Mammalian herbivores restrict the altitudinal range limits of alpine plants

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Abstract

Although rarely experimentally tested, biotic interactions have long been hypothesised to limit low-elevation range boundaries of species. We tested the effects of herbivory on three alpine-restricted plant species by transplanting plants below (novel), at the edge (limit), or in the centre (core) of their current elevational range and factorially fencing-out above- and belowground mammals. Herbivore damage was greater in range limit and novel habitats than in range cores. Exclosures increased plant biomass and reproduction more in novel habitats than in range cores, suggesting demographic costs of novel interactions with herbivores. We then used demographic models to project population growth rates, which increased 5–20% more under herbivore exclosure at range limit and novel sites than in core habitats. Our results identify mammalian herbivores as key drivers of the low-elevation range limits of alpine plants and indicate that upward encroachment of herbivores could trigger local extinctions by depressing plant population growth.

KEYWORDS
biogeography, biotic interactions, climate change, Dobzhansky–MacArthur hypothesis, herbivory, MPM/IPM demographic modelling, population ecology

INTRODUCTION

Antagonistic species interactions have long been hypothesised to limit species distributions (Brown, 1995; Dobzhansky, 1950; Louthan et al., 2015; MacArthur, 1972). Dobzhansky (1950) and MacArthur (1972) separately proposed that a species' high-elevation range limit is determined by harsh abiotic conditions, whereas its low-elevation range limit is set by antagonistic species' interactions (the Dobzhansky–MacArthur hypothesis or DMH; Brown, 1995). The high-elevation prediction of the DMH is broadly supported (Hargreaves et al., 2014; Hobbie & Chapin, 1998; Klimeš & Doležal, 2010; Sunday et al., 2011, 2012). Recent work suggests plant competition can determine low elevation range boundaries.

Plants moved below their elevation range limit and competed with a novel, low-elevation plant community often had lower survival, biomass and reproduction than plants competed against their home range community transplanted into the same low-elevation environment (Alexander et al., 2015). However, other antagonisms, such as herbivory, have received less attention than competition as potential mechanisms that restrict range limits in plants (Benning et al., 2019).

Understanding the causes of species' range limits has become more important as climate change causes species ranges to shift (Gottfried et al., 2012; Kelly & Goulden, 2008; Lenoir et al., 2008; Parmesan, 2006). Climate change can cause population declines via physiological stress (Cahill et al., 2012) or altered species interactions

(Angert et al., 2013; Fridley et al., 2016; Tylianakis et al., 2008). Less studied is how range shifts associated with climate change create novel communities as species from previously disparate geographical 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 (Alexander et al., 2016; Hargreaves et al., 2014).

Several conditions must be met to demonstrate that herbivory restricts the lower range limits of a plant species: (1) Herbivory (live plant biomass removed by herbivores) must increase from inside a species' range outward towards its lower range limit. The DMH predicts that herbivory negatively covaries with abiotic stress, such that harsh, low-productivity abiotic environments have less herbivory than abiotically benign, high-productivity environments (Brown, 1995; Louthan et al., 2015). Some data support this condition: *Arnica montana* had 75% of leaf area consumed by slugs when transplanted below elevation range limits, compared to <1% herbivory in their home range (Bruelheide & Scheidel, 1999).

Second, (2) herbivory decreases plant fitness (Louda & Potvin, 1995), therefore, excluding herbivory increases plant population growth (Agrawal et al., 2012; Lehndal & Ågren, 2015; Maron, 1998; Maron & Crone, 2006). Additionally, populations moved beyond their lower elevational range limit must be inviable (population growth rates or $\lambda < 1$) in the presence of herbivores but viable when herbivores are excluded. Fitness effects of herbivores are difficult to parse from prior cross-range transplant experiments because these were not paired with herbivory manipulations and/or measurement of plant fitness metrics (e.g. Bruelheide & Scheidel, 1999; Rivest & Vellend, 2018). The few studies that have investigated how herbivory affects plant population growth within a species' range found that population growth was more suppressed by herbivores in the less abiotically stressful part of the plants' geographical range (Hegland et al., 2010; Louthan et al., 2018; Miller et al., 2009). However, these studies missed a key piece of the second condition: for a given biotic interaction to define a range limit, it must prevent a species from persisting ($\lambda < 1$) beyond their current limit, which, to our knowledge, has not been demonstrated.

Here, we experimentally excluded both above- and belowground mammalian herbivores using fencing to limit ungulate and gopher access to focal alpine plants that were planted within, at, or below their elevational range limits in the West Elk Mountains, Colorado, USA. We asked: (1) Does herbivory increase from the core habitat to the range limit and peak in novel habitats? (2) Does mammalian herbivory reduce plant survival, growth, or reproduction more from the core habitat to the range limit and peak in novel habitats? Then, we incorporated treatment effect sizes into demographic models parameterised from natural populations to ask: (3) Does herbivore exclusion increase population growth rates, and

does the benefit of herbivore exclusion increase from core to limit and peak in novel range habitats? Mammalian herbivores suppressed reproduction and growth thereby reducing population growth rates more so at range limits and in novel habitats than in the range core, suggesting that mammal herbivory is key in limiting alpine species' low elevation range limits.

METHODS

Study species and sites

We focused on three native, caespitose (non-clonal and only reproduce by seed), alpine-restricted grass species: *Poa alpina*, *Festuca brachyphylla* and *Elymus scribneri* (Shaw, 2008). More detail on the focal species life-history strategies, importance and information on herbivores can be found in the Supporting Information Methods. We established experiments in the West Elk Mountains, CO, USA, in which temperature, atmospheric pressure and plant available N and P decline with elevation (Dunne et al., 2003; Kittel et al., 2002). The regional lapse rate is ~1°C decrease in temperature with ~140 m increase in elevation (Pepin & Losleben, 2002). We used previous vegetation surveys (Lynn et al., 2019) to locate experimental 'habitats' in the range core ('core'), at the low range limit ('limit'), or below the range limit ('novel'; ~230 m a.s.l. below limit sites). Novel habitats reflected ~2°C greater mean annual temperature than the range edge of each plant species, consistent with predicted climate warming for the region by 2050 (Pepin & Losleben, 2002; Rangwala & Miller, 2012). The three habitat types were replicated on three mountains for a total of nine sites (site coordinates and map in Table S1 and Figure S1).

Experimental design

Experimental implementation

Plants were reared in a greenhouse prior to transplantation in the field (details in Supporting Information Methods). We used a 2 × 2 factorial design to allow/exclude aboveground ungulates and allow/exclude belowground gophers using fencing, and replicated this design at the core, limit and novel habitats. Gophers were excluded by inserting wire mesh ~20 cm into the ground around a plot (Figure S2). Ungulates were excluded using 40 × 40 cm fences of 20-gauge chicken wire that were 30 cm tall (mean plant height across species was 8.8 cm; Figure S2). At each site, we marked 20 plots (30 × 30 cm) and randomly planted one individual of each species per plot into an equilateral triangle at 15 cm spacing between plants. All vegetation was removed and plots trenched prior to planting and weeded monthly during the growing

season until harvest to control for effects of competitors in transplant sites and isolate the influence of herbivory. Herbivory treatments (no exclosure 'controls', 'above' ground exclosure, 'below' ground exclosures, and 'both') were randomly assigned to plots within a site and replicated in five plots per site. Experimental set-up occurred from 22 June to 20 July 2016.

Experimental data collection

Starting in August 2016, we took monthly measurements of plant size and foliar damage by ungulate and insect herbivores (see background insect herbivory in natural populations Figure S3). Plant size was determined by counting the number of vegetative tillers. We counted the number of inflorescences to estimate reproduction but collected them prior to pollen dispersal. We took visual percentage estimates of the amount of damage present on each plant. Mammal damage was assessed as even clipping by grazing animals with whole leaf/tiller damage traced back to the crown. Insect herbivory (e.g. grasshopper) was assessed as stippling and partial leaf chewing damage.

We harvested plants from 14 to 27 August 2018. Prior to harvest, all plants were assessed for size and damage as described above. Plant aboveground biomass was cut at the meristem just below the soil surface and 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 from natural populations

In 2015, we set up five 1mx5m permanent plots that contained natural populations of the three focal species at one core site given the time demands of collecting demographic data (Avery core; Table S1). We marked every individual with metal tags and measured height (nearest mm), tiller number and inflorescence number in August 2015 and repeated annual censuses through August 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

We fit Bayesian hierarchical models to treatment effects on herbivore damage and fitness (Hobbs & Hooten, 2015). All analyses were performed in the R programming language (R Core Team, 2018) using JAGS (Plummer, 2003) and the 'R2jags' package (Su & Masanao Yajima 2015). Each species was modelled separately, and each dependent variable was modelled by the interaction of elevation habitat (core, limit, novel), aboveground fencing (yes, no) and belowground fencing (yes, no). Full model fitting and checking details are in Supporting Information Methods. Full parameter estimates from each model of fixed and group random variance effects (site and individual, depending on model; Table S2), sample sizes and number of groups per group variance effects per model per species (Table S3) are in the Supporting Information. Figures for parameter estimates of main and interaction effects of habitat and fencing treatments on herbivory and fitness are included in Figure S4 and S5 respectively. Figures highlight the 68% credible intervals (CIs), representing ± one standard deviation from posterior means.

(1) Does herbivory increase from the core habitat to the range limit and peak in novel habitats? and (2) Does mammalian herbivory reduce plant survival, growth, or reproduction more from the core habitat to the range limit and peak in novel habitats?

We assessed variation in herbivore damage with four dependent variables: herbivory presence, percent insect damage, percent mammal damage, and total percent damage (insect + mammal). Herbivory presence was modelled as a Bernoulli process (0,1). For percent damage analyses, we first removed observations with no damage (zeros) and normalised percent damage with a logit-transformation. In addition to the treatment main effects, each herbivory-dependent variable was modelled with day of the year to account for temporal effects. Models of damage included experimental site and replicate individuals as random intercept variance terms.

If ungulate and fossorial mammal herbivory depress plant fitness, then individuals in exclosures should have higher survival, biomass, and/or reproduction than controls without exclosures and we expected this effect to be greatest in novel habitats. We modelled individual survival, biomass and inflorescence number separately for each species using similar models as above. Survival was a Bernoulli process (0,1) without random intercepts (see Supporting Information Methods). Biomass was interpolated with allometric equations using tiller number and was normally distributed. Models of biomass included day of the year as an additional fixed effect and site and individual as random intercepts. We modelled reproduction as inflorescence counts with a negative binomial, year as an additional fixed effect (only 2017 and 2018, few inflorescences produced in 2016), and site and individual plant as random intercepts.

(3) Does herbivore exclusion increase population growth rates, and does the benefit of herbivore exclusion increase from core to limit and peak in novel range habitats?

We briefly describe the population models but provide full details in Supporting Information Methods,

including vital rate models and sample sizes. We built demographic models for each species by applying experimental treatment combination effects (i.e. predicted effects of main and interaction terms from fitness models) to demographic data from natural populations, which allowed for an assessment of herbivore effects on λ for core, limit and novel habitats. We fit models for four size-dependent vital rates (survival, growth, flowering probability, inflorescences number) and recruitment (Chung et al., 2015). We used size-structured (tiller number) matrix projection models (MPMs) to estimate deterministic population growth rates (λ). Given the natural population equates to a core habitat control treatment in the experiment, we used mean effect size (percentage difference) of each treatment relative to core habitat controls to adjust vital rate intercept terms for survival, growth and inflorescence number. For example if a species had 20% higher growth in the novel habitat/both exclosure treatment combination compared to core habitat/control treatment, we increased the mean posterior growth intercept by 20% to reflect treatment effects. Using the predictions from the statistical models reflects potential climate change scenarios. For example novel habitat/both exclosures treatment approximates how populations will respond with warming and no increased ungulate or fossorial mammal damage. We only manipulated vital rate intercepts given the similar age and size of experimental individuals did not allow for estimation of size-dependent treatment effects. The intercepts quantified how herbivory decreased the magnitude of growth, survival and reproduction transitions. We estimated uncertainty in λ using 1000 random draws from the 95% credible posterior distributions of vital rate parameters (Compagnoni et al., 2016; Elderd & Miller, 2016). Additionally, we performed life table response experiments (LTRE; Caswell, 2008) that compared treatment effects with core/control treatments (natural population) as the reference matrix to investigate the contribution of experimentally adjusted vital rate parameters to differences in λ. We assess relative effects of treatments on λ with the difference between reference and treatment populations ($\Delta\lambda = \lambda_{\text{treatment}} - \lambda_{\text{reference}}$).

RESULTS

Herbivory increased from core to limit and novel sites

Herbivory generally increased from core to limit to novel habitats, regardless of plant species or herbivory metric (Figure 1), thus satisfying criterion 1 (posterior estimates Figure S4 and Table S2). The mean probability that an individual was damaged increased from core-to-limit and core-to-novel elevations by 45% and 60% for *E. scribneri*, >300% at both elevations for *F. brachyphylla*, and ~150% at both elevations for *P.*

alpina (Figure 1a). Across all leaf damage types, herbivory did not differ between core and limit elevations for *E. scribneri* or *F. brachyphylla*, but both species received >90% more damage at novel sites than in core habitats. *Poa alpina* had 90% more damage at its range limit, and ~140% more in novel habitats than in core sites (Figure 1b). *Elymus scribneri* had similar insect damage at core and limit habitats but ~50% more at novel sites, *P. alpina* had ~20% more and ~80% more in limit or novel habitats, respectively, than in core sites (Figure 1c). *Festuca brachyphylla* insect damage varied little across habitats (Figure 1c). Mammal damage increased from core to limit and to novel habitats by ~100% for *E. scribneri*, ~90% and ~500% for *F. brachyphylla* and ~200% and ~100% for *P. alpina* (Figure 1d). However, there was considerable uncertainty associated with estimates of mammal damage, especially for *F. brachyphylla* and *P. alpina* (Figure 1d). Exclosure effects on herbivory were much weaker than elevational differences for all metrics of herbivore damage. Both *E. scribneri* and *P. alpina* plants had more insect damage in aboveground exclosures (above and both treatments) than in unprotected controls or belowground exclosures in novel habitats (Figure 1c). Additionally, in *E. scribneri*, mammal herbivory in belowground exclosures increased more over controls from core (~10% more with belowground exclosures) to limit (~35% more) to novel (~85% more) habitats (Figure 1d).

Mammalian herbivory reduced growth and reproduction more in range limit and novel than in core habitats

The effects of herbivory on biomass and reproduction generally followed expectations from criterion 2: Excluding herbivores increased fitness components the most in novel habitats and the least in core habitats (posterior estimates in Figures S5 and S6 and Table S3).

Biomass

Plant biomass was greatest in novel habitats for all species (Figure S6) and the effect of any given exclosure treatment over controls tended to be greatest at the range limit, followed by the novel habitats (Figure 2a). All three exclosure treatments increased *E. scribneri* biomass compared to controls by ~10% at core, ~45% at limit and ~35% at novel habitats (Figure 2a). Similarly, *F. brachyphylla* biomass increased by ~5% at core, ~40% at limit and ~15% at novel compared to controls for all three exclosure treatments (Figure 2a). *Poa alpina* biomass was larger with any exclosure over controls by ~20% at core, ~35% at limit and ~40% at novel habitats (Figure 2a).
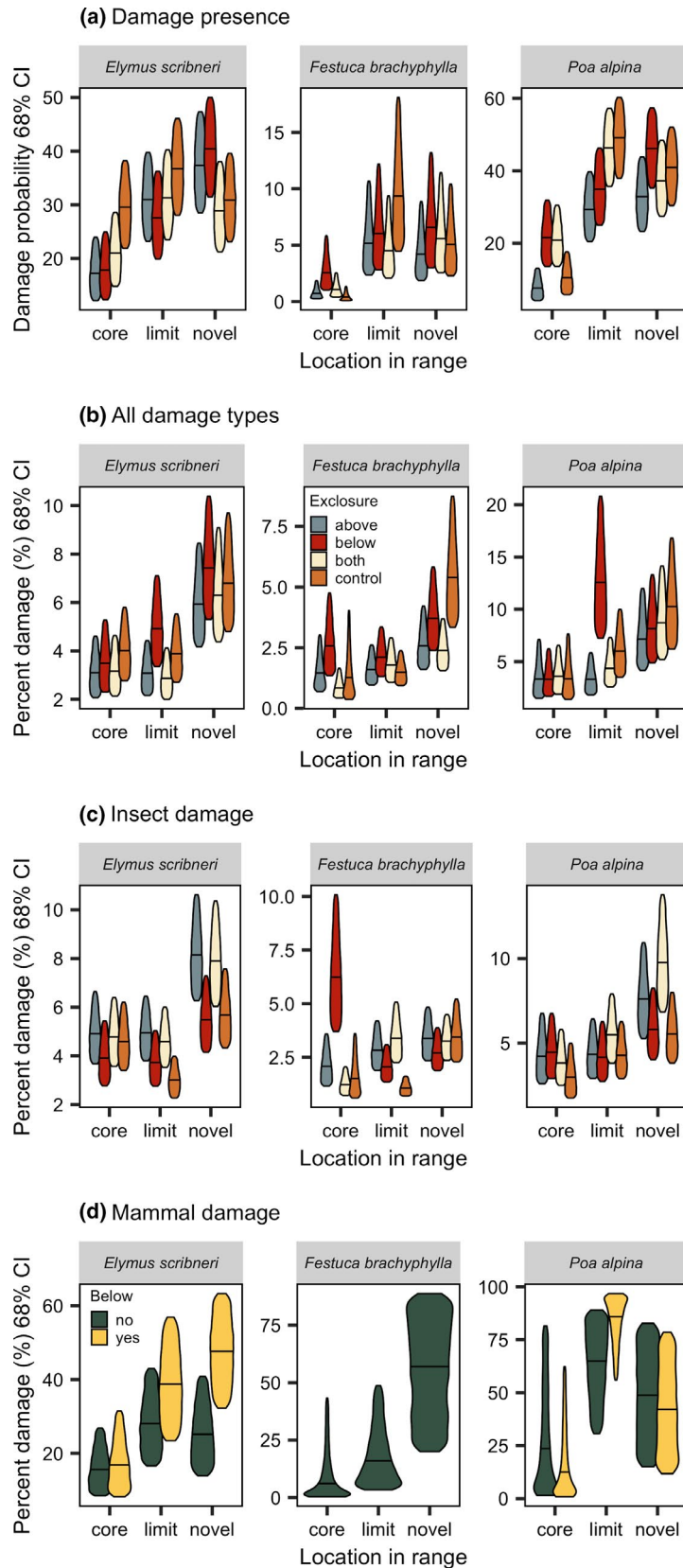
FIGURE 1 Treatment effects on herbivory presence (% of individuals) and damage amount (% leaf area) by type of herbivory. (b) 'All damage types' is insect and aboveground mammal damage combined. In the legend, 'control' lacked exclosures, 'below' had belowground exclosures, 'above' had aboveground exclosures, and 'both' had both. The treatment legend in (b) applies to panels (a) and (c). In panel (d) 'Mammal damage' the *E. scribneri* and *P. alpina* models included belowground exclosures, whereas there was insufficient data to assess this effect for *F. brachyphylla* where control represents plots with and without belowground exclosures. Violins are constructed from the 68% credibility interval (CI) with the median represented by the middle line (full treatment and interaction effect posterior estimates in Figure S4 and Table S2)
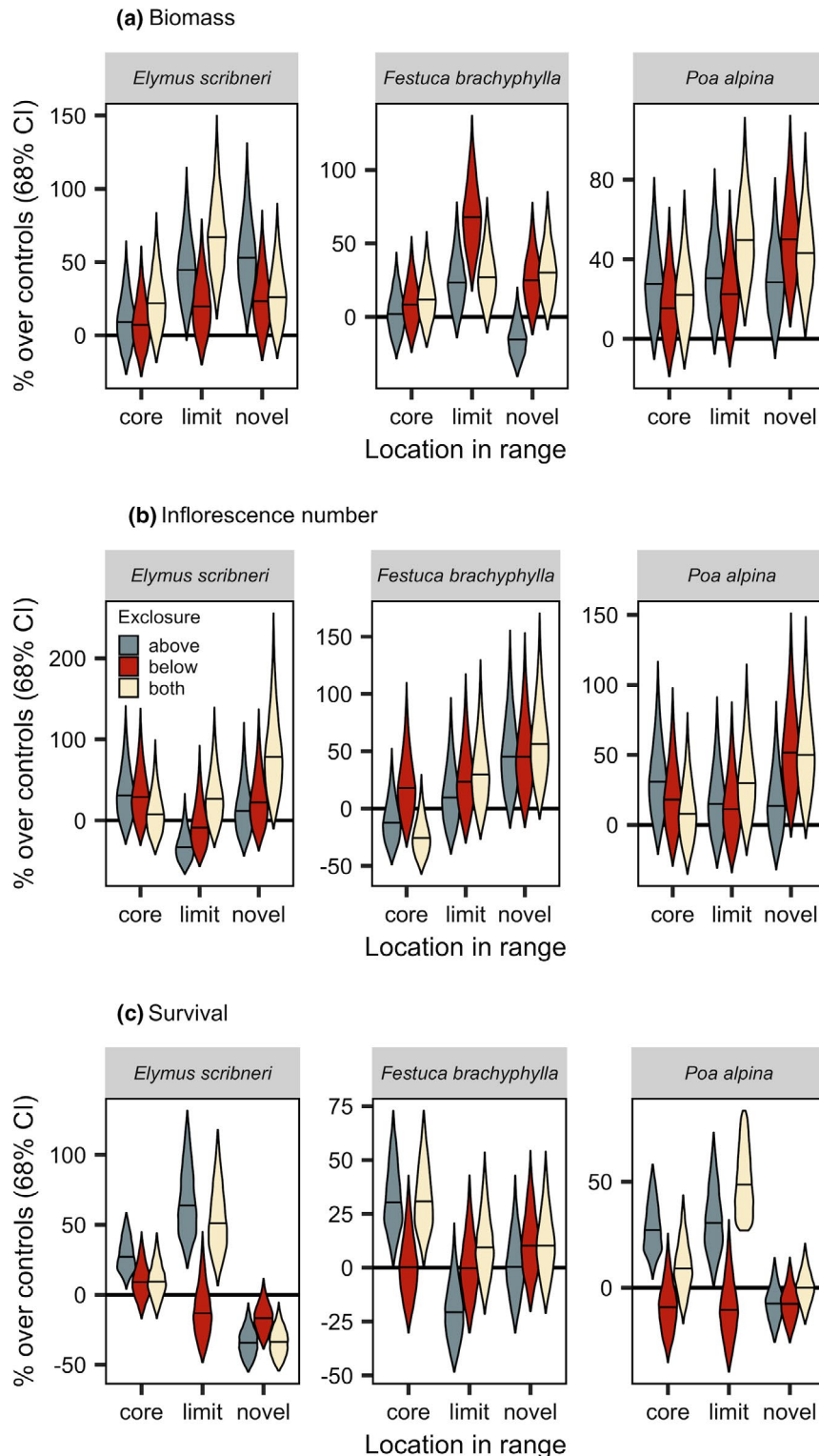
FIGURE 2 Exclosure effects over no fence controls on biomass of individuals over the experiment's duration (a), inflorescence production (reproduction; b), survival probability (c) of an individual to the end of the experiment. All panels share the legend in (b). In the legend 'above' had aboveground exclosures, 'below' had belowground exclosures, and 'both' had both. Violins are constructed from the 68% credibility interval (CI) with the median represented by the middle line (full treatment and interaction effect posterior estimates in Figures S5 and S6 and Table S2)

Reproduction

Elymus scribneri reproduction increased under combined above-belowground exclosures relative to controls by

~75% in novel habitats, whereas all other treatments had similar reproduction to controls (Figure 2b). All treatments together increased *F. brachyphylla* reproduction over controls by ~25% at limit, ~50% at novel habitats,

and decreased by ~6% in core habitats (Figure 2b). Belowground and both exclosure treatments boosted *P. alpina* reproduction by ~50% relative to controls in novel habitats, but exclosure effects at limit and core sites were negligible (Figure 2b). For all three species, but especially *F. brachyphylla*, reproduction was lowest, on average over treatments, at the range limits (Figure S6).

Survival

Aboveground exclosures increased *E. scribneri* survival by ~25% in core habitats, aboveground and both exclosures increased survival by ~50% at limit habitats, and all exclosures *reduced* survival by ~25% in novel habitats over controls (Figure 2c). Survival of *F. brachyphylla* increased by ~30% for plants with aboveground or both exclosures over controls at core habitats, with little evidence for exclosure effects at limit or novel habitats (Figure 2c). Survival of *P. alpina* improved 25–50% with aboveground or both exclosures over controls in limit habitats, with only small increases in survival with aboveground exclosures in core habitats, and little effect of exclosure in novel habitats (Figure 2c). No *P. alpina* individuals died that were transplanted to the range limit and protected with both exclosures (Figure 2c). Across species, survival was lowest (second lowest for *F. brachyphylla*) in treatments lacking aboveground exclosures at range limits (Figure S6c).

Herbivore exclusion increased population growth rates more in novel and limit than in core habitats

Results of projection models supported criterion 2, that: (1) excluding herbivores (above, below, and both) increased plant population growth (λ), and (2) the effect of exclosure was greatest in limit and novel habitats (Figure 3), and smallest in core habitats near the elevational centres of species' distributions. For *E. scribneri*, all three exclosure treatments increased λ over controls across the three habitats, but plants in both exclosures had the greatest population increase, with 7% greater growth rate in core habitats, 20% at range limits, and 9% in novel habitats (Figure 3). For *F. brachyphylla*, exclosures increased λ ~3% across all habitat types, but the only treatments with median λ above replacement (>1) were novel habitats with both or belowground exclosures (Figure 3). For *P. alpina*, exclosures increased population growth by 4% in core but by ~7% at range limit and novel sites and the largest benefits accrued at limit habitats with both above- and belowground mammal exclosures (Figure 3).

The LTRE suggested that differences in λ were most attributable to the effects of exclosures and habitats on growth (Figure 4). Though survival and reproduction often contributed to larger λ in exclosures compared to reference control-core populations, these contributions were often less than half as large as the exclosure effects on plant growth. The importance of growth contributions to *E. scribneri* and *P. alpina* λ generally increased from to core to limit to novel habitats and with exclosures (Figure 4). While in *F. brachyphylla*, λ was most sensitive to the overall effect of the range limit habitat on growth, where all treatments and controls had lower λ than the core control (reference) population (−Δλ; Figure 4). Finally, Δλ at range limits was negative in controls of all species, indicating that population growth rates decreased when plants were exposed to herbivores at the range limit. Table S4 provides full LTRE results.
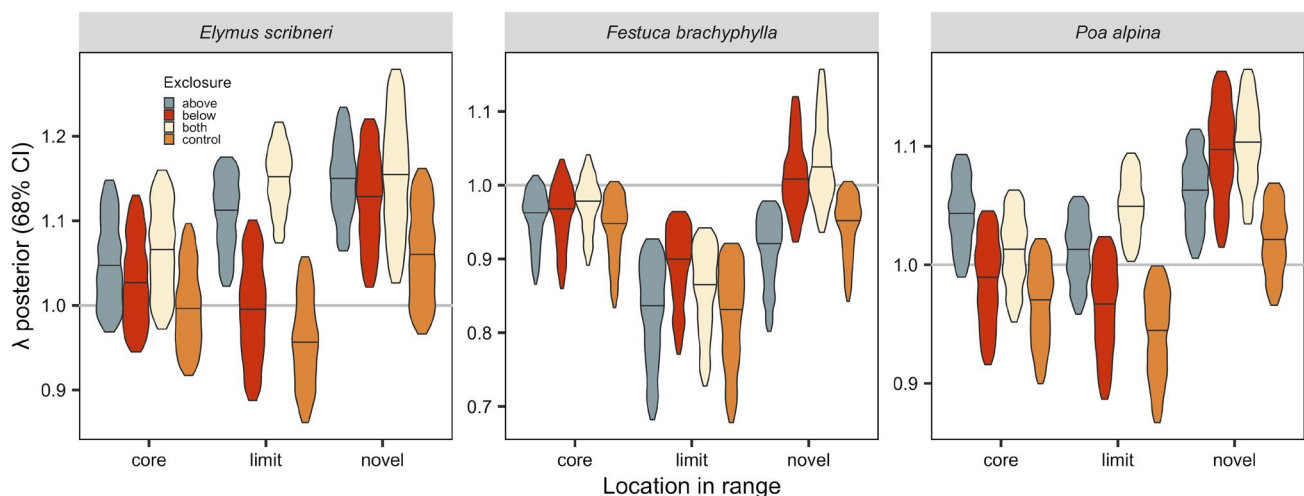

FIGURE 3 Population growth rates (λ) of each species incorporating experimental treatment effects. The core-control λ estimate represents the natural population from which all other λ estimates were derived by applying percent differences of each experimental treatment to the core-control treatment to the intercepts of the survival, growth, and inflorescence production vital rates of the natural population. In the legend, 'control' lacked exclosures, 'below' had belowground exclosures, 'above' had aboveground exclosures, and 'both' had both. Violins are constructed from the 68% credibility interval (CI) with the median represented by the middle line
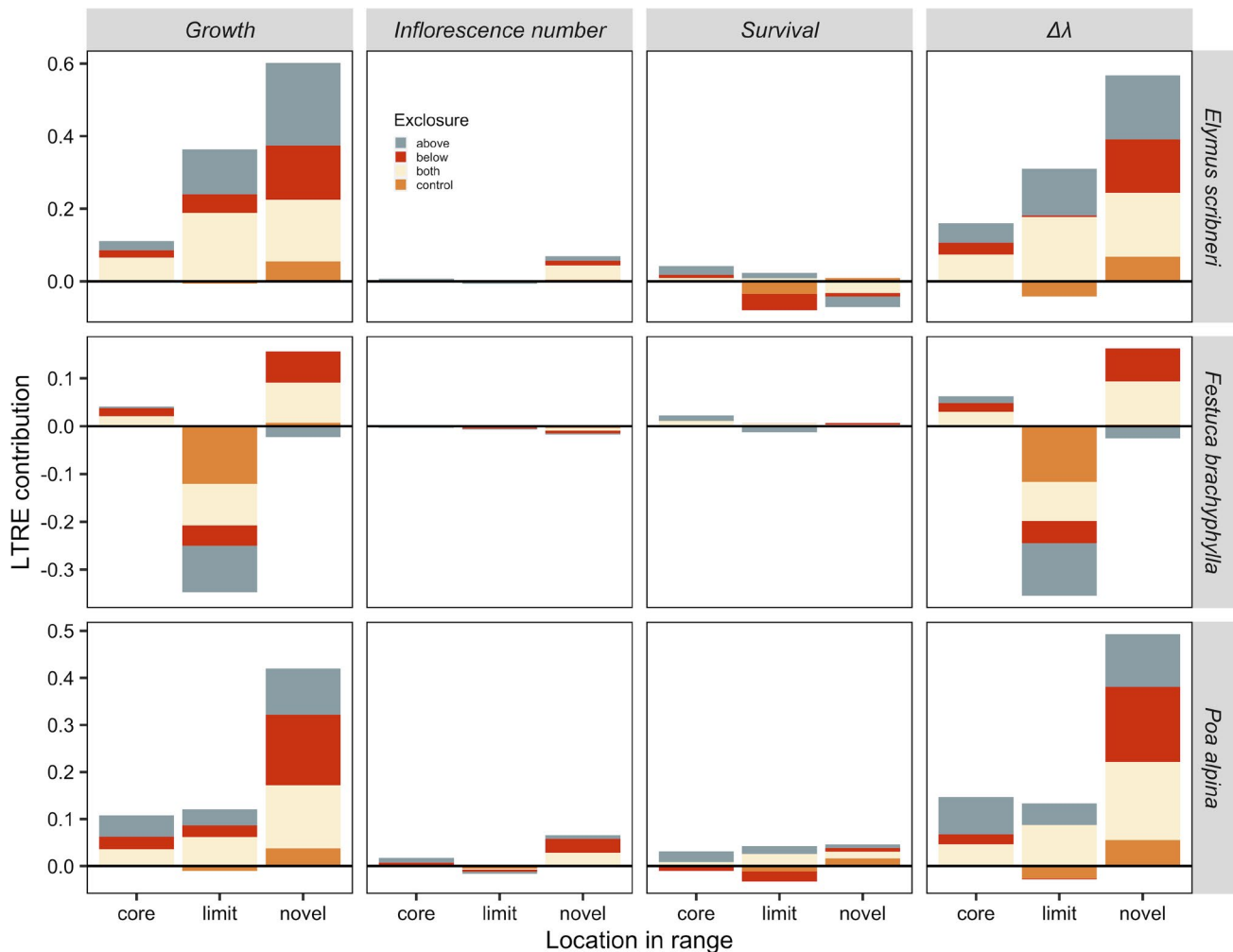
FIGURE 4 Contribution of growth, inflorescence number, and survival intercepts to λ across the experimentally adjusted projection matrices ($\Delta\lambda = \lambda_{\text{treatment}} - \lambda_{\text{natural/core-control}}$). All estimates were derived by taking the median values of the vital rate parameters for each treatment adjusted model. In the legend, 'control' lacked exclosures, 'below' had belowground exclosures, 'above' had aboveground exclosures, and 'both' had both. The individual contributions of each vital rate by habitat × exclosure treatment are stacked and do not represent cumulative effects (i.e. height of the bar represents the vital rate contribution). Full LTRE results can be found in Table S4

DISCUSSION

We provided experimental evidence that herbivory can restrict the low-elevation range limits of alpine plants. First, herbivore damage increased from the core of the species' range towards its limit and beyond. Thus, observations support DMH criterion 1, for all three species, that individuals occupying lower elevation environments experience greater intensity of antagonistic biotic interactions. Second, exclusion experiments revealed that mammalian herbivores depressed plant fitness components and population growth more in the novel or range limit habitats than in the core of species elevational range, supporting DMH criterion 2. The second criterion held for *E. scribneri* and *P. alpina*, whereas results for *F. brachyphylla* suggested that aspects of the environment other than herbivory were most important for fitness at range limits. This work generally supports a growing body of evidence that species interactions can

affect range dynamics, which is important for predicting future community dynamics under climate change (Alexander et al., 2015; Louthan et al., 2018).

Herbivory increased from within to outside of species' ranges

To our knowledge, this is the first study to find that plants transplanted below their elevation range limits experienced greater mammal herbivory than individuals in their core elevation range. Herbivory often increases towards warm temperatures associated with elevational gradients (Bruelheide & Scheidel, 1999; Moreira et al., 2018). Classic theory predicts that grasses may respond to herbivory with overcompensation, where grazing initiates higher aboveground biomass, rhizome and stolon production (McNaughton, 1979). However, the focal species are caespitose grasses which more

rarely reproduce vegetatively and are generally not well adapted to large grazing mammals (Koerner et al., 2014; Mack & Thompson, 1982). There was no evidence of overcompensation, given that excluding ungulate herbivores tended to increase biomass over uncaged controls (Figure 2a).

Alpine plants moved below their range limits were 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 defence decreases with elevation for both plant populations (Pellissier et al., 2014, 2016) and communities (Callis-Duehl et al., 2017; Descombes et al., 2017). Favourable conditions for herbivores at low elevation can increase their abundance (Descombes et al., 2017). Additionally, direct effects of temperature on the development and metabolic rates of insect herbivores (Barrio et al., 2016; Irlich et al., 2009) or mammal foraging (Aublet et al., 2009) could amplify consumption and/or herbivore abundance at low elevation sites. Another possibility includes longer exposure times of plants to herbivores due to longer growing seasons than at high elevations (Dunne et al., 2003).

A surprising effect of our fencing treatments was that insect herbivory sometimes increased under exclusion of aboveground mammals, even though this effect was weaker than habitat effects and much less than the magnitude of mammal herbivory. Insects may prefer plants that are undisturbed by mammal herbivores. For instance insect folivory (Lind et al., 2012) and abundance (Den Herder et al., 2004; Huntzinger et al., 2008) can be depressed by ungulate browsing. Additionally, exclosures may limit bird predation of insects (e.g. potentially by Horned Larks or Bushtits; Cornell Lab of Ornithology 2021), creating islands of resources free of predation for insects (Bernays & Graham, 1988; Strong et al., 2000) that in turn limit plant growth (Marquis & Whelan, 1994). Additionally, aboveground herbivory sometimes increased with belowground exclosures, suggesting a possibility that aboveground and belowground herbivores may compete (van Dam & Heil, 2011).

Herbivore exclusion increased plant fitness

Mammalian herbivores suppressed biomass more below and at their low elevation range limit than in their core range. This result aligns with past theory (Brown, 1995; Dobzhansky, 1950; Louthan et al., 2015; MacArthur, 1972) predicting that the abiotic conditions at low elevations are more conducive to growth in the absence of antagonistic species interactions, such as herbivory. However, increased herbivory towards range limits and beyond reduced plant fitness more so than in their core range. It is not uncommon to find greater biomass in plant populations and communities with ungulate exclusion (Clark et al., 2012; Evans et al., 2015; Maron &

Pearson, 2011), but increased growth of individuals planted below their range without mammals is a novel result. Additionally, low biomass at *F. brachyphylla's* low elevation range limit suggested depressed fitness near the range margin that could restrict its expansion into lower elevation habitats (Hargreaves et al., 2014). Interestingly, pocket gopher density peaked at similar elevations as the range limit for *F. brachyphylla* (Lynn et al., 2018) where belowground exclosures had the largest effect on *F. brachyphylla* biomass. Grasses decline more than forbs in response to gopher disturbance and herbivory (Sherrod et al., 2005), pointing to gophers as a key factor limiting the distribution of *F. brachyphylla*. Exclosures may have introduced artefacts (Diamond, 1983) like slight shading from the wire, but such negative effects appeared negligible given biomass and reproduction were greater with exclosures. Additionally, exclosures were necessary to eliminate herbivore access and avoid pseudoreplication of exclosure treatments given the spatial and material resources available.

Declines in reproduction were greatest in the presence of herbivores at limit and novel habitats, suggesting fitness limitations at range limits could act synergistically with dispersal limitations by restricting the number of dispersal units (seeds) needed to expand species' ranges (Angert et al., 2018). Further experimentation, such as seed addition, that tests how reproductive output interacts with propagule pressure and recruitment at range limits could be a key next step to understanding interactions with dispersal. All species reproduced less at their range limits than in novel or core habitats, which suggests that environmental constraints at species' range limits reduce fecundity. Reduced reproduction at range limits was exacerbated when above- and belowground mammals had access to plants. Consistent with other studies, mammalian herbivory often reduces plant reproduction (Gómez, 2005; Knight, 2003; Pringle et al., 2014), and plants growing at low elevation (Stinson, 2005) and latitude (Bontrager & Angert, 2016; Levin & Clay, 1984) range limits reproduce less than interior populations.

In contrast to plant growth and reproduction responses, results for plant survival in these long-lived species (>50 years; Shaw, 2008) did not clearly support criterion 2. Survival was not lowest in novel habitats when exposed to herbivores. In fact, for *E. scribneri* survival at novel habitats was lower with exclosures than in controls. The weak and variable effects of at- and cross-range transplants on survival were unexpected given strong negative effects from past studies (reviewed by Hargreaves et al., 2014), though the vast majority of such studies transplant individuals across high elevation limits. However, there was evidence that excluding aboveground mammals sometimes increased survival at the core and limit habitats, in line with past evidence that grazing and browsing ungulates can decrease plant survival (Guignabert et al., 2020).

Herbivore exclusion promoted population growth the most in range limit and novel habitats

Integrating across the fitness components and applying treatment effects to matrix projection models of natural populations reinforced that (1) mammal herbivores depressed the population growth of alpine grasses; and (2) herbivore suppression of population growth intensified from core to limit and novel habitats. The effects of herbivory and habitat on plant growth were the most important contributors to differences in population growth rates across treatments. Past work reported similar evidence of herbivore-caused reductions in plant population growth in natural populations at or near species range margins (Louthan et al., 2018; Miller et al., 2009). However, such studies are insufficient to attribute range limits to biotic or abiotic causes because they do not assess why a species is not present across their range limit (Alexander et al., 2016), which limits their predictive utility under the novel conditions brought on by climate change.

To our knowledge, this is the first evidence assessing herbivore effects on individuals transplanted outside their range limits to use projection models to predict changes in population growth. Applying experimental or simulation effects of herbivores in population projection models has been useful in invasion ecology (Maron et al., 2010; Parker, 2000; Williams et al., 2010), and can improve predictions of biotic interaction effects on population responses to climate change. We suggest the integration of experimental and demographic approaches is key to progress in predicting the ecological consequences of climate change. Our conclusions are based on a single natural population, but demographic data strategically distributed throughout a species range could improve predictions on the responses of populations to future environments under climate change (Angert, 2006; Doak & Morris, 2010).

We suggest two aspects where caution should be used in interpreting the population modelling results. First, the treatment effects in the transplant experiment were assumed to be independent of plant size. This may lead to over- or underestimation of treatment effects if they vary greatly with plant size (Tredennick et al., 2018). However, given the difficulty in creating representative populations of individuals of variable sizes into environments where species had not previously occurred (Töpper et al., 2018), we suggest that this method of applying treatment effects to vital rate models built from natural populations is a useful alternative (Maron et al., 2010; Williams et al., 2010), especially given the challenges of predicting population fates with climate change (Doak & Morris, 2010). Second, our projection matrices had to be expanded beyond the maximum size of individuals found in natural populations (Supporting Information Methods). This was needed to account for the large sizes of some experimental transplants (Williams et al., 2012).

While it is risky to expand predictions beyond the extent of data, this step was necessary to explore size distributions with no natural analogue—as in novel, abiotically mild, low elevation habitats that increased plant growth more than in core populations.

CONCLUSIONS

The patterns and consequences of mammalian herbivory satisfied the conditions expected for this antagonistic interaction to limit species' elevational range distributions. Mammalian herbivory increased from habitats in the core of species' ranges to their range limits and was greatest on individuals moved below their natural range limits. Mammal exclosures increased plant fitness the most in habitats beyond range edges. Population modelling supported the hypothesis that mammalian herbivory at species range limits and below can inhibit population growth. Taken together, results predict that if mammals shift their foraging activity upslope with climate change (Büntgen et al., 2017) and plant competitors also migrate upslope (Alexander et al., 2015), alpine plant species that occupy the tops of mountains are likely to decline and face local extinction, particularly when there is no higher elevation land available for upward migration.

AUTHORS' CONTRIBUTIONS
JSL and JAR designed the experiments. JSL collected the data and performed the experimental analysis. JSL and TEXM performed the demographic analyses, and JSL led the writing with the contributions from all authors.

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DATA AVAILABILITY STATEMENT
All data are available at the Environmental Data Initiative (EDI) at: https://doi.org/10.6073/pasta/193a9 609b5ff5cec2690b3ac67b57c82 And code for the analyses is in a GitHub repository at : https://github.com/jslyn n33/Mammals-restrict-alpine-plants

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REFERENCES

Agrawal, A.A., Hastings, A.P., Johnson, M.T.J., Maron, J.L. & Salminen, J.-P. (2012) Insect herbivores drive real-time ecological and evolutionary change in plant populations. *Science*, 338, 113–116.

Alexander, J.M., Diez, J.M., Hart, S.P. & Levine, J.M. (2016) When climate reshuffles competitors: a call for experimental macroecology. *Trends in Ecology & Evolution*, 31, 831–841.

Alexander, J.M., Diez, J.M. & Levine, J.M. (2015) Novel competitors shape species' responses to climate change. *Nature*, 525, 515–518.

Angert, A.L. (2006) Demography of central and marginal populations of monkeyflowers (*Mimulus cardinalis* and *M. lewisii*). *Ecology*, 87, 2014–2025.

Angert, A.L., Bayly, M., Sheth, S.N. & Paul, J.R. (2018) Testing range-limit hypotheses using range-wide habitat suitability and occupancy for the scarlet monkeyflower (*Erythranthe cardinalis*). *American Naturalist*, 191, E76–E89.

Angert, A.L., LaDeau, S.L. & Ostfeld, R.S. (2013) Climate change and species interactions: ways forward: Climate change and species interactions. *Annals of the New York Academy of Sciences*, 1297, 1–7.

Aublet, J.-F., Festa-Bianchet, M., Bergero, D. & Bassano, B. (2009) Temperature constraints on foraging behaviour of male Alpine ibex (*Capra ibex*) in summer. *Oecologia*, 159, 237–247.

Barrio, I.C., Bueno, C.G. & Hik, D.S. (2016) Warming the tundra: reciprocal responses of invertebrate herbivores and plants. *Oikos*, 125, 20–28.

Benning, J.W., Eckhart, V.M., Geber, M.A. & Moeller, D.A. (2019) Biotic interactions contribute to the geographic range limit of an annual plant: herbivory and phenology mediate fitness beyond a range margin. *American Naturalist*, 193, 786–797.

Bernays, E. & Graham, M. (1988) On the evolution of host specificity in phytophagous arthropods. *Ecology*, 69, 886–892.

Bontrager, M. & Angert, A.L. (2016) Effects of range-wide variation in climate and isolation on floral traits and reproductive output of *Clarkia pulchella*. *American Journal of Botany*, 103, 10–21.

Brown, J.H. (1995) *Macroecology*. Chicago: University of Chicago Press.

Bruelheide, H. & Scheidel, U. (1999) Slug herbivory as a limiting factor for the geographical range of *Arnica montana*. *Journal of Ecology*, 87, 839–848.

Büntgen, U., Greuter, L., Bollmann, K., Jenny, H., Liebhold, A., Galván, J.D. et al. (2017) Elevational range shifts in four mountain ungulate species from the Swiss Alps. *Ecosphere*, 8, e01761.

Cahill, A.E., Aiello-Lammens, M.E., Fisher-Reid, M.C., Hua, X., Karanewsky, C.J., Yeong Ryu, H. et al. (2012) How does climate change cause extinction? *Proceedings of the Royal Society B-Biological Sciences*, 280, 20121890. https://royalsocietypublishing.org/doi/pdf/10.1098/rspb.2012.1890

Callis-Duehl, K., Vittoz, P., Defossez, E. & Rasmann, S. (2017) Community-level relaxation of plant defenses against herbivores at high elevation. *Plant Ecology*, 218, 291–304.

Caswell, H. (2008). *Matrix population models: construction, analysis, and interpretation*. 2nd ed, [Nachdr.], Sunderland, MA: Sinauer Associates.

Chung, Y.A., Miller, T.E.X. & Rudgers, J.A. (2015) Fungal symbionts maintain a rare plant population but demographic advantage drives the dominance of a common host. *Journal of Ecology*, 103, 967–977.

Clark, M.R., Coupe, M.D., Bork, E.W. & Cahill, J.F. (2012) Interactive effects of insects and ungulates on root growth in a native grassland. *Oikos*, 121, 1585–1592.

Compagnoni, A., Bibian, A.J., Ochocki, B.M., Rogers, H.S., Schultz, E.L., Sneck, M.E. et al. (2016) The effect of demographic correlations on the stochastic population dynamics of perennial plants. *Ecological Monographs*, 86, 480–494.

Cornell Lab of Ornithology (2021) All About Birds.

Den Herder, M., Virtanen, R. & Roininen, H. (2004) Effects of reindeer browsing on tundra willow and its associated insect herbivores. *Journal of Applied Ecology*, 41, 870–879.

Descombes, P., Marchon, J., Pradervand, J.-N., Bilat, J., Guisan, A., Rasmann, S. et al. (2017) Community-level plant palatability increases with elevation as insect herbivore abundance declines. *Journal of Ecology*, 105, 142–151.

Diamond, J.M. (1983) Ecology: laboratory, field and natural experiments. *Nature*, 304, 586–587.

Doak, D.F. & Morris, W.F. (2010) Demographic compensation and tipping points in climate-induced range shifts. *Nature*, 467, 959–962.

Dobzhansky, T. (1950) Evolution in the tropics. *American Scientist*, 38, 208–221.

Dunne, J.A., Harte, J. & Taylor, K.J. (2003) Subalpine meadow flowering phenology responses to climate change: integrating experimental and gradient methods. *Ecological Monographs*, 73, 69–86.

Elderd, B.D. & Miller, T.E.X. (2016) Quantifying demographic uncertainty: Bayesian methods for Integral Projection Models (IPMs). *Ecological Monographs*, 86, 125–144.

Evans, D.M., Villar, N., Littlewood, N.A., Pakeman, R.J., Evans, S.A., Dennis, P. et al. (2015) The cascading impacts of livestock grazing in upland ecosystems: a 10-year experiment. *Ecosphere*, 6, e42.

Fridley, J.D., Lynn, J.S., Grime, J.P. & Askew, A.P. (2016) Longer growing seasons shift grassland vegetation towards more-productive species. *Nature Climate Change*, 6, 865–868.

Gómez, J.M. (2005) Long-term effects of ungulates on performance, abundance, and spatial distribution of two montane herbs. *Ecological Monographs*, 75, 231–258.

Gottfried, M., Pauli, H., Futschik, A., Akhalkatsi, M., Barančok, P., Benito Alonso, J.L. et al. (2012) Continent-wide response of mountain vegetation to climate change. *Nature Climate Change*, 2, 111–115.

Grime, J.P. (2006) *Plant strategies, vegetation processes, and ecosystem properties*, 2nd ed. Chichester: Wiley.

Guignabert, A., Augusto, L., Gonzalez, M., Chipeaux, C. & Delerue, F. (2020) Complex biotic interactions mediated by shrubs: revisiting the stress-gradient hypothesis and consequences for tree seedling survival. *Journal of Applied Ecology*, 57, 1341–1350.

Hargreaves, A.L., Samis, K.E. & Eckert, C.G. (2014) Are species' range limits simply niche limits writ large? A review of transplant experiments beyond the range. *American Naturalist*, 183, 157–173.

Hegland, S.J., Jongejans, E. & Rydgren, K. (2010) Investigating the interaction between ungulate grazing and resource effects on *Vaccinium myrtillus* populations with integral projection models. *Oecologia*, 163, 695–706.

Hobbie, S.E. & Chapin, F.S. (1998) An experimental test of limits to tree establishment in Arctic tundra. *Journal of Ecology*, 86, 449–461.

Hobbs, N.T. & Hooten, M.B. (2015) *Bayesian models: a statistical primer for ecologists*. Princeton Oxford: Princeton University Press.

Huntzinger, M., Karban, R. & Cushman, J.H. (2008) Negative effects of vertebrate herbivores on invertebrates in a coastal dune community. *Ecology*, 89, 1972–1980.

Irlich, U.M., Terblanche, J.S., Blackburn, T.M. & Chown, S.L. (2009) Insect rate-temperature relationships: environmental variation and the metabolic theory of ecology. *American Naturalist*, 174, 819–835.

Kelly, A.E. & Goulden, M.L. (2008) Rapid shifts in plant distribution with recent climate change. *Proceedings of the National Academy of Sciences*, 105, 11823–11826.

Kittel, T.G.F., Thorton, P.E., Royle, J.A. & Chase, T.N. (2002) Climates of the Rocky Mountains: historical and future patterns. In: Baron, J.S. (Ed.) *Rocky mountain futures: an ecological perspective*. Covelo, CA: Island Press, pp. 59–82.

Klimeš, L. & Doležal, J. (2010) An experimental assessment of the upper elevational limit of flowering plants in the western Himalayas. *Ecography*, 33, 590–596.

Knight, T.M. (2003) Effects of herbivory and its timing across populations of *Trillium grandiflorum* (Liliaceae). *American Journal of Botany*, 90, 1207–1214.

Koerner, S.E., Burkepile, D.E., Fynn, R.W.S., Burns, C.E., Eby, S., Govender, N. et al. (2014) Plant community response to loss of large herbivores differs between North American and South African savanna grasslands. *Ecology*, 95, 808–816.

Lehndal, L. & Ågren, J. (2015) Herbivory differentially affects plant fitness in three populations of the perennial herb *Lythrum salicaria* along a latitudinal gradient. *PLoS One*, 10, e0135939.

Lenoir, J., Gegout, J.C., Marquet, P.A., de Ruffray, P. & Brisse, H. (2008) A significant upward shift in plant species optimum elevation during the 20th century. *Science*, 320, 1768–1771.

Levin, D.A. & Clay, K. (1984) Dynamics of synthetic *Phlox drummondii* populations at the species margin. *American Journal of Botany*, 71, 1040–1050.

Lind, E.M., Myron, E.P., Giaccai, J. & Parker, J.D. (2012) White-tailed deer alter specialist and generalist insect herbivory through plant traits. *Environmental Entomology*, 41, 1409–1416.

Louda, S.M. & Potvin, M.A. (1995) Effect of inflorescence-feeding insects on the demography and lifetime of a native plant. *Ecology*, 76, 229–245.

Louthan, A.M., Doak, D.F. & Angert, A.L. (2015) Where and when do species interactions set range limits? *Trends in Ecology & Evolution*, 30, 780–792.

Louthan, A.M., Pringle, R.M., Goheen, J.R., Palmer, T.M., Morris, W.F. & Doak, D.F. (2018) Aridity weakens population-level effects of multiple species interactions on *Hibiscus meyeri*. *Proceedings of the National Academy of Sciences*, 115, 543–548.

Lynn, J.S., Canfield, S., Conover, R.R., Keene, J. & Rudgers, J.A. (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, e1487659.

Lynn, J.S., Kazenel, M.R., Kivlin, S.N. & Rudgers, J.A. (2019) Context-dependent biotic interactions control plant abundance across altitudinal environmental gradients. *Ecography*, 42, 1600–1612.

MacArthur, R.H. (1972) *Geographical ecology: patterns in the distribution of species*. Princeton, N.J.: Princeton University Press.

Mack, R.N. & Thompson, J.N. (1982) Evolution in steppe with few large, hooved mammals. *American Naturalist*, 119, 757–773.

Maron, J.L. (1998) Insect herbivory above- and belowground: individual and joint effects on plant fitness. *Ecology*, 79, 1281–1293.

Maron, J.L. & Crone, E. (2006) Herbivory: effects on plant abundance, distribution and population growth. *Proceedings of the Royal Society B-Biological Sciences*, 273, 2575–2584.

Maron, J.L., Horvitz, C.C. & Williams, J.L. (2010) Using experiments, demography and population models to estimate interaction strength based on transient and asymptotic dynamics. *Journal of Ecology*, 98, 290–301.

Maron, J.L. & Pearson, D.E. (2011) Vertebrate predators have minimal cascading effects on plant production or seed predation in an intact grassland ecosystem: no trophic cascade. *Ecology Letters*, 14, 661–669.

Marquis, R.J. & Whelan, C.J. (1994) Insectivorous birds increase growth of white oak through consumption of leaf-chewing insects. *Ecology*, 75, 2007–2014.

McNaughton, S.J. (1979) Grazing as an optimization process: grass-ungulate relationships in the Serengeti. *American Naturalist*, 113, 691–703.

Miller, T.E.X., Louda, S.M., Rose, K.A. & Eckberg, J.O. (2009) Impacts of insect herbivory on cactus population dynamics: experimental demography across an environmental gradient. *Ecological Monographs*, 79, 155–172.

Moreira, X., Petry, W.K., Mooney, K.A., Rasmann, S. & Abdala-Roberts, L. (2018) Elevational gradients in plant defences and insect herbivory: recent advances in the field and prospects for future research. *Ecography*, 41, 1485–1496.

Parker, I.M. (2000) Invasion dynamics of *Cytisus scoparius*: a matrix model approach. *Ecological Applications*, 10, 726–743.

Parmesan, C. (2006) Ecological and evolutionary responses to recent climate change. *Annual Review of Ecology Evolution and Systematics*, 37, 637–669.

Pellissier, L., Moreira, X., Danner, H., Serrano, M., Salamin, N., van Dam, N.M. et al. (2016) The simultaneous inducibility of phytochemicals related to plant direct and indirect defences against herbivores is stronger at low elevation. *Journal of Ecology*, 104, 1116–1125.

Pellissier, L., Roger, A., Bilat, J. & Rasmann, S. (2014) High elevation *Plantago lanceolata* plants are less resistant to herbivory than their low elevation conspecifics: is it just temperature? *Ecography*, 37, 950–959.

Pepin, N. & Losleben, M. (2002) Climate change in the Colorado Rocky Mountains: free air versus surface temperature trends. *International Journal of Climatology*, 22, 311–329.

Plummer, M. (2003) JAGS: a program for analysis of Bayesian graphical models using Gibbs sampling. In: Kurt, H., Friedrich, L. & Achim, Z. (Eds.) *Proceedings of the 3rd international workshop on distributed statistical computing*. Vienna, Austria: DSC 2003, p. 125. https://www.r-project.org/conferences/DSC-2003/

Pringle, R.M., Goheen, J.R., Palmer, T.M., Charles, G.K., DeFranco, E., Hohbein, R. et al. (2014) Low functional redundancy among mammalian browsers in regulating an encroaching shrub (*Solanum campylacanthum*) in African savannah. *Proceedings of the Royal Society B-Biological Sciences*, 281, 20140390.

R Core Team (2018) *R: a language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing.

Rangwala, I. & Miller, J.R. (2012) Climate change in mountains: a review of elevation-dependent warming and its possible causes. *Climatic Change*, 114, 527–547.

Rivest, S. & Vellend, M. (2018) Herbivory and pollen limitation at the upper elevational range limit of two forest understory plants of eastern North America. *Ecology and Evolution*, 8, 892–903.

Shaw, R.B. (2008) *Grasses of Colorado*. Boulder, CO: University Press of Colorado.

Sherrod, S.K., Seastedt, T.R. & Walker, M.D. (2005) Northern pocket gopher (*Thomomys talpoides*) control of alpine plant community structure. *Arctic, Antarctic, and Alpine Research*, 37, 585–590.

Stinson, K.A. (2005) Effects of snowmelt timing and neighbor density on the altitudinal distribution of *Potentilla diversifolia* in Western Colorado, USA. *Arctic, Antarctic, and Alpine Research*, 37, 379–386.

Strong, A.M., Sherry, T.W. & Holmes, R.T. (2000) Bird predation on herbivorous insects: indirect effects on sugar maple saplings. *Oecologia*, 125, 370–379.

Su, Y.-S. & Yajima, M. (2015). *R2jags: Using R to Run "JAGS"*. Available at: https://cran.r-project.org/web/packages/R2jags/index.html [Accessed 5th January 2019].

Sunday, J.M., Bates, A.E. & Dulvy, N.K. (2011) Global analysis of thermal tolerance and latitude in ectotherms. *Proceedings of the Royal Society B-Biological Sciences*, 278, 1823–1830.

Sunday, J.M., Bates, A.E. & Dulvy, N.K. (2012) Thermal tolerance and the global redistribution of animals. *Nature Climate Change*, 2, 686–690.

Töpper, J.P., Meineri, E., Olsen, S.L., Rydgren, K., Skarpaas, O. & Vandvik, V. (2018) The devil is in the detail: nonadditive and context-dependent plant population responses to increasing temperature and precipitation. *Global Change Biology*, 24, 4657–4666.

Tredennick, A.T., Teller, B.J., Adler, P.B., Hooker, G. & Ellner, S.P. (2018) Size-by-environment interactions: a neglected dimension of species' responses to environmental variation. *Ecology Letters*, 21, 1757–1770.

Tylianakis, J.M., Didham, R.K., Bascompte, J. & Wardle, D.A. (2008) Global change and species interactions in terrestrial ecosystems. *Ecology Letters*, 11, 1351–1363.

van Dam, N.M. & Heil, M. (2011) Multitrophic interactions below and above ground: en route to the next level: Below-ground-aboveground interactions. *Journal of Ecology*, 99, 77–88.

Williams, J.L., Auge, H. & Maron, J.L. (2010) Testing hypotheses for exotic plant success: parallel experiments in the native and introduced ranges. *Ecology*, 91, 1355–1366.

Williams, J.L., Miller, T.E.X. & Ellner, S.P. (2012) Avoiding unintentional eviction from integral projection models. *Ecology*, 93, 2008–2014.

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.