

Journal of Applied Ecology

DR NATHALIE CHARDON (Orcid ID : 0000-0001-9120-4778)

Article type : Research Article

Editor : Anibal Pauchard

TITLE

Human trampling disturbance exerts different ecological effects at contrasting elevational range limits

AUTHORS

Nathalie Isabelle Chardon ^{1,2*}, Christian Rixen ², Sonja Wipf ², Daniel Forest Doak ¹

Author affiliations:

1) Environmental Studies Program, 397 University of Colorado, Boulder, CO 80309, USA

2) WSL Institute for Snow and Avalanche Research SLF, Flüelastrasse 11, 7260 Davos Dorf,
Switzerland

*Author for correspondence: nathalie.chardon@colorado.edu

ABSTRACT

1. Shifts in species geographic distributions in response to climate change have spurred numerous studies to determine which abiotic (e.g., climatic) and, less commonly, biotic (e.g., competitive), processes determine range limits. However, the impact of disturbances on range limits and their interactions with climatic and biotic effects is not well understood, despite their potential to alter competitive relationships between species or override climatic effects. Disturbance might have differential effects at contrasting range limits, based on Darwin's theory that biotic interactions set abiotically benign range limits and abiotic factors set abiotically stressful range limits.
2. We predicted that plants at lower elevation (abiotically benign) range limits experience a net positive effect of disturbance whereas those at higher elevation (abiotically stressful) range limits experience a net neutral effect. We examined plant populations along elevational gradients in the Colorado Rocky Mountains, in order to quantify the effects of human trampling disturbance at lower and upper elevational range limits of the common alpine cushion plants *Silene acaulis* and *Minuartia obtusiloba*.
3. Our results are consistent with Darwin's theory. A disturbance-mediated reduction of competitive effects increases the performance of cushion plants at lower elevations, suggesting a range limit set by biotic factors. At higher elevations, where biotic interactions are minimal, disturbance has neutral or negative effects on cushion plants.
4. *Synthesis and applications.* Human trampling disturbance exerts differential effects on alpine cushion plant populations at contrasting range limits, emphasizing the need to account for the effects of climate change into the management and conservation of disturbed areas. Disturbance can diminish plant-plant competitive interactions at lower elevational range limits, and thus possibly stabilize alpine species populations susceptible to climate change mediated encroachment by lower elevation species. Conservation and management approaches should therefore particularly account for the differential effects of disturbance across climatic gradients.

Keywords: alpine, climate change, competition, cushion plants, disturbance, *Minuartia obtusiloba*, range limits, *Silene acaulis*

INTRODUCTION

Understanding how species range limits are determined and will shift with climate change is an increasingly important applied issue in ecology, with the ultimate goal of providing local and global management agencies the knowledge base necessary to mitigate species extinction risks. The need to understand range limits has inspired a surge in studies documenting shifting range limits (Parmesan, 2006; Harsch & HilleRisLambers, 2016) as well as work on how different abiotic and biotic processes create range limits in the first place (Sexton, McIntyre, Angert & Rice, 2006; Louthan, Doak & Angert, 2015; Angert, Bayly, Sheth & Paul, 2018). However, a plethora of landscape factors, such as disturbances, may modify or even override the effects of climate on species distributions (Dirnböck, Dullinger & Grabherr, 2003). In fact, disturbance itself can be an important driver of shifts in invasive species distributions (McKenzie, Yoshida & Unsworth, 2014; Lembrechts et al., 2017). While the effects on native species range limits have also been examined (Lenoir et al., 2010; Slaton, 2015), we still do not have a comprehensive understanding of how the effects of disturbance interact with range-limiting mechanisms. This is particularly important in order to anticipate how species range limits will shift in response to both climatic and disturbance impacts to shape species future distributions (Sheil, 2016). Detailed knowledge of how the effects of disturbance change across climatic gradients and between contrasting elevational range limit populations is thus critical to inform decisions regarding both landscape disturbances as well as conservation planning.

A long-standing theory, dating back to Darwin (1859), suggests that range limits at lower elevations and latitudes are controlled more by biotic forces than by direct effects of the physical environment, whereas colder or otherwise more stressful range limits are determined predominately by abiotic forces (reviewed in Louthan, Doak & Angert, 2015). This is especially true in mountain systems characterized by strong abiotic stress gradients, where biotic interactions can reduce alpine

plant abundances at lower elevations as they become outcompeted (e.g., Kopp & Cleland, 2014). In contrast, extremely high elevations are often characterized by few biotic interactions, and population dynamics here are often driven by abiotic factors, such as climate (Michalet et al. 2016; Dvorsky et al. 2016). Therefore, if anthropogenic disturbances, such as trampling by humans or livestock, alter biotic interactions or override the effects of abiotic factors (e.g., Pickett & White, 1985; Franklin, Serra-Diaz, Syphard & Regan, 2016), we would expect disturbance to especially impact lower range limits.

If disturbance reduces vegetation cover of the dominant, characteristically lower elevation species, this reduction in competitive pressure and increase in habitat availability will favour higher elevation alpine plants (e.g., Lenoir et al. 2010). In fact, trampling disturbance can reduce the dominant vegetation cover and increase alpine cushion plant cover in the Tasmanian alpine zone (Whinam & Chilcott, 2003). A similar pattern exists in areas frequently disturbed by avalanches, where abundance of dominant competitive species is lower and alpine species are more common (Rixen, Haag, Kulakowski & Bebi, 2007). Disturbance might therefore ultimately protect alpine species' lower elevational range limits (i.e. trailing edges) from the upward encroachment of more competitive lower elevation species (e.g., Kopp & Cleland, 2014; Alexander, Diez & Levine, 2015), although populations in disturbed areas might also be less stable. In high elevation areas characterized by low biotic interactions, where low plant cover exerts minimal competitive or facilitative influence (e.g., Olofsson, Moen & Oksanen, 1999), the net effects of disturbance on alpine plant populations at their upper elevational range limit are likely minimally negative.

Alpine ecosystems are especially susceptible to the effects of climate change due to high rates of warming (IPCC, 2014) and resulting species extinctions (Panetta, Stanton & Harte, 2018). As evidenced by the countless trails in popular hiking destinations around the world, human trampling, in particular, is a major anthropogenic impact in these alpine ecosystems that can cause significant organismal damage (Monz, 2002; Barros, Gonnet & Pickering, 2013) as well as alter community composition (Ballantyne & Pickering, 2015). Visitation by hikers particularly in the Colorado, USA alpine zone has markedly increased over the last few decades, resulting in heavily disturbed soils and vegetation (*personal communication*, B. Hanus, Colorado Fourteeners Initiative). Together with their

large elevational and resulting temperature gradients, the Colorado Rocky Mountains are therefore an ideal setting for studying the effect of disturbance at lower and upper elevational range limits.

To better understand the impacts of local disturbances on alpine plant populations and how these effects interact with those of climate, we examine the effects of moderate human trampling (i.e. hiker trail edges) at lower, centre, and upper elevational range locations of two common and widespread alpine cushion plant species. We chose to study human trampling at hiking trails as this is a spatially defined as well as replicated type of disturbance important in its own right, and is similar to landscape-level (i.e. across multiple kilometres) trampling disturbance by grazers. We examine *Silene acaulis* (L.) Jacq. (Caryophyllaceae; henceforth, *Silene*) and *Minuartia obtusiloba* (Rydb.) House (Caryophyllaceae; henceforth, *Minuartia*) in the southern part of their range in western North America. Both are widespread across alpine zones across the Northern Hemisphere (*Silene*) or throughout North America (*Minuartia*). Seeing as cushion plants populate alpine communities across the globe (Butterfield et al., 2013), our work is applicable to alpine ecosystems world-wide. Furthermore, the facilitative properties of cushion plants make them important drivers of alpine community diversity (Butterfield et al., 2013), and they may buffer the negative effects of climate change on other species (Anthelme, Cavieres & Dangles, 2014).

Across elevational and disturbance gradients, we quantify maximum reproductive potential and abundance indicators as measures of individual and population performance, along with estimates of competing vegetation cover and habitat availability. By sampling at elevational range limits and centres, we are able to analyse populations that are presumably driven by different mechanisms, in order to answer the following questions:

- A) How do the effects of disturbance and range position interact to affect cushion plants?
- B) Does a disturbance-mediated decrease in competitive vegetation or increase in habitat availability favour cushion plant performance, and do these effects vary with range position?

We hypothesize that at warmer lower elevational range limits the presumably negative effects of trampling on cushion plants will be outweighed by the positive effects of reducing competitive vegetation or increasing habitat availability. Conversely, at cooler upper elevational range limits we expect that trampling will have reduced benefits and net neutral or even negative effects (Fig. 1).

MATERIALS & METHODS

Sites. We chose 18 sites (i.e. mountain sides) between 3,500 and 4,270 m (11,500 – 14,000 ft) in four mountain ranges and with different aspects within the Colorado Rocky Mountains, USA in order to capture a wide range of the climatic variability seen across alpine habitats in the state of Colorado (Fig. S1.1 in Appendix S1 in Supplementary Information; for details see Appendix S2). In order to maximize disturbance effects, we chose sites in the state's iconic and popular peaks above 4,267 m ('14er' peaks, > 14,000 ft) plus one frequently hiked 4,204 m (13,794 ft) peak. The most heavily frequented peaks are visited annually by up to 20,000 hikers per peak (*unpublished data*, Colorado Fourteeners Initiative). Several peaks provided two or three study sites, due to trails on different aspects of the same mountain. We surveyed along the most frequently used trail at each site (Roach, 1999). Recorded data for some of these trails indicate that they were constructed between 9 and 22 years ago (*unpublished data*, Colorado Fourteeners Initiative). Although trail usage varies between sites, hikers that start at the beginning of a trail generally continue on the same trail to reach the summit (hiking 14ers is an integral part of the Colorado identity; Blake, 2002). These sites experience little to no livestock grazing, and as evidenced by low dung counts (*personal observation*), grazing intensity by wild ungulates is low.

Our study sites are generally characterized by metamorphic and igneous rock, with a gravelly to rocky substrate. They experience strong winds (exceeding 50-100 mph; Colorado Climate Center 2017) and a continental climate, with an average annual precipitation of 309 mm and an average 68 days with snow (1979-2013 data from Leadville at 3012 m, 39.14° N 106.19° W; Weatherbase). Average summer (June, July, August) microhabitat temperatures range from 11.2°C at lower

elevations to 5.9°C at higher elevations (temperature logger data 2016-2017; see Appendix S2).

Lower elevations are characterized by higher vegetation abundance, whereas higher elevations are characterized by increased rock and bare ground abundance (*personal observation*; Fig. 2).

Study species. Both *Silene* and *Minuartia* are long-lived gynodioecious perennials (Fig. S1.2). *Silene* has a circumboreal distribution (0 – 4200 m; Flora of North America, 2008a), whereas *Minuartia* is widespread in western North America (0 – 4000 m; Flora of North America, 2008b). Cushions slowly grow radially outwards and are known to live 300 years or longer (Morris & Doak, 1998). They have one taproot, allowing them to survive harsh alpine conditions, such as water drought. As a measure of performance, we measured *Silene* maximum plant sizes (see below for details), as maximum size is strongly correlated with environmental conditions (see Appendix S3). For example, larger *Silene* individual sizes, not mean sizes, vary significantly along the climatic gradient found along the species' North American latitudinal range, with a peak in size in central range locations (Fig. S3.1). Furthermore, larger individuals produce disproportionately more fruits (Fig. S3.2), indicating that populations with larger cushion areas have higher reproductive potential.

Data collection. We conducted focused population surveys between June – August 2015 and September – October 2016. At each site, we set up two to three 10x1 m² transects directly adjacent to trails (i.e. trail-side, disturbed) and paired off-trail (i.e. undisturbed) transects away from the trail at local lower (~ 3710 m), middle (~ 3930 m), and upper (~ 4060 m) elevational range locations (Fig. 2; for details see Appendix S2). As an additional measure of disturbance, we obtained trail age and yearly hiker visitation rates data from the Colorado Fourteeners Initiative (*unpublished data*) for a subset of sites (see Appendix S2). Within 1 m² quadrats in each 10 m² transect, we quantified three *Silene* (maximum size of individual plants, density, percent cover) and one *Minuartia* (percent cover) population performance indicators (Table 1, Fig. S1.3). As a measure of competing vegetation and habitat availability we measured vegetation and bare ground percent cover, respectively. Our measure

of habitat availability is a proxy for multiple likely highly correlated effects, including disturbance-mediated changes in habitat quality, soil compaction, and resource availability of space itself, nutrients, and water. We transformed these percent cover values to indices that reflect the amount of rock-free space (see Appendix S2).

Statistical analyses. We first fit sets of alternative linear mixed models (LMMs) for *Silene* maximum cushion area (n = 3490 individuals) and density (n = 1561 quadrats) and of zero-inflated beta-distributed general linear mixed models (GLMMs) for *Silene* percent cover (n = 936 quadrats with *Silene* presence, otherwise n = 1561) and *Minuartia* percent cover (n = 1561 quadrats). As this type of GLMM is bounded by (0,1), we adjusted our data with: $(\text{param} * (n - 1) + 0.5) / n$ where param = % cover in decimal values and n = number of observations (Smithson & Verkuilen, 2006). All models included a random effect of site (n = 18). We performed all analyses in R ver. 3.4.3 (R Core Team, 2017) using the function ‘lmer’ in package lme4 (Bates, Maechler, Bolker & Walker, 2015) and the function ‘glmmadmb’ with family=beta, link=logit, and zeroInflation=TRUE in package glmmADMB (Fournier et al., 2012; Skaug, Fournier, Bolker, Magnusson & Nielsen, 2016). We log-transformed *Silene* cushion area ($\log(\text{area})$) and density ($\log(\text{density} + 1)$) to meet LMM residual distribution assumptions.

For each cushion plant dependent variable, we fit two sets of models. The first set included only combinations and interactions of trail disturbance and elevational level (Table S1.1a). We also fit models using additional variables for temperature, yearly hikers, and trail age, but these models were not well supported (see Appendix S2). As we used *Silene* presence as a criterion to establish trail-side transects, our models comparing *Silene* percent cover between trail and off-trail transects only included data of quadrats where *Silene* is present.

Our second set included the effects of vegetation, forb, graminoid, and habitat availability indices, as well as elevational level and its interaction with these indices (Table S1.2). In addition, we also fit GLMMs testing the effects of trail disturbance and elevational level, as well as their

interaction, on vegetation, forb, graminoid, and habitat availability indices (Table S1.1b). As the vegetation index has disproportionately high values of both 1 and 0, we used the additional argument `zeroInflation=FALSE` for this variable. We identified the most parsimonious model in each set with AICc, allowing us to determine which variables are most influential.

Based on the best-supported models, we also fit Structural Equation Models (SEMs) to understand the interplay between predictor variables and their relative strengths in affecting cushion plant performance indicators. We fit SEMs (function ‘sem’ in package lavaan; Rosseel, 2012) to *Silene* maximum size, density, as well as *Silene* (from quadrats where it is present) and *Minuartia* percent cover. We characterized trail disturbance as an exogenous variable and habitat availability as an endogenous variable (see Tables S1.3, S1.4, S1.5, S1.6). As habitat availability and vegetation indices are highly correlated (-0.62), we used habitat availability, the better predictor in LMMs and GLMMs, to simplify our SEMs. To make variable variances similar, we centred and scaled all cushion plant variables.

RESULTS

In line with our predictions, disturbance has a net positive impact on cushion plant performance at lower elevations, and a neutral or negative effect at upper elevations (Table 2a, Fig. 3). Trail disturbance increases maximum *Silene* cushion area, density, and percent cover at the lower two elevational levels, an effect that becomes negative at the uppermost elevational level (Fig. 3a-f). Trail disturbance similarly increases *Minuartia* cover at lower elevations and has a neutral effect at higher elevations (Fig. 3g, h). Although highly significant effects are present in each model, goodness of fit values are low to moderate (Table 2A). Models with additional measures of disturbance (trail age, yearly hikers) and climate (average summer temperature) indicate the same results, with trail disturbance and elevational level being the best predictors (see Appendix S2).

Trail disturbance reduces competitive vegetation and increases habitat availability (Table 2a, Fig. 4, Fig. S1.4), as we hypothesized. Trail disturbance has a significant negative effect on the vegetation index, which is highest at the mid-elevational level (Fig. 4a, b). Trail disturbance significantly increases habitat availability, especially at the uppermost elevational level (trail x elevational level interaction; Fig. 4c, d). Forb cover increases with trail disturbance at the lowest elevation, but decreases at the uppermost elevational level. Graminoid cover is not influenced by trail, and decreases with elevation (Fig. S1.5, see Appendix S2). Our model fits with additional variables (trail age, yearly hikers, average summer temperature) indicate similar patterns or insignificant results (see Appendix S2).

As expected, reduction of vegetative competition and augmentation of habitat availability favour cushion plant performance, with strongest effects at lower elevations (Table 2b). *Silene* maximum cushion area is negatively affected by vegetation at all elevations (Fig. 5a). *Silene* density, in contrast, increases with habitat availability (Fig. 5b), an effect strongest at the lower two elevations but negative at the highest elevation. *Silene* (Fig. 5c) and *Minuartia* (Fig. 5d) percent cover increase with habitat availability at the lower two elevations, with neutral effects at the highest elevation.

Our SEMs confirm our LMM and GLMM results, showing that habitat availability differentially influences cushion plants along their elevational range, effects that can override the direct effects of trail disturbance. Habitat availability favours *Silene* percent cover most at lower elevations, and the positive effect of trail is strongest at mid-elevation and decreases to negative at high elevations (Fig. 6a, Table S1.3). Habitat availability is the dominant positive driver of *Minuartia* percent cover at the lower two elevational levels, an effect that is minimal at high elevations (Fig. 6b, Table S1.4). Habitat availability is also most important in increasing *Silene* density at the lower two elevational levels, whereas trail has the most dominant negative effect at higher elevations (Fig. S1.6a, Table S1.5). The pattern for *Silene* maximum cushion size is similar, with strongest positive effects of trail at lower elevation and negative at high elevations (Fig. S1.6b, Table S1.6). Habitat availability has negative effects at lower elevations that switch to positive at the highest elevation.

DISCUSSION

In line with Darwin's predictions (1859), our results indicate that the importance of competitive interactions decreases with abiotic stress, and that abiotic processes exert stronger effects in abiotically stressful areas that see reduced population performance. At lower, warmer elevations, we found that trampling disturbance decreases competing vegetation and increases habitat availability, exerting a net positive impact on cushion plant performance. This is consistent with recent work that illustrates the importance of abiotic drivers, and their interaction with biotic factors, in setting lower elevational range limits (Cahill, Aiello-Lammens, Fisher-Reid, Hua & Karanewsky, 2014). At upper elevations, which are colder (see Appendix S2) and likely have fewer biotic interactions, disturbance has a neutral or net negative impact on cushion plants. Our results suggest that this shift in disturbance effects along an abiotic stress gradient is driven by the amount to which disturbance reduces competitive interactions. These results imply that disturbance can shift biotic interactions at climatic trailing edges, illustrating the importance of accounting for climatic difference within disturbed landscapes. In particular, land managers making decisions regarding landscape-level disturbance activities need to account for the differential effects of disturbance at lower vs. upper elevational limits.

In mountain systems, upper elevational range edges generally shift upward with warmer conditions (Freeman, Lee-Yaw, Sunday & Hargreaves, 2018), whereas lower elevational range edges will likely contract with encroachment of more competitive species from lower elevations (Alexander, Diez & Levine, 2015). Our results suggest that disturbance might preserve populations near the trailing edge by reducing the effects of competitors. We show that the importance of habitat availability, a measure of competitive-free space, and competitive vegetation are less important at the upper elevational limit, where disturbance has net neutral or negative effects. This suggests that while competitive interactions play a key role at lower elevations, these competitive interactions switch to neutral or possibly facilitative at higher elevations (Michalet, Schöb, Lortie, Brooker & Callaway, 2014). While our study is not designed to test the Stress Gradient Hypothesis (Bertness & Callaway, 1994), community facilitative effects at higher elevations, if present, would benefit *Silene* and

Minuartia cushions. Disturbance likely also disrupts facilitative interactions, possibly resulting in the observed negative effects of disturbance at upper elevational range limits. However, given the low vegetation cover at upper elevational range limits (see Fig. 2), we suspect that only minimal plant-plant interactions exist. Even so, we are cautious in our interpretation that disturbance exerts neutral effects at high elevations, as our examination of net disturbance effects does not allow us to differentiate between individual negative and positive effects on plant populations.

Interestingly, we found that while competitive vegetation is more important in determining cushion plant size, habitat availability is more important for population density. As cushion plants grow radially outward, the presence of competing vegetation at the perimeter of an already established plant can limit further growth (Griggs, 1956), and thus reduction of this competing vegetation may allow cushion plants to achieve larger maximum sizes. Maximum size increases with elevation in the absence of disturbance (Fig. 3b), possibly due to decreasing competitive pressure, as also found in the South American Andes (Armesto, Arroyo & Villagran, 1980). As largest cushions bear the largest proportion of fruits (see Appendix S3, Fig. S3.2), cushions in low elevation disturbed areas might therefore have a higher reproduction potential, if fruits are not damaged by disturbance (see Chardon, Wipf, Rixen, Beilstein & Doak, 2018). Increased habitat availability in disturbed areas, which is a proxy for other effects besides direct space competition, such as soil compaction and resource availability, allows for increased establishment of cushion plants such as *Silene* (Griggs, 1956). Disturbance thus creates conditions similar to those in recently de-glaciated regions, where cushion plants are good colonizers of similarly competitor-free space (Cichini, Schwienbacher, Marcante, Seeber & Erschbamer, 2011).

Disturbance via human trampling does not selectively reduce dominant vegetation and leave cushion plant populations intact (e.g., Monz, 2002), but our findings suggest that it does shift the competitive balance away from dominant plants. The taproot and low-lying growth form of our two study species makes these plants potentially more resistant to trampling disturbance than other species. *Silene* cushions, in particular, can be relatively resistant to trampling compared to other alpine tundra species (Willard, Cooper & Forbes, 2007). However, disturbance has been shown to exert

significant organismal damage in other systems (Barros, Gonnet & Pickering, 2013), and direct trampling on cushions can cause portions to die off (Willard & Marr, 1970). Furthermore, we have found in previous work that disturbance is detrimental to *Silene* reproduction (Chardon, Wipf, Rixen, Beilstein & Doak, 2018). We therefore highlight the need to measure multiple traits to understand the comprehensive effects of disturbance. We also emphasize the need to improve our mechanistic understanding of disturbance by examining the link between disturbance-mediated effects on soil properties (e.g., nutrient availability, structure, moisture) and how this impacts plant growth and establishment (e.g., Billings, 1973; Chambers, 1995).

As human trampling, and other landscape impacts such as trampling by grazers, are ubiquitous anthropogenic activities, our work is relevant to alpine regions around the globe as well as to other ecosystems. Other forms of disturbance, from major storm events to avalanches, may well have similar effects. We emphasize that the effects of disturbance vary along abiotic stress gradients, and that management decisions should be tailored to anticipate these differential effects along elevational gradients. In particular, disturbance has been shown to create heterogenous landscapes to maintain high biodiversity levels (Dullinger, Dirnböck, Greimler & Grabherr, 2003) and allows higher elevation plants to persist near their lower elevational range limit (Lenoir et al., 2010). While we show that disturbance effects interact with the effects of climate and biotic interactions across a species' range, research in other systems is clearly needed to test the generality of our results before they are used to define management objectives. Understanding how the effects of disturbance vary across elevational gradients is thus a promising area of future research, ultimately improving predictions of species future distributions (e.g., Randin, Vuissoz, Liston, Vittoz & Guisan, 2009) and allowing for tailored management decisions regarding disturbance activities.

ACKNOWLEDGMENTS

We thank Colorado Fourteeners Initiative for sharing their data, and for helpful discussions on site choices. We thank Emily Valencia, Emily Gulick, Timothy Salazar, Trevor Gundlach, Clea Bertholet,

Lizzie Lombardi, Florence Chardon, Kelsey Dailey, Jessica Frost, and Elin Bonnevier for data collection assistance and endurance in challenging alpine terrain. Support provided by American Alpine Club, John Marr Ecology Fund, Indian Peaks Wilderness Alliance, and University of Colorado Herbarium Hazel Schmoll Research Fellowship to NIC, and by NSF-DEB 1340024, 1242355 and LabEx/TULIP to DFD. NIC is grateful to David Ackerly for his mentorship, which led to the idea of studying leading and trailing edges in alpine systems. We thank Jason Sexton for helpful discussions, and members of the Doak Lab as well as William Bowman for reviewing early versions of this manuscript. Thank you to Anibal Pauchard for constructive editorial comments, as well as to Jonas Lembrechts and an anonymous reviewer for comments and suggestions that greatly improved this work. The authors declare no conflict of interest.

DATA ACCESSIBILITY

Data and R code available via the Open Science Framework <https://doi.org/10.17605/OSF.IO/C8AJ2> (Chardon, 2019).

AUTHORS' CONTRIBUTIONS

NIC, CR, SW, and DFD conceived the ideas and designed methodology. NIC collected as well as analysed the data, and wrote the manuscript with substantial input from DFD, CR, and SW. All authors contributed critically to the drafts and gave final approval for publication.

REFERENCES

Alexander JM, Diez JM & Levine JM (2015) Novel competitors shape species' response to climate change. *Nature*. 525:515-520. doi:10.1038/nature14952.

Angert AL, Bayly M, Sheth SN & Paul JR (2018) Testing range-limit hypothesis using range-wide habitat suitability and occupancy for the Scarlet Monkeyflower (*Erythranthe cardinalis*). *The American Naturalist*. 191(3). doi:10.1086/695984

Anthelme F, Cavieres LA & Dangles O (2014) Facilitation among plants in alpine environments in the face of climate change. *Frontiers in Plant Science*. doi: 10.3389/fpls.2014.00387.

Armesto JJ, Arroyo MK & Villagran C (1980) Altitudinal distribution, cover and size structure of umbelliferous cushion plants in high Andes of central Chile. *Acta Oecologica*. 1:327-332.

Ballantyne M & Pickering CM (2015) Recreational trails as a source of negative impacts on the persistence of keystone species and facilitation. *Journal of Environmental Management*. 159:48-57. doi:10.1016/j.jenvman.2015.05.026

Barros A, Gonnet J & Pickering CM (2013) Impacts of informal trails on vegetation and soils in the highest protected area in the Southern Hemisphere. *Journal of Environmental Management*. 127:50-60. doi:10.1016/j.jenvman.2013.04.030

Bates D, Maechler M, Bolker B & Walker S (2015). Fitting Linear Mixed-Effects Models Using lme4. *Journal of Statistical Software*. 67(1):1-48. doi:10.18637/jss.v067.i01.

Bertness M & Callaway RM (1994) Positive interactions in communities. *Trends in Ecology and Evolution*. 9:191–193. doi:10.1016/0169-5347(94)90088-4

Billings WD (1973) Arctic and alpine vegetations: Similarities, differences, and susceptibility to disturbance. *Bioscience*. 23(12):697-704.

Blake KS (2002) Colorado Fourteeners and the nature of place identity. *The Geographical Review*. 92(2):155-179. doi:10.1111/j.1931-0846.2002.tb00002.x

Butterfield BJ, Cavieres LA, Callaway RM, Cook BJ, Kikvidze Z, Lortie CJ, ... & Brooker RW (2013) Alpine cushion plants inhibit the loss of phylogenetic diversity in severe environments. *Ecology Letters*. 16:478-86.

Cahill AE, Aiello-Lammens ME, Fisher-Reid MC, Hua X, Karanewsky CJ (2014) Causes of warm-edge range limits: systematic review, proximate factors and implications for climate change. *Journal of Biogeography*. 41:429-442.

Chambers JC (1995) Disturbance, life history strategies, and seed fates in alpine herbfield communities. *American Journal of Botany*. 82(3):421-433.

Chardon NI (2019) Data from: Human trampling disturbance exerts different ecological effects at contrasting elevational range limits. Open Science Framework.

<https://doi.org/10.17605/OSF.IO/C8AJ2>

Chardon NI, Wipf S, Rixen C, Beilstein A & Doak DF (2018) Local trampling disturbance effects on alpine plant populations and communities: negative implications for climate change vulnerability. *Ecology and Evolution*. 00:0-15.

Cichini K, Schwienbacher E, Marcante S, Seeber GUH & Erschbamer B (2011) Colonization of experimentally created gaps along an alpine successional gradient. *Plant Ecology*. 212:1613-1627.

Colorado Climate Center (2017) “Climate of Colorado”. *Colorado State University*. Accessed 4 April 2018. <http://climate.colostate.edu/climate_long.html>.

Darwin (1859) *On the Origin of the Species by Means of Natural Selection*. England: Murray.

Dirnböck T, Dullinger S & Grabherr G (2003) A regional impact assessment of climate and land-use change on alpine vegetation. *Journal of Biogeography*. 30:401-417. doi:10.1046/j.1365-2699.2003.00839.x

Dullinger S, Dirnböck T, Greimler J & Grabherr G (2003) A resampling approach for evaluating effects of pasture abandonment on subalpine plant species diversity. *Journal of Vegetation Science*. 14:243-252.

Dvorsky M, Chlumska Z, Altman J, Capkova K, Rehakova K, Macek M, ... Dolezal J (2016) Gardening in the zone of death: an experimental assessment of the absolute elevation limit of vascular plants. *Scientific Reports*. 6:24440. doi:10.1038/srep24440

Flora of North America (2008a) “*Silene acaulis*”. *www.eFloras.org*. Accessed 22 May 2018. <http://www.efloras.org/florataxon.aspx?flora_id=1&taxon_id=250060827>.

Flora of North America (2008b) “*Minuartia obtusiloba*”. *www.eFloras.org*. Accessed 22 May 2018. <http://www.efloras.org/florataxon.aspx?flora_id=1&taxon_id=250060648>.

Fournier DA, Skaug HJ, Ancheta J, Ianelli J, Magnusson A, Maunder M, ... & Sibert J (2012). “AD Model Builder: using automatic differentiation for statistical inference of highly parameterized complex nonlinear models.” *_Optim. Methods Softw._*, *27*, pp. 233-249.

Franklin J, Serra-Diaz JM, Syphard A & Regan H (2016) Global change and terrestrial plant community dynamics. *PNAS*. 113(14):3725-3734. doi: 10.1073/pnas.1519911113

Freeman BG, Lee-Yaw JA, Sunday JM & Hargreaves AL (2018) Expanding, shifting, and shrinking: The impact of global warming on species' elevational distributions. *Global Ecology and Biogeography*. doi: 10.1111/geb.12774

Griggs RF (1956) Competition and succession on a Rocky Mountain fellfield. *Ecology*. 37(1):8-20. doi:10.2307/1929664

Harsch MA & HilleRisLambers J (2016) Climate warming and seasonal precipitation change interact to limit species distribution shifts across western North America. *PLoS ONE*. 11(7): e0159184. doi:10.1371/journal.pone.0159184.

IPCC (2014) *Climate Change 2014: Synthesis Report, Fifth Assessment Report. Contribution of Working Groups I, II, and III to the Fifth Assessment Report of the Intergovernmental Panel of Climate Change* [Core Writing Team, Pachauri RK & Meyer LA (eds.)] IPCC, Geneva, Switzerland.

Kopp CW & Cleland EE (2015) Shifts in plant species elevational range limits and abundances observed over nearly five decades in a western North America mountain range. *Journal of Vegetation Science*. 25:135-146. doi:10.1111/jvs.12072

Lembrechts JJ, Lenoir J, Nuñez MA, Pauchard A, Geron C, Bussé G, ... & Nijs I (2017) Microclimate variability in alpine ecosystems as stepping stones for non-native plant establishment above their current elevational limit. *Ecography*. 10.1111/ecog.03263. doi:10.1111/ecog.03263

Lenoir J, Gégout J-C, Guisan A, Vittoz P, Wohlgemuth T, Zimmermann, ... & Svenning J-C (2010) Going against the flow: potential mechanisms for unexpected downslope range shifts in a warming climate. *Ecography*. 33:295-303. doi: 10.1111/j.1600-0587.2010.06279.x

Louhan AM, Doak DF & Angert AL (2015) Where and when do species interactions set range limits? *Trends in Ecology & Evolution*. 30(12):780-792. doi:10.1016/j.tree.2015.09.011

McKenzie LJ, Yoshida RL & Unsworth RKF (2014) Disturbance influences the invasion of a seagrass into an existing meadow. *Marine Pollution Bulletin*. 86:186-196.
doi: 10.1016/j.marpolbul.2014.07.019

Michalet R, Schöb C, Lortie C, Brooker RW & Callaway RM (2014) Partitioning net interactions among plants along altitudinal gradients to study community responses to climate change. *Functional Ecology*. 28:75-86. doi:10.1111/1365-2435.12136

Michalet R, Schöb C, Xiao S, Zhao L, Chen T, An L-z & Callaway RM (2016) Beneficiary feedback effects on alpine cushion benefactors become more negative with increasing cover of graminoids and in dry conditions. *Functional Ecology*. 30:79-87.

Monz CA (2002) The response of two arctic tundra plant communities to human trampling disturbance. *Journal of Environmental Management*. 64:207-217. doi:10.1006/jema.2001.0524

Morris WF & Doak DF (1998) Life history of the long-lived Gynodioecious cushion plant *Silene acaulis* (Caryophyllaceae), inferred from size-based population projection matrices. *American Journal of Botany*. 85(6):784-793. doi:10.2307/2446413

Olofsson J, Moen J & Oksanen L (1999) On the balance between positive and negative plant interactions in harsh environments. *OIKOS*. 86:539-543. doi: 10.2307/3546658

Panetta AM, Stanton ML & Harte J (2018) Climate warming drives local extinction: evidence from observation and experimentation. *Science Advances*. 4:eaq1819. doi:10.1126/sciadv.aaq1819

Parmesan C (2006) Ecological and evolutionary responses to recent climate change. *Annual Review of Ecology, Evolution, and Systematics*. 37:637-669. doi:10.2307/annurev.ecolsys.37.091305.300

Pickett STA & White PS (1985) *The ecology of natural disturbance and patch dynamics*. Orlando, Florida: Academic Press, Inc. pp. 287-316.

R Core Team (2017) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. <<http://www.R-project.org/>>.

Randin CF, Vuissoz G, Liston GE, Vittoz P & Guisan A (2009) Introduction of snow and geomorphic disturbance variables into predictive models of alpine plant distributions in the Western Swiss Alps. *Arctic, Antarctic, and Alpine Research*. 41(3):347-361. doi: 10.1657/1938-4246-41.3.347

Rixen C, Haag S, Kulakowski D & Bebi P (2007) Natural avalanche disturbance shapes plant diversity and species composition in subalpine forest belt. *Journal of Vegetation Science*. 18:735-742. doi:10.1111/j.1654-1103.2007.tb02588.x

Roach G (1999) Colorado's Fourteeners: From Hikes to Climbs (2nd ed.) Golden, Colorado, USA: Fulcrum Publishing.

Rosseel Y (2012). lavaan: An R Package for Structural Equation Modeling. *Journal of Statistical Software*. 48(2):1-36. <<http://www.jstatsoft.org/v48/i02/>>.

Sexton JP, McIntyre PJ, Angert AL & Rice KJ (2009) Evolution and ecology of species range limits. *Annual Review of Ecology, Evolution, and Systematics*. 40:415-436. doi:10.1146/annurev.ecolsys.110308.120317

Sheil D (2016) Disturbance and distributions: avoiding exclusion in a warming world. *Ecology and Society*. 21(1):10. doi:10.5751/ES-07920-210110

Skaug H, Fournier D, Bolker B, Magnusson A & Nielsen A (2016-01-19). _Generalized Linear Mixed Models using 'AD Model Builder'_. R package version 0.8.3.3.

Slaton MR (2015) The roles of disturbance, topography and climate in determining the leading and rear edges of population range limits. *Journal of Biogeography*. 42:255-266. doi: 10.1111/jbi.12406

Smithson M & Verkuilen J (2006). A Better Lemon Squeezer? Maximum-Likelihood Regression with Beta-Distributed Dependent Variables. *Psychological Methods*. 11(1):54–71. doi:10.1037/1082-989X.11.1.54

Weatherbase. “Mt Elbert, Colorado”. Accessed 20 Apr 2018.

<<http://www.weatherbase.com/weather/weather.php3?s=588450&cityname=Mount-Elbert-Colorado&set=metric>>.

Whinam J & Chilcott NM (2003) Impacts after four years of experimental trampling on alpine/sub-alpine environments in western Tasmania. *Journal of Environmental Management*. 67:339–351. doi:10.1016/S0301-4797(02)00218-9

Willard BE & Marr JW (1970) Effects of human activities on alpine tundra ecosystems in Rocky Mountain National Park, Colorado. *Biological Conservation*. 2:257-265. doi:10.1016/0006-3207(70)90008-X

Willard BE, Cooper DJ & Forbes BC (2007) Natural Regeneration of alpine tundra vegetation after human trampling: a 42-year data set from Rocky Mountain National Park, Colorado, U.S.A. *Arctic, Antarctic and Alpine Research*. 39(1):177–183. doi:10.1657/1523-0430(2007)39[177:NROATV]2.0.CO;2

FIGURE LEGENDS

Figure 1: Conceptual diagram of predictions. We test the null hypothesis (H_0 , dashed line) that disturbance has no effect across an elevational gradient. Following Darwin's Hypothesis (solid line), we predict that disturbance exerts net positive effects at lower elevations due to a disturbance mediated reduction in competitive effects. Conversely, at climatically stressful upper elevations with fewer biotic interactions, we predict net neutral disturbance effects.

Figure 2. Site schematic. We sampled across *Silene acaulis*' local elevational range (black arrow) on a site (i.e. mountain side) with a popular hiker trail (white curve). Red and grey lines represent trail-side (disturbed) and off-trail (undisturbed) 10 m² sampling transects, respectively. *Minuartia obtusiloba* has a similar elevational distribution, but transects were established based on *Silene*'s absolute elevational range limits (for details see Appendix S2). Photo insets of trail-side transects (measuring tapes) with 1 m² quadrats (white squares) illustrate that vegetation abundance decreases with elevation, while rock cover and bare ground increase.

Figure 3: Trail disturbance favours cushion plants most at lower elevations. Trail disturbance increases *Silene acaulis* maximum cushion area (A), density (C), as well as *Silene* (E) and *Minuartia obtusiloba* (G) percent cover most at the species' lower elevational range limit. As seen in the coefficient plots (B, D, F, H) of the most parsimonious model (trail * elevational) for each variable, the positive effect of trail is reduced to neutral or even negative at the species' upper elevational range limit. Group means are indicated above each boxplot. Coefficients for Trail (mid-Elev) and Trail (high Elev) are the sum of the effects of trail and the respective by elevation interaction effect +/- this sum's standard error. All other coefficients are from raw

model outputs +/- standard error. Colours in (C, E, G) are as in (A), and colours in (B), (D), (F), and (H) differentiate parameters.

Figure 4: Trail decreases competitive vegetation and increases habitat availability. Trail disturbance decreases vegetation (A) evenly across all elevations as indicated by a lack of an interaction effect between trail and elevation (B). In contrast, trail increases unoccupied habitat availability (C), with a slightly larger effect at higher elevations (D). Group means are indicated above each boxplot. Coefficients for Trail (mid-Elev) and Trail (high Elev) are the sum of the effects of trail and the respective by elevation interaction effect +/- this sum's standard error. All other coefficients are from raw model outputs +/- standard error. Colours in (C) are as in (A), and colours in (B) and (D) differentiate parameters.

Figure 5: Vegetation disfavours and habitat availability favours cushion plants. Vegetation negatively affects *Silene* maximum area (A) at all elevations. Habitat availability increases *Silene* density (B) as well as *Silene* (C) and *Minuartia* (D) percent cover, an effect that decreases to neutral or negative at highest elevations. Coefficients for Habitat Index at mid-Elev and high Elev are the sum of the effects of that index and the respective by elevation interaction effect +/- this sum's standard error. All other coefficients are from raw model outputs +/- standard error. Colours merely differentiate parameters.

Figure 6: Habitat availability is a dominant driver of cushion plants. (A) Structural Equation Models (SEMs) for *Silene acaulis* percent cover indicate that habitat availability favours *Silene* most at lower elevations, and that the direct positive effect of trail is strongest at mid-elevation and decreases to negative at high elevations. (B) SEMs for *Minuartia obtusiloba* percent cover indicate that habitat availability has the largest effect on increasing *Minuartia*

percent cover, an effect that wanes with elevation. The direct effects of habitat availability are overall stronger than that of trail disturbance, and much of trail's overall effect is accounted for by an increase in habitat availability. Model estimates are shown within each arrow, thickness of arrows reflect effect strength, and green and red colours indicate positive (+) and negative (-) effect, respectively. See Tables S1.3, S1.4 for details on model results.

Table 1. Description of independent and dependent variables used in statistical models. See Materials & Methods for details.

Parameter	Type	Response or Predictor	Measurement scale	N
Trail disturbance	binary [0, 1]	predictor	Transect	157
Elevational level (i.e. range location)	categorical [0, 1, 2]	predictor	Transect	157
Summer Average Temperature	continuous [June, July, August]	predictor	Elevational level	17
Age of Trail	continuous	predictor	Site	6
Yearly Hikers	continuous	predictor	Site	6
Vegetation Index	continuous (0:1)	response and predictor	Quadrat	1561
Habitat Index	continuous (0:1)	response and predictor	Quadrat	1561
Forb Index	continuous (0:1)	response and predictor	Quadrat	1561
Graminoid Index	continuous (0:1)	response and predictor	Quadrat	1561
<i>Silene acaulis</i> maximum size	continuous [5 largest plants/quad.]	response	Individual plant	3490
<i>Silene acaulis</i> density	integer [plants/quad.]	response	Quadrat	1561
<i>Silene acaulis</i> % cover	discrete counts by 1%	response	Quadrat	1561 (present in 936)
<i>Minuartia obtusiloba</i> % cover	discrete counts by 1%	response	Quadrat	1561

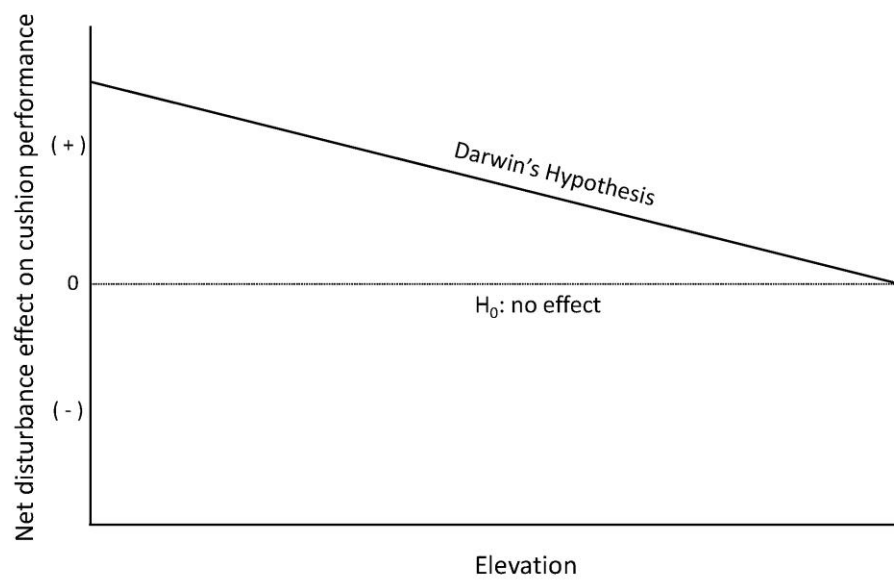
Table 2. Two most parsimonious model results of all fitted LMMs and GLMMs, with tested fixed effects listed at the top (see Materials & Methods for model details). (A) Effects of trail and elevational level (level) on cushion plants as well as vegetation and habitat availability indices. (B) Effects of habitat availability and vegetation indices as well as elevational level on cushion plants. Forb and graminoid fixed effects were not in any of the most parsimonious models, hence they are left out here. *Silene* area and density are log-transformed. Trail and elevational level are factor variables, with 2 and 3 levels, respectively. Parameter estimates for trail, vegetation, and habitat availability shown with p-values (< 0.0001***; < 0.001**; < 0.01*; < 0.05') +/- standard error. Level coefficient values are summarized as follows: (+) positive trend, (-) negative trend, (unimodal) with a maximum (+) or minimum (-) at mid-elevation, and indicated p-values reflect lowest significance value for any level. Goodness of fit measures LMM: marginal and conditional r^2 , respectively; Goodness of fit measures GLMM: correlation between fitted values and data. See Tables S1.1, S1.2 for full list of models.

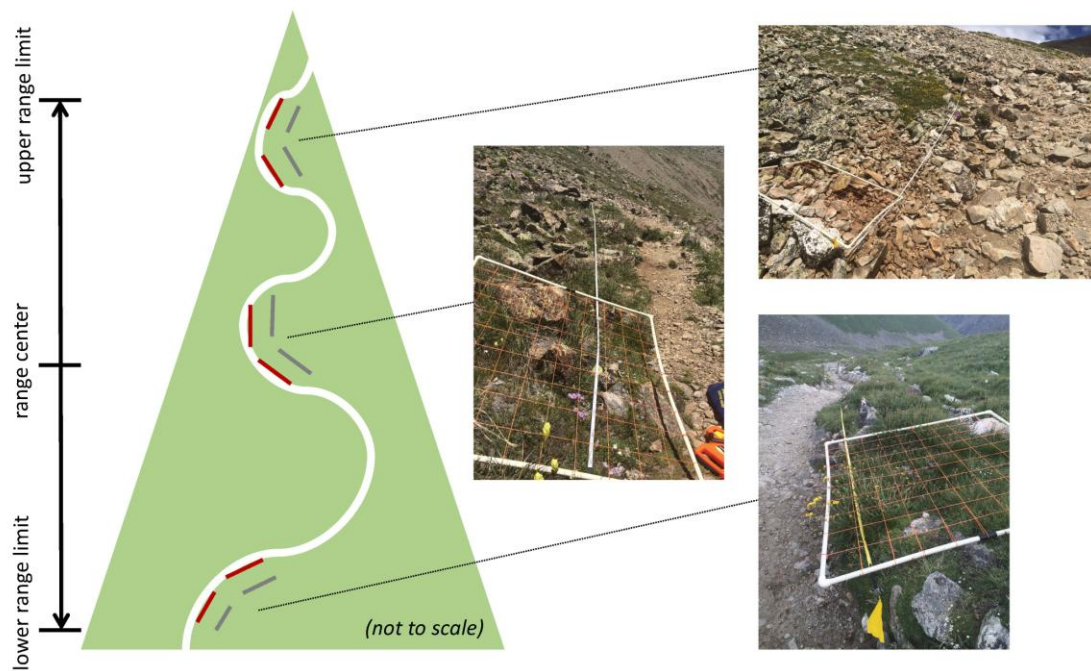
A

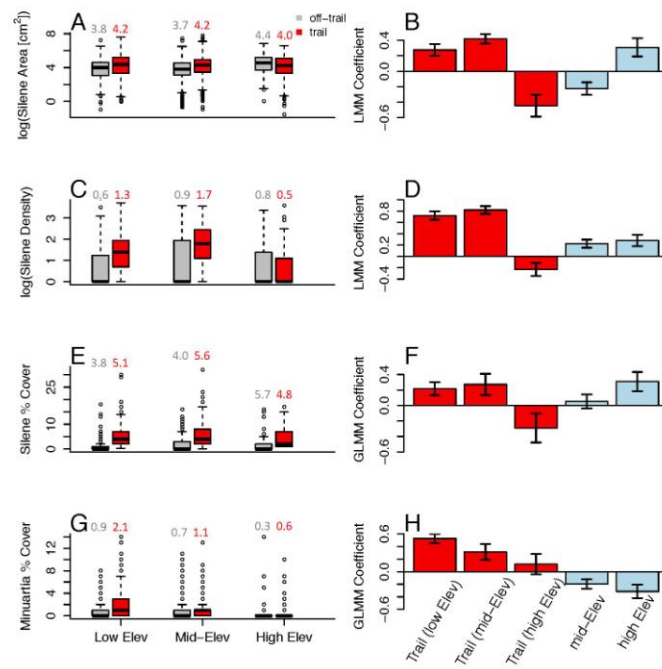
Type	Response Variable	Formula	Intercept	Trail	Level	Δ AICc	N	Goodness of fit
LMM	Silene area	trail * level	3.94	0.28*** +/- 0.08	unimodal (-)**	0	3490	0.02, 0.16
LMM	Silene area	trail				20.99	3490	0.01, 0.15
LMM	Silene density	trail * level	0.67	0.72*** +/- 0.07	(+)*	0	1561	0.15, 0.25
LMM	Silene density	trail + level				53.85	1561	0.12, 0.22
GLMM	Silene cover	trail * level	-3.17	0.22** +/- 0.08	unimodal (+)	0	936	0.37
GLMM	Silene cover	trail				6.95	936	0.36
GLMM	Minuartia cover	trail * level	-4.62	0.52*** +/- 0.07	unimodal (-)*	0	1561	0.51
GLMM	Minuartia cover	trail				5.4	1561	0.51
GLMM	vegetation	trail + level	0.55	-0.46*** +/- 0.07	unimodal (+)	0	1561	0.46
GLMM	vegetation	trail * level				1.9	1561	0.47
GLMM	habitat availability	trail * level	-1.57	1.36*** +/- 0.1	unimodal (+)	0	1561	0.62
GLMM	habitat availability	trail + level				3.24	1561	0.61

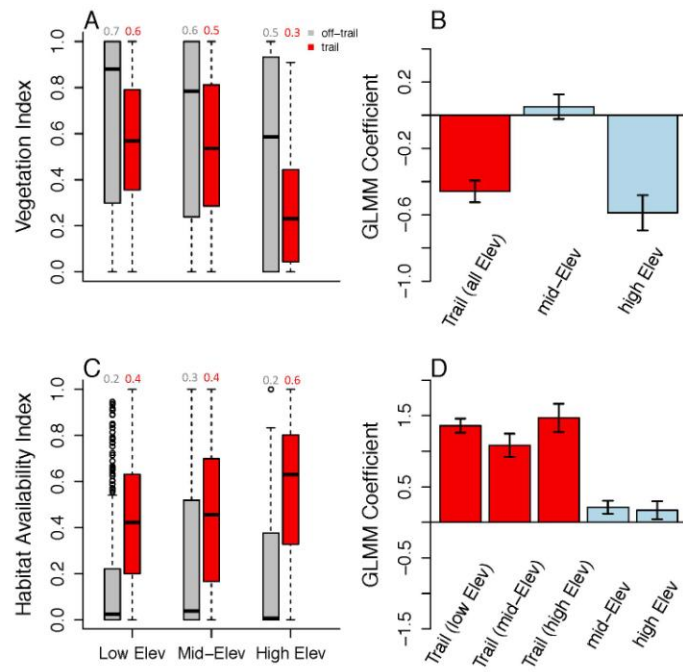
B

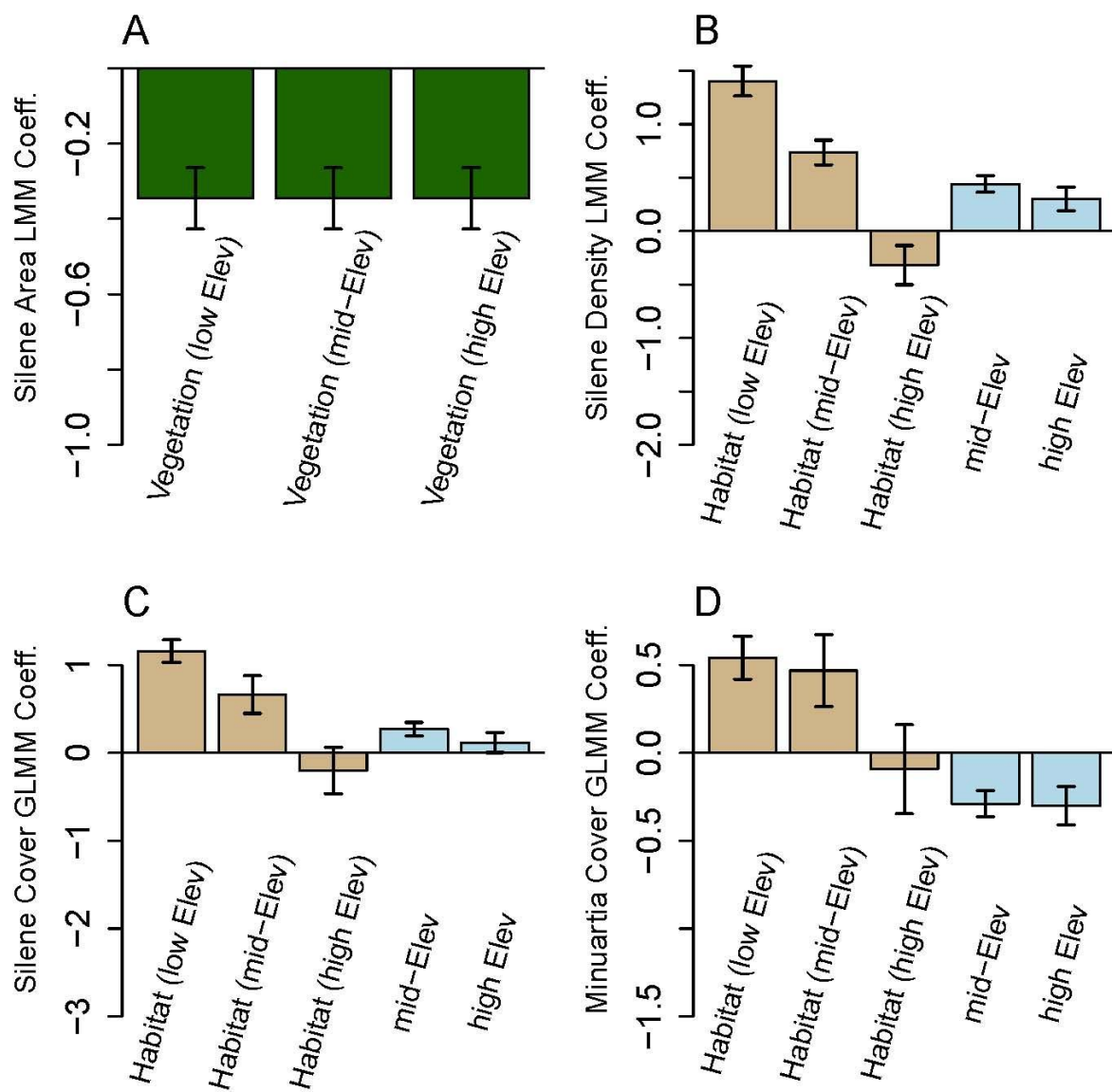
Type	Response Variable	Formula	Intercept	Habitat Availability	Vegetation	Level	Δ AICc	N	Goodness of fit
LMM	Silene area	vegetation	4.25		-0.35*** +/- 0.08		0	3490	0.01, 0.16
LMM	Silene area	vegetation + level					13.67	3490	0.01, 0.16
LMM	Silene density	habitat availability * level	0.59	1.4*** +/- 0.14		unimodal (+)**	0	1561	0.12, 0.2
LMM	Silene density	habitat availability + level					48.22	1561	0.09, 0.15
GLMM	Silene cover	habitat availability * level	-3.92	1.16*** +/- 0.13		unimodal (-)	0	1561	0.36
GLMM	Silene cover	habitat availability + level					31.28	1561	0.36
GLMM	Minuartia cover	habitat availability * level	-4.56	0.65*** +/- 0.13		(-)	0	1561	0.49
GLMM	Minuartia cover	habitat availability + level					5.8	1561	0.49



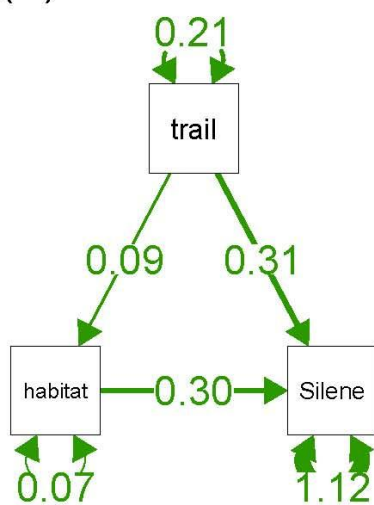




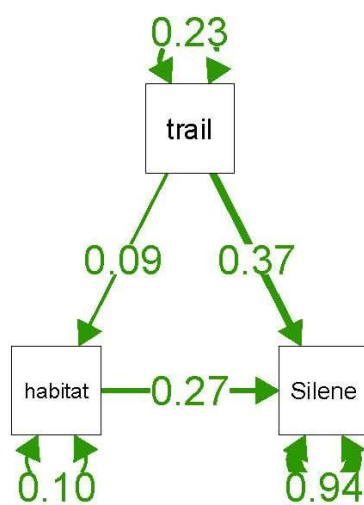




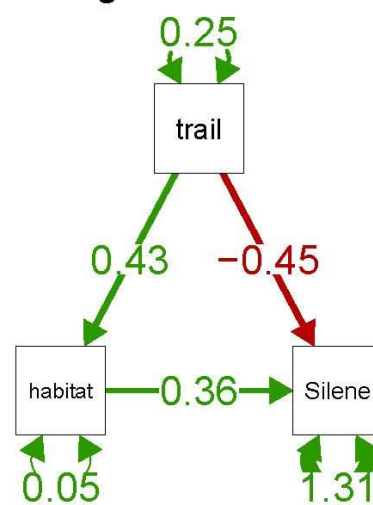
(A) Low Elevation



Mid-Elevation



High Elevation



(B)

