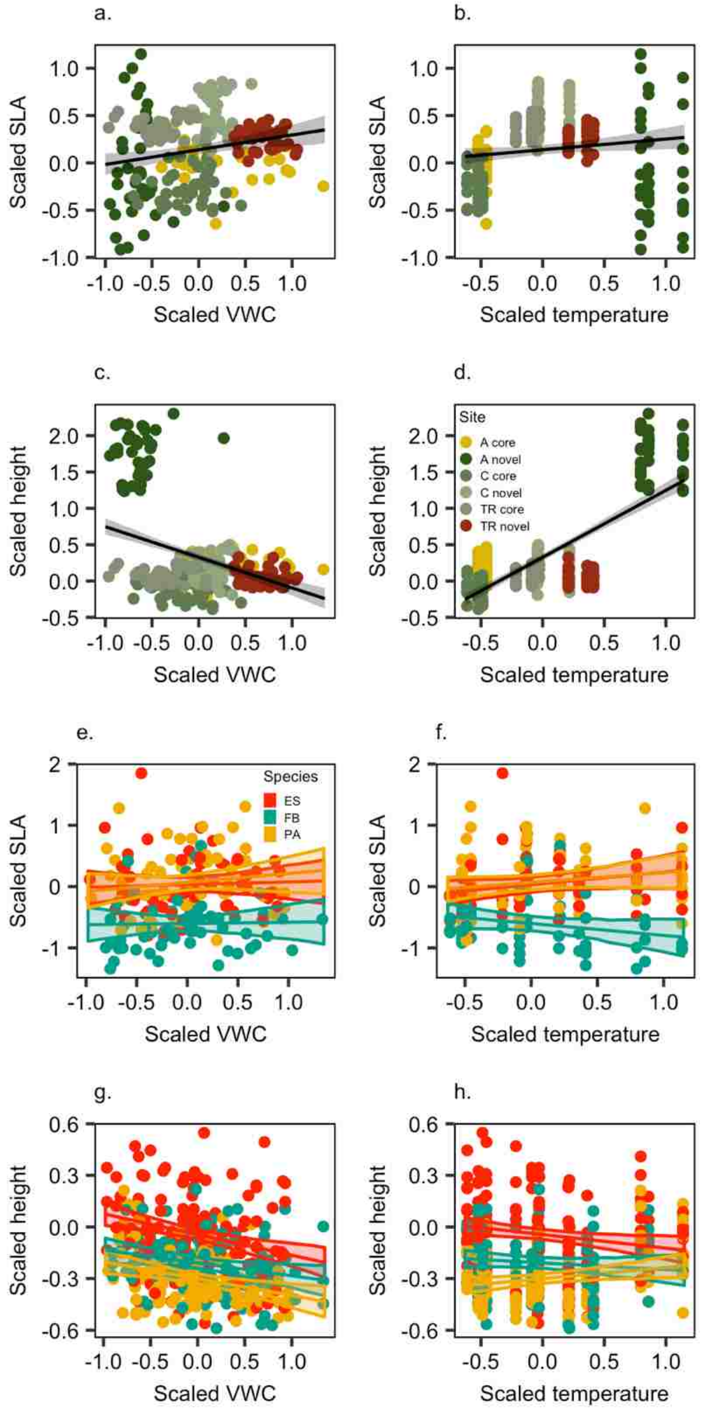
Chapter 3 Figure 1.



Chapter 3 Figure 2.



Chapter 3 Figure 3.



Chapter 3 Supplementary Material

Table S1. Coordinates for experimental sites.

Peak	*Site*	*Elevation (m)*	*Latitude (°)*	*Longitude (°)*
Avery	Core	3655	38.98407	-106.97021
Avery	Novel	3192	38.97142	-106.98428
Cinnamon	Core	3726	38.99495	-107.07043
Cinnamon	Novel	3366	38.97018	-107.02955
Treasury	Core	3598	39.00000	-107.08065
Treasury	Novel	3197	38.97073	-107.05871

Figure S1. Posterior (95%) mean estimates of treatment effects on survival (A), biomass (B), and flowering probability (C). Each distribution is a probability density function representing the predicted mean of treatment by species and dependent variable. All models were fit with flat priors and group-level variance effects for mountain transect and year the plant was transplanted. Biomass models additionally had date as a covariate, to account for temporal correlation across sampling periods, and flowering probability models had a year measured group-level variance effect.

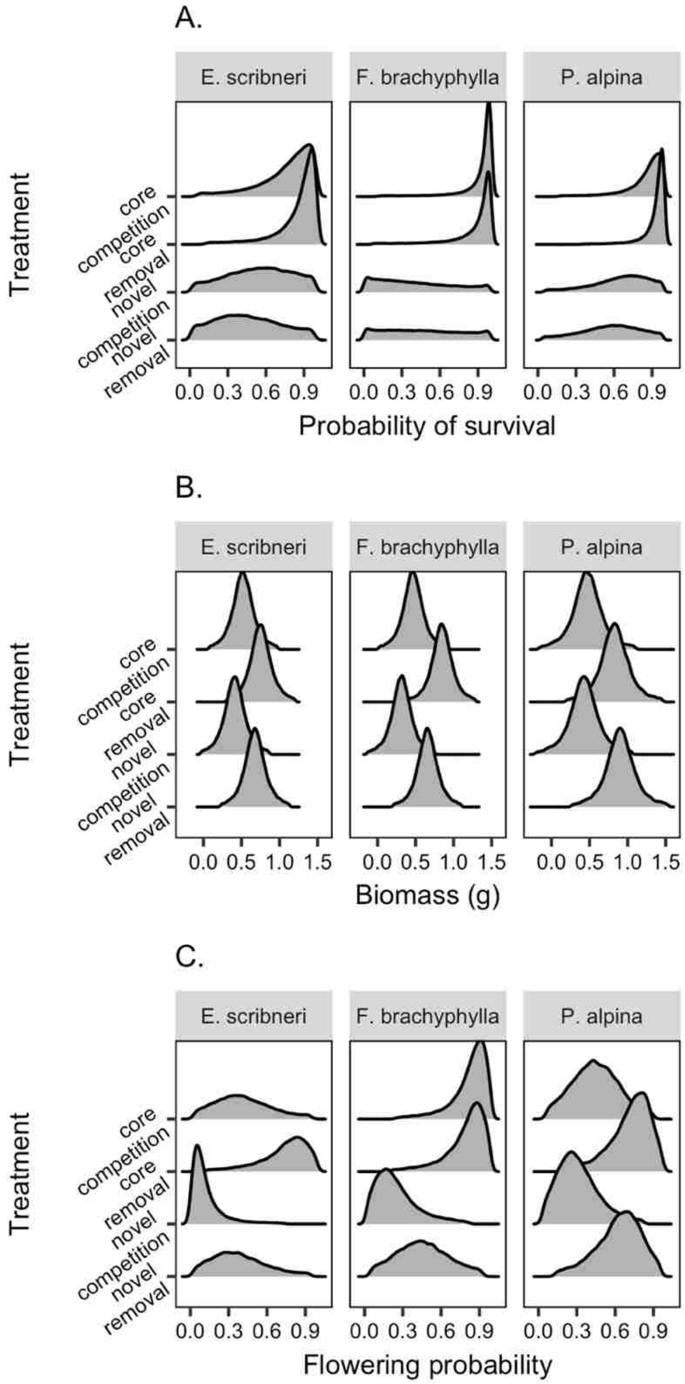

A.
E. scribneri
F. brachyphylla
P. alpina
Treatment
core competition
core removal
novel competition
novel removal
0.0 0.3 0.6 0.9
Probability of survival
B.
E. scribneri
F. brachyphylla
P. alpina
Treatment
core competition
core removal
novel competition
novel removal
0.0 0.5 1.0 1.5
Biomass (g)
C.
E. scribneri
F. brachyphylla
P. alpina
Treatment
core competition
core removal
novel competition
novel removal
0.0 0.3 0.6 0.9
Flowering probability

Figure S2. Gopher disturbance on the right-hand side of the of the photo abuts the mesh fence and limits its intrusion into the plot.