

**THE EFFECTS OF HUMAN TRAMPLING DISTURBANCE, PLANT-PLANT
INTERACTIONS, AND CLIMATE ON THE PERFORMANCE AND
DISTRIBUTION OF THE ALPINE CUSHION PLANT *SILENE ACAULIS***

by

NATHALIE ISABELLE CHARDON

B.A., University of California, Berkeley, 2010

A thesis submitted to the
Faculty of the Graduate School of the
University of Colorado in partial fulfillment
of the requirement for the degree of
Doctor of Philosophy
Environmental Studies Program

2018

This thesis entitled:
The Effects of Human Trampling Disturbance, Plant-Plant Interactions, and
Climate on the Performance and Distribution of the
Alpine Cushion Plant *Silene acaulis*
written by Nathalie Isabelle Chardon
has been approved for the Environmental Studies Program

Prof. Daniel F. Doak (Chair)

Prof. William D. Bowman

Prof. Katherine N. Suding

Dr. Sonja Wipf

Dr. Christian Rixen

Date: _____

The final copy of this thesis has been examined by the signatories, and we find that both the content and the form meet acceptable presentation standards of scholarly work in the above-mentioned discipline.

Chardon, N. I. (Ph.D., Environmental Studies)

The Effects of Human Trampling Disturbance, Plant-Plant Interactions, and Climate on the Performance and Distribution of the Alpine Cushion Plant *Silene acaulis*

Thesis directed by Prof. Daniel F. Doak

Delineating the abiotic and biotic processes that set species geographic distributions has been a central theme in ecological research for hundreds of years, yet we still do not understand many aspects of this broad question. Discerning what processes determine past and current range limits is particularly critical for predicting how species distributions will respond to climate change. In Chapters 2 and 3, I address how the interactions of climate, inter-species interactions such as competition, and human disturbances together influence range limits. I show that disturbance has positive effects on the alpine cushion plants *Silene acaulis* and *Minuartia obtusiloba* at the species' lower elevational range limits, likely through a reduction in competitive interactions. In contrast, at upper elevational range limits, where biotic interactions are minimal, disturbance exerts neutral or negative effects. However, disturbance has negative effects at the *S. acaulis* population level, as evidenced by a reduction in population density and reproductive indices. While facilitation by cushion plants is thought to increase with abiotic stress, it is also left unanswered if disturbance influences these facilitative effects. I show that disturbance does not alter plant-plant interactions, and that, in fact, competitive interactions prevail in *S. acaulis* communities. In Chapter 4, I address a second major issue in the understanding and prediction of range limits by examining if local populations respond differently to climatic drivers limiting their distribution. By constructing Species Distribution Models (SDMs) based on *S. acaulis*' global distribution and separately with subpopulations based on genetic and habitat differences, I show that potential local population adaptation to climate renders a

global SDM inaccurate. Furthermore, the manner in which subpopulations are defined greatly affects habitat suitability predictions, which are poorly linked to measures of *S. acaulis* population performance and facilitative interaction strength. The final aspect of my work is outlined in Chapter 5, for which I developed a citizen science application for smart phones to aid in the identification and hence appreciation of alpine plants in the Colorado Rocky Mountains. Altogether, my work illustrates the need to carefully examine all factors important in both setting species range limits and determining distribution shifts.

DEDICATION

To the mountains, which always bring me home.

* * *

There is an intimate sense of calm that descends over the dusky valleys, the rolling alpine fields, and the bright snowy peaks with the alpine sunset. It is a peace found only here, away from nocturnal electricity, confining walls of civilization, and expectations of society. Here is where sitting on a stone wall listening to the alpine cowbells is the main attraction for the evening.

The simplicity of drinking tea to a valley waking up with dew on its leaves and hiking through the morning light is how we sharpen our senses for the day.

Coming back to an alpine hut after a long day at altitude, cooking to such a mesmerizing sunset, and swapping stories about where life has taken us is how we bid farewell to a beautiful day. These bare essentials are forgotten, buried behind layers of fast-paced living, when alpine days are too far and few in between. This is what we lose in the circus, our inner balance with the big around us.

7 July 2016
Calanda Hut, Switzerland

* * *

ACKNOWLEDGMENTS

Dan Doak, for your patience, wisdom, and guidance to turn me into a scientist

Doak Lab, for being my “Alice in Wonderland” family

Committee Members, for guiding me with countless discussions and advice

Team Mountain Ecosystems, for welcoming me year after year

Samuel Pironon, for your constant modeling advice and ideas

Field Assistants, for hiking thousands of vertical feet to collect data

My Asolos, for taking every step with me

Carol Wessman, for tea and influential discussions on disturbance

David Ackerly, for lighting in me a passion for research and species range limits

Elizabeth Bergstrom, for encouraging my love of alpine ecology

3821 Paseo del Prado, for dogs and conversations about all things science

Alain Chardon, for always fighting on my side

Elisabeth Chardon, for knowing I could succeed

Alessandra Chardon, for keeping me sane with your understanding

Florence Chardon, for your excitement in my path and emergency proof-reading

Christian Lauber, for your commitment, humor, and countless air miles

Katherine Lawry, for soggy talks about a decision and Lawry’s Editing Services

Friends, for romping around with me in mountains, canyons, and deserts

My skis and climbing harness, for letting me play and reminding me to do so

Funding generously provided by:

CU Boulder Environmental Studies Program, Zeno Karl Schindler Foundation, Santa Barbara Scholarship Foundation, CU Boulder Graduate School, American Alpine Club, Indian Peaks Wilderness Alliance, John Marr Ecology Fund, CU Herbarium Hazel Schmoll Fellowship, Swiss Botanical Society

CONTENTS

CHAPTER

1. Introduction	1
1.1. Range Limits and Climate Change	1
1.2. Local Disturbance and Range Limits	3
1.3. Alpine Plant Interactions	5
1.4. Predicting Range Shifts	6
1.5. Disturbance Impacts	7
1.6. Species Distribution Models	8
 2. Disturbance benefits two alpine cushion plants at lower, but not upper, elevational range limits	 9
2.1. Abstract	9
2.2. Introduction	10
2.3. Materials & Methods	15
2.3.1. Sites	15
2.3.2. Study species	17
2.3.3. Data collection	18
2.3.4. Statistical analyses	20
2.4. Results	22
2.5. Discussion	30

2.6.	Acknowledgments	34
2.7.	Data Accessibility	34
2.8.	Author Contributions	35
3.	Local trampling disturbance effects on alpine plant populations and communities: Negative implications for climate change vulnerability	36
3.1.	Abstract	36
3.2.	Introduction	37
3.3.	Materials & Methods	44
3.3.1.	Sites	44
3.3.2.	Field measurements: cushion plants	45
3.3.3.	Field measurements: community effects and species interactions	47
3.3.4.	Statistical analyses: cushion plants	48
3.3.5.	Statistical analyses: community effects	50
3.3.6.	Statistical analyses: species interactions	52
3.4.	Results	53
3.4.1.	Cushion plants	53
3.4.2.	Community effects: inside species	58
3.4.3.	Community effects: neighboring species	62
3.4.4.	Species interactions	64
3.5.	Discussion	65

3.5.1. Cushion plants	65
3.5.2. Community effects and species interactions	67
3.6. Acknowledgments	73
3.7. Data Accessibility	74
3.8. Author Contributions	74
4. Subpopulation species distribution models outperform global model for an arctic-alpine plant	75
4.1. Abstract	75
4.2. Introduction	76
4.3. Methods	85
4.3.1. Climate data	85
4.3.2. Species occurrences	85
4.3.3. Species traits	87
4.3.4. SDMs	89
4.3.5. Analyses	91
4.4. Results	94
4.5. Discussion	104
4.6. Acknowledgments	110
4.7. Data Accessibility	111
4.8. Author Contributions	111
5. A species identification app to increase citizen engagement at Niwot Ridge	112

5.1.	Introduction	112
5.2.	Methods	115
5.2.1.	Development	115
5.2.2.	Data	117
5.2.3.	Testing	118
5.3.	Results	119
5.3.1.	App	119
5.3.2.	Website	121
5.3.3.	Outreach	121
5.4.	Discussion	122
5.5.	Documentation	123
5.6.	Acknowledgments	124
6.	Conclusion	126
6.1.	Overview	126
6.2.	Alpine Cushion Plant Communities	126
6.3.	Species Distribution Models	129
6.4.	Citizen Science	130
	BIBLIOGRAPHY	131
	APPENDIX	151
	A. Chapter 2 Appendix	151

A.A. Additional Figures and Tables	151
A.B. Details on sampling and additional variables	165
A.B.1. Data collection	165
A.B.2. Data Analyses	168
A.C. Use of maximum size structure justification	174
A.C.1. Data	174
A.C.2. Data Analyses	174
A.C.3. Results	175
B. Chapter 3 Appendix	178
B.A. Parameters, supplemental results, and supplemental figures ...	178
B.B. Full lists of models	190
C. Chapter 4 Appendix	213
C.A. Supplemental tables and figures	213

TABLES

Table

2.1. Variables for statistical models	19
2.2. Most parsimonious model results	22
3.1. Most parsimonious cushion plant model results	54
3.2. Most parsimonious species community model results	59
3.3. Most parsimonious species interactions model results	64
4.1. Other subpopulation SDM studies	79
4.2. Evaluation metrics	95
4.3. Predicting traits with suitability	103
5.1. Luminous ID filter options	118
5.2. Luminous ID glossary terms	118
5.3. Documentation	124

FIGURES

Figure

2.1. Conceptual diagram of predictions	15
2.2. Site schematic	17
2.3. Trail disturbance favors cushion plants most at lower elevations	24
2.4. Trail decreases competitive vegetation and increases habitat availability ..	26
2.5. Vegetation disfavors and habitat availability favors cushion plants	27
2.6. Habitat availability is a dominant driver of cushion plants	29
3.1. Study species	43
3.2. Sampling design	46
3.3. Disturbance effects on <i>Silene acaulis</i>	56
3.4. Disturbance effects on <i>Silene acaulis</i> reproduction	57
3.5. Inside species community	60
3.6. Neighboring species community	63
3.7. Conceptual diagram summarizing main findings	66
4.1. Species occurrences	88
4.2. SDM validation	96
4.3. SDM suitability	97
4.4. SDM suitability by genetic group	99
4.5. Predicted climate niches	100
4.6. Genetic subpopulation climate niches	103

4.7. Species traits	104
5.1. Luminous ID user interface	120

CHAPTER 1

Introduction

Delineating the abiotic and biotic processes that set species geographic distributions has been a central theme in ecological research for hundreds of years, and contemporary computing power allows us to use this knowledge to predict how species ranges will shift with ongoing climate change. Central to this prediction is a clear understanding of how such processes vary between contrasting range limits, such as at lower and upper elevational limits. These ideas, which I review here, are central to my dissertation and motivated my work. I then briefly outline how my chapters address unanswered questions in the field to increase our understanding of range limits and improve species distribution predictions.

1.1. RANGE LIMITS AND CLIMATE CHANGE

Range limits have sparked the curiosity of biologists for hundreds of years, including that of Darwin, who proposed that both abiotic and biotic factors set range limits based on the amount of abiotic stress a species experiences from its environment (Darwin 1859). MacArthur (1972) further developed the idea, suggesting that biotic competition can be a strong driver of range limits when climate is not a limiting factor. Connell (1978) was the first to experimentally show

on a microhabitat scale that biotic and abiotic factors set range limits in environmentally benign versus stressful areas, respectively.

In present day, global climate change is causing abiotic factors to shift and also has the potential to alter the strength of biotic interactions (Parmesan 2006, Lenoir et al. 2010). Together, these effects are resulting in species distributions shifts worldwide (e.g., Parmesan 2006, Harsch & HilleRisLambers 2016, Freeman et al. 2018). The importance of accurately predicting species range shifts to optimize the conservation of threatened species and global biodiversity has spurred an increase in research examining how different processes set range limits (e.g., Sexton et al. 2009, Angert et al. 2018) and how these are expected to shift in the future (e.g., Ackerly & Cornwell et al. 2015, Carroll et al. 2015, Ehrlén & Morris 2015). However, we still have a poor understanding of the exact processes and mechanisms that determine such geographic distribution limits (reviewed in Louthan et al. 2015).

Trailing edge populations are particularly threatened by the impacts of climate change, with possible mechanisms including increasingly warm temperatures and encroachment by lower latitude or lower elevation species (Parmesan 2006, Alexander et al. 2015). In mountain systems, where lower and upper limits are often set by biotic and abiotic factors, respectively (e.g., Choler et al. 2001, Ettinger et al. 2011), such encroachment can result in lower range contractions (e.g., Kopp & Cleland 2015). This pattern in turn relies on lower elevation species having higher competitive abilities than those characteristically

living at higher elevations. If this pattern holds, we would expect that alpine species would be unable to maintain their lower elevational limits in the face of increased competition resulting from climate change. However, we have few tests of this prediction, which can also be moderated by multiple other factors, including local disturbance.

1.2. LOCAL DISTURBANCE AND RANGE LIMITS

Disturbance has long been recognized for its ecological importance (Liddle 1975) and as an influential driver of ecosystem dynamics (Connell 1978). It interacts with biotic processes (Picket & White 1985) and can even override the effects of climate (Franklin et al. 2016). Disturbance is influential in community structuring, playing as big of a role as competition and stress (Grime 1974). It can determine distributional patterns, such as in the cases of recurring fires (Sousa 1984), and anthropogenic disturbances have caused distributional shifts in invasive species worldwide (e.g., McKenzie et al. 2014, Lembrechts et al. 2017). Given that the effects of disturbance play an important role in determining invasive species distributions, it is surprising that disturbance is often left out of native species range limit research (but see Serra-Diaz et al. 2015, Slaton 2015). This limits a comprehensive understanding of how the effects of disturbance interact with range-limiting mechanisms, and how this will shape species distributions with ongoing climatic changes (Sheil 2016).

Despite the paucity of research in this area, we can still expect disturbance to influence range limits. Many alpine plant species, in particular, are limited by competition at their lower elevational range limit (Choler et al. 2001, Alexander et al. 2015). In abiotically benign areas, where facilitative effects of alpine species are marginal (Callaway et al. 2002), competitive interactions dominate ecosystem processes. If disturbance lessens competitive interactions by reducing the density of dominant competitors (e.g., Whinam & Chilcott 2003), we would expect alpine species to exhibit enhanced performance or density with moderate disturbance, possibly stabilizing lower range limits in the face of climate change. While disturbance, such as human trampling, does not selectively reduce dominant vegetations and leave cushion plants unharmed (e.g., Monz 2002), cushion plants can be more resistant to trampling compared to other alpine species (Willard et al. 2007). A positive effect of disturbance will therefore only be observed if the benefit from reduced competition outweighs the organismal damage exerted by disturbance (e.g., Barros & Pickering 2015).

As evidenced by the abundant trails in popular hiking destinations around the world (e.g., over 10,000 miles within the US National Trail System; Chavez et al. 1999), human trampling, in particular, is a major anthropogenic impact in alpine ecosystems. While population and community responses to localized disturbances have been documented for decades (Willard & Marr 1971, Willard et al. 2007, Ballantyne & Pickering 2015a, b), the role of these impacts on species range limits is largely unknown. Other landscape disturbances, such as avalanches (Rixen et al.

2007), that increase soil erosion and reduce dominant vegetation cover, have long been recognized as playing important roles in ecosystem dynamics, by influencing biotic factors such as colonization and competitive relationships between species (Pickett & White 1985). While observed species and community responses certainly result from a myriad of effects, such as soil nutrients, microbial activity (Bowman et al. 2004), species interactions (Butterfield et al. 2013), and direct organismal damage (Barros & Pickering 2015), studying population and community structures in disturbed systems can provide us with a better understanding of how disturbance affects species populations at range limits.

1.3. ALPINE PLANT INTERACTIONS

Alpine cushion plants, which act as nurse plants for other species (known as beneficiary species), are particularly important for maintaining local community diversity and maintain high species community diversity around the globe (Butterfield et al. 2013, Cavieres et al. 2013). The facilitative effects of cushion plants generally increase along elevational gradients, as they provide the necessary microhabitat for beneficiary species at high elevations characterized by increased abiotic stress (Callaway et al. 2002). These facilitative interactions, however, can break down at extremely high levels of abiotic stress (Michalet et al. 2006, reviewed in Liancourt et al. 2017) or be absent entirely in cushion plant communities (de Bello et al. 2011, Dvorsky et al. 2013, Bowman & Swatling-Holcomb 2017). As disturbance can influence facilitative and competitive interactions (e.g., Michalet et

al. 2014, Catorci et al. 2016), community-level responses to disturbance therefore likely play an integral role in determining community assembly and species diversity.

Although many studies have shown that the facilitative effects of cushion plants favor beneficiary species by increasing overall species richness and diversity (e.g., Callaway et al. 2002, Butterfield et al. 2013, Cavieres et al. 2016), only recently have the effects of beneficiaries on facilitators been considered (Bronstein 2009, Schöb et al. 2014). Even though we are gaining a better understanding of how facilitator-benefactor relationships function, research in this area is sparse and we are left with a number of unresolved questions (Brooker et al. 2008, Schöb et al. 2014). We have particularly limited knowledge of how such relationships are affected by disturbance, and if the effects of disturbance are consistent across the abiotic stress gradients found in alpine systems.

1.4. PREDICTING RANGE SHIFTS

With substantial interest in both management and conservation fields in predicting species distributions with ongoing climatic changes, we require a comprehensive understanding of what processes determine range limits. Increased knowledge of how the effects of biotic interactions, landscape perturbations, and climate interact to influence range limit populations will ultimately provide us with the necessary information to accurately predict range shifts. A common approach uses Species Distribution Models (SDMs), which predict a species' current or future

distribution across the globe with predominately climatic factors (Wiens et al. 2009, Elith et al. 2011). Such models fundamentally assume that all populations will respond equally to the range of climates found throughout a species' distribution, however this assumption is rarely tested (Araújo & Peterson 2012, Merow et al. 2013). As different lineages of a species may or may not respond to climate similarly (e.g., Fournier-Level et al. 2011), it is critical that we understand if, and how, such differences affect SDM predictions in order to appropriately model climate-driven distribution patterns.

1.5. DISTURBANCE IMPACTS

To better understand how disturbance influences cushion plant populations at range limits set by different processes, I addressed the question: Does human disturbance exert contrasting effects at range limits characterized by different processes? I therefore quantified population characteristics of the alpine cushion plants *Silene acaulis* and *Minuartia obtusiloba* in disturbed and undisturbed areas (i.e. areas adjacent to and away from hiker trails, respectively) in the Colorado Rocky Mountains (Chapter 2) and the Swiss Alps (Chapter 3). I also addressed the question: Does disturbance influence interspecific plant species interactions? To answer this question, I quantified species community measures to examine how interactions between plant species are influenced by disturbance (Chapter 3).

1.6. SPECIES DISTRIBUTION MODELS

To improve approaches on how to model species distributions, or more generally, their suitable habitat, I addressed the fundamental question: Do local populations respond differently to climatic drivers characterizing their distribution? I constructed three distinct SDMs using *S. acaulis*' full global distribution and separately with subpopulations based on genetic and habitat differences (Chapter 4). This allowed me to assess which SDM type (global, genetic, or habitat) best predicts *S. acaulis* current distribution, indicating to what extent the species might, or might not be, adapted to local conditions. Using extensive trait data on the species, I also tested if suitability predictions can be linked to population performance or facilitative interaction strength.

CHAPTER 2

Disturbance benefits two alpine cushion plants at lower, but not upper, elevational range limits

Chardon NI, Rixen C, Wipf S & Doak DF

2.1. ABSTRACT

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 role 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. 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*. 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. We propose that disturbance can diminish competitive interactions at lower elevations, and thus, possibly stabilize populations of alpine species susceptible to encroachment by lower elevation species. As the effects of disturbance and elevation interact to differentially impact species success at range limits, we highlight the importance of incorporating the effects of climate change into disturbance studies for a comprehensive understanding of landscape-level impacts. Conservation and management approaches should therefore particularly account for the differential effects of disturbance across climatic gradients.

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

2.2. 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, Freeman et al. 2018) as well as work on how different abiotic and biotic processes create range limits in the first place (Sexton et al. 2009, Louthan et al. 2015, Angert et al. 2018). However, a plethora of landscape factors, such as disturbances, may modify or even override the effects of climate on species distributions (Dirnböck et al. 2003). In fact, disturbance itself can be an important driver of shifts in invasive species distributions (McKenzie et al. 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 et al. 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., Picket & White 1985, Franklin et al. 2016), we would expect disturbance to impact 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 favor 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 (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 et al. 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 et al. 2015). In high elevation areas characterized by low biotic interactions, where low plant cover exerts minimal competitive or facilitative influence (e.g., Olofsson et al. 1999), the net effects of disturbance on alpine plant populations at their upper elevational range limit are likely minimal.

Alpine ecosystems are especially susceptible to the effects of climate change due to high rates of warming (IPCC 2014) and resulting species extinctions (Panetta

et al. 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 et al. 2013) as well as alter community composition (Ballantyne & Pickering 2015a, b). 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, center, 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 and replicated type of disturbance important in its own right, as well as is similar to landscape-level 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 et al. 2014).

Across elevational and disturbance gradients, we quantified 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 centers, we were able to analyze 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 favor cushion plant performance, and do these effects vary with range position?

We hypothesized 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. 2.1).

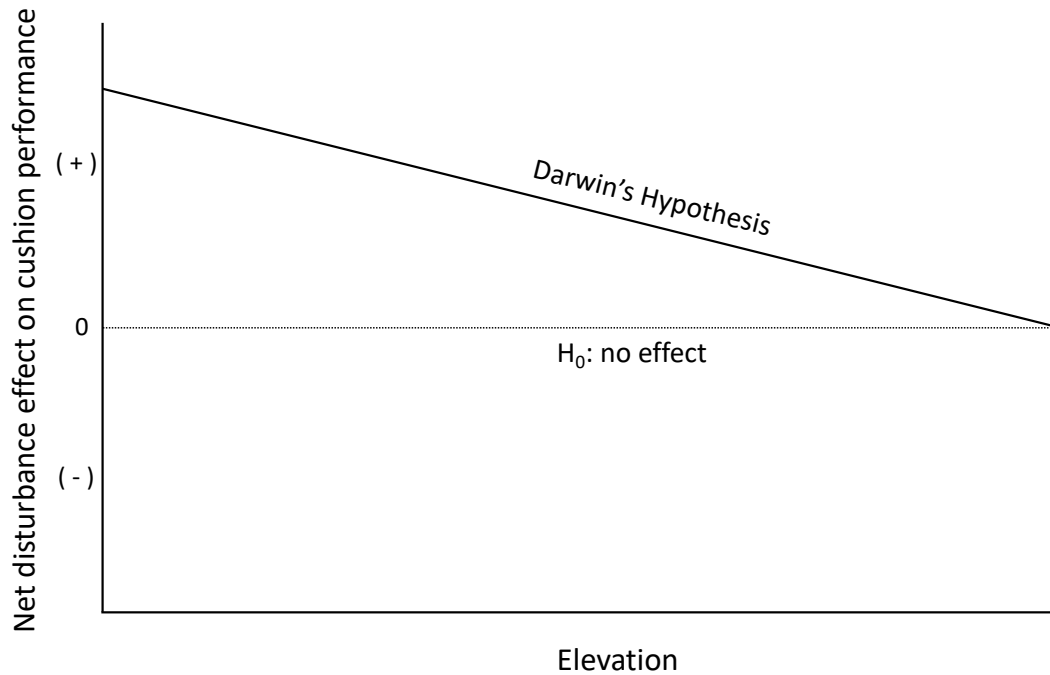


Figure 2.1: Conceptual diagram of predictions. We test the null hypothesis (H_0 , dashed line) that disturbance has no effect across an elevational gradient. Following Darwin's Hypothesis (solid line), we predict that disturbance exerts net positive effects at lower elevations due to a disturbance mediated reduction in competitive effects. Conversely, at climatically stressful upper elevations with fewer biotic interactions, we predict net neutral disturbance effects.

2.3. MATERIALS & METHODS

2.3.1. 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. A.A1; for details see

Appendix A.B). 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 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 A.B). Lower elevations are characterized by higher vegetation abundance,

whereas higher elevations are characterized by increased rock and bare ground abundance (*personal observation*; Fig. 2.2).

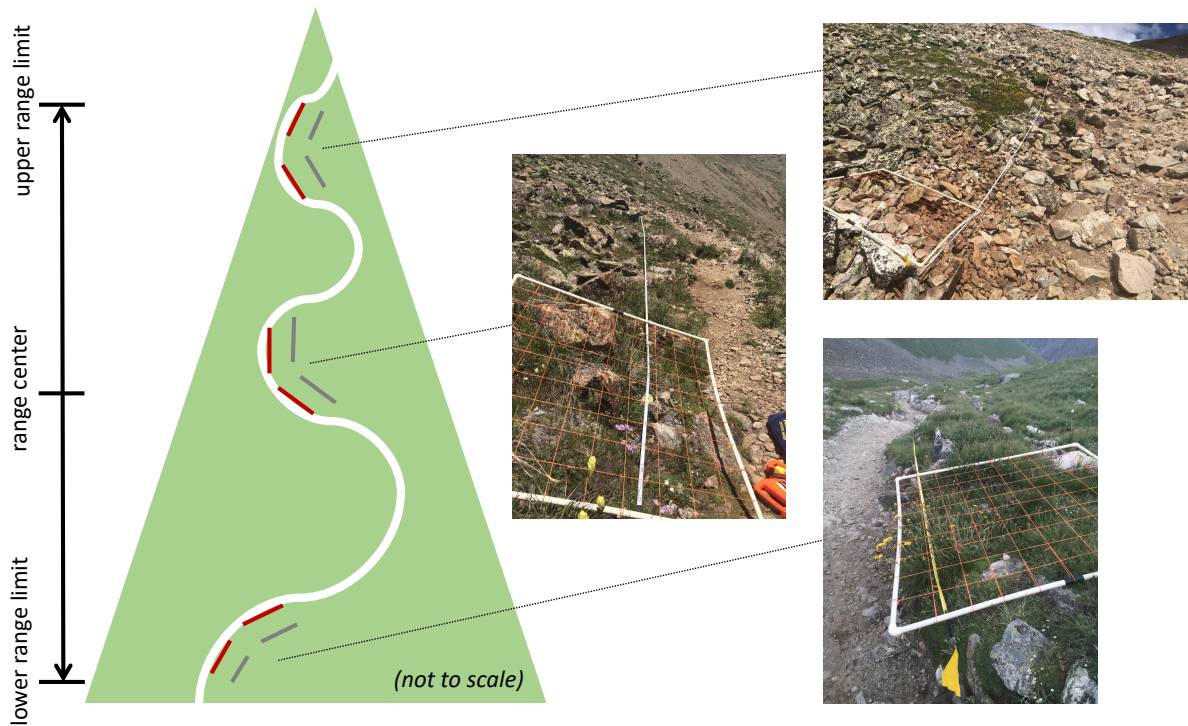


Figure 2.2: Site schematic. We sampled to encompass *Silene acaulis*' local elevational range (black arrows) on a site (i.e. mountain side) with a popular hiker trail (white curve). Red and grey lines represent trail-side (disturbed) and off-trail (undisturbed) 10 m² sampling transects, respectively. *Minuartia obtusiloba* has a similar elevational distribution, but transects were established based on *Silene*'s absolute elevational range limits (for details see Appendix A.B). Photo insets of trail-side transects (yellow measuring tape) with 1 m² quadrats (white square) illustrate that vegetation abundance decreases with elevation while rock cover and bare ground increases.

2.3.2. Study species

Both *Silene* and *Minuartia* are long-lived gynodioecious perennials (Fig. A.A2). *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 A.C). 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. Furthermore, larger individuals produce disproportionately more fruits, indicating that populations with larger cushion areas have higher reproductive potential.

2.3.3. 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 (mean = 3710 m), middle (3930 m), and upper (4060 m) elevational range locations (Fig. 2.2; for details see Appendix A.B). 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 (Appendix A.B). 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 indicator (Table 2.1, Fig. A.A.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 (Appendix A.B).

Table 2.1. Description of independent and dependent variables used in statistical models. See Materials & Methods for details.

Parameter	Type	Response/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/predictor	Quadrat	1561
Habitat Index	continuous (0:1)	response/predictor	Quadrat	1561
Forb Index	continuous (0:1)	response/predictor	Quadrat	1561
Graminoid Index	continuous (0:1)	response/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

2.3.4. Statistical analyses

We first fit sets of alternative linear mixed models (LMMs) for *Silene* maximum cushion area ($n = 3490$ individuals) as well as 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 $\text{param} = \% \text{ cover in decimal values}$ and $n = \text{number of observations}$ (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 et al. 2015) and the function ‘glmmadmb’ with family=beta, link=logit, and zeroInflation=TRUE in package glmmADMB (Fournier et al. 2012, Skaug et al. 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 A.A.1a). We also fit models using additional variables for temperature, yearly hikers, and trail age, but these models were not well supported (see Appendix A.B). 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 A.A.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 A.A.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 A.A.4, A.A.5, A.A.6, A.A.7). 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 centered and scaled all cushion plant variables.

2.4. 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 2.2a, Fig. 2.3). 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. 2.3a-f). Trail disturbance similarly increases *Minuartia* cover at lower elevations and has a neutral effect at higher elevations (Fig. 2.3g, h). Although highly significant effects are present in each model, goodness of fit values are low to moderate (Table 2.2). 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 (Appendix A.B).

Table 2.2. 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. 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 A.A.1, A.A.2 for full list of models.

A

Type	Response Variable	Formula	Intercept	Trail	Level	$\Delta AICc$	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	$\Delta AICc$	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

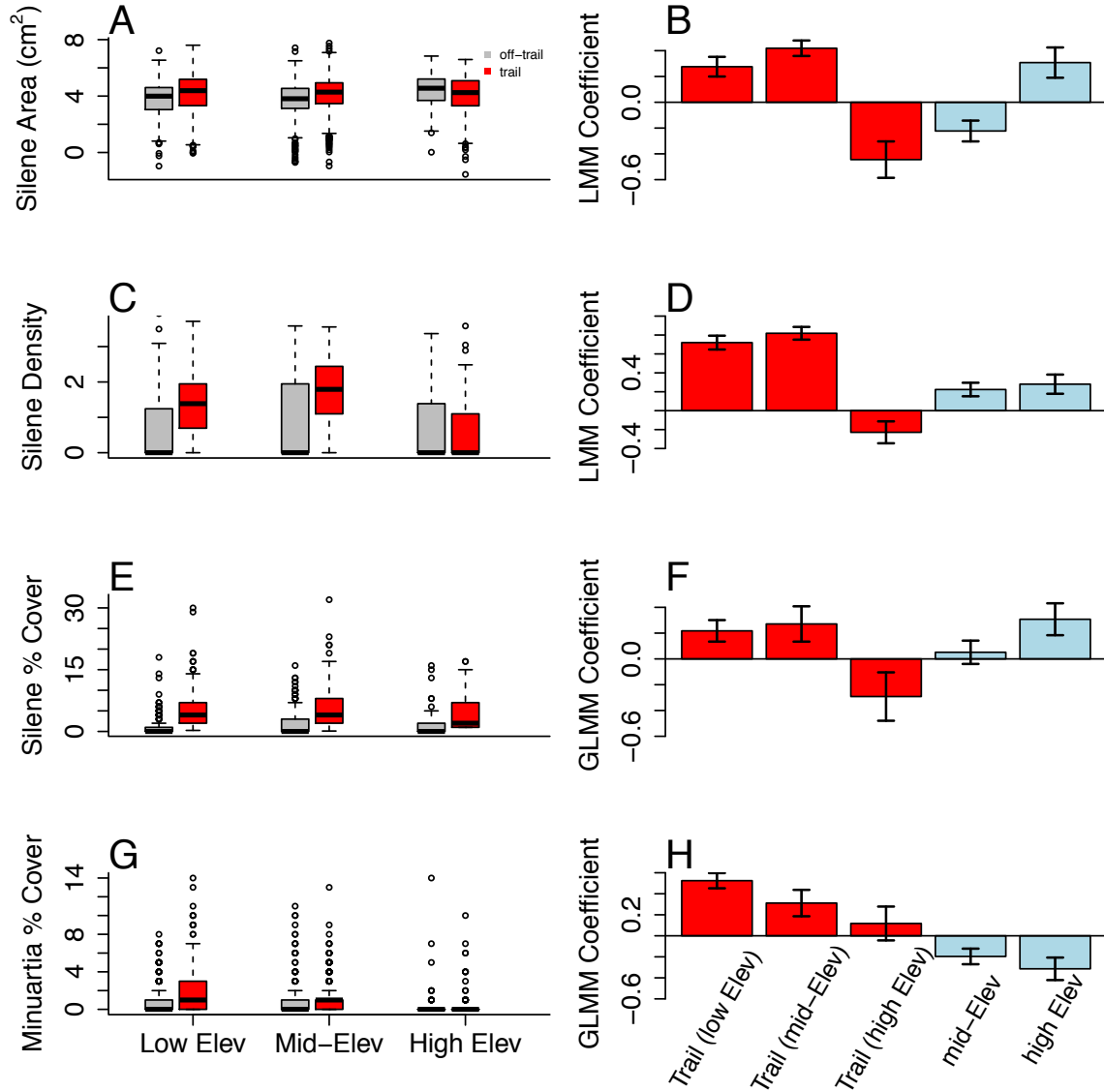


Figure 2.3: Trail disturbance favors cushion plants most at lower elevations. Trail disturbance increases *Silene acaulis* maximum cushion area (A), density (C), as well as *Silene* (E) and *Minuartia obtusiloba* (G) percent cover most at the species' lower elevational range limit. Note that both *Silene* area and density are log-transformed. 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. 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. Colors in (C, E, G) are as in (A).

Trail disturbance reduces competitive vegetation and increases habitat availability (Table 2.2, Fig. 2.4, Fig. A.A.4), as we hypothesized. Trail disturbance has a significant negative effect on the vegetation index, which is highest at the mid-elevational level (Fig. 2.4a, b). Trail disturbance significantly increases habitat availability, especially at the uppermost elevational level (trail x elevational level interaction; Fig. 2.4c, 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. A.A.5, Appendix A.B). Our model fits with additional variables (trail age, yearly hikers, average summer temperature) indicate similar patterns or insignificant results (Appendix A.B).

As expected, reduction of vegetative competition and augmentation of habitat availability favor cushion plant performance, with strongest effects at lower elevations (Table 2.2b). *Silene* maximum cushion area is negatively affected by vegetation at all elevations (Fig. 2.5a). *Silene* density, in contrast, increases with habitat availability (Fig. 2.5b), an effect strongest at the lower two elevations but negative at the highest elevation. *Silene* (Fig. 2.5c) and *Minuartia* (Fig. 2.5d) percent cover increase with habitat availability at the lower two elevations, with neutral effects at the highest elevation.

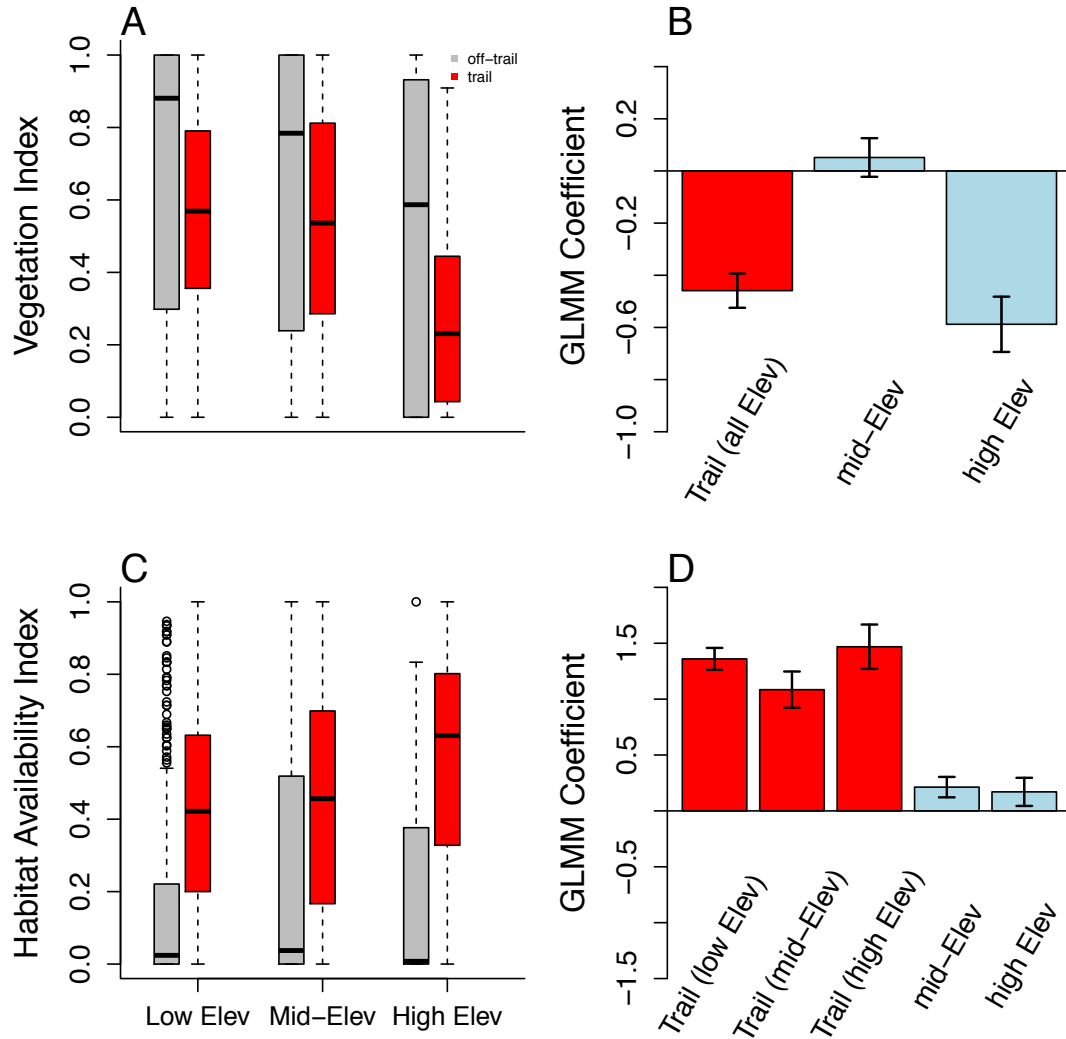


Figure 2.4: Trail decreases competitive vegetation and increases habitat availability. Trail disturbance decreases vegetation (A) evenly across all elevations as indicated by a lack of an interaction effect between trail and elevation (B). In contrast, trail increases unoccupied habitat availability (C), with a slightly larger effect at higher elevations (D). 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. Colors in (C) are as in (A).

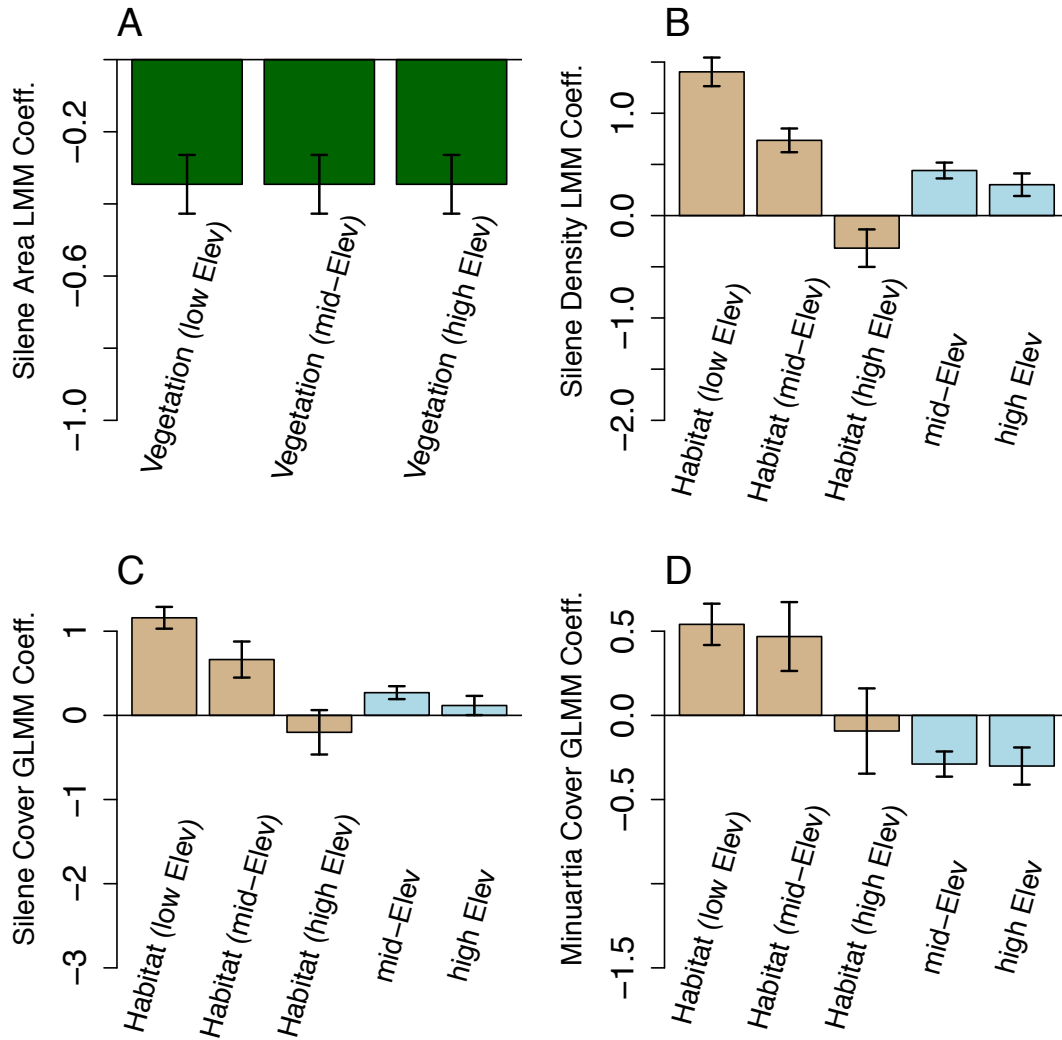


Figure 2.5: Vegetation disfavors and habitat availability favors cushion plants. Vegetation negatively affects *Silene* maximum area (A) at all elevations. Habitat availability increases *Silene* density (B) as well as *Silene* (C) and *Minuartia* (D) percent cover, an effect that decreases to neutral or negative at highest elevations. Note that both *Silene* area and density are log-transformed. 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.

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

favors *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. 2.6a, Table A.A.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. 2.6b, Table A.A.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. A.A.6a, Table A.A.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. A.A.6b, Table A.A.6). Habitat availability has negative effects at lower elevations that switch to positive at the highest elevation.

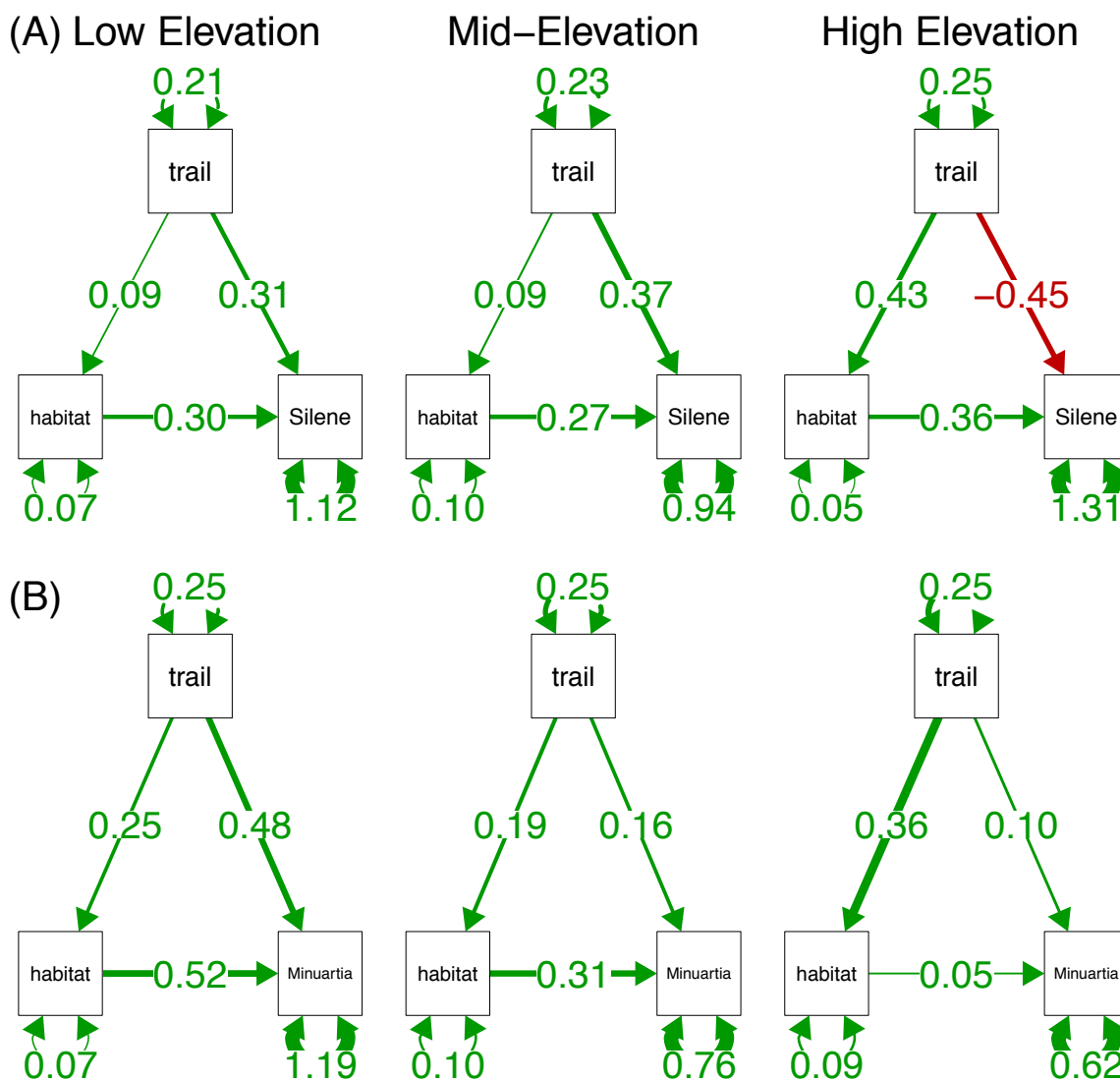


Figure 2.6: Habitat availability is a dominant driver of cushion plants. (A) SEMs for *Silene acaulis* percent cover indicate that habitat availability favors *Silene* most at lower elevations, and that the direct positive effect of trail is strongest at mid-elevation and decreases to negative at high 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 colors indicate positive (+) and negative (-) effect, respectively. See Tables A.A.3, A.A.4 for details on model results.

2.5. 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 et al. 2014). At upper elevations, which are colder (Appendix A.B) 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 et al. 2018), whereas lower elevational range edges will likely contract with encroachment of more competitive species from lower elevations (Alexander et al. 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 et al. 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. 2.2), 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. 2.3b), possibly due to decreasing competitive pressure as also found in the South American Andes (Armesto et al. 1980). As largest cushions bear the largest proportion of fruits (see Appendix A.C), cushions in low elevation disturbed areas might therefore have a higher reproduction potential, if fruits are not damaged by disturbance (see Chardon et al. 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 deglaciated regions, where cushion plants are good colonizers of similarly competitor-free space (Cichini et al. 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 et al. 2007). However, disturbance has been shown to exert significant organismal damage in other systems (Barros et al. 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 et al. 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 et al. 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 et al. 2009) and allowing for tailored management decisions regarding disturbance activities.

2.6. 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.

2.7. DATA ACCESSIBILITY

All data and R code used in this work are publicly and freely available (<https://doi.org/10.17605/OSF.IO/C8AJ2>) and are part of the Open Science Framework project “Anthropogenic disturbances in alpine ecosystems” (<https://doi.org/10.17605/OSF.IO/GKJV2>).

2.8. AUTHOR CONTRIBUTIONS

NIC, CR, SW, and DFD conceived the ideas and designed methodology. NIC collected as well as analyzed 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. The contents of this chapter are currently in revision as an article in *Journal of Applied Ecology*, which permits the publication of this article as part of this dissertation.

CHAPTER 3

Local trampling disturbance effects on alpine plant populations and communities: Negative implications for climate change vulnerability

Chardon NI, Wipf S, Rixen C, Beilstein A, Doak DF

3.1. ABSTRACT

Global change is modifying species communities from local to landscape scales, with alterations in the abiotic and biotic determinants of geographic range limits causing species range shifts along both latitudinal and elevational gradients. An important but often overlooked component of global change is the effect of anthropogenic disturbance, and how it interacts with the effects of climate to affect both species and communities, as well as interspecies interactions, such as facilitation and competition. We examined the effects of frequent human trampling disturbances on alpine plant communities in Switzerland, focusing on the elevational range of the widely distributed cushion plant *Silene acaulis* and the interactions of this facilitator species with other plants. Examining size distributions and densities, we found that disturbance appears to favor individual *Silene* growth at middle elevations. However, it has negative effects at the population level, as evidenced by a reduction in population density and reproductive indices. Disturbance synergistically interacts with the effects of elevation to reduce species richness at low and high elevations, an effect not mitigated by *Silene*. In

fact, we find predominantly competitive interactions, both by *Silene* on its hosted and neighboring species and by neighboring (but not hosted) species on *Silene*. Our results indicate that disturbance can be beneficial for *Silene* individual performance, potentially through changes in its neighboring species community. However, possible reduced recruitment in disturbed areas could eventually lead to population declines. While other studies have shown that light to moderate disturbances can maintain high species diversity, our results emphasize that heavier disturbance reduces species richness, diversity, as well as percent cover, and adversely affects cushion plants and that these effects are not substantially reduced by plant–plant interactions. Heavily disturbed alpine systems could therefore be at greater risk for upward encroachment of lower elevation species in a warming world.

Keywords: alpine, climate change, disturbance, facilitation, *Silene acaulis*, Switzerland

3.2. INTRODUCTION

Expected shifts in species geographic distributions in response to climate change have spurred numerous studies to determine which abiotic (e.g., climatic) and biotic (e.g., competitive and facilitative) processes determine range limits and affect population performance (Sexton et al. 2009). One topic of these studies is understanding the effects of disturbance regimes and potential shifts in disturbance

patterns with climate change. However, despite their significant potential to alter competitive balances or override climatic effects, the role of localized anthropogenic factors (e.g., site-specific disturbance regimes) in shaping range limits, including their interactions with broader climate changes, remains surprisingly understudied (Turner 2010). To predict how populations at range limits will respond in an era of climate warming, it is therefore crucial to understand how the cumulative effects of local disturbance, climate, and species interactions influence population parameters. This is especially relevant in systems where declining performance of threatened trailing edge (i.e. warmer climatic edge) populations could cause range contractions, such as for species that occur across substantial elevational gradients. For these species, effects of local disturbance would be expected to interact with the known negative effects of encroachment of lower elevational, more competitive, species (Alexander et al. 2015) in ways that could either stabilize lower range limits or, conversely, cause them to fail such that the entire range shifts upward in response to climate change.

Trailing edge populations are particularly threatened by the impacts of climate change, with possible mechanisms including increasingly warm temperatures and encroachment by formerly restricted lower latitude or lower elevation species (Parmesan 2006, Alexander et al. 2015). In mountain systems, where lower and upper limits are often believed to be set by biotic and abiotic factors, respectively (e.g., Ettinger et al. 2011), such encroachment can result in lower elevational range contractions (e.g., Kopp & Cleland 2015). This pattern in

turn relies on lower elevation species having higher competitive abilities than those characteristically living at higher elevations. If this pattern holds, we would expect that alpine species would be unable to maintain their lower elevational limits in the face of increased competition resulting from climate change. However, this set of processes may be moderated by multiple other factors, including local disturbance. In particular, it is unclear how the biotic interactions that influence species range limits will shift with climate change, and particularly how the strength of these interactions will be altered by disturbances.

Disturbance has long been recognized as an important driver of ecosystem dynamics (e.g., Connell 1978), and high intensity disturbance can exert significant organismal damage (Barros & Pickering 2015). Disturbance interacts strongly with multiple biotic processes (see Picket & White 1985 for review, pp. 287-316) and can even override the effects of climate (Franklin et al. 2016). It can determine distributional patterns, such as in the cases of recurring fires (Sousa 1984) or through changes in landscape patch structure (Picket & White 1985, p. 309). Anthropogenic disturbances can broaden the range in which non-native species can grow (Lembrechts et al. 2017), favor invasive species richness (Sandoya et al. 2017), and cause distributional shifts in invasive species (e.g., McKenzie et al. 2014). Given its influential role in invasive species range expansion, it is therefore surprising that disturbance is often left out of most studies of native species range limits. This limits a comprehensive understanding of how disturbance affects range-limiting mechanisms, or how such interactive effects will respond to global climate change.

We would expect that disturbance will influence range limits, in particular for species such as many alpine plant species that are limited by competition at their lower elevational range limit (Choler et al. 2001). In abiotically benign areas, where facilitative effects of alpine species are marginal (Callaway et al. 2002), competitive interactions dominate ecosystem processes. If disturbance reduces competitive interactions by reducing the density of dominant competitors, we might expect alpine species to exhibit enhanced performance or density with moderate disturbance, possibly stabilizing lower range limits in the face of climate change. Of course, this effect will only occur if disturbance is not so intense as to exert strong direct negative effects on alpine species themselves.

While disturbance may reduce competitive interactions at lower elevational limits, we would expect quite different effects at higher elevations. The facilitative effects of cushion plants, in particular, is generally believed to increase along elevational gradients, as they provide the necessary microhabitat for hosted species living within the cushions at high elevations characterized by increased abiotic stress (Callaway et al. 2002). These nurse plants may therefore play an important role in maintaining high species diversity around the globe (Butterfield et al. 2013). However, studies suggesting that cushion plants augment overall species richness (e.g., Cavieres et al. 2016) have been countered by other work showing that cushion species actually host less-diverse communities than surrounding areas (e.g. Dvorsky et al. 2013). Considering that disturbance is a form of abiotic stress, we expect alpine facilitator species to host increased species not only because these facilitators

provide a more sheltered microhabitat, but also because of the reduced resistance of facilitator species to other species. This is especially likely at higher elevations, where abiotic stress is known to play a large part in determining ecological processes.

To the extent that disturbance alters community interactions, such as facilitation and competition, it could have strong indirect effects on community assembly and species diversity. There is evidence that disturbance can affect facilitative and competitive interactions, such as reducing facilitator species' reproductive output and increasing hosted species presence (Michalet et al. 2011). On the other hand, facilitative interactions can break down with high levels of abiotic stress (for review see Michalet et al. 2016). Not only do we lack a clear picture of which environmental factors influence these interactions, but we also do not have a comprehensive understanding of the role that disturbance plays on species interactions along biotic and abiotic stress gradients, and how this influences species range limits.

In order to address the question of how disturbance can influence range limits, we focused on the biotic to abiotic gradient often present along elevational gradients in alpine ecosystems. While disturbances can be short to long-term and natural or anthropogenic in origin, we studied the margins of human-made trails, which represent frequent, relatively high intensity disturbances that are similar to livestock trails. Livestock trails are, however, more damaging, not only because livestock exert more pressure on the ground, but also because livestock herds create

multiple trails (Cole & Spildie 1998, Pickering et al. 2010, Barros & Pickering 2015). We specifically examined trail-side and off-trail plant communities in a system known to exhibit facilitative and competitive interactions along elevational gradients in the Swiss Alps. To assess the net effects of disturbance on such interactions, we quantified performance indicators of the well-studied facilitative common alpine cushion plant species, *Silene acaulis* (L.) Jaq. (Caryophyllaceae; Fig. 3.1), and quantified community measures of its inside (plants growing within cushions) and neighboring (plants growing next to cushions) species. Collecting data on the responses of a facilitative species as well as its inside and neighboring species allowed us to better understand i) how disturbance influences survival, growth, and reproduction indicators of this individual facilitative species and ii) how this community and its interactions are altered by disturbance. Specifically, we tested the following hypotheses:

1. a) At low elevations, presumably characterized by low abiotic stress and increased competition, disturbance will largely benefit cushion plant growth (as indicated by size of plants). At abiotically stressful high elevations, disturbance will have net negative effects.
- b) Disturbance may, however, have a negative effect on population density at all elevations, possibly due to low establishment and survival of younger plants.

2. Higher abundance of species inside disturbed cushions will have negative effects on cushion plant reproduction at all elevations.
3. Facilitation by cushion plants will be stronger and more important in maintaining species diversity in disturbed areas, an effect amplified at higher elevations.



Figure 3.1: Study species. *Silene acaulis* is a facilitative alpine cushion plant found throughout the northern Hemisphere.

To test these hypotheses, we measured *Silene acaulis* (henceforth, *Silene*) populations and species community structure along elevational range locations at sites frequently disturbed by human trampling (i.e. hiker trails) vs. relatively undisturbed (i.e. off-trail) areas in southeast Switzerland. We additionally measured two soil parameters (Soil Organic Matter and Soil Water Content) to

understand how disturbance alters habitat conditions. *Silene* is an ideal model species for this work, as it is a common circumboreal alpine plant with important facilitative effects on other vegetation (Butterfield et al. 2013). Its widespread distribution and facilitative effects make it an important alpine species across the Northern Hemisphere, and drivers of change to its populations, such as disturbance, need to be examined in order to improve our understanding of how to maintain alpine biodiversity in the face of impacts by multiple interactions.

3.3. MATERIALS & METHODS

3.3.1. Sites

We established three sampling sites located along popular alpine hiking trails on two summits and one mountain pass (Piz Beverin, Haldensteiner Calanda, Fallerfurrgga) within the canton of Grisons in southeastern Switzerland. We chose the summits using known occurrence locations (InfoFlora 2016) to ensure that sampling sites span *Silene*'s elevational range. At four evenly spaced elevations (i.e. elevational levels) encompassing *Silene*'s local (i.e. within site) elevational range, we sampled disturbed (trail-side) and paired undisturbed (off-trail) plots with a standard width (1 m for trail-side plots and 5 m for off-trail plots) and variable length (mean size = 16 m²) between June and August 2016. We defined plots as the area including the first 30 *Silene* individuals we encountered at each elevational level. For trail-side plots, we marked the first 30 *Silene* individuals within 0.5 m on either side of the trail while walking uphill. For off-trail plots, we walked at least 10

m away from the trail to find an undisturbed (i.e. no hiker or livestock trail) area of similar topography as the trail, and marked the first 30 *Silene* individuals while walking uphill, back and forth in a 5 m width (Fig. 3.2).

Plots span an elevational range of 1950 – 2680 m, are characterized by a continental alpine climate, and have a bedrock type predominantly classified as biogenic sedimentary rock. The summer growing season (June, July, August) has a mean monthly temperature of 5°C and mean monthly precipitation of 180 mm, and annual precipitation is 1411 mm (Federal Office of Meteorology and Climatology MeteoSwiss 2017). These sites have been moderately grazed by livestock (mainly cattle and sheep) for centuries, and the trails we sampled have been used as mountain passages for over a century. These sites are currently still used by livestock, with higher use at lower elevations, and livestock use is similar between sites. As evidenced by low dung counts at all sites (*personal observation*), grazing intensity is low. Hikers utilize these popular trails to hike to the summit or nearest pass, with similar hiker numbers at all elevations.

3.3.2. Field measurements: cushion plants

At each plot, we measured the size (i.e. cushion area, following the methods of Doak & Morris 2010) of all 30 *Silene* individuals regardless of cushion size for data to test Hypothesis 1a. To estimate population density within each plot in order to test Hypothesis 1b, we delineated an area of 0.5 m (to achieve a standard width within trail-side and off-trail plots) by the maximum length of the plot and recorded

which *Silene* individuals we found within it. We picked this area to be the 0.5 m width within the plot that had the highest density of plants, and fit this area to trail curvature for trail-side plots (Fig. 3.2). Of the 30 individuals measured per plot, we randomly picked five individuals (henceforth, “focal plants”) for additional measurements of either flower or fruit number (depending on individual plant phenology at the time of censusing) and sex (hermaphrodite or female) in order to test Hypothesis 2.

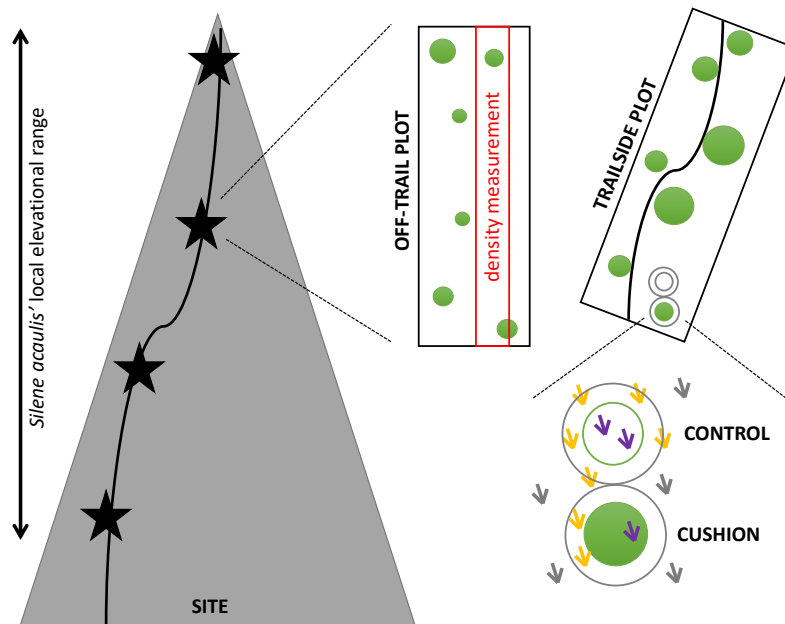


Figure 3.2: Sampling design. The black curved line represents a hiking trail at a SITE and stars indicate sampling locations along *Silene acaulis*' local elevational range. Black rectangles delineate each PLOT, and the smaller, inner red rectangle within the plot was used to calculate population density at both off-trail and trailside plots. Green circles are cushion plants ($n = 30$ per plot) and each plot had randomly chosen focal cushions for CUSHION/CONTROL pairs ($n = 5$ per plot). Grey circles represent the 5 cm sampling belt outside cushion and control (inner green circle) area. Cartoon plants are other vegetation, with purple cartoons measured as inside species and orange cartoons as neighboring species. Grey cartoons were not measured as they were outside the sampling area. See text for additional details.

3.3.3. Field measurements: community effects & species interactions

For each of the five focal plants in each plot, we established a control area of the same size but without any *Silene* cushion (methodically selected within 0.1-0.5 m of the focal plant with similar slope, aspect, and microtopography), using wire loops to maintain size of cushion area (following methods of Butterfield et al. 2013). We identified the identity and percent cover of other plant species growing inside each cushion and control area (i.e. inside species), as well as within 5 cm of the cushion edge and control edge (i.e. neighboring species) for the data to test Hypothesis 3. Our sampling protocol yielded 5 cushion/control pairs per disturbance type by elevation and 30-40 pairs per site, totaling 100 pairs.

To characterize soils from cushions and controls, we extracted soil samples at 4 cm depth using a spoon of approximately 20 cm³ at three cushion/control pairs per plot. We placed each soil sample in a plastic bag in the field. We determined soil water content (% SWC) by weighing the soil samples before and after drying them >48 hours at 60°C. We determined soil organic matter content (% SOM) of sieved soil samples (at 2 mm mesh size) by the loss on ignition method: 2 subsamples of 2 g dry soil per sample burned at 410°C for 40 hours (following the methods of Schöb et al. 2012), and weighed again after cooling. We averaged the values of the two samples for our measure of % SOM. At each plot, we measured microhabitat temperature over one year with temperature loggers (Maxim Integrated iButtons, CA, USA) buried at 2 cm depth under one of the focal cushions and its corresponding control.

3.3.4. Statistical analyses: cushion plants

To test whether disturbance largely benefits cushion plant growth at low elevations and has a net negative effect at high elevations (Hypothesis 1a), we first examined size distribution differences between disturbed and undisturbed *Silene* individuals with a Kolmogorov-Smirnov test. Second, to further test Hypothesis 1a and to test whether population density is reduced by disturbance at all elevations (Hypothesis 1b), we quantified the effects of disturbance and elevation on the plot-level densities and on individual size of *Silene* plants (Table B.A.1a) using two separate sets of linear mixed models (LMMs; see below for details). Third, to test if higher abundance of species inside disturbed cushions has a negative effect on reproduction across all elevations (Hypothesis 2), we examined the effects of disturbance, elevation, and several community indices (Table B.A.1b) on *Silene* reproduction indicators (fruit density, relative reproduction) by fitting another set of LMMs. We fit a separate model set using either inside or neighboring community measures, in order to understand effect differences from species growing within cushions compared to those growing adjacent. Lastly, we tested the effects of disturbance, level, SOM, and SWC on *Silene* cushion size and reproduction indicators, to understand how disturbance-mediated changes in habitat are important.

In each set of LMMs, we fit a series of alternative models for each dependent variable with differing combinations of main effects (Table B.B.1), with all models including a random intercept and a random site effect. We included the explanatory

variable of elevational level in all model sets, as this metric had much higher overall predictive power than absolute elevation, elevation above lowest local *Silene* occurrence, average June temperature, or average July temperature. As demonstrated by our microhabitat temperature data, elevational level is a fairly good predictor of average June temperature (conditional $r^2 = 0.50$, $p\text{-values}_{\text{levels}} < 0.05$). We identified the most parsimonious model in each model set using AICc. To identify meaningful explanatory variables within model sets with multiple models within 2 AICc, we computed AICc weighted average ratios of t values (Cade 2015). We performed all analyses with the R (Version 3.4.1) programming language (R Core Team 2017). We fit LMMs in the ‘lme4’ package (Bates et al. 2015), and calculated additional outputs using the AICcmodavg (Mazerolle 2016) and MuMIn (Bartón 2016) packages.

We calculated two reproduction indices, fruit density and relative reproductive success. Due to differences in sampling times and phenology, some plants were in flower and others in fruit when sampled. We therefore converted flower to fruit number for plants of each sex using relationships from 628 individual *Silene* plants from Colorado, USA (*unpublished data*, D.F. Doak, W.F. Morris, and M.L. Peterson; no comparable local data were available). These data show strong and significant correlations between flower number and seed-bearing fruits within the same growing season (females: $p\text{-value} < 0.001$, $r^2 = 0.79$; hermaphrodites: $p\text{-value} < 0.001$, $r^2 = 0.70$; Fig. B.A.1a).

We used fruit density (number of fruits/cushion size) as a broad measure of reproductive output. We also quantified relative reproductive output through several steps to arrive at a size- and sex-independent measure of relative reproduction. We first regressed fruit number on cushion area for each sex, and then as an index of relative reproductive success divided each plant's residual by the predicted value for its sex and size. Values greater than one indicate high reproductive rate while those below one show less than expected production. We also tested whether fruit production correlates with other aspects of individual performance by regressing relative reproductive rate on relative growth rate for the Colorado data set, and found that the two values are weakly correlated ($r^2 = 0.14$; Fig. B.A.1b). Neither relative growth nor relative fruit production are significantly dependent on cushion size (Fig. B.A.1c, d).

3.3.5. Statistical analyses: community effects

We quantified communities in several ways. First, we used direct data on the non-*Silene* plants in each cushion or control area to determine absolute species richness, Shannon diversity ('vegan' package; Oksanen et al. 2017), percent cover of non-*Silene* plants, and community competitiveness. We derived species competitive values from species indicator values assigned to each species in Switzerland (Landolt et al. 2010). Each species has a value indicating its position on Grime's Triangle, such that most competitive species are coded as 'ccc', most ruderal as 'rrr', and most stress-tolerant as 'sss', with any combination of three letters possible. We

assigned each species a competitive value from 0 to 3 according to how many 'c's its three-letter code contained. For each sampling unit (i.e. individual cushion, control, or their respective neighboring rings), we calculated the species average competitive value.

To test if facilitation by disturbed cushion plants is stronger and more important in maintaining species diversity at higher sites (Hypothesis 3), we examined the effects of disturbance, elevation, and *Silene* presence on community characteristics with a set of LMMs separately for species richness, Shannon Diversity, and percent vegetation cover (Table B.A.2). These models include different combinations of elevation, disturbance, *Silene* presence, and sample size area, with sample size never tested without added effect of cushion presence (Table B.B.2). To improve model stability, we centered and scaled sampling area. Model details are as described above, with a nested random effect of site and cushion-control pair. To examine how community competitiveness is influenced by disturbance, elevation, and cushion presence, we fit LMMs with these all combinations of these three parameters separately on inside and neighboring average community competitive index (Table B.B.3). Model details are as described above, with a nested random effect of site.

In order to understand how soil parameters influence species richness, diversity, and percent cover, we removed cushion presence and included SOM and SWC in our inside species LMMs (Table B.A.2, B.B.2). To improve model stability, we centered and scaled SOM and SWC. We did not include these soil parameters in

our first model set, as this dataset has a smaller sample size. To then understand how cushion presence, disturbance, and elevation influence SOM and SWC, we tested these effects with LMMs (Table B.A.3, B.B.4). Since soil samples were taken underneath cushions and their respective controls, and not separately for neighboring environments, we could only test for effects on inside species. Model details are as described above, with a nested random effect of site and cushion-control pair.

3.3.6. Statistical analyses: species interactions

In order to account for the species differences observed between each focal plant and its associated control area, we calculated two separate indices. The Bray-Curtis dissimilarity index is a measure of compositional dissimilarity between two sites (Bray & Curtis 1957), which we calculated using the ‘vegan’ package (Oksanen et al. 2017). We calculated separate dissimilarities between a focal plant and its control (i.e. inside species), and between the 5 cm neighboring ring around a focal plant and the replicated ring around its control (i.e. neighboring species). The Relative Interaction Index (RII; Armas et al. 2004) is a measure of interaction intensity between plants, with positive values indicating facilitation and negative values competition. We calculated a RII between the cushion vs. control inside species and the cushion vs. control neighboring species as follows: $RII = (N_{\text{cushion}} - N_{\text{control}}) / (N_{\text{cushion}} + N_{\text{control}})$, where N is species richness (RII_s), species diversity (RII_{shan}), or total percent cover (RII_{cov}).

Following many alpine facilitation studies and as part of our test of Hypothesis 3, we tested for effects on RII and Bray-Curtis dissimilarity values with LMMs. These models include disturbance and elevation as fixed effects, and site as a random effect (Table B.A.4, B.B.5). All models were structured as described in the previous section, and we tested the effects on inside and neighboring species separately.

3.4. RESULTS

3.4.1. Cushion plants

We predicted that disturbance will benefit cushion plant growth at low elevations and have a net negative effect at high elevations (Hypothesis 1a), and have a negative effect on population density at all elevations (Hypothesis 1b). We found that disturbed and undisturbed *Silene* individuals have significantly different sizes (Fig. 3.3a) as well as different size distributions (Fig. B.A.2), with disturbed areas having much larger maximum plant sizes and undisturbed areas having more small individuals. While these results suggest benefits for plant growth from disturbance, our models indicate a possible role of disturbance in decreasing population density. Although the most parsimonious model for *Silene* population density indicates that density is highest in the middle of *Silene*'s elevational range and does not include a disturbance effect (Table 3.1a, Fig. 3.3b), the full model set indicates a moderate negative effect of disturbance on population density (AICc weighted average ratio of t value = 0.78). *Silene* mean cushion sizes are increased by

disturbance (Table 3.1a; Fig. 3.3c), implying older age of plants, faster growth rates, or both. This relatively weak effect is largest in the middle of the species' elevational range (level 3), with a significant disturbance by elevation interaction supported by model selection (Fig. 3.3d). Compared to undisturbed cushions, disturbed cushions were on average 128% larger at middle elevations (level 3) but only 30% larger at range edges (levels 1, 2 and 4).

Table 3.1. Results of most parsimonious models testing the effects of A) disturbance and elevational level on cushion size and population density and B) disturbance, level, and species community indices on reproduction indicators. Response variables subscripts indicate if tested community indices correspond to inside or neighboring species. Light green colors differentiate response variables tested using the same dataset, black differentiates different datasets. Interactions (Int(s)) are listed without the corresponding estimates. Elevational level and disturbance are factor variables, with 4 and 2 levels, respectively. Level coefficient values are hence summarized as follows: (+) positive trend, (-) negative trend, or unimodal with a maximum (+) or minimum (-) at levels 2 or 3. All models with Δ AICc values of less than 2 are shown for each response variable with marginal (marg) r^2 and conditional (cond) r^2 listed, and significant p-values ($< 0.001^{***}$, $< 0.01^{**}$, $< 0.05^{*}$) shown above the first listed model within each section. P-values for level indicate that at least one level was significant at < 0.05 . The full list of models tested and their AICc weights are shown in Table B.B.1.

(A)												
Response variable	Intercept	Disturbance	Level	Int(s)	marg r^2	cond r^2	Δ AICc					
Silene size	62.48	37.44	Unimodal (-)	*	Dist \times level	0.05	0.06	0.00				
Population density	2.45		Unimodal (+)			0.16	0.16	0.00				
Population density	3.66	-1.98	Unimodal (+)			0.19	0.19	0.64				
Population density	4.86	-3.58	Unimodal (+)		Dist \times level	0.35	0.44	0.79				
(B)												
Response variable	Intercept	Disturbance	Level	Richness	Diversity	% Veg cover	Competition	Int(s)	marg r^2	cond r^2	Δ AICc	
Fruits per area _{inside}	0.13								0.00	<0.01	0.00	
Fruits per area _{inside}	0.46						-0.28		0.01	0.01	0.68	
Relative reproduction _{inside}	-0.20		Unimodal (-)				0.26	Level \times comp	0.12	0.19	0.00	
Relative reproduction _{inside}	-4.13	1.11	+				3.21	Level \times comp	0.17	0.31	1.49	
Fruits per area _{neighboring}	2.32	-2.23									0.00	
Relative reproduction _{neighboring}	1.31		Unimodal (-)				-0.94	Level \times comp	0.25	0.42	0.00	

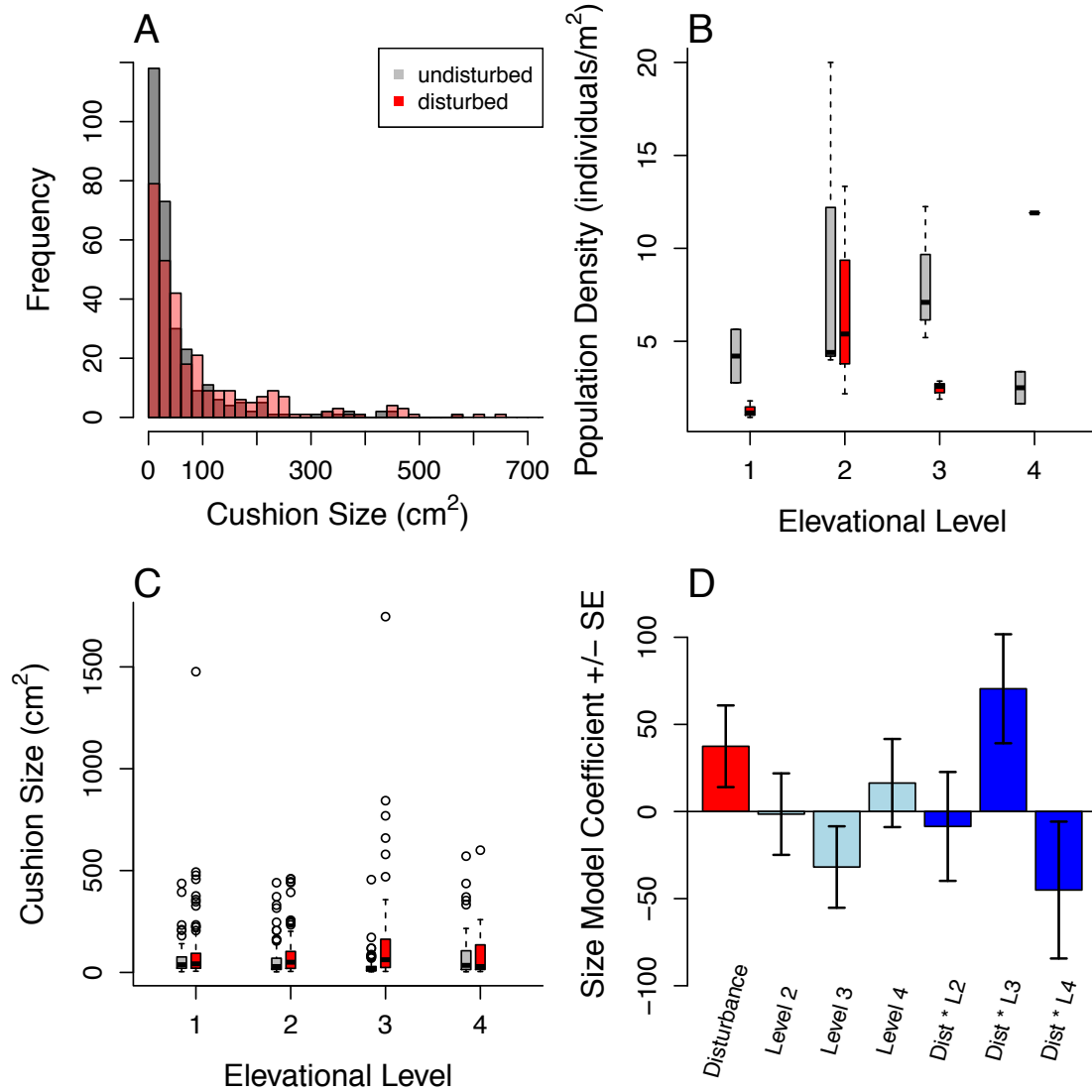


Figure 3.3: Disturbance effects on *Silene acaulis*. (A) Disturbed sites have smaller numbers of small *Silene acaulis* individuals, and increased numbers of larger individuals (12 largest sizes removed to improve figure clarity). Population density (B) is highest at the center of the species range (levels 2 and 3), with no effect of disturbance in the most parsimonious model but a moderate negative disturbance effect over the full model set (colors as in (A)). Disturbance increases *Silene acaulis* mean cushion sizes (C, colors as in (A)). The best supported model for cushion size (D) includes a positive disturbance effect, a negative unimodal elevation effect, and a significant disturbance by elevation effect. This suggests that although disturbance benefits cushion growth at middle elevations (level 3), it greatly inhibits it at the upper elevational range limit (level 4). Contrasting colors merely differentiate parameters.

We further predicted that higher abundance of species inside disturbed cushions will have negative effects on reproduction at all elevations (Hypothesis 2). We found that *Silene* reproduction is best explained by models with neighboring, but not inside, community indices (Table 3.1b). Both disturbance and neighboring species diversity significantly reduce fruit density (although not neighboring species abundance, as measured by percent cover), with a significant disturbance by diversity interaction effect (Fig. 3.4). Contrary to our expectations, fruit density is not influenced by any inside species measures, and neither inside nor neighboring species measures have a significant effect on relative reproduction.

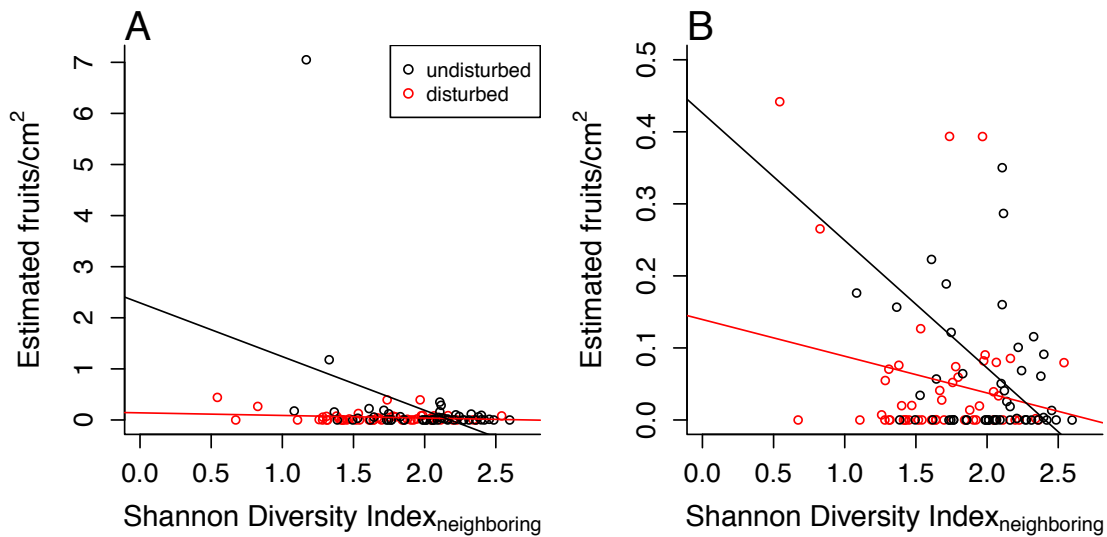


Figure 3.4: Disturbance effects on *Silene acaulis* reproduction. Fruit density is negatively affected by both neighboring species diversity and disturbance, with a significant disturbance by diversity interaction that implies the negative effect of disturbance overrides those of diversity. Linear regression lines based on only the fixed effect of Shannon Diversity Index and shown separately for disturbed and undisturbed cushions, where undisturbed cushions are significantly negatively affected by diversity (A) without and (B) with two outliers removed (colors as in (A)) (respective p-values = 0.007, 0.018). Note the different y-axes scales. Points jittered for clarity.

In model sets testing the effects of SOM and SWC, which replaced species community parameters, we found that higher values in both soil parameters relate to decreased *Silene* reproductive measures. SWC decreases fruit density and SOM moderately decreases relative reproduction, with a negative effect of disturbance on fruit density (Table B.A.5a). In these models, fruit density is highest at both upper and lower elevational range edges, and relative reproduction decreases with elevation. The best model for cushion size has no significant explanatory variables.

3.4.2. Community effects: inside species

We predicted that facilitation by cushion plants will be stronger and more important in maintaining species diversity in disturbed areas, an effect amplified at higher elevations (Hypothesis 3). However, we did not find an amplified facilitative effect on inside species by *Silene* cushions in disturbed areas, or support for any other interaction between cushion presence and disturbance (Table 3.2). In contrast to findings of some previous studies, cushion presence has a significant negative effect on species richness (Fig. 3.5a, c), and a moderate negative effect on both Shannon diversity (Fig. 3.5b, d) and percent vegetation cover (Fig. B.A.3a, c).

TABLE 3.2. Results of most parsimonious models testing the effects of disturbance, elevational level, *Silene acaulis* cushion presence, and sampling area on species community indices. Light green colors differentiate response variables tested using the same dataset, black differentiates different datasets. Interactions (Int(s)) are listed without the corresponding estimates. Elevational level and disturbance are factor variables, with 4 and 2 levels, respectively. Level coefficient values are hence summarized as follows: (+) positive trend, (-) negative trend, or unimodal with a maximum (+) or minimum (-) at levels 2 or 3. All models with Δ AICc values of less than 2 are shown for each response variable with marginal (marg) r^2 and conditional (cond) r^2 listed, and significant p-values ($< 0.001^{***}$, $< 0.01^{**}$, $< 0.05^{*}$) shown above the first listed model within each section. P-values for level indicate that at least one level was significant at < 0.05 . The full list of models tested and their AICc weights are shown in Table B.B.2.

Response variable	Intercept	Disturbance	Level	Cushion	Area	Int(s)	marg r^2	cond r^2	Δ AICc
			*	***					
Species richness _{inside}	8.64	-0.67	Unimodal (+)	-1.60	2.44	Dist \times level	0.44	0.72	0.00
		**	*		***	*			
Shannon diversity _{inside}	1.69	-0.31	Unimodal (+)	-0.05	0.46	Dist \times area	0.24	0.57	0.00
Shannon diversity _{inside}	1.64	-0.27	Unimodal (+)	-0.05	0.21		0.21	0.57	1.16
Shannon diversity _{inside}	1.54	-0.27		-0.05	0.48	Dist \times area	0.16	0.56	1.50
			*	***					
% Vegetation cover _{inside}	62.32	0.78	Unimodal (+)	-37.42	3.09	Dist \times level \times area	0.53	0.59	0.00
			*						
Species richness _{neighboring}	12.03	-0.71	Unimodal (+)	-0.42	-0.01	Dist \times level \times area	0.37	0.75	0.00
Shannon diversity _{neighboring}	2.08	-0.27	—				0.21	0.58	0.00
% Vegetation cover _{neighboring}	64.85	1.89	Unimodal (+)	-1.08	-15.99	Dist \times level \times area	0.41	0.79	0.00

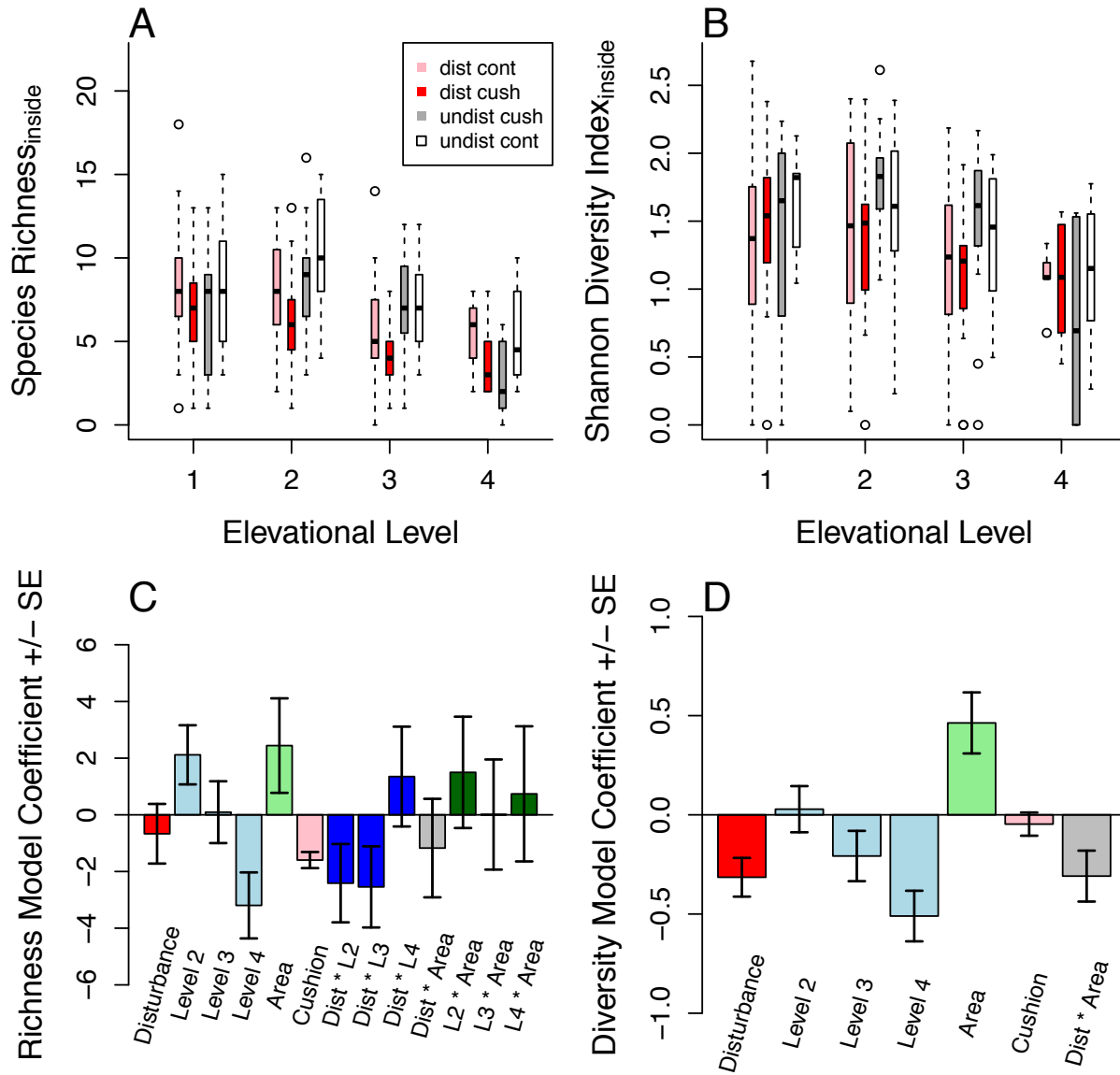


Figure 3.5: Inside species community. Disturbance reduces inside species richness (A) and diversity (B), which both decrease with cushion presence (colors for B as in (A)). Legend abbreviations are as follows: dist = disturbed, undist = undisturbed, cush = cushion, cont = control. The best supported model for species richness (C) highlights the importance of interactions between disturbance and elevation, which synergistically interact to decrease richness at middle elevations (levels 2 and 3). The most parsimonious model for species diversity (D) suggests that the interaction between disturbance and cushion area cancel out the positive effect of area. Contrasting colors merely differentiate parameters.

As expected, we found that disturbance exerts an overall negative effect on both the species richness and diversity of inside species (Table 3.2). Although disturbance has an overall net positive effect on percent vegetation, visual interpretation of the three-way interaction with elevational level and area demonstrates that disturbance effects are weak at low and high elevations but strongly negative at middle elevations (Table B.B.6). All three community measures of inside species are highest at middle elevations and increase with sampling area. The interaction effect of area for all three community measures is likely due to larger cushion sizes (and therefore larger sampling areas) in disturbed areas, and varying cushion sizes across elevations.

We found that inside community competitiveness is significantly lower at higher elevations, with no effect of cushion presence and disturbance (Fig. B.A.4a, Table B.A.6). This pattern is most likely not driven by certain highly competitive individual species alone, but rather by the average competitive index values found at overall median species richness (Fig. B.A.5a).

After including the sampled soil parameters as predictor variables in our models, we found that higher values of SWC are related to higher inside species community richness and percent vegetation cover, but SWC has no effect on diversity (Table B.A.5b). Higher SOM values decrease species richness and percent vegetation cover, and SOM also has no effects on diversity. Both species richness and percent vegetation cover are increased with disturbance and are highest at middle elevations, with a 4-way interaction (SOM x SWC x disturbance x elevation)

present for both. These soil parameters, in turn, are negatively influenced by disturbance, both peak at middle elevations, and are positively affected by *Silene* presence (Table B.A.7).

3.4.3. Community effects: neighboring species

As for inside species, we did not find evidence that facilitation by *Silene* cushions on neighboring species increases with disturbance (Table 3.2). Surprisingly, *Silene* presence has a moderate negative effect on species richness (Fig. 3.6a) and percent vegetation cover (Fig. B.A.3b, d). As expected, we found an overall moderate negative effect of disturbance on both species richness and Shannon diversity, with the effects of disturbance on diversity most pronounced at middle elevations (Fig. 3.6b). As for inside communities, neighboring species richness peaks at middle elevations, and Shannon diversity decreases with elevation. Both neighboring species richness and percent vegetation cover decrease with sampling area. Disturbance has an overall positive effect on vegetation cover, but as seen through visual interpretation of the three-way interaction with elevational level and area, disturbance exerts weak effects at low and high elevations with strong negative effects at middle elevations (Table B.B.6).

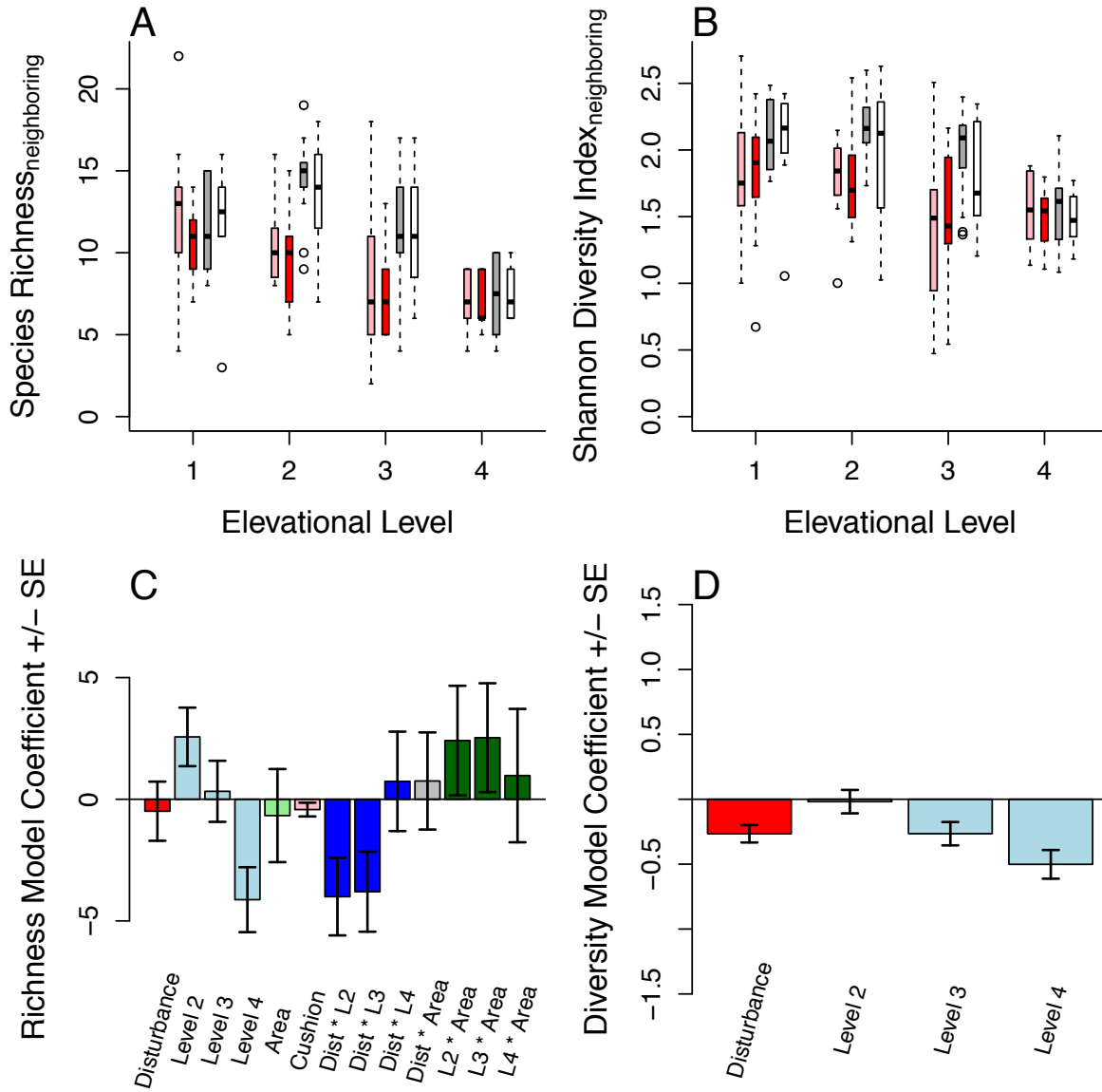


Figure 3.6: Neighboring species community. Disturbance reduces neighboring species richness (A) and diversity (B) (colors as in Fig. 5a), with an additional negative effect of cushion presence and area on richness. The best supported model for species richness (C) highlights the importance of interactions between disturbance and elevation, whose effects synergistically interact to decrease richness at middle elevations (levels 2 and 3; see also Table B6), an effect partly mitigated by the interaction between elevation and area. The most parsimonious model for species diversity (D) indicates a negative effect of disturbance and level, with no effect of cushion. Contrasting colors merely differentiate parameters.

We found that neighboring species community competitiveness is highest at middle elevations, with no influence by disturbance (Fig. B.A.4b). As with inside species, we suspect that this pattern is driven by sampling areas that exhibit median species richness (Fig. B.A.5b).

3.4.4. Species interactions

Contrary to our third hypothesis, we observed neither an increase in facilitation with disturbance nor an overall facilitative effect by *Silene* on neither inside nor neighboring species. Our data show more negative RII values than expected (Fig. B.A.6, B.A.7), indicating net competition within cushions and between cushions and neighboring species. We found no support of a disturbance effect on RII_{cov} , RII_{shan} , RII_{veg} , and the Bray-Curtis Dissimilarity Index nor along our sampled elevational gradient (Table 3.3).

TABLE 3.3. Results of most parsimonious models testing the effects of disturbance and elevational level on Relative Interaction Indices (RII) and Bray-Curtis Dissimilarity indices (calculated between cushions and corresponding controls). Inside: species inside cushions compared to species inside control; neighboring: cushion neighbors compared to control neighbors. Light green colors differentiate response variables tested using the same dataset, black differentiates different datasets. Interactions (Int(s)) are listed without the corresponding estimates. Elevational level and disturbance are factor variables, with 4 and 2 levels, respectively. Level coefficient values are hence summarized as follows: (+) positive trend, (-) negative trend, or unimodal with a maximum (+) or minimum (-) at levels 2 or 3. All models with $\Delta AICc$ values of less than 2 are shown for each response variable with marginal (marg) r^2 and conditional (cond) r^2 listed, and significant p-values ($< 0.001^{***}$, $< 0.01^{**}$, $< 0.05^*$) shown above the first listed model within each section. P-values for level indicate that at least one level was significant at < 0.05 . The full list of models tested is shown in Table B.B.5.

Response variable	Intercept	Disturbance	Level	Int(s)	marg r^2	cond r^2	Δ AICc
RII: Species richness _{inside}	-0.13				0.00	0.10	0.00
RII: Shannon diversity _{inside}	-0.04				0.00	0.17	0.00
RII: % Vegetation cover _{inside}	-0.42				0.00	0.02	0.00
Bray-Curtis dissimilarity _{inside}	0.75				0.00	0.03	0.00
RII: Species richness _{neighboring}	-0.01				0.00	<0.01	0.00
Shannon diversity _{neighboring}	0.03				0.00	0.00	0.00
RII: % Vegetation cover _{neighboring}	-0.01				0.00	0.10	0.00
Bray-Curtis dissimilarity _{neighboring}	0.53				0.00	0.03	0.00
Bray-Curtis dissimilarity _{neighboring}	0.48	0.09			0.07	0.11	1.13

3.5. DISCUSSION

3.5.1. Cushion plants

We studied systems adjacent to popular hiking trails where trampling is a frequent and relatively high intensity disturbance, similar in its severe erosion effects to high intensity grazing and landslides. Our data shows that disturbance spurs growth, but reduces population density and reproduction of *Silene* (Fig. 3.7). We suspect that disturbance, either through the mechanical manipulation of cushions or by altering soil conditions, increases adult plant size while greatly reducing the ability of smaller plants to survive. This corresponds to the size structure differences we see between disturbed and undisturbed areas, as well as to our findings that population density is lower with disturbance. In the short term, this suggests a positive effect of disturbance on *Silene* growth, however the long-term effect could be a decline in *Silene* populations as reproduction is decreased and young individuals are unable to survive the impacts of disturbance. The balance

between these effects with increased performance of large plants will determine the long-term net population effects of disturbance, which we cannot judge from our short-term data. One potential scenario is disturbed populations progressing to larger and larger size structures, with an eventual population decline as these older cushions die off without replacement by younger individuals.

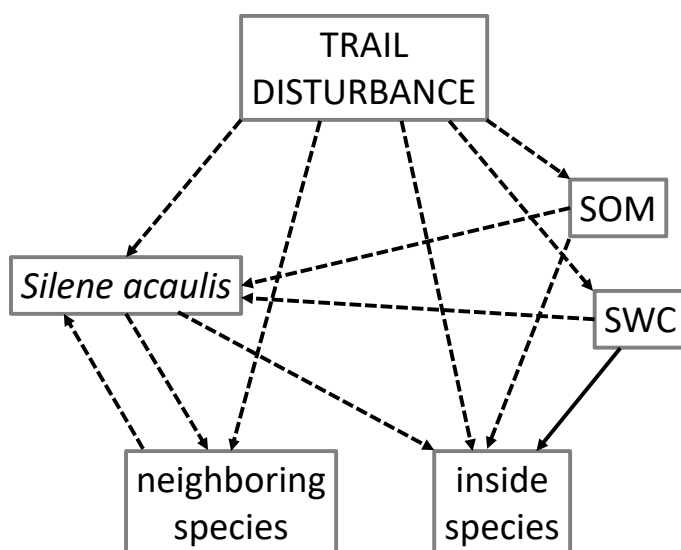


Figure 3.7: Conceptual diagram summarizing main findings. The net (i.e. majority of) effects of trail disturbance, *Silene acaulis* presence, Soil Organic Matter (SOM), Soil Water Content (SWC), and neighboring species are indicated (dashed = negative effect; solid = positive effect). Notes on diagram: only individual, not sequential, arrows for each relationship were tested and elevational effects not shown. Notes on parameters: inside species do not have an effect on *Silene*; the positive effects of disturbance on *Silene* size are not shown because reproduction, density, and small plant size are all negatively affected.

Although other studies have showed that disturbance can negatively affect nurse plant abundance, size, and density (e.g., Ballantyne & Pickering 2015a), we are not aware of other studies that have examined responses in cushion plant size

structure and reproduction to relatively high disturbance levels. However, past studies also point to changes in abundance and percent cover. Trampling disturbance can reduce the dominant vegetation cover and therefore increase cushion plant cover (Whinam & Chilcott 2003), as well as cause graminoid species to replace cushion plants growing at lower elevations. Direct trampling on cushions causes portions of *Silene* cushions to die off (Willard & Marr 1970), which we also observed (*personal observation*) for cushions growing in the center of the trail. Compared to other alpine tundra species, however, *Silene* cushions can be relatively resistant to trampling (Willard et al. 2007).

3.5.2. Community effects and species interactions

Overall, we found that species diversity and richness within and next to cushions is lower compared to control areas, indicating net competitive interactions between cushions and other plant species. Such negative or neutral interactions have been documented in other studies as well (e.g., de Bello et al. 2011, Dvorsky et al. 2013, Bowman & Holcomb 2017), but surprised us given that *Silene* has been shown to increase species percent cover and richness (Bonanomi et al. 2015). Although disturbance reduces both species richness and diversity, it has no effect on species interactions, as measured by RII. In undisturbed areas, species richness peaked at middle elevations instead of declining linearly with elevation (Fig. 3.7). We suspect this is due to high levels of biotic competition at low elevations (Table B.A.6) and high levels of abiotic stress at upper elevations, as well as an

intermediate disturbance effect by grazing at middle elevations. Compared to higher elevations, grazing is most intense at lower elevations and reaches intermediate disturbance levels at middle elevations on mountain slopes, likely increasing species richness in these areas. Furthermore, the unnatural elevational tree line in Switzerland, which has been anthropogenically established due to many centuries of land use and grazing, could cause species richness to be highest at middle elevations where the subalpine-alpine ecotone is reached.

The cushion plant *Silene* has been found to host an increasing number of species at higher elevations (Antonsson et al. 2009), while also demonstrating greatest facilitative effects on other species at the center of its elevational range (Bonanomi et al. 2015) as well as in abiotically stressful environments (Kjaer et al. 2017). We therefore expected cushion plants to first, host higher species diversity and richness compared to control areas, and second, maintain this higher diversity in areas where disturbance exerts negative effects. Our careful selection of control areas near to *Silene* cushions that had similar microhabitats is one likely reason that our findings differ from other plant facilitation studies, where control areas are randomly selected near to cushions (e.g., Butterfield et al. 2013). Since cushion plants, including *Silene*, as well as other alpine species, tend to disproportionately occur in favorable microhabitats, we believe that our approach in selecting control areas allows better differentiation of the effects of cushions on other species. This is especially true for alpine environments, which are known to be highly variable in topography, with slight variations in slope and aspect playing a large role in

determining species community (Körner 2003). Completely random choice of control sites can therefore include very different and often less favorable microclimates than those occupied by cushion plants, whereas choosing control areas that match microtopography is likely a more accurate representation of what a species community would look like in the absence of cushion plants. Careful attention to the spatial representation of the microhabitat environment is especially important in ecosystems with cushion plants, as the beneficial microhabitat provided by cushion plants may buffer the effects of climate change (Anthelme et al. 2014).

Since richness and diversity inside cushions increase with cushion size, we suspect that the positive effects of cushions are only seen once cushions reach a certain size. Comparison of our data with data gathered for another facilitation study (Butterfield et al. 2013) at one of our sites (Val Bercla at Fallerfurrga) shows that our control areas had significantly higher species richness (Fig. B.A.8a), however our data represents the lower end of cushion size distribution (Fig. B.A.8b). As found in many other studies, we would expect a positive correlation between nurse plant size and species richness and diversity (e.g., Tewksbury & Lloyd 2001, Molenda et al. 2012, Incerti et al. 2013, Yang et al. 2017). Smaller nurse plants understandably cannot provide the same microhabitat shelter that larger ones do, and likely act as competitors to other species in the area as they establish. Furthermore, larger plants have had longer time periods in which to accumulate inside species, and their larger surface area increases the chance of establishment by other species. We therefore expected the larger cushions in disturbed

environments to have increased richness and diversity, but our results suggest that the overall negative impacts of disturbance on species richness and diversity prevail. In fact, closer examination of richness and diversity as a function of total cushion size shows that disturbed cushions and control areas have a much lower accumulation of species richness and diversity than undisturbed ones (Fig. B.A.9). Although our model results point to a negative influence of cushion presence on species richness and diversity, disturbance appears to be a stronger driver of these species measures. Disturbance has been found to mediate plant traits that influence facilitative interactions in other systems (Catorci et al. 2016), however studies examining the impacts of both disturbance and plant traits on facilitative interactions are, to our knowledge, rare. Such relatively high intensity disturbances can ultimately prevent plant species from recovering, as shown in a comparable system in the Alaskan arctic tundra (Monz 2002).

Other studies have shown that facilitative interactions break down at high levels of abiotic stress (for review see Michalet 2006, Liancourt et al. 2017), implying that positive interactions only increase up to a certain threshold. Considering that trails are sources of frequent disturbances, the lack of facilitative effects in these areas is perhaps not surprising. This is especially true at the species' upper elevational range limit, where there is increased abiotic stress due to the colder climate. However, we expected to find some indication of facilitation in our off-trail plots, but competitive interactions dominate here as well. While surprising to us, these results are in agreement with multiple studies that have

found lower species richness in cushion plants compared to control areas (e.g., de Bello et al. 2011, Dvorsky et al. 2013), although they contrast with some other alpine facilitation studies (e.g., Callaway et al. 2002, Butterfield et al. 2013).

Our absolute community measures show a negative response to disturbance, but we surprisingly did not detect any significant changes in RII between disturbance types nor along our sampled elevation gradient. Many facilitation studies argue for the use of RII to detect differences in species interactions (e.g., Butterfield et al. 2013, Schöb et al 2014), however this method does not allow small differences between cushions and control areas to be picked up. Many published facilitation studies observed a much larger difference between cushions and control areas than we did, and therefore the use of RII is reasonable. Using RII to determine if a system is characterized by competitive or facilitative interactions assumes that the relationship between cushion and neighboring communities is proportional, but this relationship undoubtedly changes across climatic regions and ecosystems. The analysis of absolute community measures could therefore present a clearer picture, especially with small differences between cushions and control areas.

Species composition changes have been observed in other disturbed systems (e.g., Monz 2002, Suding & Goldberg 2001), and a negative impact of trail disturbance on soils has been found to reduce species richness and abundance (Lucas-Borja et al. 2011, Ballantyne & Pickering 2015a, b). It is well documented that soil conditions can influence facilitative and competitive species interactions,

and therefore be drivers of species community composition (e.g., Gross et al. 2009). This holds in our system as well, with SWC increasing species richness and percent vegetation cover. SOM and SWC in turn are both negatively affected by disturbance, and positively affected by the presence of *Silene*. However, the presence of *Silene* cushions does not mitigate this disturbance effect, as seen by decreased species richness and diversity in cushions. These negative impacts of disturbance on the soil environment provide a possible mechanistic explanation of why disturbance reduces species richness and diversity in both cushions and control areas.

Disturbance likely favors plant morphologies that increase resistance to disturbance (e.g., cushion plants with a taproot) and functional groups that can quickly recover after disturbance (e.g., ruderal species). The Swiss Alps have experienced centuries of intermediate disturbance by livestock grazing, resulting in productive and species rich meadows above tree line. In fact, reduction in grazing has reduced species richness at these elevations (Dullinger et al. 2003). Within these intermediately disturbed areas, we examined areas specifically characterized by relatively high intensity disturbance (i.e. hiker trails). We use the terms ‘undisturbed’ and ‘disturbed’ for ease in differentiation of our sampling areas. However, even our ‘undisturbed’ areas experience intermediate levels of disturbance via grazing, while the disturbed areas experience both intermediate grazing and frequent intensity hiker trampling disturbance. Such higher levels of disturbance very likely push these areas above optimal levels of disturbance, and into levels of

high abiotic stress. Considering that absolute percent vegetation cover in these disturbed areas was still quite high (mean = 48%) compared to undisturbed areas (mean = 58%), it is clear that although our disturbed sites experience a high frequency of human trampling, they are not disturbed enough that they could support only minimal plant life.

With global climate change, species ranges, and therefore biotic interactions, are shifting along latitudinal and elevational gradients. We show that species communities are susceptible to the effects of relatively high intensity trampling disturbance, which has negative effects on cushion plants at the population level. In combination with the projected upward expansion of more competitive lower elevation species, this could ultimately lead to sites with high disturbance intensity experiencing rapidly diminishing cushion plant populations at the lower elevational limit. The negative effects of sustained high intensity disturbance at upper elevational range limits could ultimately reduce the persistence of upper elevational populations.

3.6. ACKNOWLEDGMENTS

We thank the Zeno Karl Schindler Foundation (Geneva, Switzerland) for a year-long doctoral exchange grant to NIC, without which this work would not have been possible. We also thank the Botanical Society of Switzerland for financial support of our fieldwork, and the University Libraries Open Access Fund (University of Colorado, Boulder) for financing the publishing fees. Members of the

Doak Lab provided insightful comments and suggestions, and an anonymous reviewer greatly helped us present our work more clearly to improve this manuscript.

3.7. DATA ACCESSIBILITY

Our data and R code are freely available at the following Open Science Framework (OSF) site: <https://osf.io/6pk3m/>. This data is part of the OSF project “Anthropogenic disturbances in alpine ecosystems” (doi:10.17605/OSF.IO/GKJV2).

3.8. AUTHOR CONTRIBUTIONS

NIC, SW, CR, and DFD designed this study. NIC and AB collected all data, and AB processed all soil samples. NIC conducted all analyses with substantial theoretical and practical suggestions by DFD, SW, and CR. NIC wrote the article with input and revisions by DFD, CR, SW, and AB. All authors approved the final version. This article, which has been formatted to fit this dissertation, is made available under a Creative Commons Attribution license (CC BY; <https://creativecommons.org/licenses/by/3.0/>) from: 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*. 8:7921-7935. doi: 10.1002/ece3.4276

CHAPTER 4

Subpopulation species distribution models outperform global model for an arctic-alpine plant

Chardon NI, Pironon S, Peterson ML, Doak DF

4.1. ABSTRACT

A common approach to predicting how species distributions will shift with climate change is to construct species distribution models (SDMs). These models use a species' climatic niche to determine currently suitable areas for the species and forecast how these areas will be distributed under future climate scenarios. A core, rarely tested, assumption of SDMs is that all populations will respond equivalently to climatic drivers. Few studies have examined this assumption, and those that have rarely dissect the reasons for intraspecific differences. Focusing on the arctic-alpine cushion plant *Silene acaulis*, we compared predictive accuracy from SDMs constructed using the species' full global distribution with separate SDMs constructed using subpopulations defined either by genetic or habitat differences. As SDM habitat suitability has been assumed to correlate with other aspects of performance or ecological function, we also tested if suitability can predict individual performance (i.e. plant size) and biotic interactions (i.e. facilitative interaction strength) using a global trait dataset. We found that SDMs constructed

separately using subpopulations are more accurate than a global SDM, and that the genetic model substantially differs from and outperforms the habitat model. While SDMs have been used to infer population performance and possibly even biotic interactions, in our system these relationships were extremely weak. Our results indicate that individual subpopulations might respond differently to climate, although we also explore several alternative explanations for the superior performance of the genetic model. We emphasize the need to carefully examine how to best define SDM subpopulations for a species of interest, especially if occurrences have sampling bias, as under-sampled regions may be better accounted for in subpopulation SDMs. We emphasize that genetic, environmental, or sampling variation within species ranges may critically affect SDM predictions of habitat suitability, which in turn could have little correspondence with population performance and biotic interactions.

Keywords: climate change, distribution modeling, local adaptation, MaxEnt, SDM, *Silene acaulis*

4.2. INTRODUCTION

Discerning how and where populations will respond to climate change is now a central topic in ecological research, with great interest in applying this knowledge to inform conservation and management decisions in order to mitigate species extinction risks. A common approach is to determine how suitable habitat for a

given species will shift in space with climatic changes using correlative Species Distribution Models (SDMs; Pacifi et al. 2015). Such SDMs (also known as ‘ecological niche models’ or ‘habitat suitability models’) correlate species occurrences to current climate in order to predict suitable habitat areas in space and time (reviewed in Wiens et al. 2009). Assuming that species track the modeled suitable habitat, this method allows ecologists to draw conclusions on how species’ distributions will shift into the future (e.g., Elith et al. 2011, Hughes et al. 2012). Given the accessibility of global species occurrence records (e.g., *data online at* GBIF.org), high resolution climate data (e.g., WorldClim, CHELSA; Fick & Hijmans 2017, Karger et al. 2017), and user-friendly software (e.g., MaxEnt; Phillips et al. 2006), SDMs are now widely utilized for a variety of applications (Merow et al. 2013, Pacifi et al. 2015).

Despite their ubiquitous use, however, there has been increasing criticism of SDMs regarding their over-simplification of the factors that limit species distributions (e.g., Araújo & Peterson 2012, Early & Sax 2014). Recent improvements address some of these concerns, incorporating factors such as dispersal limitations and biotic interactions into habitat suitability modeling (e.g., Guisan & Rahbek 2011, Mod et al. 2015). However, SDMs that use predominately climatic factors to describe a species’ distribution still make the key assumptions that the species is in equilibrium with its climatic niche (Veloz et al. 2012), climate is indeed the main distribution driver (Araújo & Peterson 2012), and all populations respond identically to climate, such that the climate niche for the species is also

that for individual populations (Wiens et al. 2009). Even given the long history of work that shows strong evidence for local adaptation to climate conditions in many plants and animals (e.g., Mayr 1956, Aitken et al. 2008, Pelini et al. 2009, Fournier-Level et al. 2011, Ruegg et al. 2018), it is poorly understood how differences in local population responses to climate can affect SDM results (but see Hällfors et al. 2016, Schwalm et al. 2016, Theodoridis et al. 2018). As the predictions of SDMs are widely and increasingly used to inform conservation and land management decisions, it is therefore imperative to carefully evaluate this assumption.

A standard approach in constructing climate-based SDMs is to use all available data on a species' occurrences to predict the full geographic extent of its suitable habitat, implicitly assuming that all populations across a species' range share the same climatic responses (Araújo & Peterson 2012, Merow et al. 2013). To account for differences in climate responses, the simplest approach has been to separately model smaller units (henceforth, 'subpopulations') of a species range (Table 4.1) generally grouped according to genetic differences, differing climate histories, or geographic region. Combining these subpopulation SDMs yields a suitability prediction (i.e. probability of occurrence) over the same geographical extent as a global population SDM, while predicting suitability for subpopulations according to their corresponding climate. Differences in predictions between these types of SDMs and the corresponding global SDM have generally been interpreted as indicating local adaptation to climate (Table 4.1) or more broadly, differences in climate responses, be they adaptive or not. However, even in the absence of any

genetically-based niche divergence, subpopulation SDMs could produce different predictions simply due to over-fitting, better representation of under-sampled climates, or differences in the environmental distributions (including biotic interactions) among the defined subpopulations leading to different inferred climate responses. Regardless of the mechanisms involved, the extent and importance of differences in SDM results have only rarely been tested by comparing subpopulation and global SDMs. Furthermore, few studies have examined possible explanations for differences between global vs. subpopulation models (Table 4.1), limiting our understanding of how important this complication is for climate response predictions.

Table 4.1. For sixteen studies that have used subpopulation SDMs, we summarize i) how subpopulations were identified, ii) if or how SDMs were compared, and iii) how the results were interpreted. Columns describe (from left to right): **Subpopulations** = how occurrences were divided into intraspecific groups; **Entire range represented** = all species occurrences represented in subpopulation SDMs; **Evidence** = evidence that motivated the use of these subpopulations and/or how subpopulation SDMs were validated; **Global** = includes a global SDM using all occurrences; **Mult. subpop.** = includes multiple subpopulation SDMs, based on alternative groupings of occurrences; **Results** = results of comparisons between global and subpopulation SDMs; **LA** = higher performance of subpopulation SDM primarily interpreted in the context of genetically-based local adaptation to climate; **Alternative explanations** = what, if any, alternative explanations discussed for interpreting subpopulation SDMs. Note that we focus on studies using traditional SDM approaches calibrated with occurrence data and do not include related approaches that incorporate intraspecific structure through modeling ecosystem types or data from transplant experiments (e.g., Benito-Garzón et al. 2011; Gray et al. 2011; Hamann and Aitken 2013).

	IDENTIFYING SUBPOPULATIONS			SDM COMPARISON			INTERPRETATION	
Reference	Subpopulations	Entire range represented	Evidence	Global	Mult. subpop.	Results	LA	Alternative explanations
Cacciapaglia & van Woesik (2018)	5 regions of a coral (<i>Porites lobata</i>); 4 defined by genetic isolation & 1 by a biogeographic barrier	Yes	Validated with calibration data	X		Global model has greater AUC	X	
D'Amen et al. (2013)	2-7 genetic lineages within each of 9 species of African mammal	No; 3 lineages with limited distributions excluded	Validated with calibration data	X		Global models tend to have lower AUC	X	Sampling bias
Hällfors et al. (2016)	2 climatically-distinct regions of a butterfly (<i>Lycaeides melissa</i>) & 2 subspecies of an herb (<i>Primula nutans</i>).	Yes	Validated with calibration data	X		Global models have lower AUC	X	Sampling bias, climate interactions, overfitting
Homburg et al. (2014)	2 disjunct evolutionarily significant units of an insect (<i>Carabus irregularis</i>)	Yes	Validated with calibration data	X		Global model has lower AUC & specificity, but higher sensitivity	X	Habitat availability
Hu et al. (2017)	5 seed zones of a tree (<i>Platycladus orientalis</i>) shown to be locally adapted	Yes	Validated with calibration data, niche divergence, transplant experiments				X	
Ikeda et al. (2017)	3 genetic lineages of a tree (<i>Populus fremontii</i>)	No; limited to USA & occurrences with >10% genetic group admixture excluded	Validated with calibration data, niche divergence, transplant experiments	X		Global model has lower predictive accuracy as measured with binomial probability test	X	Habitat availability
Lecocq et al. (2016)	5 subspecies of an insect (<i>Bombus impatiens</i>)	No; 3 subspecies with limited distributions & occurrences in areas of subspecies overlap were excluded	Validated with calibration data, temperature tolerance experiments	X		Global model has lower AUC, sensitivity, specificity, & TSS	X	
Marcet et al. (2016)	3 chloroplast haplotypes, 4 nuclear genetic groups, or 2 vernalization phenotypes	No; limited to the Iberian Peninsula	Validated with calibration data, transplant experiments	X	X	Global model tends to have lower AUC	X	Neutral genetic divergence
Meynard et al. (2017)	2 subspecies of an insect	Yes	Validated with calibration data					Niche conservatism

	(<i>Schistocerca gregaria</i>)							
Oney et al. (2013)	3 subspecies of a tree (<i>Pinus contorta</i>)	No; occurrences in areas of subspecies overlap were excluded	Validated with calibration data, transplant experiments	X		Global model has lower AUC	X	
Pearman et al. (2010)	2-4 subspecies of several birds and reptiles	Yes	Validated with calibration data	X		Global models tend to have lower AUC	X	Sampling bias, habitat availability
Schwalm et al. (2016)	8 national parks with American Pika (<i>Ochotona princeps</i>)	No; occurrences outside chosen parks were excluded	Validated with calibration data					Climate interactions, habitat connectivity
Serra-Varela et al. (2017)	7 & 8 genetic groups for <i>Pinus pinaster</i> and <i>Pinus halepensis</i>	No; portions of each range with low sampling and occurrences not assigned to a genetic group were excluded	Validated with calibration data				X	
Sork et al. (2010)	4 regions of a tree (<i>Quercus lobata</i>)	No; limited to 4 circles of 150 km diameter	Genetic isolation at this scale, correlation of genotypes and climate				X	
Theodoridis et al. (2018)	4 genetic groups of an herb (<i>Primula farinosa</i>)	Yes	Validated with calibration data, niche divergence				X	Neutral genetic divergence
Ureta et al. (2012)	47 cultivars of maize, 4 cultivars of <i>Teocinte</i> , and 11 cultivars of <i>Tripsacum</i>	No; limited to Mexico & cultivars with >9 occurrences	Validated with calibration data				X	

We examine how subpopulation and global SDMs differ for a circumboreal alpine-arctic plant, using broad genetic and habitat (i.e. biome) differences to construct subpopulation SDMs. Previous studies have used broad patterns of genetic differentiation, such as subspecies, phylogeographic lineages, or haplotypes, to distinguish SDM subpopulations (e.g., Pearman et al. 2010, D'Amen et al. 2013, Serra-Varela et al. 2017). Yet whether such neutral genetic differentiation captures functional differences in climate responses relevant to species distributions remains an active debate (Holderegger et al. 2006, Gotelli and Stanton-Geddes 2015,

Theodoridis et al. 2018). Alternatively, other studies have grouped occurrence data into climatically distinct regions or habitat types as a proxy for local adaptation (e.g., Sork et al. 2010, Hällfors et al. 2016, Hu et al. 2017). Despite the potential for these two approaches to yield differing predictions of subpopulation climate responses, and thus the species' distribution as a whole, no study has compared both genetic and habitat-based approaches to constructing subpopulation SDMs (but see Marcer et al. 2016 for comparison of genetic and trait-based models).

We also go further than most SDM validation approaches that focus on distributions, by using probability of occurrence as a proxy for other aspects of population performance and ecological function. While SDMs only formally predict probability of occurrence (henceforth, 'suitability'), their outputs have been assumed to correlate to population performance, such as population persistence (Araújo & Williams 2000) and functional traits (Thuiller et al. 2009). However, predicting species performance with suitability is currently controversial and recent studies have argued to what extent suitability can accurately predict population performance parameters. While some researchers have demonstrated strong links between suitability and abundance (VanDerWal et al. 2009, Van Couwenberghe et al. 2013, Lee-Yaw et al. 2016), varied findings illustrate that the link to demographic rates is unclear (e.g., Thuiller et al. 2014, Csergő et al. 2017). Even the existing evidence for using distance to environmental, not geographic, centers to predict population performance (Martínez-Meyer et al. 2012) and genetic diversity (Lira-Noriega & Manthey 2014) has been recently contested (Pironon et al. 2017,

Santini et al. 2018) as a drastic oversimplification of the biogeographic drivers on populations (Dallas et al. 2017).

In this study, we compare both genetically- and habitat-informed subpopulation SDMs to a traditional global SDM for the facilitative cushion plant *Silene acaulis* (L.) Jacq. (Caryophyllaceae; henceforth, *Silene*). *Silene* is common and widely distributed, making it an ideal species for SDMs (Pacifi et al. 2015). Further, it is particularly important to understand how facilitative plants, such as *Silene*, will respond to climatic changes, as they increase community phylogenetic diversity (Cavieres et al. 2016, Michalet & Pugnaire 2016) and can potentially buffer rapid climatic changes in alpine and arctic regions (Anthelme et al. 2014). We also aim to shed light on how well suitability can predict population performance with an extensive global cushion plant dataset (Cavieres et al. 2013) and a long-term demographic dataset (Peterson et al. 2018). We specifically test if SDM suitability can predict *Silene* size distribution, a good measure of population performance (Chardon et al. 2018), and if this prediction might be improved with subpopulation SDMs. We also test if strength of facilitative interactions with beneficiary species (i.e. plant species growing within *Silene* cushions) can be predicted with suitability, which, to our knowledge, has not been tested before. As facilitative interactions tend to be higher in climatically stressful areas (e.g. Callaway et al. 2002), we might expect a peak at medium suitability values, corresponding to sub-optimal climatic conditions for *Silene*. In this work, we specifically examine the following hypotheses:

H1. Genetic- and habitat-based subpopulation SDMs yield similar suitability predictions and outperform the global SDM.

H2. *Silene* performance (measured by cushion plant size) is positively and strongly correlated with predicted suitability from SDMs.

H3. Strength of facilitative interactions (measured by beneficiary species percent cover, richness, and diversity) is correlated with predicted suitability from SDMs.

If genetic and habitat information captures variation in local climate responses, then we expect that subpopulation SDMs will outperform the global SDM. Given that each subpopulation SDM is, by definition, tailored to the local data, we anticipate that the two subpopulation models will yield very similar results. Further, we expect that the differences we see are not explained simply by differences in climate across subpopulations. We dissect the results and underlying patterns in the data to explore the possible mechanisms behind any observed differences. Finally, if SDM suitability captures the potential for high population performance (e.g., Araújo & Williams 2000), we expect that *Silene* in areas of high predicted suitability will also have large individual plant sizes and areas of medium suitability will have high cover, richness, and diversity of beneficiary species.

4.3. METHODS

4.3.1. Climate data

In our SDMs, we used four bioclimatic variables from the CHELSA dataset in the timeframe 1979 to 2013 (during which most of our species data is available) and at a 30 arc-sec ($\sim 1 \text{ km}^2$) resolution (Karger et al. 2017). These newly available global climatology data correct for the problematic spatial and temporal heterogeneity in meteorological station data, making them particularly suitable for ecological studies (Karger et al. 2017).

We used the bioclimatic variables maximum temperature of the warmest month, temperature seasonality (i.e. difference between annual minimum and maximum), precipitation of the wettest month, and precipitation seasonality (Fig. C.A.1), four variables recently used in a *Silene* SDM study (Pironon et al. 2015). We cropped these bioclimatic variables to encompass the broad geographic regions that define *Silene*'s global distribution (North America, Europe, Russia; thematicmapping.org). To account for large land-locked bodies of water found within the species' distribution range (e.g., Canada), we also removed large lakes ($\geq 50 \text{ km}^2$) and reservoirs ($\geq 0.5 \text{ km}^3$; WWF).

4.3.2. Species occurrences

We combined geographic occurrences from two existing data sets on *Silene* traits (see below for details; Cavieres et al. 2013, Peterson et al. 2018), occurrences from a *Silene* genetic study (see Appendix 1 in Gussarova et al. 2015), and *Silene*

occurrence records from digital databases. We downloaded all “*Silene acaulis*” (and listed subspecies) digital occurrence records from the databases BIEN (biendata.org), GBIF (gbif.org), and BioTIME (BioTIME Consortium 2018, Dornelas et al. 2018). To match the resolution and timeframe of the occurrence data to the bioclimatic data, we first filtered all data at 1 km geographic position accuracy or better and at 1979 data collection year or later, where these metadata were available. As these metadata were not available for all species occurrences, we acknowledge that there may be a resolution mismatch between the occurrence data and the bioclimatic data (i.e. latitude and longitude data of a record is at a coarser resolution than 30 arcsec). Second, we removed any exact latitude and longitude duplicate occurrences.

Third, to reduce erroneous occurrences, we filtered all data by biomes that contain alpine or tundra terrain within *Silene*’s geographic distribution (“Tundra”, “Temperate Conifer Forests”, “Temperate Broadleaf & Mixed Forests”, “Boreal Forests/Tiaga”; Ecoregions2017). These are the same biome categories we then used to define habitat subpopulations. While this filter removed some known occurrences from the manually collected data sets, we employed this filter to all data in order to keep the data used across our three different SDMs consistent. Fourth, we manually checked isolated southern or lower elevation occurrences in the USA and mainland Europe (GoogleEarth Pro 2009) to remove 6 occurrences not in alpine terrain. Finally, we manually added back into the data the only record from Eastern Russia found in our search, because of its rare verification of existence in this region

(Gussarova et al. 2015) and our use of this record to determine geographic delineations of genetic groups.

4.3.3. Species traits

We used two data sets that provide both cushion size ($n = 5890$) and beneficiary species percent cover and richness ($n = 1674$) that span *Silene*'s geographic distribution in both North America and Europe (Fig. 4.1a). Given that larger *Silene* plants produce more fruits (Doak & Morris 2010), and that to achieve large size plants must either grow quickly and/or survive well, cushion size (measured as elliptical area) is a useful proxy of population or individual performance.

The strength of facilitative interactions in cushion plants is commonly measured with beneficiary percent cover and richness (Cavieres et al. 2016). The extensive cushion plant data collected by Cavieres and colleagues (2013) represents a total of 40 cushion plant species across 77 alpine plant communities (sites) in North and South America, Europe, Asia and New Zealand. The data collected at each site between 2007 – 2010 are cushion plant size, and percent cover as well as identity of beneficiary species growing inside the cushion plant (Butterfield et al. 2013, Cavieres et al. 2013). *Silene* is present in 30% of these sites (21 sites in 8 countries; Fig. 4.1a, Table C.A.1), making it by far the most widely represented cushion plant. We calculated beneficiary species diversity with the Shannon diversity index (vegan package, Oksanen et al. 2018).

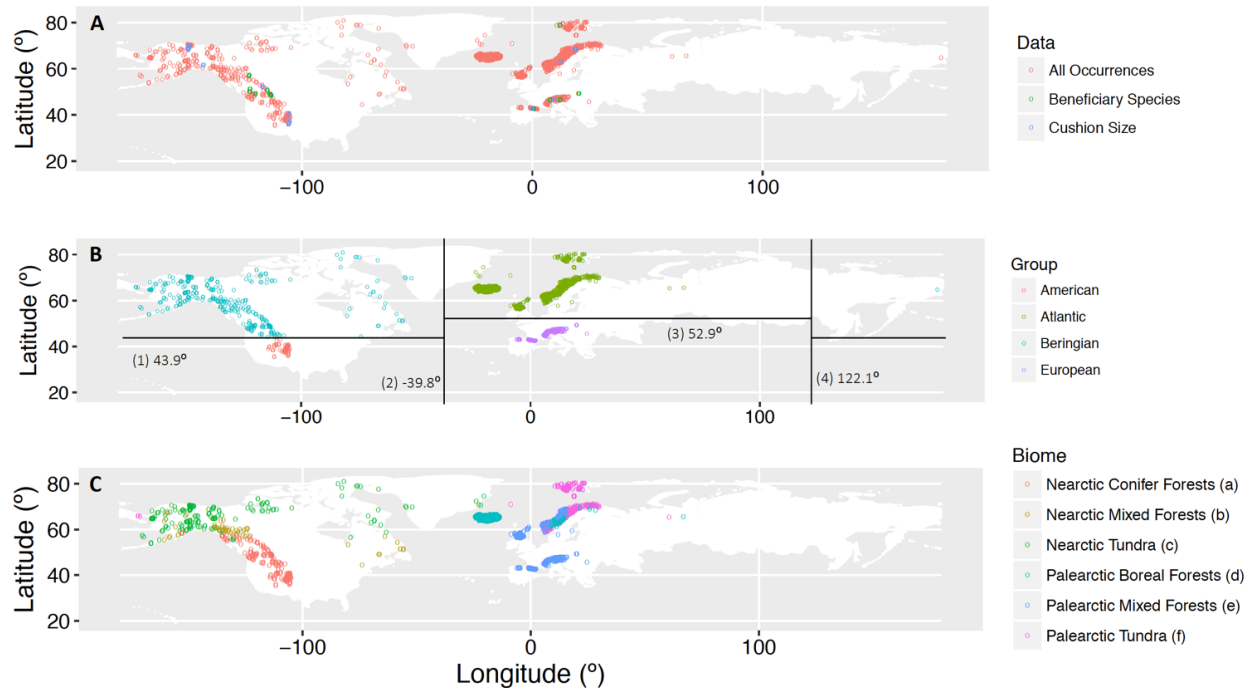


Figure 4.1: Species occurrences. A) Data on cushion sizes ($n = 50$ sites), and additionally on beneficiary species growing within cushions ($n = 21$ sites), span the geographic range of *Silene acaulis*.

B) Splits in occurrence data according to genetic groups defined by Gussarova et al. (2015), with adjacent groups split with means of: (1) maximum latitude in SW American and minimum latitude in Beringian/American; (2) maximum longitude in Beringia/American and minimum in E Atlantic; (3) southernmost occurrence in E Atlantic and northernmost occurrence in SC-European; (4) easternmost occurrence in Beringia/American and westernmost occurrence in E Atlantic. Occurrence data grouped into the four genetic groups Beringian ($n = 440$), American ($n = 99$), Atlantic ($n = 3252$), or European ($n = 316$).

C) Occurrence data grouped according to biomes in either the Nearctic or Palearctic realms defined by Ecoregions2017. Nearctic occurrences split into the biomes (a) “Temperate Conifer Forest” ($n = 252$), (b) “Boreal Forests/Taiga” + “Temperate Broadleaf & Mixed Forest” ($n = 62$), and (c) “Tundra” ($n = 225$). Palearctic occurrences split into the biomes (d) “Boreal Forests/Taiga” ($n = 1434$), (e) “Temperate Conifer Forests” + “Temperate Broadleaf & Mixed Forests” ($n = 950$), and (f) “Tundra” ($n = 1183$). Adjacent biome types combined where occurrences were < 20 for an individual biome (b) and to combine the European Alps and Pyrenees (e). Maps in Albers projection.

We also used data on North American and European *Silene* populations from a long-term demographic study (Peterson et al. 2018, Doak & Morris 2010; including *unpublished data*, D.F. Doak, W.F. Morris, M.B. García, S. Wipf & C. Rixen). For each site (21 sites in 5 countries; Fig. 4.1a, Table C.A.1), we used data on individual plant sizes from the first year's census (2001 – 2014). Given the methodology differences between the two datasets, with either targeted sampling of larger individuals (Cavieres et al. 2013) or sampling all individuals in a population (Doak & Morris 2010, for comparison see Fig. B.A.8 in SuppInfo from Chardon et al. 2018), we used only cushion sizes of plants above the 65th percentile overall from the latter dataset (Fig. C.A.2).

4.3.4. SDMs

To correct for some of the sampling bias present in the occurrence records, which are far denser in Europe than in either North America or Russia, we subsampled all records by randomly sampling one occurrence per 30 arc-sec cell ('gridSample' function in dismo package; Hijmans et al. 2017) to match the resolution of the bioclimatic data (total $n = 4107$ occurrences; Fig. 4.1a). Although this does not correct for unsampled areas, it is nonetheless a well-performing bias correction approach (Fourcade et al. 2014, Guisan et al. 2017). We then split the occurrences into four genetic groups identified by STRUCTURE analyses of multilocus AFLP markers (335 markers for 106 populations) by Gussarova et al. (Fig. 4.1b; corresponding to Fig. 4 in Gussarova et al. 2015). These genetic

differences are most pronounced between North America and Europe. We also split the occurrences into six habitat biome groups in the Nearctic (biomes: Tundra, Mixed Forests, Conifer Forests) or Palearctic (biomes: Mixed Forests, Tundra, Boreal Forests) realms (Fig. 4.1c; Ecoregions2017) representing broad habitat and climatic differences. While there is considerable correspondence between the habitat and genetic groupings, they are not identical, and also differ in the total number of subpopulations recognized, likely reflecting the fact that genetic groups reflect post glacial history as well as current habitat effects.

We used Maximum Entropy Species Distribution Modeling (MaxEnt version 3.4.1; Phillips et al.) to model *Silene*'s current climatic suitability (i.e. probability of current occurrence) using 1) all occurrences together (global SDM), and separately for 2) occurrences within each genetic group (genetic SDMs) and 3) occurrences within each habitat group (habitat SDMs). We calibrated and projected individual SDMs only in the polygon corresponding to that subpopulation. We chose MaxEnt to create our SDMs, as it is a common and well-performing algorithm for presence-only data (Phillips et al. 2006, Elith et al. 2010, Merow et al. 2013). We elected to only model current suitability (following Hällfors et al. 2016), as this allows the best evaluation of which SDM type (global, genetic, or habitat) can best predict *Silene*'s distribution and population performance.

We ran 10 cross-validated replicates for each individual SDM with a jackknife test of variable importance and response curves for environmental variables. For binary presence-absence predictions, we selected the maximum test

sensitivity plus specificity threshold in MaxEnt, a commonly used and well-performing suitability threshold that maximizes the sum of sensitivity and specificity (Liu et al. 2005). This allowed us to compare the predicted binary presence-absence maps among SDMs. We constructed these maps retaining only those cells above the threshold in more than five of the replicates per individual SDM (following Hällfors et al. 2016). We then combined maps across subpopulations to generate the final presence-absence and also suitability (i.e. probability of occurrence as indicated by cloglog output; Phillips et al. 2017) maps for the global, genetic, and habitat models. Given that output values are only relative to the modeled region and are dependent on occurrence density and sampling design, we recognize that comparing these values across models can be difficult (Merow et al. 2013).

4.3.5. Analyses

To test which SDM best predicts *Silene*'s current distribution (H1), we evaluated SDM performance with two approaches. First, we used a global, but large-scale and low-precision, *Silene* distribution map (digitized terrestrial locations from map 791 in Hultén & Fries 1986) to validate our models with data independent from those used to calibrate our SDMs. We used the final presence-absence maps to calculate the standard performance metrics of sensitivity (proportion of correctly identified presences), specificity (proportion of correctly identified absences), and True Skills Statistic ($TSS = sensitivity + specificity - 1$;

Allouche et al. 2006) for the global, genetic, and habitat SDMs. TSS is particularly useful in comparing model accuracy (Allouche et al. 2006, Shabani et al. 2016), whereas the commonly employed Area Under the Receiver Operating Curve (AUC) has been increasingly criticized as inappropriate (e.g., Lobo et al. 2008, Jiménez-Valverde 2012, Shabani et al. 2016). Second, we also compared spatial overlap between cells with current occurrence (as defined by Hultén & Fries 1986) and cells predicting current presence (as defined by our final presence-absence maps) across SDMs (following Hällfors et al. 2016) to identify which best covers current distribution.

To dissect differences between SDM predictions, we examined suitability correlation between the global and subpopulation SDMs for each distinct group to see where SDM type influenced predictions and where it did not. We also examined if SDM dissimilarities are caused by climate differences between subpopulations, choosing the two climate variables that were identified as most important by MaxEnt's analysis of variable contribution and jackknife test of variable importance. First, we compared how predicted individual subpopulation climate niches differ between the genetic or habitat SDM and the global SDM. Second, we compared the regional climate conditions (i.e. all cells from occurrence and background points) between the distinct genetic or habitat groups used to construct SDMs. Third, we compared the climate conditions for just the predicted presences between distinct subpopulations within one SDM type.

To test if SDM suitability values can predict *Silene* population performance (H2), we fit suitability values from the final suitability map of each SDM to *Silene* cushion plant sizes. Given the quadratic distribution of our data and their nested structure within 50 separate populations, we fit linear mixed models (LMMs with function 'lmer' in package lme4; Bates et al. 2015) with linear and quadratic suitability terms and a random effect of population. We calculated additional model outputs with the packages lmerTest (Kuznetsova et al. 2017) and MuMIn (Bartón 2018). We log-transformed size to meet LMM assumptions of residual distribution. We also subset these data (i.e. all Cavieres et al. sizes and the already subset Peterson et al. sizes) above the 40th percentile, as small values are present in all sites and thus do not provide a good index for performance. In past work, we have shown that particularly larger plant sizes correlate best with population performance (*unpublished data*, N.I. Chardon, C. Rixen, S. Wipf & D.F. Doak; see Fig. A.C.2) and larger plants also produce a disproportionately large amount of fruits (Morris & Doak 1998). We chose the 40th percentile as this provided the best fit out of a set of cutoffs tested. Using other cutoffs does not change the qualitative patterns in the results.

In order to test if facilitative interactions between beneficiary species and *Silene* can be predicted by suitability (H3), we fit three separate sets of quadratic LMMs as described above. Specifically, we fit suitability values from each SDM to beneficiary species percent cover, richness, and diversity. We log-transformed

percent cover $[\log(\text{cover} + 1)]$ to meet LMM assumptions of residual distribution, a transformation not necessary for richness and diversity.

We performed all data manipulations (using packages raster, Hijmans 2017; sp, Pebesma & Bivand 2005; rgdal ver. 1.3-1, Bivand et al. 2018) and data analyses in the statistical environment R (version 3.5.1; R Core Team 2018).

4.4. RESULTS

We found that the genetic SDM gives the highest proportion of true presences (sensitivity, or cell overlap with current distribution) and thus the highest TSS value (Table 4.2a). All three SDM types yield quite different presence-absence (Fig. 4.2) as well as suitability predictions (Figs. 4.3, C.A.3), with the biggest differences between the global and subpopulation SDMs. While cell overlap between current and predicted distribution is low for all SDM types, it varies substantially between the genetic (overlap = 35%), habitat (23%), and global (17%) SDMs (Fig. 4.2). In contrast, the proportion of true absences (specificity) was well predicted by all SDM types (Table 4.2a).

Table 4.2. Evaluation metrics from validating the global, genetic, and habitat SDM final presence-absence maps (A) and those for each separate genetic group (B) with the Hultén & Fries (1986) distribution data. ‘Overlap’ refers to the number of cells within the current distribution predicted as present. Highlighted are the best performing models, as judged by TSS. See Methods for details.

A

SDM	Sensitivity	Specificity	TSS	Overlap (millions of cells)
genetic	0.35	0.97	0.32	9.9
habitat	0.23	0.98	0.21	5.8
global	0.17	0.97	0.14	4.9

B

Group	SDM	Sensitivity	Specificity	TSS
Europe	genetic	0.24	0.98	0.22
	global	0.19	0.96	0.15
Atlantic	genetic	0.37	0.98	0.35
	global	0.44	0.96	0.4
America	genetic	0.18	0.99	0.17
	global	0.02	0.99	0.01
Beringian	genetic	0.36	0.95	0.31
	global	0.13	0.98	0.11

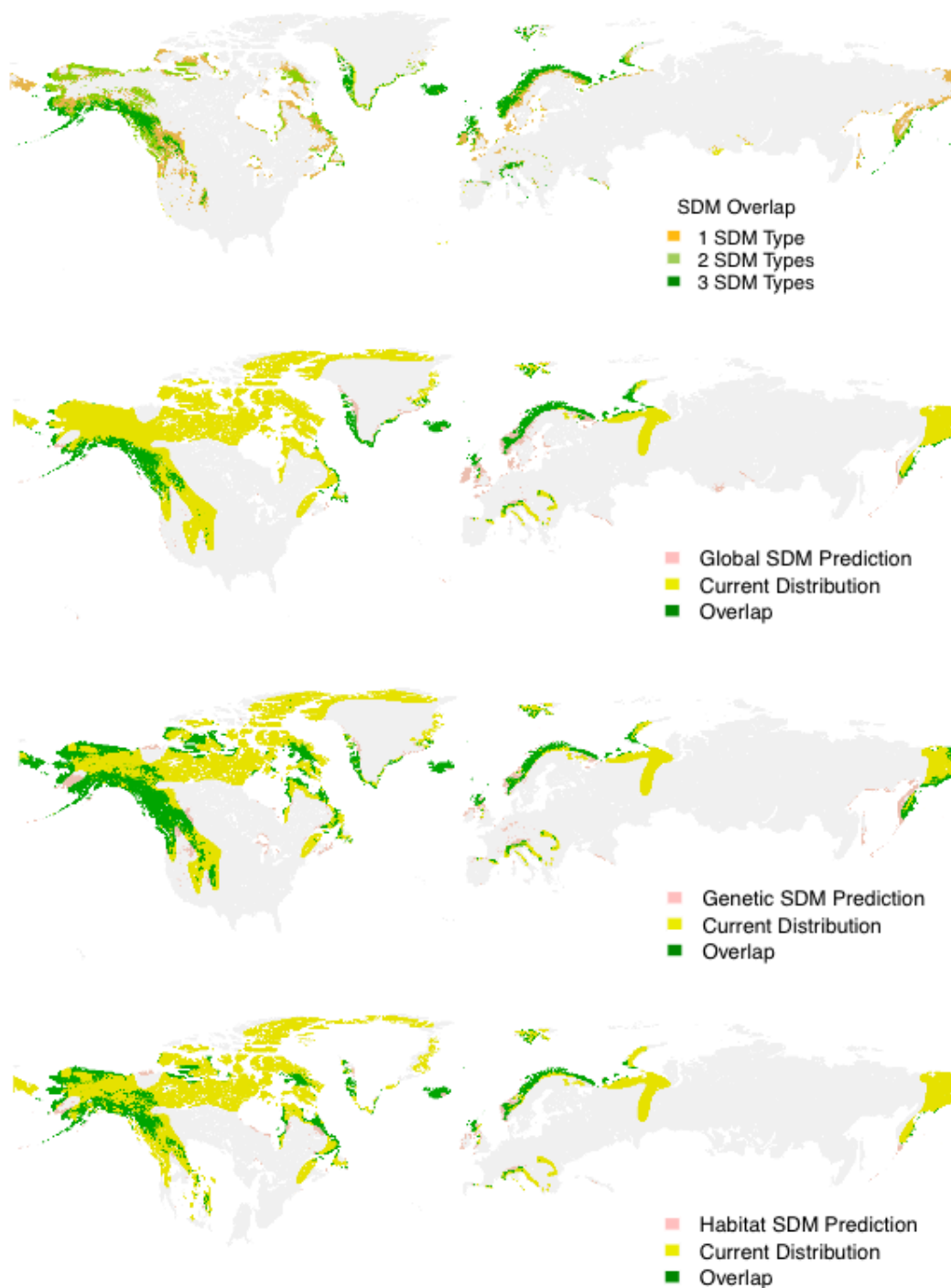


Figure 4.2: SDM validation. Top panel: Overlap between global, genetic, and habitat SDM predicted presences (based on presence-absence cells defined by maximum testing sensitivity plus specificity threshold values). Lower three panels: Overlap between predicted presences and *Silene acaulis*' current distribution (as defined by Hultén & Fries 1986) illustrate that the genetic SDM gives the highest overlap with the species' current distribution. Note that the habitat SDM predicts less cells than the global or genetic SDMs (see Methods for details).

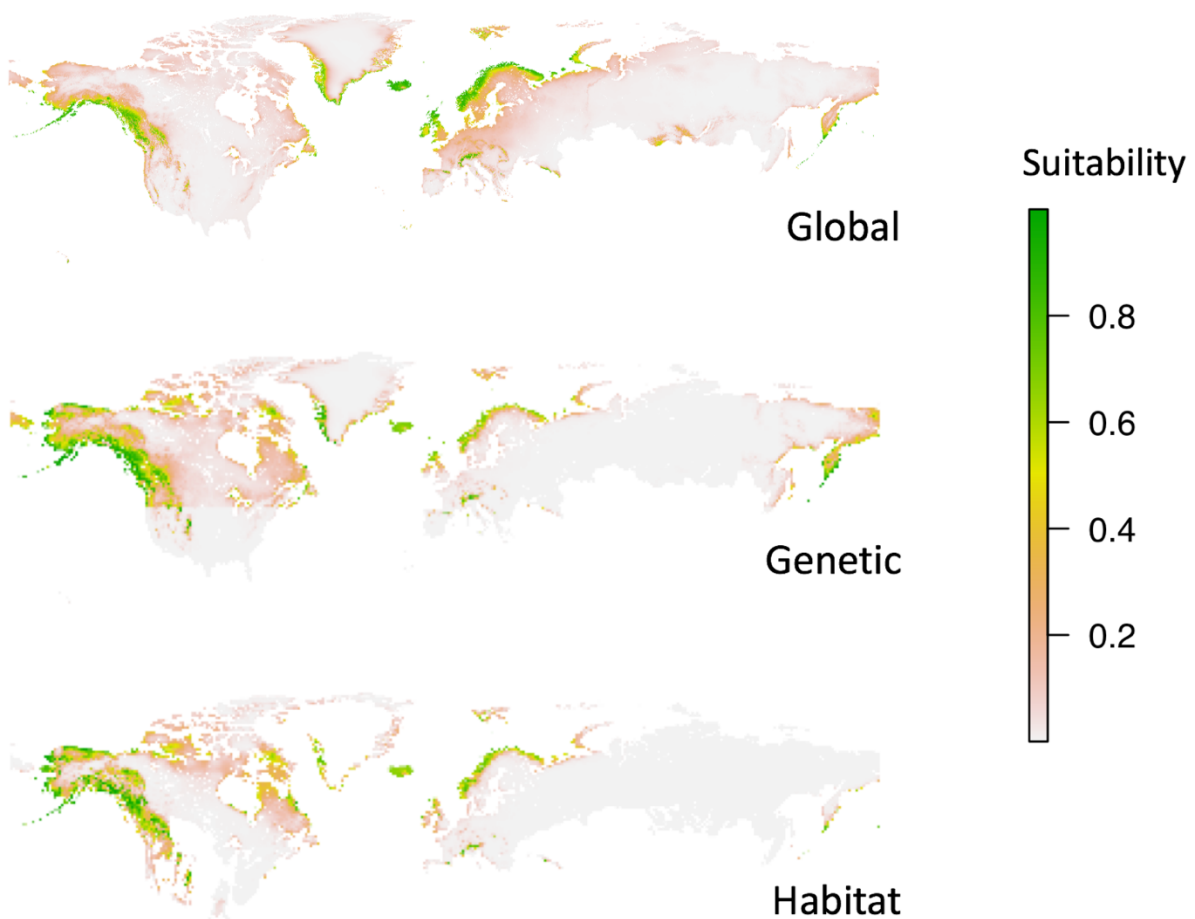


Figure 4.3: SDM suitability. Suitability maps constructed for each SDM type, with greener colors showing higher suitability. In the genetic map (middle panel) it can be seen in North America that we combined separate SDMs constructed for the distinct subpopulations. Note that the habitat SDM set predicts less cells than the global or genetic SDM sets (see Methods for details).

Interestingly, the largest overlap in predictions are where occurrence records are most abundant, such as the coasts of northern Europe and western North America (compare Fig. 4.2 with Fig. 4.1). In contrast, predictions differ quite substantially in areas with sparser occurrence records, such as northern North America and eastern Russia. The types of disagreements in predictions also vary by

subpopulation. For the European and American genetic groups, largest differences in predicted suitability are where the global SDM predicts high suitability for cells predicted as unsuitable by the genetic SDM (Fig. 4.4). In contrast, the differences in suitability predictions are more symmetrical in the Beringian and Atlantic groups. In fact, the global SDM predicts presences slightly better in the Atlantic subpopulation, with a 7% higher cell overlap with *Silene*'s current distribution (Table 4.2b). Similarity in suitability predictions matches similarity in predicted climate niches (i.e. predicted presences), as the Atlantic climate niche is similarly predicted by both SDM types, whereas the other genetic groups are predicted quite differently (Fig. 4.5).

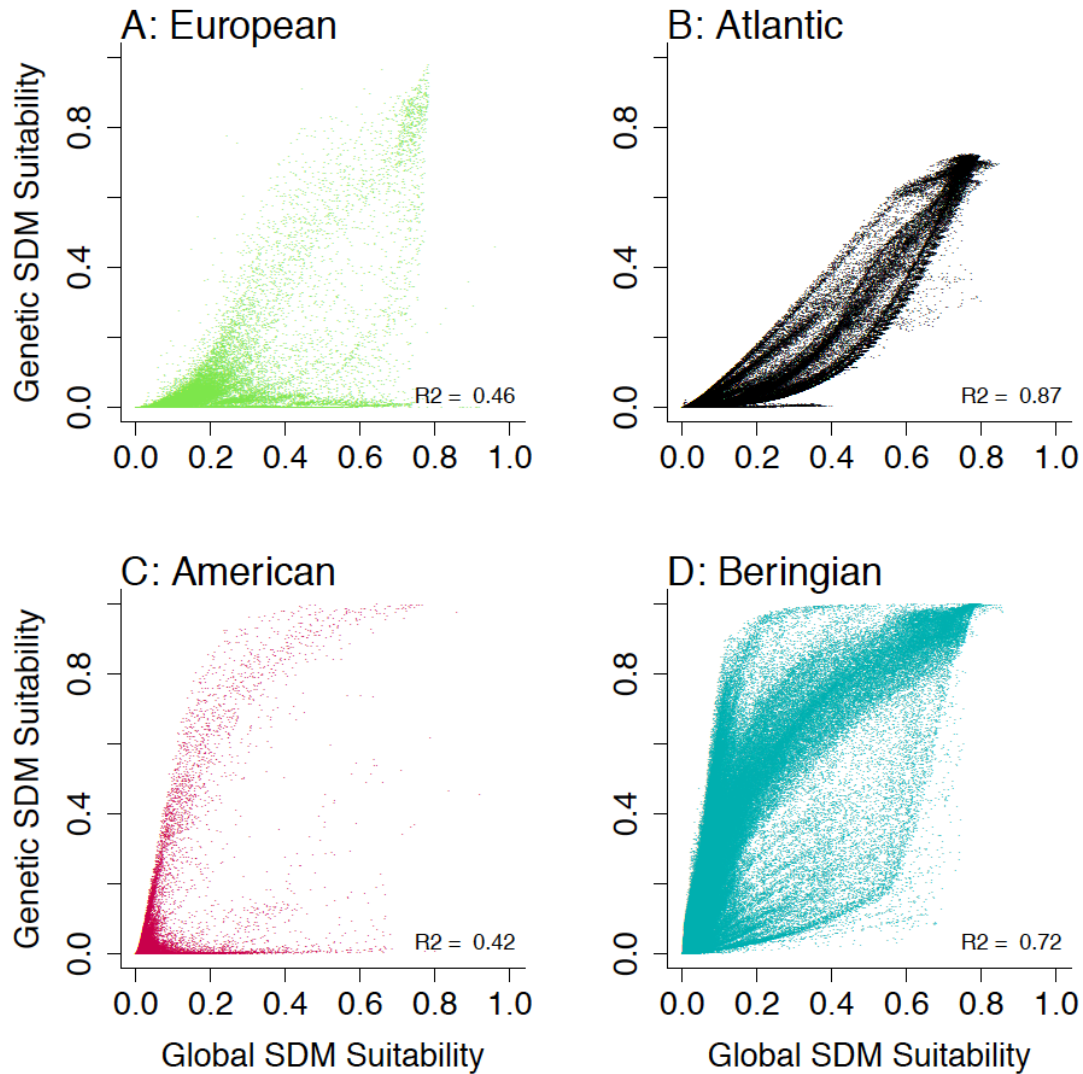


Figure 4.4: SDM suitability by genetic group. SDM suitability predictions between the genetic and global SDM types vary between genetic groups. Predictions for the Atlantic (B) genetic group are most similar, likely due to high quality occurrence data, whereas they are more dissimilar for regions with lower quality data and sampling bias (A, C, D). Shown are 1% of data per genetic group for figure clarity, and R^2 values are from linear regressions.

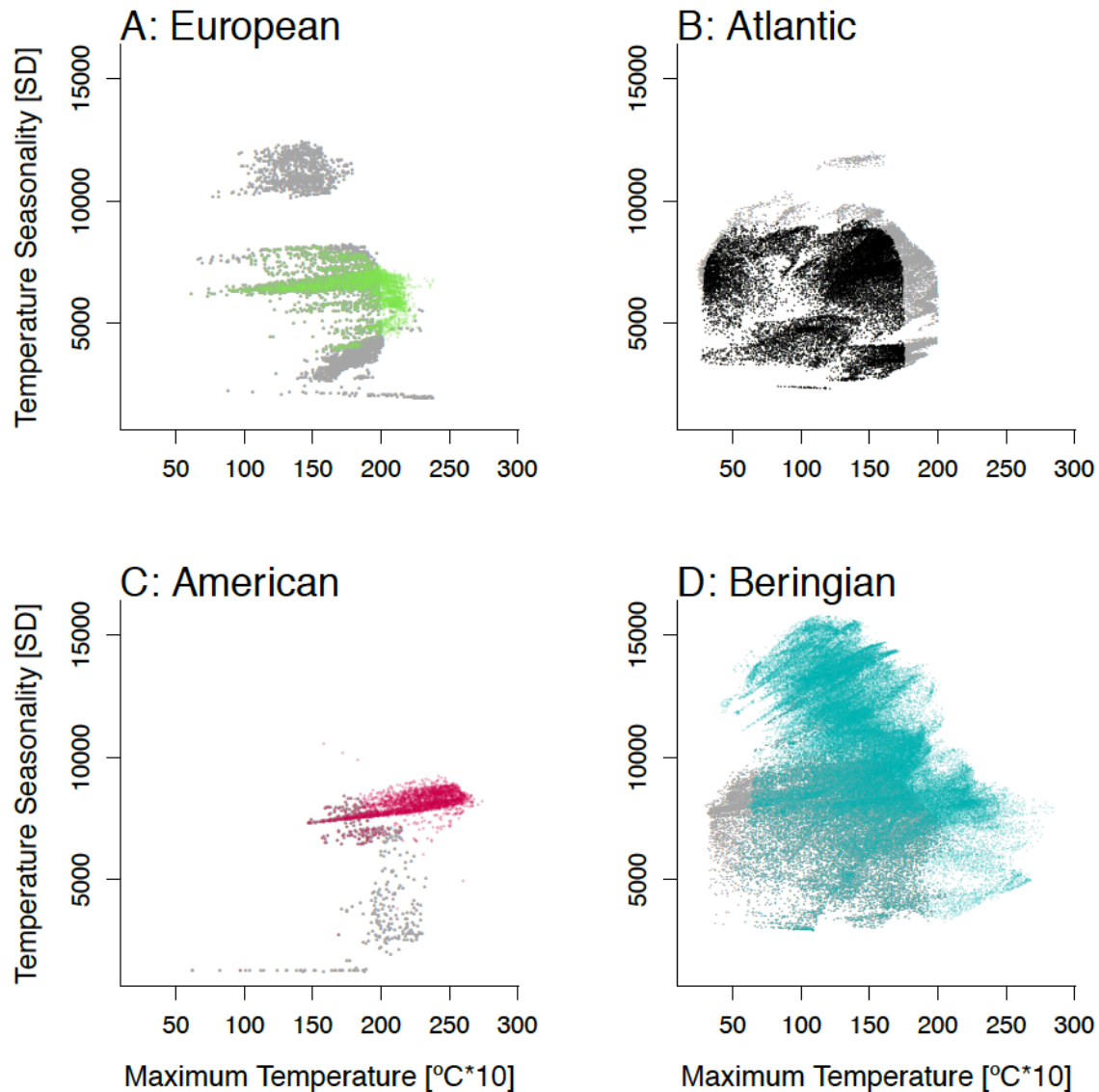


Figure 4.5: Predicted climate niches. The type of error in the global (shown in grey) compared to the genetic (shown in color) SDM predictions varies by genetic group. Shown are 1% of data per genetic group for figure clarity, and the predicted presence (determined by equal testing sensitivity plus specificity threshold) cells plotted are the same as in Fig. 4.6b.

Differences between the habitat and global SDMs broadly illustrate that suitability values are more similar in the Palearctic realm (Europe), also corresponding to the higher sampling intensity here (Fig. C.A.4). The global SDM generally overpredicts suitability in the Palearctic realm and underpredicts in the

Nearctic realm (North America). When compared to the global SDM, the habitat SDM also shows the largest difference in predicted climate niches where similarity between suitability predictions is low, most notably in the Nearctic Tundra and Conifer Forests biomes (Fig. C.A.5).

Especially surprising is that the genetic and habitat SDMs differ in their predictions, given that they both use fairly similar subpopulation divisions (see Fig. 4.1). While suitability predictions are more similar between these two SDMs than to the global SDM (compare Fig. C.A.3a with Figs. C.A.3b, c), their cell overlap with *Silene*'s current distribution differ by 12%. This is seen particularly in North America, where the habitat SDM underestimates *Silene*'s suitability (compare Fig. 4.2c with Fig. 4.2b).

Out of the four climate variables we used to construct our SDMs, maximum temperature of the warmest month (average percent variable contribution to MaxEnt models for genetic SDM: 55%; habitat SDM: 59%) and temperature seasonality (34%; 27%) are the two most important environmental variables across the four and six separate genetically-based and habitat-based SDMs, respectively. These two variables are also most important for the global SDM (temperature: 33%; temperature seasonality: 67%). Jackknife tests of variable importance in both training and testing gains for each separate SDM also identified the variable with the highest contribution as being most important in all but one case (Nearctic Tundra biome).

We examined these climate variables to gauge how much variation between the subpopulation and global SDMs results from climate differences between the individual genetic or habitat regions. The temperature climate niches are considerably broader and more overlapping for the Atlantic and Beringian groups, while those for the Atlantic and European areas are smaller and somewhat more separate (Fig. 4.6a). The climate niche of predicted presences is narrower than the regional climate space (Fig. 4.6b), suggesting that prediction differences are not solely due to climate differences in the distinct regions. This predicted climate niche also corresponds to the climate niche of known occurrences (Fig. 4.6c), which is no surprise given that we used these occurrences for SDM calibration. The same pattern is seen in the habitat biome climate niches, with increased total overlap in the narrower climate niche of predicted presences within the distinct biomes (Fig. C.A.6).

We found that the relationships between suitability values and either *Silene* performance (H2) or strength of facilitative interactions (H3) are very weak (marginal R^2 : 0.01 - 0.15) for the three models and these relationships are not improved with subpopulation SDM suitability. Suitability values from the global SDM best predicts both *Silene* cushion plant size and beneficiary species percent cover, with a peak at median to high suitability values (Tables 4.3, C.A.2, Fig. 4.7a, b). We found that other measures of facilitative interaction strength, beneficiary species richness and diversity, cannot be significantly predicted by suitability (Table C.A.2, Fig. 4.7c, d).

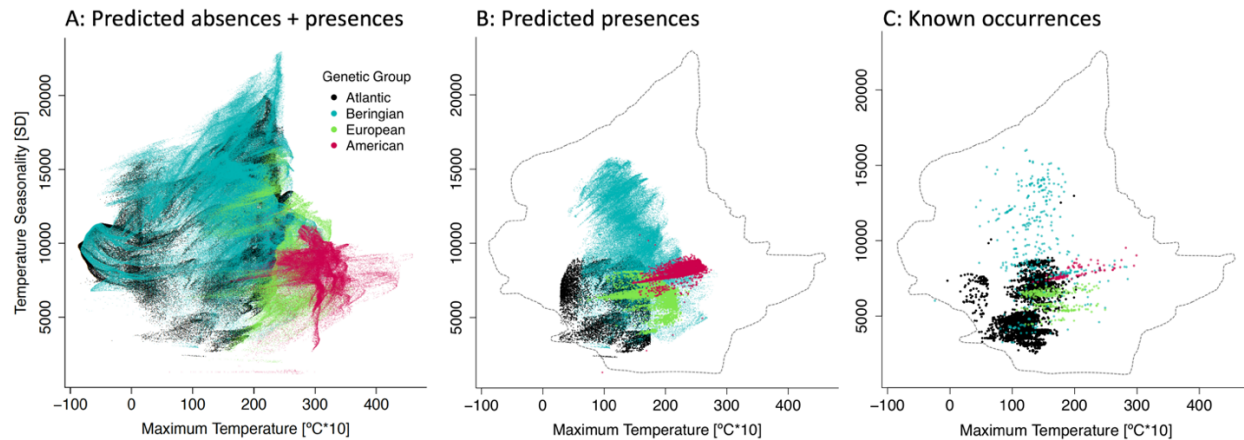


Figure 4.6: Genetic subpopulation climate niches. The climate niche for all 1 km² cells used to calibrate SDMs (A) illustrate overlap between the Atlantic and Beringian groups, which occupy a separate climate space from the overlapping European and American groups. The predicted presence cells (B) occupy a narrower climate niche and illustrate greater total overlap in climate between genetic groups. The predicted presences accurately represent the known temperature niche for the species (C). Shown are 1% of data per genetic group in (A) and (B) for figure clarity, all colors are as in (A), and the temperature niche in (A) is outlined in (B) and (C). Note that we constructed SDMs with the additional variables precipitation seasonality and precipitation of the wettest month, but plot only the two most important climate variables as identified by MaxEnt.

Table 4.3. Results from quadratic LMMs fitting suitability values from each SDM type to *Silene acaulis* cushion area. All but the intercept-only model test the effects of suitability + suitability² per SDM with a random effect of population (n = 50). Model estimates for suitability and suitability² effects are given by estimate and estimate_{sq}, respectively, and p-values by p-value and p-value_{sq}, respectively. R² values are marginal R² values. See Methods for model details.

parameter	SDM	intercept	estimate	estimate _{sq}	p-value	p-value _{sq}	n	R ²	Δ AICc
	suitability								
area	global	0.12	7.1	7.22	0.05	0.25	3531	0.06	0
	genetic	0.12	7.19	7.28	0.61	0.15	3531	0.03	2.65
	habitat	0.12	7.72	7.57	0.83	0.32	3531	0.01	3.78
	intercept only	5.06	-	-	-	-	3531	0	12.67

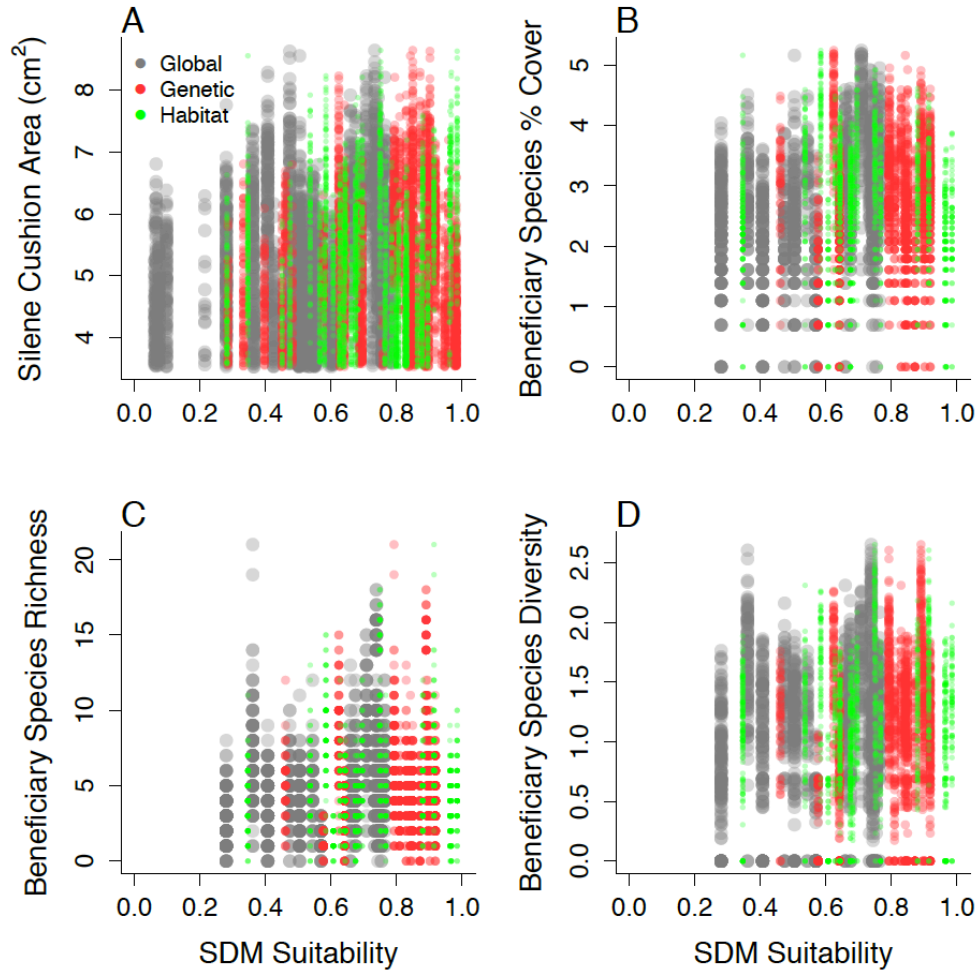


Figure 4.7: Species traits. A) Global SDM suitability values are the only ones that significantly predict *Silene acaulis* cushion area, with a peak at higher suitability values. There is no significant relationship between SDM suitability values of any SDM type and beneficiary species percent cover (B), richness (C), or diversity (D). Colors are all as in (A), and all LMMs are fit with a quadratic suitability term. Shown are the log-transformed data above the 40th percentile used to fit the models for (A) and log-transformed data for (B). Note that sample size for the trait data in (A) is larger, and therefore a wider range of suitability values are observed.

4.5. DISCUSSION

We critically evaluated the performance of three approaches to model species distributions: a traditional global SDM using a species-wide climate niche, and subpopulation models based on either genetic groups or climatically-distinct habitat

types. Interestingly, we found that the subpopulation SDMs outperform the global SDM for predicting the current distribution of *Silene*. However, we did not find that model performance simply increased with greater subdivisions of the data, as the genetic SDM with four groups outperformed the habitat SDM based on six groups and calibrated on an overall smaller climate niche (see Fig. 4.3). This implies that how a species is divided into subpopulations is critical to the results and inference from SDMs, and that subpopulations based on habitat types or geographic regions may not best capture genetic differences in responses to climate. Seeing as MaxEnt is the SDM of choice in many studies due to its high performance with presence-only data (Phillips et al. 2006, Elith et al. 2010, Merow et al. 2013), this algorithm likely provided the best results compared to other algorithms.

While SDMs have been widely employed for decades to forecast species distribution shifts (reviewed in Pacifici et al. 2015), it is only recently that researchers have started examining the implications of differences between subpopulations responses to climate (Table 4.1; see also Schurr et al. 2012, Ehrlén & Morris 2015, Pironon et al. 2018). To date, we could find only sixteen studies that have constructed subpopulation SDMs. Notably, while all these studies show differences between subpopulations in predicted climate niches (but see Meynard et al. 2017), most do not report results that allow for an assessment of the importance of these differences or their likely causes. First, only half compare predictions of a global model to those of the subpopulation models, a comparison necessary to understand how important subpopulation models might be. Where such

comparisons have been made, however, subpopulation models tended to have higher predictive accuracy, emphasizing the potential importance of this approach. Second, only one study compared multiple approaches to delineating subpopulations (Marcer et al. 2016), and none used independent validation data with which to judge predictive quality.

Similarly, few prior studies have examined the potential factors that could cause differences in subpopulation SDM predictions (Table 4.1). While most authors have interpreted their results as evidence of local adaptation to climate, several other effects are also possible. First, if there are strong climate differences in separately modeled regions, subpopulation SDMs may well fit correspondingly different climate niches (e.g., Meynard et al. 2017). Several recent studies have attempted to test this hypothesis by quantifying niche divergence with respect to background habitat availability (Warren et al. 2008, Broennimann et al. 2012, Hu et al. 2017, Ikeda et al. 2017, Meynard et al. 2017, Theodoridis et al. 2018). In our study, the regional climate niche within a subpopulation is substantially larger than the observed or predicted climate niche for that subpopulation (Figs. 4.6, C.A.6). This suggests that suitability differences are not simply due to distinctions between regional climates.

Second, differences in sample size (i.e. recorded occurrences) between different regions may mean that a global model may perform poorly for subpopulations with lower sampling intensity (e.g., Pearman et al. 2010; Hällfors et al. 2016). Our study supports this explanation, as we see that unequal sampling

intensity across regions corresponds to differences between global and subpopulation predictions. Finally, two effects that are not easily examined are i) differences in the ways that local climate effects are mediated by other biotic or abiotic factors, that themselves can vary with region (e.g., Schwalm et al. 2016), and ii) local adaptation itself. Few studies that use subpopulation SDMs have independent evidence for local adaptation of the subpopulations used to model distribution (but see Hu et al. 2017). Such information would greatly strengthen the inferences that can be drawn, particularly with regards to shifts in distribution under future climate.

We emphasize that SDMs themselves are not capable of fully dissecting these different mechanisms, but examination of the calibration data and model predictions can help with interpretation. Whether genetic differences between *Silene* subpopulations actually cause differential climate responses needs to be tested experimentally, as dissimilarity in SDM predictions can only indicate the potential for local adaptation and resulting population-level climate response. However, in the case of *Silene*, climate manipulation experiments have found local adaptation to temperature between populations corresponding to the Beringian and American genetic groups (Peterson et al. 2018). *Silene* might also respond strongly to other climatic drivers than the ones we examined, although recent studies have identified temperature to be an important climate variable for the species (Pironon et al. 2014, Ferrarini et al. 2018).

Our SDM suitability values poorly predict *Silene* cushion size and facilitative interaction strength, and this quadratic relationship likely corresponds to the wide range of elevations represented in the trait data. Largest plant size and strongest facilitative interactions are found at mid-elevations (Fig. C.A.7a, b), whereas suitability values predicting species occurrence show a broad pattern of increasing with elevation (Fig. C.A.7c). Adding elevation as a fixed effect to our LMMs, however, does not improve model fit for any of the variables we fit. Even substituting climate variables for suitability in LMMs does not yield strong relationships (Table C.A.3, Fig. C.A.8), illustrating that the species traits in our study system cannot be accurately predicted by either suitability nor broad-scale climatic factors.

Given that suitability is used to extrapolate to species performance or traits (e.g., Araújo & Williams 2000) and has been found to be a good predictor of performance (VanDerWal et al. 2009, Van Couwenberghe et al. 2013, Lee-Yaw et al. 2016), we had expected a strong relationship in our data. While the ability to predict species' traits with habitat suitability has been examined before (Thuiller et al. 2009), recent work has shown that such results need to be interpreted cautiously, especially when considering species demographic rates (Thuiller et al. 2014, Csergő et al. 2017). Although biotic interactions have been successfully modeled on a geographic scale (Araújo & Rozenfeld 2014) and SDM predictions can improve when incorporating facilitative interactions (Filazzola et al. 2018), our

results indicate that predicting biotic interactions from suitability values needs to be approached with caution.

As SDM types strongly varied only in their sensitivity, and thus in their TSS, measures (see Table 4.2a), our results also suggest that subpopulations need to be carefully defined to achieve the highest accuracy and hence utility. This is especially relevant given that the use of such predictions is important in conservation planning (e.g., Franklin 2013). Our validation data represented the coarse-scale distribution, meaning that it provides, at a fine scale, gross overpredictions of *Silene*'s distribution (e.g., *Silene* is not present in all of Alaska, see Fig. 4.2). This resulted in overall low sensitivity values for all models and we note that the nature of the validation data can affect these measures.

Given that we found large inconsistencies between SDM types, we emphasize that subpopulations should be modeled separately for more accurate predictions and that the choice of how to define subpopulations needs to be well-justified. Our results illustrate the necessity of examining potential local population response differences to climate, which, if present, greatly violate a foundational assumption of SDMs built using a species' full climatic niche. Species traits or performance can differ with the various climate niches found within its range (Emery et al. 2015, Amburgey et al. 2017) and predictions for locally modeled populations often do not match those from global models (Hällfors et al. 2016, Schwalm et al. 2016). However, given the different predictions provided by the genetic and habitat SDMs, we emphasize the need to compare multiple types of subpopulation models,

particularly in the absence of independent data suggesting local adaptation. Importantly, simple habitat classifications may not capture relevant genetic differences. Given that we found the largest differences in SDM predictions expressly where sampling intensity is low, we argue that subpopulation SDMs are thus needed to accurately model a species' suitable habitat in regions with biased occurrence data.

Future work should focus on examining how subpopulation SDMs vary from global ones for species with narrower distributions, as well as use experimental approaches to test if subpopulations respond differently to climate. Practitioners using SDM outputs for conservation planning should be wary of predictions generated from single SDMs using large scale distribution data, and aim to compare outputs from multiple SDM types. Furthermore, prediction dissimilarities from SDMs constructed with different subpopulation types need to be carefully examined, to rule out alternative explanations and to ultimately best decide what areas a species will most likely occupy.

4.6. ACKNOWLEDGMENTS

We are grateful to GIBF, BIEN, and BioTIME for making their data on global species occurrences publicly and freely available, and to Gussarova et al. (2015) for their genetic work as well as publishing their sampling locations. Thank you to the many collaborators in the studies by Cavieres et al. (2013) and Peterson et al. (2018) for your countless hours in the field and for sharing your data, without which

this work would not have been possible. We thank Andreas Stoffel for his work to digitize the distribution map from Hultén & Fries (1986). We appreciate the many helpful initial and ongoing discussions with Sonja Wipf and Christian Rixen, and thank the members of the Doak lab for reviewing early versions for this manuscript. Partial funding for NIC, DFD, and MLP was provided by NSF DEB 1242355, 1340024, and 1753954.

4.7. DATA ACCESSIBILITY

All data and R code used in this work are available on the Open Science Framework (<https://osf.io/muvay/>). The full dataset from Cavieres et al. (2013) is now publicly available (Lortie 2018).

4.8. AUTHOR CONTRIBUTIONS

NIC, SP, and DFD conceived the ideas and designed methodology, NIC performed the analyses with help from SP, and MLP conducted the literature review to compile Table 4.1. NIC wrote the manuscript with substantial input from DFD, MLP, and SP. All authors contributed critically to the drafts and gave final approval for publication.

CHAPTER 5

A species identification app to increase citizen engagement at Niwot Ridge

Chardon NI

5.1. INTRODUCTION

Public involvement in scientific research has tremendous potential to increase awareness of our changing natural environment, and could even ensure the continued funding of this field. With the widespread use of smartphones, every user could become an amateur scientist as part of multiple citizen science projects if given the means to do so. Mobile application software (apps) collect an incredible amount of data on a daily basis, yet most of this information remains unused. In an effort to increase public engagement and scientific understanding at the University of Colorado's (CU) Boulder Mountain Research Station (MRS) and Long-Term Ecological Research (LTER) site at Niwot Ridge, I sought to develop an app that allows visitors to easily identify alpine plants and to centrally record their observations.

Niwot Ridge hosts hundreds of visitors and researchers every year, including those who recreate, engage in amateur natural history activities, or conduct a variety of research projects. However, few fully appreciate the species diversity present in this area. The Niwot Ridge LTER encompasses approximately 95 km² of

montane and alpine ecosystems (Greater NWT LTER; Niwot-LTER) that are readily accessible to both researchers and visitors. Such ecosystems are particularly threatened by climatic warming (IPCC 2014), yet are not a common focus of citizen science projects examining the effects of global climate change. The combination of the accessibility of the MRS and Niwot LTER along with the collection of long-term climatic data at the site makes it an ideal location for a citizen science project. An app designed to allow increased species identification while recording geographic position and phenological state through a photograph would therefore allow for increased understanding of Niwot Ridge's biodiversity while collecting useful data. Similar observation-based citizen science projects have not only been very successful in increasing public participation in the sciences (Sullivan et al. 2009), but have also contributed invaluable data to track species abundances (Boyle & Sigel 2015, Langham et al. 2015) and to project species distributions with climate change (Distler et al. 2015). The vast amount of data collected from citizen science projects could therefore become important for conservation and management decisions.

Citizen science initiatives are becoming a useful way to integrate the broader public into scientific research (Dickinson et al. 2012), and are gaining immense popularity across the globe (Silvertown 2009). Apps (e.g., iNaturalist) as well as species observation databases (e.g., Pl@ntNet, Global Biodiversity Information Facility) have greatly increased both the quantity and availability of species occurrence data across the globe, with the well-known Global Biodiversity

Information Facility currently hosting over 1 billion species observations (GBIF 2018a) for over 5.8 million species (GBIF 2018b), and the newer iNaturalist database hosting over 11 million observations for 170,000 species (iNaturalist 2018). Such citizen science initiatives provide the user with the opportunity to engage with the natural environment, while increasing ecological knowledge and awareness of the impacts of human activities (Branchini et al. 2015). Furthermore, data collected by citizen scientists are directly useful to researchers in answering pressing ecological questions, such as how phenology is affected by climatic changes (Hurlbert & Liang 2012) and how species necessary for ecological services are distributed (van der Wal et al 2015). Intended for use by Niwot Ridge visitors and researchers, the app I designed allows the user to discover and learn exactly what they are looking at while participating in a larger scale citizen science project aimed at increasing our understanding of the effects of climatic change on alpine flora phenology. With the public availability of this app, I sought to engage outdoor recreationalists as well as researchers by learning more about their environment, while also contributing meaningful data to scientific research.

A central objective in developing this app was to address the major challenge of species identification that is faced by citizen users who use apps to record species geographic occurrences. Although citizens are becoming increasingly engaged in using apps to record species occurrences (e.g. iNaturalist) and identifying species (e.g. Colorado Rocky Mt Wildflowers, Leafsnap), to my knowledge no app exists that allows the user to identify a species within the app before recording its occurrence

with a photograph. This could lead to either species misidentification or simply the lack of an observation when the user is not confident enough in their identification. By providing the public with an app that has an incorporated species identification guide (i.e. field guide), I aimed to reduce the fundamental challenge that citizens face when recording species occurrences.

In this project, my goal was to produce a functional smartphone application and corresponding website to aid research efforts and increase public scientific literacy. Additionally, this project fostered collaboration between the Environmental Studies Program (ENVS), the Computer Science (CS) Department, and the Institute for Arctic and Alpine Research (INSTAAR) at CU Boulder. With the development capabilities of CS undergraduate students in a design course and the botanical expertise from Jane Smith (INSTAAR), the tools to create such an app were readily available at CU Boulder.

5.2. METHODS

5.2.1. Development

As the sponsor of two groups of CS students in their year-long ‘Software Engineering Project’ course, I oversaw the design and development of the Luminous ID app versions 1 (2014-2015) and 2 (2016-2017). Through providing the students with ample flexibility in their development strategy, I also allowed the 6-person teams high levels of creativity in design and coding. We held meetings one to two

times per month, during which the students reported their progress, outlined their next steps, and ensured that their development plans matched my goals for the app.

The initial Luminous ID version 1 (Chardon et al. 2015) consisted of a mobile species field guide for the alpine flowers at Niwot Ridge and included a recognition algorithm for the abundant cushion plant *Silene acaulis* (Caryophyllaceae; Chardon & Smith 2015). Luminous ID ver. 1 had two main functions. First, it used a binary classifier visual recognition algorithm to identify *S. acaulis* with a photograph taken by the user, and correctly identified observations were recorded with geographic location. Once back in an area with cellular reception, the user synchronized these observations with the website. Second, it had a photographic field guide for the alpine flowers at Niwot Ridge, searchable by a filter based on seven plant characteristics (flower color, flower shape, habitat, inflorescence structure, leaf arrangement, leaf shape, petal number). Personal conversations with users highlighted that the main incentive in using Luminous ID was to utilize the species field guide, not the photo recognition algorithm for solely one plant. The amount of observations uploaded for *S. acaulis* were minimal, with less than five users uploading such observations.

To broaden the scope of Luminous ID and increase its usability at Niwot Ridge, I again oversaw a student team to develop Luminous ID version 2 (Chardon et al. 2017). We designed Luminous ID ver. 2 to be an interactive app that includes a full species list of the plants (i.e. trees, forbs, grasses) found at Niwot Ridge (MRS 2017), searchable by a filter function. This version also included an observation

upload option of species photographs and their geographic locations. The main revisions from ver. 1 were to provide users with an expanded species guide and the option to upload any species observations (not just the algorithm-recognized *S. acaulis*). We also designed a public website (luminousid.org) to allow users to see their observations and for researchers to verify species observations (following iNaturalist.org).

5.2.2. Data

The list of species included in the app corresponds to the MRS species list (V. Komarkova, M. Walker & J. Smith, MRS 2017). In order to integrate a functional filter in the species field guide, the student developers required a list of traits for all species. J. Smith and I first decided on the traits to use as filters (Table 5.1), choosing traits that were specific enough to be a useful filter while ensuring that the public could understand them. We then compiled traits for the species represented in the app by using existing trait data (*unpublished data*, J. Smith), examining herbarium specimens, and consulting regional flora. So that every species entry has a photograph of the species, we used personal photos (W. Bowman, N. Chardon & J. Smith) and online species databases (for full list see luminousid.org/about.html). To aid public understanding of the traits used as filters, J. Smith compiled a visual glossary of terms for difficult forb and graminoid terminology (Table 5.2).

Table 5.1. Filter options in Luminous ID that use species traits to narrow down the list of potential species a user is attempting to identify.

Species Group	Filter 1	Filter 2
Graminoids	Sedges	Stem Cross-section, Leaf Blade, Inflorescence, Spike Color, Habitat
	Rushes	Stem Cross-section, Leaf Blade, Habitat
	Grasses	Stem Cross-section, Leaf Blade, Inflorescence, Florets Per Spikelet, Awns, Habitat
Forbs	Family, Flower Color, Petal Number, Flower Shape, Leaf Arrangement, Leaf Shape, Habitat	
Trees & shrubs	Deciduous	Family, Leaf Arrangement, Leaf Margin, Leaf Shape
	Needle	Family, Needle Arrangement, Needle Per Fascicle, Needle Apex, Cone

Table 5.2. Terms in the Luminous ID glossary that are explained with drawings (J. Smith).

Graminoids	Forbs
Awn Absent	Alternate
Awn Bent	Basal
Awn Straight	Campanulate
Awn Twisted	Composite
Awn	Cushion
Contracted	Funnelform
Flat	Labiate
Floret	Oblong
Involute	Opposite
Keeled	Palmate
Open	Papilionaceous
Spikelet	Radial
Spikes Globose	Reflexed
Spikes One	Round
Spikes Two or more	Ternate
	Urceolate
	Whorled

5.2.3. Testing

In order to ensure the functionality of Luminous ID ver. 2 on both Google Android and Apple iOS devices, the students spent the last two weeks of this project testing the app. Students made new accounts in the app and took pictures of items with the app to upload these observations, and checked that they could see their

observations both within the app and the website. They furthermore ensured that the sync options worked properly, settings which they designed so that users could choose to automatically or manually sync their observations to the website.

5.3. RESULTS

Released in May 2017, Luminous ID ver. 2 (Chardon et al. 2017) is an interactive app that allows users to search for a plant species using a filtering function and upload that observation to the app's website (luminousid.org). The app has been downloaded over 900 times on Google or Apple devices (July 2018). It is frequently used by visitors to the MRS and Niwot Ridge LTER, who claim that it has helped them to easily identify plants in the field (*personal observation*). The app's corresponding website gives users access to the field guide and allows them to track their observations.

5.3.1. App

From the home screen (Fig. 5.1a), the user can choose to remain a guest or log in in order to record species observations. The user can also choose to navigate to four other pages from the home screen: the field guide ("Field Guide"), their observations ("My Observations"), a glossary of terms ("Glossary"), and information about the app ("About Us"). A user can utilize the field guide (Fig. 5.1b) with the implemented filters (Table 5.1) to identify a plant species. Once the user has identified a species, they can record that observation with a photo (Fig. 5.1c), which

automatically registers the user's current geographic coordinates. A user can see their recorded observations under "My Observations", where the sync status of each observation is listed and observations can be automatically or manually synced. The "Glossary" provides a sketch to certain plant traits used in the filter (Table 5.2). "About Us" gives a brief description of the Luminous ID goals, contact and image information, and how to use the app.

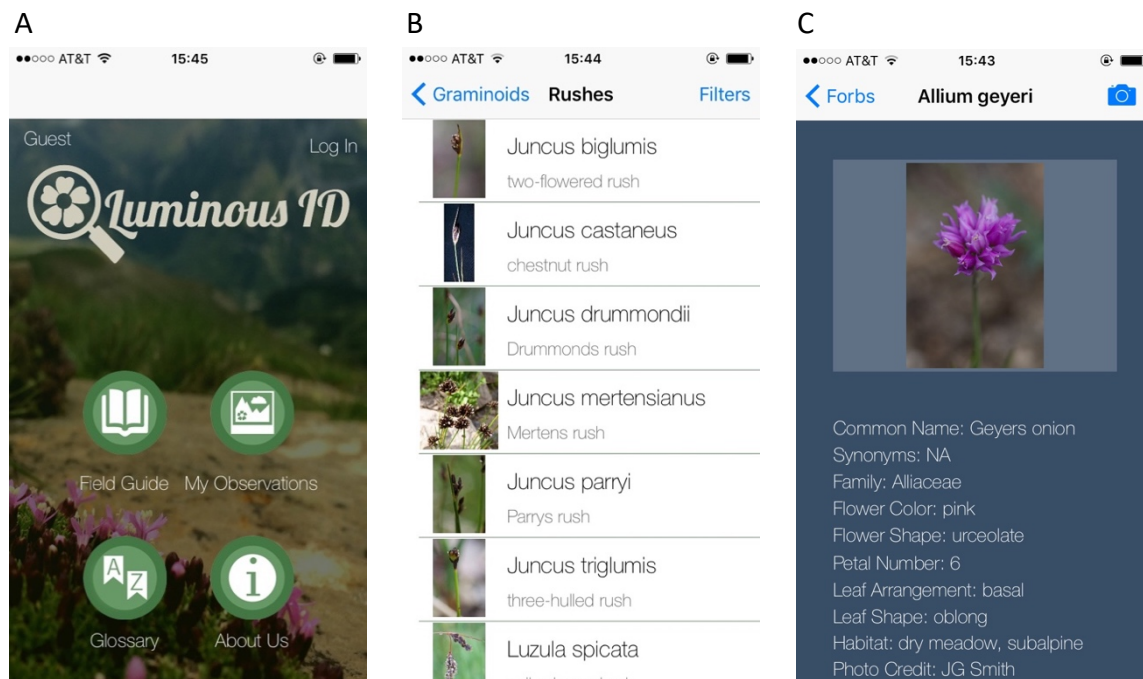


Figure 5.1: Luminous ID user interface. The home screen (A) of Luminous ID ver. 2 gives the user the option to access the field guide, their existing observations, a glossary of plant trait terms, and information about the developers as well as pertinent contact details. The field guide (B) allows the user to filter plants by traits and the entries for individual species (C) summarize these traits.

5.3.2. Website

The website provides guidance how to use the app and the website, gives users access to the same field guide as in the app and all existing observations, links to the AppStore and GooglePlay to download the app, and gives the same contact and sign in information as the app. Existing species observations can be verified by researchers (following www.iNaturalist.org), and after two verifications an observation is marked as “verified”. This ensures that species observations are accurate, making them more useful to ecological researchers. Observations can be downloaded as one file (.csv format) that includes the species name, latitude, longitude, GPS accuracy, verification status, and photo reference. A current major glitch in Luminous ID ver. 2 is that it does not reliably upload species observations GPS coordinates or photos, with some incorrect coordinates recorded, missing photos to observations, or heavily distorted photos.

5.3.3. Outreach

To disseminate information about this app to the larger scientific community, J. Smith presented Luminous ID ver. 1 at an LTER conference (Smith & Chardon 2015). To increase awareness of Luminous ID ver. 2 to MRS and Niwot Ridge LTER visitors, we printed informative fliers and posted them in targeted locations (e.g., MRS, CU greenhouse, ENVS front office). We displayed Luminous ID cards at the MRS for visitors to take. We also announced the release of Luminous ID ver. 2 on several email lists (e.g., Niwot LTER, ENVS).

5.4. DISCUSSION

A fruitful collaboration between ENVS, CS, and INSTAAR yielded the useful mobile app Luminous ID that helps visitors and researchers at the MRS and Niwot Ridge LTER identify and upload plant species observations. While this collaboration was productive and impressive given that this app was the developers' first, two main problems arose. First, the app has a major malfunction in uploading recorded species observations to the website, with inaccurate GPS coordinates, no accompanying photo, or a severely distorted photo. Given that the accuracy of species observations relies on only GPS coordinates and a photograph is needed for verification purposes, this malfunction hinders the full realization of the app's goals. If researchers cannot rely on the accuracy of the species observations, this data will only be marginally useful in work aiming to understand how different species' phenology timing shifts with climatic changes. Second, the filtering function within the app has some minor glitches, including missing trait data for some species and some categories that cannot be selected.

A main challenge in the development of this app was to effectively align the project goals and visions between myself, an ecologist, and the computer scientists involved. To facilitate this process, it is imperative to have a clear and detailed delineation of the desired functions and capabilities of the product. This includes details such as what steps a user will take at the app's home screen, how the filtering function will split the species data, what data should be transferred to the website, and how the website should be arranged. Such details can only be defined

once the data (e.g., species names and traits) are available, which we should have provided the developers with early on (e.g., first 1-2 months) in the project. Given that most computer scientists are unfamiliar with biological data, time to explain the structure and meaning of the data should also be budgeted at the start of such a project. Finally, ample time for testing of a product is required to ensure that all desired functionalities work properly. Luminous ID ver. 1 had no malfunctions, likely due to two months of testing by both developers and myself. Had we tested Luminous ID ver. 2 earlier on, and with more users across both Android and iOS platforms, we could have identified the malfunctions in time to correct them.

The development documentation to Luminous ID is open source (Table 5.3) and the MRS as well as Niwot Ridge LTER would greatly benefit from an updated version of Luminous ID that addresses the known glitches. Given the success of this app within the Niwot Ridge LTER community, the development documentation could also be used to expand Luminous ID to include species from all LTER sites or other areas in Colorado. In order to test the effectiveness of including a species field guide in a species observation app, it would also worthwhile to conduct a human subjects research project to compare data collection with this app to other apps.

5.5. DOCUMENTATION

All development documentation for Luminous ID versions 1 and 2 is open source, and sensitive information has restricted access (Table 5.3).

Table 5.3. Luminous ID documentation details and contact information (Nathalie Chardon: nathalie.chardon@gmail.com; Sarah Elmendorf: sarah.elmendorf@colorado.edu or current Information Manager at Niwot LTER; Jane Smith: jane.g.smith@colorado.edu). *Institutional Review Board documentation consists of an approved protocol (CU Boulder IRB, June 2017) and accompanying material to study the effectiveness of Luminous ID in recording species observations compared to an app that does not contain a species field guide. Due to major glitches in the species upload function, I did not carry this study out as planned. +Currently (October 2018) shared with N. Chardon, J. Smith, and S. Elmendorf.

Documentation	Publicly Available	Location	Contact
Development ver. 1	yes	https://github.com/Aardevarken/LuminousMossBosses	N. Chardon
Development ver. 2	yes	https://github.com/TheGardenClub/LuminousID	N. Chardon or S. Elmendorf
Outreach	conditional	restricted GoogleDrive folder ⁺	N. Chardon or S. Elmendorf
Future Ideas	conditional	restricted GoogleDrive folder ⁺	N. Chardon or S. Elmendorf
Institutional Review Board*	conditional	restricted GoogleDrive folder ⁺	N. Chardon or S. Elmendorf
Deployment	no	restricted GoogleDrive folder ⁺	N. Chardon or S. Elmendorf
Payment	no	restricted GoogleDrive document ⁺	N. Chardon or J. Smith

5.6. ACKNOWLEDGMENTS

This work would not have been possible without the tremendous amount of time invested by Jamie Miller, Brian Bauer, Jacob Rail, Jack Skinner, Andrey Shprengel, and Morgan Garske in 2014-2015 (Luminous ID ver. 1) as well as Ryan O'Connell, Chase Springer, D'Vreaux Fontaine, Brian Larson, Kevin Rau, and Jennifer Baumann in 2016-2017 (Luminous ID ver. 2) to turn an idea into tangible reality. The existence of this app is grounded in the meticulous species lists compiled mainly by Marilyn Walker, Marko Spasovic, and Jane Smith, with

corresponding species traits added by Jane Smith. Rick Parker provided invaluable support and encouragement during development. The Computer Science Department's encouragement to CU entities to propose projects to the students in their design course made this work financially possible. I thank Daniel Doak for the numerous discussions and ideas on how to develop such an app.

CHAPTER 6

Conclusion

6.1. OVERVIEW

The motivations of my dissertation work were to improve our understanding of what processes set range limits as well as how to better predict species distribution shifts, while increasing public engagement in ecological research. To examine the effects of range limits, I conducted extensive field surveys at elevational range limit populations of the alpine cushion plants *Silene acaulis* (henceforth, *Silene*) and *Minuartia obtusiloba* (henceforth, *Minuartia*) at trail-side and off-trail plots (Chapters 2 & 3). To improve predictions of species distributions with Species Distribution Models (SDMs), I compared the accuracy of a traditional modeling approach with a newer approach that accounts for potential local population adaptation (Chapter 4). To contribute to citizen science efforts, I designed a mobile application software (app) that allows users to quickly identify and record alpine plants in the field (Chapter 5).

6.2. ALPINE CUSHION PLANT COMMUNITIES

While localized field studies are required for detailed examination of the processes that are important at, and potentially set, range limits, such studies need

to be conducted at a global scale in order to make broad ecological generalizations. By examining the effects of human trampling disturbance at range limit populations of the alpine cushion plants *Silene* and *Minuartia* in both the North American Rocky Mountains in Colorado and the European Alps in Switzerland, I show that distinct similarities and contrasts exist between these two geographically isolated mountain ranges. On a broad scale, the effects of disturbance are tightly linked to those of elevation in the Rocky Mountains (henceforth, 'Rockies'), whereas this is less the case in the Alps. Disturbance generally favors cushion plant sizes, indicating a positive effect on growth or survival, or both, particularly at lower elevations.

In the Rockies, I show that disturbance has differential effects at lower and upper elevational range limits. In particular, disturbance positively affects *Silene* cushion plant size, density, and percent cover as well as *Minuartia* percent cover at these species' lower elevational limits, likely by reducing the effects of competitive interactions. These disturbance effects become neutral to negative at upper elevational limits, where fewer biotic interactions exist. While disturbance also favors *Silene* sizes at lower elevational limits in the Alps, this effect is similarly present at upper elevational limits. In contrast, population density and reproductive indices are negatively affected by disturbance at all elevations, illustrating a negative disturbance effect at the population level in the Alps. With data on plant-plant interactions in the Alps, I found that disturbance negatively affects species richness and diversity of both other species growing inside and adjacent to *Silene*

cushions. Surprisingly, disturbance does not influence either the facilitative or competitive interactions in *Silene* communities, which are predominately characterized by competitive interactions.

My scientific findings illustrate that disturbance can have important differential effects on contrasting range limit populations, implying that disturbance can be an influential player in determining range limits. While these effects are similar between the Rockies and Alps at lower range limits, they differ at upper range limits. Not only does this highlight the importance of further examining the effects of disturbance at upper elevational range limits, but also of the extent to which effects of landscape processes can be generalized. My work implies that management and conservation should seek to maintain heterogeneous landscapes, such as through moderate disturbances, at lower elevational range limits, but that management of high elevation areas should be tailored to local ecosystems. Particular care should be taken with high intensity disturbances, such as human trampling, as they can negatively impact plant reproduction and species richness as well as diversity.

To comprehensively understand the effects of disturbance at the population level, future studies should focus on reproductive and recruitment processes, such as through demographic studies. As novel species are now found in alpine zones, either through encroachment from lower elevations or as invasive species, it is also imperative to improve our understanding of how disturbance affects the range limits of such species.

6.3. SPECIES DISTRIBUTION MODELS

In my work focusing on how to improve SDMs, I found that suitable habitat predictions differ between an SDM that uses a species' full geographic range and multiple SDMs that separately model distinct subpopulations (defined by either broad genetic or habitat differences). I show that subpopulation SDMs provide better predictions of *Silene*'s current distribution, and dissect multiple mechanisms responsible for this result. At least for *Silene*, the traditional approach to constructing a SDMs, by modeling a species' suitable habitat using the species' global distribution, yields inaccurate predictions if local populations respond differently to climate. Importantly, the manner in which subpopulations are defined greatly affects habitat suitability predictions, which are poorly linked to measures of *Silene* population performance and facilitative interaction strength. In addition to showing this basic result, I also discuss possible reasons for differences between subpopulation SDMs. I conclude that local adaptation is only one of several possible explanations for this result and that SDM results alone cannot differentiate between possible mechanisms.

I show that, at least in my study system, subpopulation SDMs provide the most accurate predictions, implying that practitioners need to be cautious in their decisions based on single SDMs using large scale distribution data. As I found that biased sampling effort is particularly problematic in global SDMs, particular care needs to be taken when making management or conservation decisions for poorly sampled regions of a species' range. My findings illustrate that subpopulation SDMs

should be used in order to provide accurate predictions of suitable habitat, although how to define such subpopulations needs to be carefully considered.

Future work should seek how to best define subpopulations across multiple taxa and various geographic scales, to establish a standard in how to divide a species' global distribution for SDMs. To further our understanding of how local population adaptation influences SDMs, detailed experimental studies should be carried out that specifically examine to what extent local populations are adapted to local climate conditions. Future research efforts on SDMs should also establish guidelines on how such adaptations can be better incorporated into SDMs.

6.4. CITIZEN SCIENCE

Finally, to increase citizen engagement in ecological research, I designed a freely accessible app that allows users to quickly identify alpine plant species at the University of Colorado's Mountain Research Station and Niwot Long-Term Ecological Research site. Using a filter function, a user can narrow down the list of potential plants they are looking at, and record their observation with a photograph that also marks the species' geographic location. Not only does this allow the user to discover and learn exactly what they are looking at, but it also contributes meaningful data to research examining the effects of climate change on alpine flora phenology. Future work should focus on developing an update to fix this app's current glitches, in order to allow for accurate and meaningful data collection on species occurrences.

BIBLIOGRAPHY

Ackerly DD, Cornwell WK, Weiss SB, Flint LE & Flint AL. (2015) A geographical mosaic of climate change impacts on terrestrial vegetation: Which areas are most at risk? *PLoS ONE*. 10(6):e0130629.

Aitken SN, Yeaman S, Holliday JA, Wang T & Curtis-McLane S. (2008) Adaptation, migration, or extirpation: climate change outcomes for tree populations. *Evolutionary Applications*. 1:95-111.

Allouche O, Tsoar A & Kadmon R. (2006) Assessing the accuracy of species distribution models: prevalence, kappa, and the true skill statistic (TSS). *Journal of Applied Ecology*. 43:1223-1232.

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

Amburgey SM, Miller DAW, Grant EHC, Rittenhouse TAG, Benard MF, et al. (2017) Range position and climate sensitivity: The structure of among-population demographic responses to climatic variation. *Global Change Biology*. DOI: 10.1111/gcb.13817

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.

Antonsson H, Björk RG & Molau U. (2009) Nurse plant effect of the cushion plant *Silene acaulis* (L.) Jacq. in an alpine environment in the subarctic Scandes, Sweden. *Plant Ecology & Diversity*. 2(1):17-25.

Araújo MB & Williams PH. (2000) Selection areas for species persistence using occurrence data. *Biological Conservation*. 96:331-345.

Araújo MB & Peterson AT. (2012) Uses and misuses of bioclimatic envelope modeling. *Ecology*. 93(7):1527-1539.

Araújo MB & Rozenfeld A. (2014) The geographic scaling of biotic interactions. *Ecography*. 37:406-415.

- Armas C, Ordiales R & Pugnaire FI. (2004) Measuring plant interaction: a new comparative index. *Ecology*. 85(10):2682–2686.
- 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. (2015a) Recreational trails as a source of negative impacts on the persistence of keystone species and facilitation. *Journal of Environmental Management*. 159:48-57.
- Ballantyne M & Pickering CM. (2015b) The impacts of trail infrastructure on vegetation and soils: Current literature and future directions. *Journal of Environmental Management*. 164:53-64.
- 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.
- Barros A & Pickering CM. (2015) Impacts of experimental trampling by hikers and pack animals on a high-altitude alpine sedge meadow in the Andes. *Plant Ecology & Diversity*. 8(2):265-276.
- Bartoń K. (2018). MuMIn: Multi-Model Inference. *R package version 1.42.1*. <<https://CRAN.R-project.org/package=MuMIn>>
- 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.
- Benito-Garzón M, Alía R, Robson TM & Zavala MA. (2011) Intra-specific variability and plasticity influence potential tree species distributions under climate change. *Global Ecology and Biogeography*. 20(5):766-778.
- 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
- biendata.org [Internet] Botanical Information and Ecology Network. Data retrieved 27 March 2018. <biendata.org>.
- Billings WD. (1973) Arctic and alpine vegetations: Similarities, differences, and susceptibility to disturbance. *Bioscience*. 23(12):697-704.

- BioTime Consortium. (2018) BioTIME (Version 2) BioTIMEQuery_06_12_2017. Zenodo. Data retrieved 5 April 2018. <<http://doi.org/10.5281/zenodo.1211105>>.
- Bivand R, Keitt T & Rowlingson B. (2018) rgdal: Bindings for the 'Geospatial' Data Abstraction Library. R package version 1.3-1. <<https://CRAN.R-project.org/package=rgdal>>
- 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
- Bowman WD, Steltzer H, Rosenstiel TN, Cleveland CC & Meier CL. (2004) Litter effects of two co-occurring alpine species on plant growth, microbial activity and immobilization of nitrogen. *OIKOS*. 104:336-344.
- Bowman WD & Swatling-Holcomb S. (2017) The roles of stochasticity and biotic interactions in the spatial patterning of plant species in alpine communities. *Journal of Vegetation Science*. 29: 25–33. <https://doi.org/10.1111/jvs.12583>
- Bonanomi G, Stinca A, Chirico GB, Ciaschetti G, Saracino A & Incerti G. (2015) Cushion plant morphology controls biogenic capability and facilitation effects of *Silene acaulis* along an elevational gradient. *Functional Ecology*. 30:1216-1226. doi: 10.1111/1365-2435.12596.
- Boyle WA & Sigel BJ. (2015) Ongoing changes in the avifauna of La Selva Biological Station, Costa Rica: Twenty-three years of Christmas Bird Counts. *Biological Conservation*. 188:1-21. doi:10.1016/j.biocon.2015.01.004
- Branchini S, Meschini M, Covi C, Piccinetti C, Zaccanti F & Goffredo S. (2015) Participating in a citizen science monitoring program: implications for environmental education. *PLoS ONE*. 10(7): e0131812. doi:10.1371/journal.pone.0131812.
- Bray JR & Curtis JT. (1957) An ordination of the upland forest communities of southern Wisconsin. *Ecological Monographs*. 27(4):325–349. <https://doi.org/10.2307/1942268>
- Broennimann O, Fitzpatrick MC, Pearman PB, Petitpierre B, Pellissier L, et al. (2012) Measuring ecological niche overlap from occurrence and spatial environmental data. *Global Ecology and Biogeography*. 21(4):481-497.
- Bronstein JL. (2009) The evolution of facilitation and mutualism. *Journal of Ecology*. 97:1160-1170.

- Brooker RW, Maestre FT, Callaway RM, Lortie CL, Cavieres LA, et al. (2008) Facilitation in plant communities: the past, the present, and the future. *Journal of Ecology*. 96:18-34.
- Butterfield BJ, Cavieres LA, Callaway RM, Cook BJ, Kikvidze Z, et al. (2013) Alpine cushion plants inhibit the loss of phylogenetic diversity in severe environments. *Ecology Letters*. 16:478-86.
- Cacciapaglia C & van Woesik R. (2018) Climate-change refugia: shading reef corals by turbidity. *Global Change Biology*. 22(3)L1145-1154.
- Cade SC. (2015) Model averaging and muddled multimodel inferences. *Ecology*. 96(9):2370-2382.
- 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.
- Callaway RM, Brooker RW, Choler P, Kikvidze Z, Lortie CJ, et al. (2002) Positive interactions among alpine plants increase with stress. *Nature*. 417:844-848.
- Carroll C, Lawler JJ, Roberts DR & Hamann A. (2015) Biotic and climatic velocity identify contrasting areas of vulnerability to climate change. *PLoS ONE*. 10(10):e0140486.
- Catorci A, Malatesta L, Velasquez JL, Tardella FM & Zeballos H. (2016) The interplay of nurse and target plant traits influences magnitude and direction of facilitative interactions under different combinations of stress and disturbance intensities in Andean dry grassland. *Journal of Plant Ecology*. 9(3):296-310.
- Cavieres LA, Brooker RW, Butterfield BJ, Cook BJ, Kikvidze Z, et al. (2013). Facilitative plant interactions and climate simultaneously drive alpine plant diversity. *Ecology Letters*. 17(2):193-202.
- Cavieres LA, Hernandez-Fuentes C, Sierra-Almeida A & Kikvidze Z. (2016) Facilitation among plants as an insurance policy for diversity in Alpine communities. *Functional Ecology*. 30:52-59.
- Chambers JC. (1995) Disturbance, life history strategies, and seed fates in alpine herbfield communities. *American Journal of Botany*. 82(3):421-433.
- Chardon NI & Smith JG. (2015) Researchers at Niwot LTER develop an alpine plant smartphone app. *LTER Network News: Network News Summer 2015*. 28(2). <<http://news.lternet.edu/Article3224.html>>.

- Chardon NI, Miller J, Bauer B, Garske M, Rail J, et al. (2015) Luminous ID (Version 1) [Mobile Application Software].
- Chardon NI, O'Connell R, Springer C, Fontaine D, Larson B, et al. (2017) Luminous ID (Version 2) [Mobile Application Software]. Available on Apple AppStore and GooglePlay. <luminousid.org>.
- 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*. 8:7921-7935.
- Chavez DJ, Harding JA & Tynon JF. (1999) National recreation trails: A forgotten designation. *Journal of Forestry*. 40-43.
- Choler P, Michalet R & Callaway RM. (2001) Facilitation and competition on gradients in alpine plant communities. *Ecology*. 82(12):3295-3308.
- Cole DN & Spildie DR. (1998) Hiker, horse and llama trampling effects on native vegetation in Montana, USA. *Journal of Environmental Management*. 53:61-71.
- Colorado Climate Center. (2017) "Climate of Colorado". *Colorado State University*. Accessed 4 April 2018. <http://climate.colostate.edu/climate_long.html>.
- Colorado Rocky Mt Wildflowers. *Colorado Wildflowers*. <<http://www.highcountryapps.com/ColoradoWildflowers.aspx>>.
- Connell JH. (1978) Diversity in tropical rainforests and coral reefs. *Science* 199: 1302–1310. <https://doi.org/10.1126/science.199.4335.1302>
- Csergő AM, Salguero-Gómez R, Broennimann O, Coutts SR, Guisan A, et al. (2017) Less favourable climates constrain demographic strategies in plants. *Ecology Letters*. 20(8):969-980.
- Dallas T, Decker RR & Hastings A. (2017) Species are not most abundant in the centre of their geographic range or climatic niche. *Ecology Letters*. 20:1526-1533.
- D'amen M, Zimmermann NE & Pearman PB. (2013) Conservation of phylogeographic lineages under climate change. *Global Ecology and Biogeography*. 22(1):93-104.
- Darwin CR. (1859) *On the Origin of the Species by Means of Natural Selection*. England: Murray.

de Bello F, Dolezal J, Dvorsky M, Chlumska Z, Rehakova K, et al. (2011) *Annals of Botany*. 108:567-573.

Dickinson JL, Shirk J, Bonter D, Bonney R, Crain RL, et al. (2012) The current state of citizen science as a tool for ecological research and public engagement. *Frontiers in Ecology and the Environment*. 10:291-297. doi:10.1890/110236

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

Distler T, Schuetz JG, Velásquez-Tibatá J & Langham GM. (2015) Stacked species distribution models and macroecological models provide congruent projections of avian species richness under climate change. *Journal of Biogeography*. 42:976-988. doi:10.1111/jbi.12479

Doak DF & Morris WF. (2010) Demographic compensation and tipping points in climate-induced range shifts. *Nature*. 467:959-962.

Dornelas M, Antão LH, Moyes F, Bates AE, Magurran AE, et al. (2018) BioTIME: A database of biodiversity time series for the Anthropocene. *Global Ecology and Biogeography*. 27:760-786.

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, Dolezal J, Kopecky M, Chlumska Z, Janatkova K, et al. (2013) Testing the stress-gradient hypothesis at the roof of the world: effects of the cushion plant *Thylacospermum caespitosum* on species assemblages. *PLOS ONE*. 8(1); e53514.

Dvorsky M, Chlumska Z, Altman J, Capkova K, Rehakova K, et al. (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

Early R & Sax DF. (2014) Climatic niche shifts between species' native and naturalized ranges raise concern for ecological forecasts during invasions and climate change. *Global Ecology and Biogeography*. 23:1356–1365.

Ecoregions2017. [Internet]. Data retrieved 14th April 2018.
<<https://ecoregions2017.appspot.com/>>.

Ehrlén J & Morris WF. (2015) Predicting changes in the distribution and abundance of species under environmental change. *Ecology Letters*. 18(3):303-314.

Elith J, Kearney M & Phillips S. (2010) The art of modelling range-shifting species. *Methods in Ecology and Evolution*. 1:330-342.

Elith J, Phillips SJ, Hastie T, Dudík M, Chee YW & Yates CJ. (2011) A statistical explanation of MaxEnt for ecologists. *Diversity and Distributions*. 17:43:57.

Emery NJ, Henwood MJ, Offord CA & Wardle GM. (2015) *Actinotus helianthi* populations across a wide geographic range exhibit different climatic envelopes and complex relationships with plant traits. *International Journal of Plant Science*. 176(8):739-750.

Ettinger AK, Ford KR & J HilleRisLambers. (2011) Climate determines upper, but not lower, altitudinal range limits of Pacific Northwest conifers. *Ecology*. 92(6):1323-1331.

Federal Office of Meteorology and Climatology MeteoSwiss. (data retrieved 26 July 2017) <<http://www.meteoswiss.admin.ch/home/climate/past/climate-normals/normal-values-per-measured-parameter.html>>.

Ferrarini A, Alsafran MHSA, Dai J & Alatalo JM. (2018) Improving niche projections of plant species under climate change: *Silene acaulis* on the British Isles as a case study. *Climate Dynamics*. DOI: 10.1007/s00382-018-4200-9

Fick SE & Hijmans RF. (2017) WorldClim 2: new 1-km spatial resolution climate surfaces for global land areas. *International Journal of Climatology*. 37:4302-4315.

Filazzola A, Sotomayor DA & Lortie CJ. (2018) Modelling the niche space of desert annuals needs to include positive interactions. *OIKOS*. 127:264-273.

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>.

Fourcade Y, Engler JO, Rödder D, Secondi J. (2014) Mapping species distributions with MAXENT using a geographically biased sample of presence data: A performance assessment of methods for correcting sampling bias. *PLoS ONE*. 9(5): e97122.

Fournier-Level A, Korte A, Cooper MD, Nordborg M, Schmitt J & Wilczek AM. (2011) A map of local adaptation in *Arabidopsis thaliana*. *Science*. 334:86-89.

Fournier DA, Skaug HJ, Ancheta J, Ianelli J, Magnusson A, et al. (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. (2013) Species distribution models in conservation biogeography: developments and challenges. *Diversity and Distributions*. 19:1217-1223.

Franklin J, Serra-Diaz JM, Syphard AD & Regan HM. (2016) Global change and terrestrial plant community dynamics. *Proceedings of the National Academy of Sciences*. 113(14): 3725-3734.

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

GBIF. (2018a) *Occurrences*. Accessed 16 July 2018.
<<https://www.gbif.org/occurrence/search>>.

GBIF. (2018b) *Species*. Accessed 16 July 2018.
<<https://www.gbif.org/species/search>>.

GBIF.org. [Internet]. Data retrieved 5th April 2018.
<<https://doi.org/10.15468/dl.w2puoz>>.

Global Biodiversity Information Facility. *Free and open access to biodiversity data*.
<www.gbif.org>.

GoogleEarth Pro (Version 7.3.2.5491). (2009) Mountain View, CA: Google Inc. [Software]. Accessed 2 July 2018. <<https://www.google.com/earth/>>.

Gotelli NJ & Stanton-Geddes J. (2015) Climate change, genetic markers and species distribution modelling. *Journal of Biogeography*. 42:1577-1585.

Gray LK, Gylander T, Mbogga MS, Chen PY & Hamann A. (2011) Assisted migration to address climate change: recommendations for aspen reforestation in western Canada. *Ecological Applications*. 21(5):1591-1603.

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

- Gross N, Kunstler G, Liancourt P, de Bello F, Suding KN & Lavorel S. (2009) Linking individual response to biotic interactions with community structure: a trait-based framework. *Functional Ecology*. 23:1167-1178.
- Guisan A & Rahbek C. (2011) SESAM – a new framework integrating macroecological and species distribution models for predicting spatio-temporal patterns of species assemblages. *Journal of Biogeography*. 38:1433-1444.
- Guisan A, Thuiller W & Zimmermann NE. (2017) Habitat Suitability and Distribution Models with Applications in R. Cambridge University Press: Cambridge, United Kingdom.
- Gussarova G, Allen GA, Mikhaylova Y, McCormick LJ, Mirré V, Marr KL, Hebda RJ & Brochmann C. (2015). Vicariance, long-distance dispersal, and regional extinction-recolonization dynamics explain the disjunct circumpolar distribution of the arctic-alpine plant *Silene acaulis*. *American Journal of Botany*. 102(10):1703-1720.
- Grime JP. (1974) Vegetation classification by reference to strategies. *Nature*. 250:26-31.
- Hällfors MH, Liao J, Dzurisin J, Grundel R, Hyvärinen M, Towle K, Wu GC & Hellmann JJ. (2016) *Ecological Applications*, 26(4):1154–1169.
- Hamann A & Aitken SN. (2013) Conservation planning under climate change: accounting for adaptive potential and migration capacity in species distribution models. *Diversity and Distributions*. 19(3):268-280.
- 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.
- Hijmans RJ. (2017) raster: Geographic Data Analysis and Modeling. R package version 2.6-7. <<https://CRAN.R-project.org/package=raster>>.
- Hijmans RJ, Phillips S, Leathwick J & Elith J. (2017) dismo: Species Distribution Modeling. R package version 1.1-4. <<https://CRAN.R-project.org/package=dismo>>.
- Holderegger R, Kamm U & Gugerli F. (2006) Adaptive vs. neutral genetic diversity: implications for landscape genetics. *Landscape Ecology*. 21(6):797-807.
- Homburg K, Brandt P, Drees C & Assmann T. (2014) Evolutionarily significant units in a flightless ground beetle show different climate niches and high extinction risk due to climate change. *Journal of Insect Conservation*. 18(5):781-790.

Hu XG, Wang T, Liu SS, Jiao SQ, Jia KH, et al. (2017) Predicting future seed sourcing of *Platycladus orientalis* (L.) for future climates using climate niche models. *Forests*. 8(12):471.

Hughes AC, Satasook C, Bates PJJ, Bumrungsri S & Jones G. (2012) The projected effects of climatic and vegetation changes on the distribution and diversity of Southeast Asian bats. *Global Change Biology*. 18:1854–1865.

Hultén E & Fries M. (1986) Atlas of North European Vascular Plants North of the Tropic of Cancer (vol. I). Koeltz Scientific Books: Königstein, Federal Republic of Germany. p. 396.

Hurlbert AH & Liang Z. (2012) Spatiotemporal variation in avian migration phenology: citizen science reveals effects of climate change. *PLoS ONE*. 7(2): e31662. doi:10.1371/journal.pone.0031662

Ikeda DH, Max TL, Allan GJ, Lau MK, Shuster SM & Whitham TG. (2017) Genetically informed ecological niche models improve climate change predictions. *Global Change Biology*. 23:164-176.

iNaturalist. *A community for Naturalists*. <www.inaturalist.org>.

iNaturalist. (2018) *Observations*. Accessed 17 July 2018. <www.inaturalist.org/observations>.

Incerti G, Giordano D, Stinca A, Senatore M, Termolino P, Mazzoleni S & Bonanomi G. (2013) Fire occurrence and tussock size modulate facilitation by *Ampelodesmos mauritanicus*. *Acta Oecologica*. 49:116-124.

InfoFlora. (2016) Das nationale Daten- und Informationszentrum der Schweizer Flora. Data retrieved 1 May 2016. <<https://www.infoflora.ch/de/>>.

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.

Jiménez-Valverde A. (2012) Insights into the area under the receiver operating characteristic curve (AUC) as a discrimination measure in species distribution modeling. *Global Ecology and Biogeography*. 21:498-507.

Karger DN, Conrad O, Böhner J, Kawohl T, Kreft H, et al. (2017). Climatologies at high resolution for the earth's land surface areas. *Scientific Data*. 4:170122. Data retrieved 5 June 2018. <chelsa-climate.org/downloads/>.

Kjaer U, Olsen SL & Klanderud K. (2017) Shifts from facilitative to neutral interactions by the cushion plant *Silene acaulis* along a primary succession gradient. *Journal of Vegetation Science*. doi: 10.1111/jvs.12584.

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.

Körner C. (2003) *Alpine Plant Life*. Springer-Verlag: Berlin, Germany, pp. 31-34.

Kuznetsova A, Brockhoff PB, Christensen RHB (2017). "lmerTest Package: Tests in Linear Mixed Effects Models." *Journal of Statistical Software*. 82(13):1-26. DOI: 10.18637/jss.v082.i13

Landolt E, Bäumler B, Erhardt A, Hegg O, Klölzli F, et al. (2010) *Flora indicativa. Ökologische Zeigerwerte und biologische Kennzeichen zur Flora der Schweiz und der Alpen*. Bern, Stuttgart, Wien: Haupt Verlag.

Langham GM, Schuetz JG, Distler T, Soykan CU & Wilsey C. (2015) Conservation status of North American birds in the face of future climate change. *PLoS ONE*. 10(9): e0135350. doi:10.1371/ journal.pone.0135350

Leafsnap. *Leafsnap: An Electronic Field Guide*. <leafsnap.com>.

Lecocq T, Rasmont P, Harpke A & Schweiger O. (2016) Improving International Trade Regulation by Considering Intraspecific Variation for Invasion Risk Assessment of Commercially Traded Species: The *Bombus terrestris* Case. *Conservation Letters*. 9(4):281-289.

Lee-Yaw JA, Kharouba HM, Bontrager M, Mahony C, Csergő AM, et al. (2016) A synthesis of transplant experiments and ecological niche models suggests that range limits are often niche limits. *Ecology Letters*. doi: 10.1111/ele.12604

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

Lenoir J, Gégout J-C, Guisan A, Vittoz P, Wohlgemuth T, Zimmermann, et al. (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

Liancourt P, Le Bagousse-Pinguet Y, Rixen C & Dolezal J. (2017) SGH: stress or strain gradient hypothesis? Insights from an elevation gradient on the roof of the world. *Annals of Botany*. doi:10.1093/aob/mcx037.

Liddle MJ. (1975) A selective review of the ecological effects of human trampling on natural ecosystems. *Biological Conservation*. 7:17-36.

Lira-Noriega A & Manthey JD. (2014) Relationship of genetic diversity and niche centrality: A survey and analysis. *Evolution*. 68(4):1082-1093.

Liu C, Berry PM, Dawson TP & Pearson RG. (2005) Selecting thresholds of occurrence in the prediction of species distributions. *Ecography*. 28:385-393.

Lobo JM, Jiménez-Valverde A & Real R. (2008) AUC: a misleading measure of the performance of predictive distribution models. *Global Ecology and Biogeography*. 17:145-151.

Lortie C. (2018). Global cushion plant community datasets. Knowledge Network for Biocomplexity. DOI: 10.5063/F1W957BW.
<<https://knb.ecoinformatics.org/#view/doi:10.5063/F1W957BW>>.

Louthan 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

Lucas-Borja ME, Bastida F, Moreno JL, Nicolás C, Andres M, López FR & Del Cerro A. (2011) The effects of human trampling on the microbiological properties of soil and vegetation in mediterranean mountain areas. *Land Degradation & Development*. 22:383-394.

Marcen A, Méndez-Vigo B, Alonso-Blanco C & Picó FX. (2016) Tackling intraspecific genetic structure in distribution models better reflects species geographical range. *Ecology and Evolution*. 6(7):2084-2097.

Martínez-Meyer E, Díaz-Porras D, Peterson AT & Yáñez-Arenas C. (2012) Ecological niche structure and rangewide abundance patterns of species. *Biology Letters*. 9:20120637.

Mayr E. (1956) Geographical character gradients and climatic adaptation. *Evolution*. 10(1):105-108.

Mazerolle MJ. (2016) AICcmodavg: Model selection and multimodel inference based on (Q)AIC(c). *R package version 2.0-4*. <<http://CRAN.R-project.org/package=AICcmodavg>>.

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

Merow C, Smith MJ & Silander, Jr. JA. (2013) A practical guide to MaxEnt for modeling species' distributions: what it does, and why inputs and settings matter. *Ecography*. 36:1058–1069.

Meynard CN, Gay PE, Lecoq M, Foucart A, Piou C & Chapuis MP. (2017) Climate-driven geographic distribution of the desert locust during recession periods: Subspecies' niche differentiation and relative risks under scenarios of climate change. *Global Change Biology*. 23(11):4739-4749.

Michalet R, Brooker RW, Cavieres LA, Kikvidze Z, Lortie CJ, et al. (2006) Do biotic interactions shape both sides of the humped-back model of species richness in plant communities? *Ecology Letters*. 9:767-773.

Michalet R, Xiao S, Touzard B, Smith DS, Cavieres LA, et al. (2011) Phenotypic variation in nurse traits and community feedbacks define an alpine community. *Ecology Letters*. 14:433-443.

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 & Pugnaire FI. (2016) Facilitation in communities: underlying mechanisms, community, and ecosystem implications. *Functional Ecology*. 30:3-9.

Mod HK, le Roux PC, Guisan A & Luoto M. (2015) Biotic interactions boost spatial models of species richness. *Ecography*. 38:913-921.

Molenda O, Reid A & Lortie CJ. (2012) The alpine cushion plant *Silene acaulis* as foundation species: a bug's-eye view to facilitation and microclimate. *PLoS ONE* 7(5): e37223. doi:10.1371/journal.pone.0037223.

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

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

MRS. (2017) *Plant Species Composition, Niwot Ridge and Green Lakes Valley*. Compiled by Komarkova V, Walker M & Smith J. <<https://www.colorado.edu/mrs/research-natural-history/species-lists/plant-species-composition>>.

Niwot-LTER. *Niwot Ridge LTER*. Niwot Ridge Long Term Ecological Research (LTER). Accessed 17 July 2018. <<http://niwot.colorado.edu/location>>.

Oksanen J, Blanchet FG, Friendly M, Kindt R, Legendre P, et al. (2017) *vegan: Community Ecology Package. R package version 2.4-2*. <<https://CRAN.R-project.org/package=vegan>>.

Oksanen J, Blanchet FG, Friendly M, Kindt R, Legendre P, McGlinn D, Minchin PR, O'Hara RB, Simpson GL, Solymos P, Stevens MHH, Szoecs E & Wagner H. (2018). *vegan: Community Ecology Package. R package version 2.5-2*. <<https://CRAN.R-project.org/package=vegan>>.

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

Oney B, Reineking B, O'Neill G & Kreyling J. (2013) Intraspecific variation buffers projected climate change impacts on *Pinus contorta*. *Ecology and Evolution*. 3(2):437-449.

Pacifi M, Foden WB, Visconti P, Watson JEM, Butchart SHM, et al. (2015). Assessing species vulnerability to climate change. *Nature Climate Change*. 5:215-225.

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.aq1819

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

Pearman PB, D'Amen M, Graham C, Thuiller W & Zimmermann NE. (2010) Within-taxon niche structure: niche conservatism, divergence and predicted effects of climate change. *Ecography*. 33(6):990-1003.

Pebesma EJ & Bivand RS. (2005) Classes and methods for spatial data in R. *R News* 5(2). <<https://cran.r-project.org/doc/Rnews/>>.

Pelini SL, Dzurisin JDK, Prior KM, Williams CM, Marsico TD, Sinclair BJ & Helmann JL. (2009) *PNAS*. 106(27):11160-11165.

Peterson ML, Doak DF & Morris WF. (2018) Both life-history plasticity and local adaptation will shape range-wide responses to climate warming in the tundra plant *Silene acaulis*. *Global Change Biology*. 24:1614-1625.

Phillips SJ, Anderson RP, Schapire RE. (2006) Maximum entropy modeling of species geographic distributions. *Ecological Modelling*. 190:231–259.

Phillips SJ, Dudík M & Schapire RE. [Internet] Maxent software for modeling species niches and distributions (Version 3.4.1). Accessed 6 June 2018. <http://biodiversityinformatics.amnh.org/open_source/maxent/>.

Phillips SJ, Anderson RP, Dudík M, Schapire RE & Blair ME. (2017) Opening the black box: an open-source release of Maxent. *Ecography*. 40:887-893.

Pl@ntNet. *Identify, explore and share your observations of wild plant*. <identify.plantnet-project.org>.

Pickering DM, Hill W, Newsome D & Leung Y-F. (2010) Comparing hiking, mountain biking and horse riding impacts on vegetation and soils in Australia and the United States of America. *Journal of Environmental Management*. 91:551-562.

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

Pironon S, Villellas J, Morris WF, Doak DF & García MB. (2015) Do geographic, climatic or historical ranges differentiate the performance of central versus peripheral populations? *Global Ecology and Biogeography*. 24(6):611-620.

Pironon S, Papuga G, Villellas J, Angert AL, García MB & Thompson JD. (2017) Geographic variation in genetic and demographic performance: New insights from an old biogeographical paradigm. *Biological Reviews*. 92:1877-1909.

Pironon S, Villellas J, Thuiller W, Eckhart VM, Geber MA, et al. (2018) The ‘Hutchinsonian niche’ as an assemblage of demographic niches: Implications for species geographic ranges. *Ecography*. 41:1103-1113.

- R Core Team. (2017) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. <<http://www.R-project.org/>>.
- R Core Team. (2018) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. <<http://www.R-project.org/>>.
- Ruegg K, Bay RA, Anderson EC, Saracco JF, Harrigan RJ, et al. (2018) Ecological genomics predicts climate vulnerability in an endangered southwestern songbird. *Ecology Letters*. 21:1085-1096.
- 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
- 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
- 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/>>.
- Sandoya V, Pauchard A & Cavieres LA. (2017) Natives and non-natives plants show different responses to elevation and disturbance on the tropical high Andes of Ecuador. *Ecology and Evolution*. DOI: 10.1002/ece3.3270.
- Santini L, Pironon S, Maiorano L & Thuiller W. (2018) Addressing common pitfalls does not provide more support to geographical and ecological abundant-centre hypotheses. *Ecography*. doi: 10.1111/ecog.04027
- Schöb C, Butterfield BJ & Pugnaire FI. (2012) Foundation species influence trait-based community assembly. *New Phytologist*. 196:824-834.
- Schöb C, Michalet R, Cavieres LA, Pugnaire FI, Brooker RW, et al. (2014) A global analysis of bidirectional interactions in alpine plant communities shows facilitators experiencing strong reciprocal fitness costs. *New Phytologist*. 202:95-105.
- Schurr FM, Pagel J, Cabral JS, Groeneveld J, Bykova O, et al. (2012) How to understand species' niches and range dynamics: a demographic research agenda for biogeography. *Journal of Biogeography*. 39:2146-2162.

- Schwalm D, Epps CW, Rodhouse TJ, Monahan WB, Castillo JA, Ray C & Jeffress MR. (2016) Habitat availability and gene flow influence diverging local population trajectories under scenarios of climate change: a place-based approach. *Global Change Biology*. 22:1572-1584.
- Serra-Varela MJ, Alía R, Daniels RR, Zimmermann NE, Gonzalo-Jiménez J & Grivet D. (2017) Assessing vulnerability of two Mediterranean conifers to support genetic conservation management in the face of climate change. *Diversity and Distributions*. 23(5):507-516.
- 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.
- Shabani F, Kumar L & Ahmadi M. (2016) A comparison of absolute performance of different correlative and mechanistic species distribution models in an independent área. *Ecology and Evolution*. 6(16):5973-5986.
- Sheil D. (2016) Disturbance and distributions: avoiding exclusion in a warming world. *Ecology and Society*. 21(1):10. doi:10.5751/ES-07920-210110
- Silvertown J. (2009) A new dawn for citizen science. *Trends in Ecology & Evolution*. 24(9):467-471. doi:10.1016/j.tree.2009.03.017
- 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
- 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.
- Smith JG & Chardon NI (2015, August). *Luminous ID: Alpine plant recognition and field guide smartphone app developed for Niwot Ridge LTER*. Poster session presented at Long Term Ecological Research All Scientist Meeting, Estes Park, Colorado.
- 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
- Sork VL, Davis FW, Westfall R, Flint A, Ikegami M, Wang H & Grivet D. (2010) Gene movement and genetic association with regional climate gradients in

California valley oak (*Quercus lobata* Nee) in the face of climate change. *Molecular Ecology*. 19(17):3806-3823.

Sousa WP. (1984) The role of disturbance in natural communities. *Annual Review of Ecology and Systematics*. 15:353-391.

Suding KN & Goldberg D. (2001) Do disturbances alter competitive hierarchies? Mechanisms of change following gap creation. *Ecology*. 82(8):2133-2149.

Sullivan BL, Wood CL, Illif MJ, Bonney RE, Fink D & Kelling S. (2009) eBird: A citizen-based bird observation network in the biological sciences. *Biological Conservation*. 142:2282-2292. doi:10.1016/j.biocon.2009.05.006

Tewksbury JJ & Lloyd JD. (2001) Positive interactions under nurse-plants: spatial scale, stress gradients and benefactor size. *Oecologia*. 127:425-434.

thematicmapping.org. [Internet]. Data retrieved 5 July 2018.
<http://thematicmapping.org/downloads/world_borders.php>.

Theodoridis S, Patsiou TS, Randin C & Conti E. (2018) Forecasting range shifts of a cold-adapted species under climate change: are genomic and ecological diversity within species crucial for future resilience? *Ecography*. 41:1357-1369.

Thuiller W, Albert CH, Dubuis A, Randin C & Guisan A. (2009) Variation in habitat suitability does not always relate to variation in species' plant functional traits. *Biology Letters*. DOI: 10.1098/rsbl.2009.0669

Thuiller W, Münkemüller T, Schiffrers KH, Georges D, Dullinger S, et al. (2014) Does probability of occurrence relate to population dynamics? *Ecography*. 37:1155-1166.

Turner M. (2010) Disturbance and landscape dynamics in a changing world. *Ecology*. 91(10):2833-2849.

Ureta C, Martínez-Meyer E, Perales HR & Álvarez-Buylla ER. (2012) Projecting the effects of climate change on the distribution of maize races and their wild relatives in Mexico. *Global Change Biology*. 18(3):1073-1082.

Van Couwenberghe R, Collet C, Pierrat JC, Verheyen K & Gégout JC. (2013) Can species distribution models be used to describe plant abundance patterns? *Ecography*. 36:665-674.

VanDerWal J, Shoo LK, Johnson CN & Williams SE. (2009) Abundance and the environmental niche: Environmental suitability estimated from niche models

predicts the upper limit of local abundance. *The American Naturalist*. 174(2):282-291.

van der Wal R, Anderson H, Robinson A, Sharma N, Mellish C, et al. (2015) Mapping species distributions: a comparison of skilled naturalist and lay citizen science recording. *Ambio*. 44(Suppl. 4):S584-S600. doi:10.1007/s13280-015-0709-x

Veloz SD, Williams JW, Blois JL, He F, Otto-Bliesner B & Liu Z. (2012) No-analog climates and shifting realized niches during the late quaternary: implications for 21st-century predictions by species distribution models. *Global Change Biology*. 18:1698-1713.

Warren D, Glor RE & Turelli M. (2008) Environmental niche equivalency versus conservatism: quantitative approaches to niche evolution. *Evolution*. 62(11):2868-2883.

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.

Wiens JA, Stralberg D, Jongsomjit D, Howell CA & Snyder MA. (2009) Niches, models, and climate change: assessing the assumptions and uncertainties. *Proceedings of the National Academy of Sciences USA*. 106 (Suppl. 2):19729–19736.

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

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.

WWF [Internet] WWF Global Lakes and Wetlands Database. Data retrieved 5 July 2018.
<<https://www.worldwildlife.org/publications/global-lakes-and-wetlands-database-large-lake-polygons-level-1>>.

Yang Y, Chen J-G, Schöb C & Hang S. (2017) Size-mediated interaction between a cushion species and other non-cushion species at high elevations of the Hengduan Mountains, SW China. *Frontiers in Plant Science*. DOI: 10.3389/fpls.2017.00465.

APPENDIX A

Chapter 2 Appendix

A.A. Additional Figures and Tables

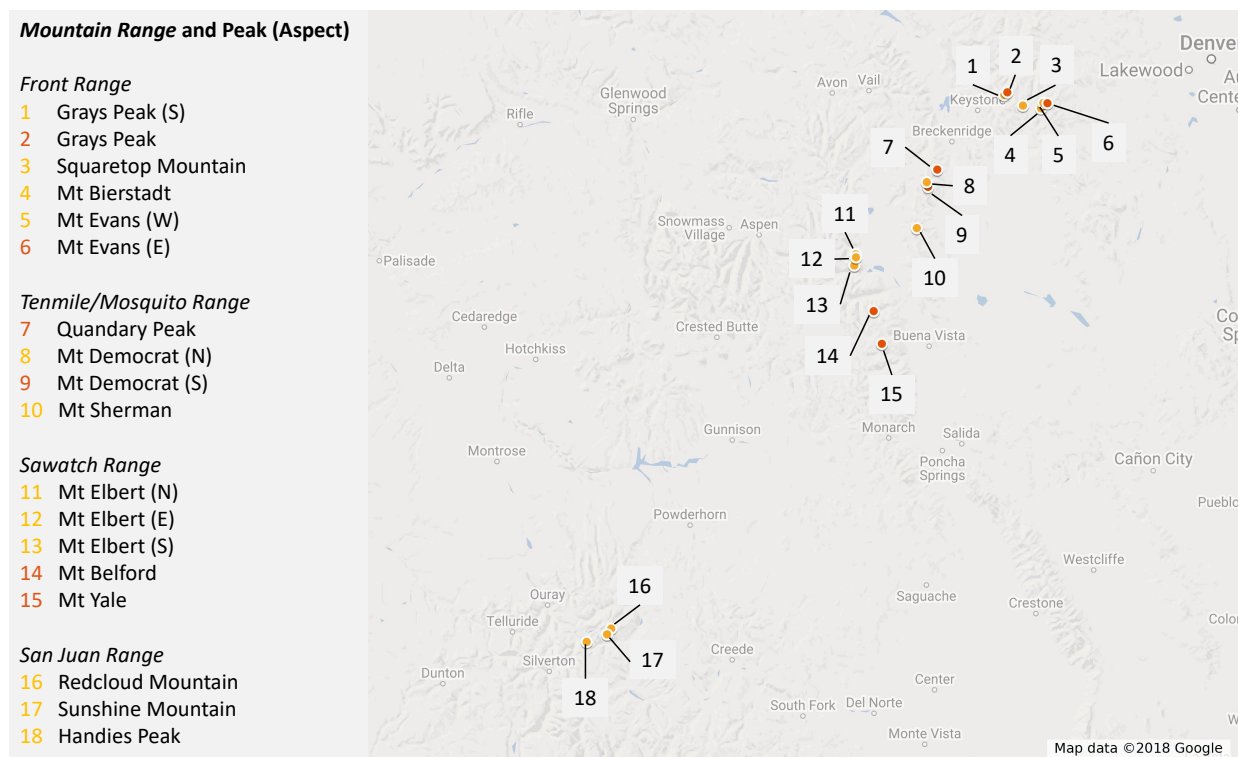


Figure A.A.1: Sampling locations. We conducted surveys on 14,000 ft peaks across four mountain ranges in the Colorado Rocky Mountains. We deployed temperature loggers at six select peaks (red circles and red number in legend; all others in orange). Aspect within a peak is indicated in the legend if we sampled more than one slope for that particular peak. Note that only part of western Colorado is shown (Map data © 2018 Google).

A



B



Figure A.A.2: Study species. *Silene acaulis* (A) and *Minuartia obtusiloba* (B; photo: William Bowman) are widely distributed facilitative alpine cushion plants that are commonly found in the Colorado Rocky Mountains.

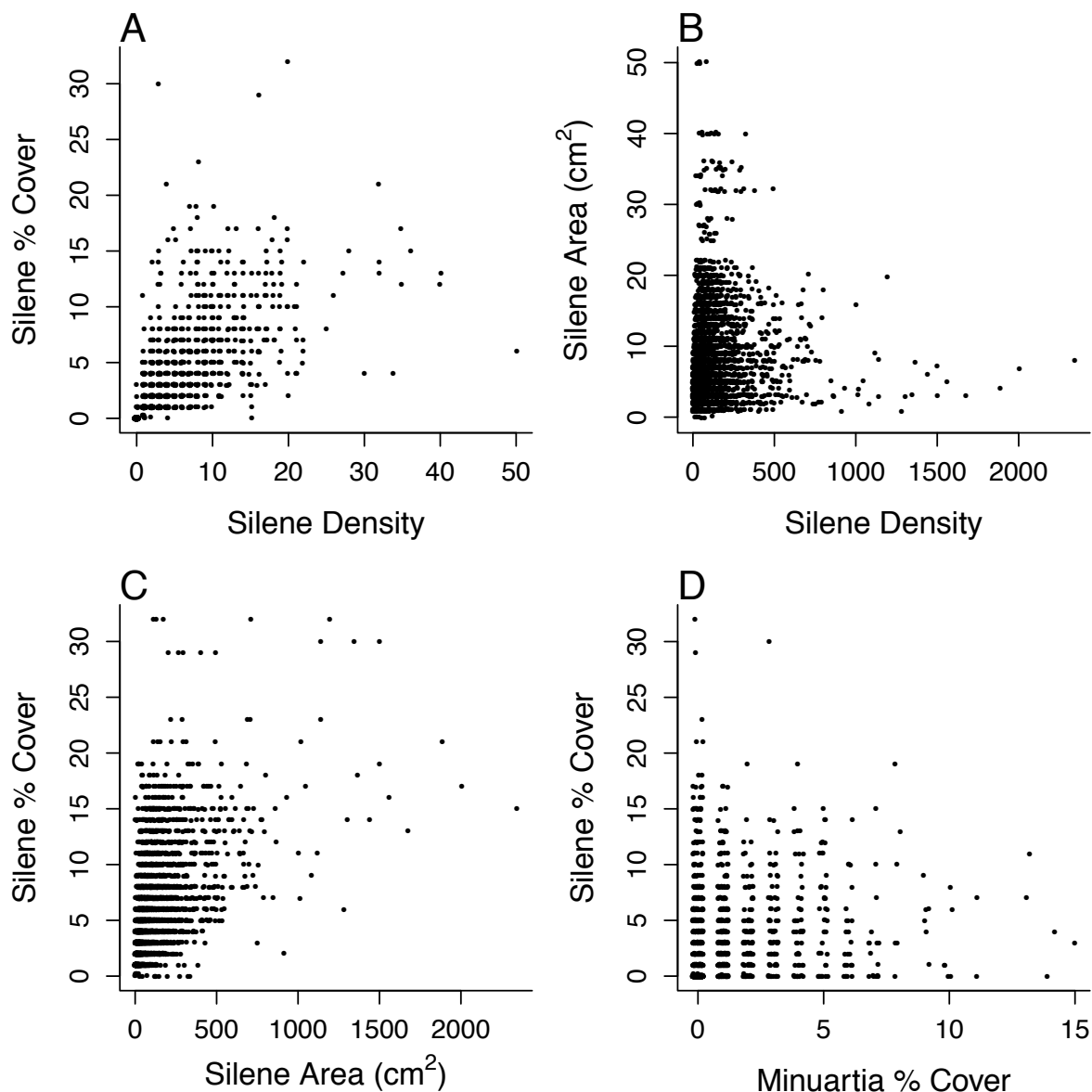


Figure A.A.3: Correlations between cushion plant variables. The three variables we measured (percent cover, density, and maximum cushion area) as proxies for *Silene* population performance indicators are all moderately to strongly correlated (A: correlation = 0.70; B: 0.45, C: 0.47). *Silene acaulis* and *Minuartia obtusiloba* percent cover values are weakly correlated (D: 0.18). Note that axes are on different scales. Data points jittered for clarity.

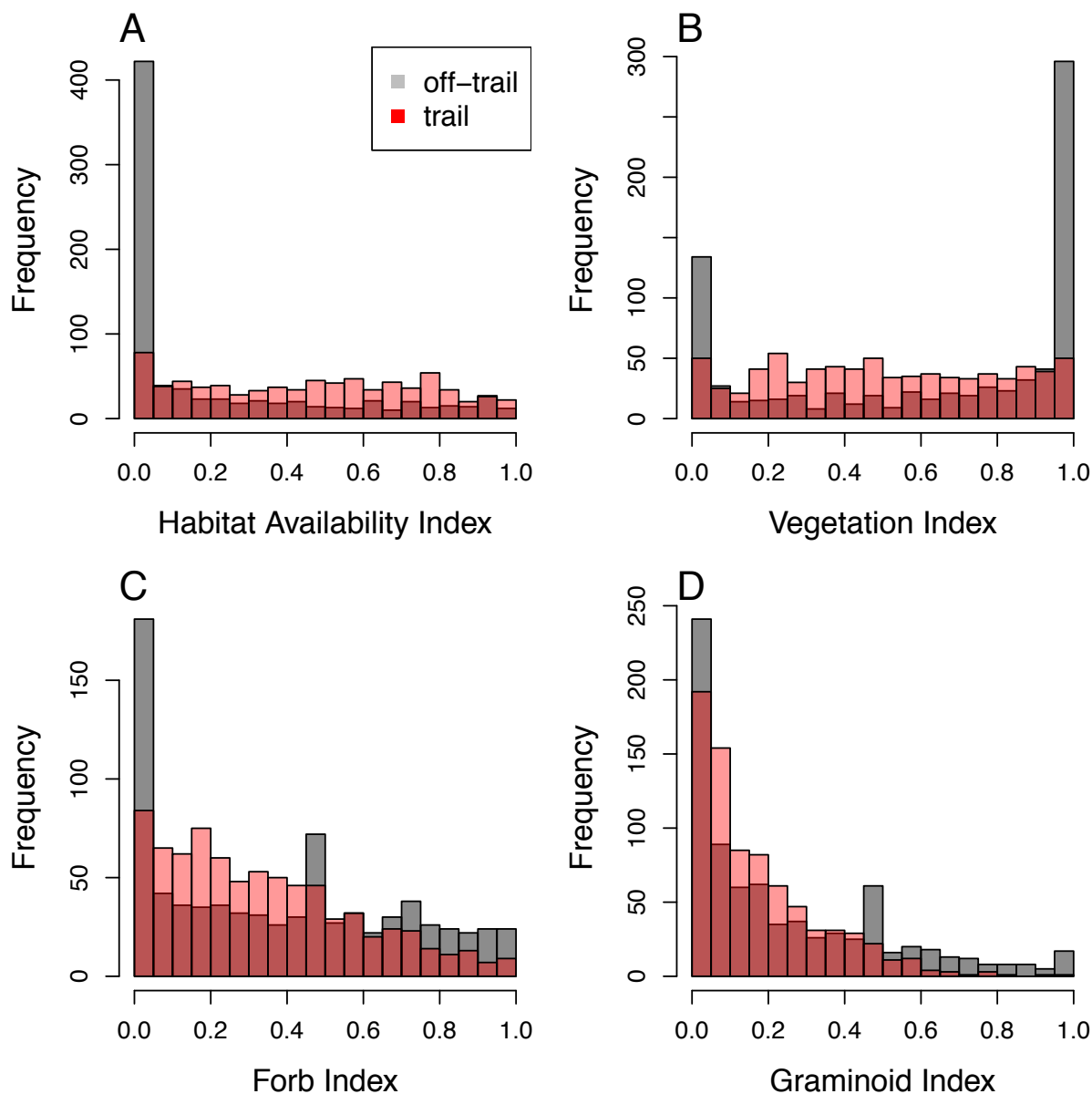


Figure A.A.4: Vegetation, forb, graminoid, and habitat availability indices at off-trail and trail transect. Compared to undisturbed transects, disturbed transects have higher habitat availability index values (A), and lower vegetation (B), forb (C), as well as graminoid (D) values.

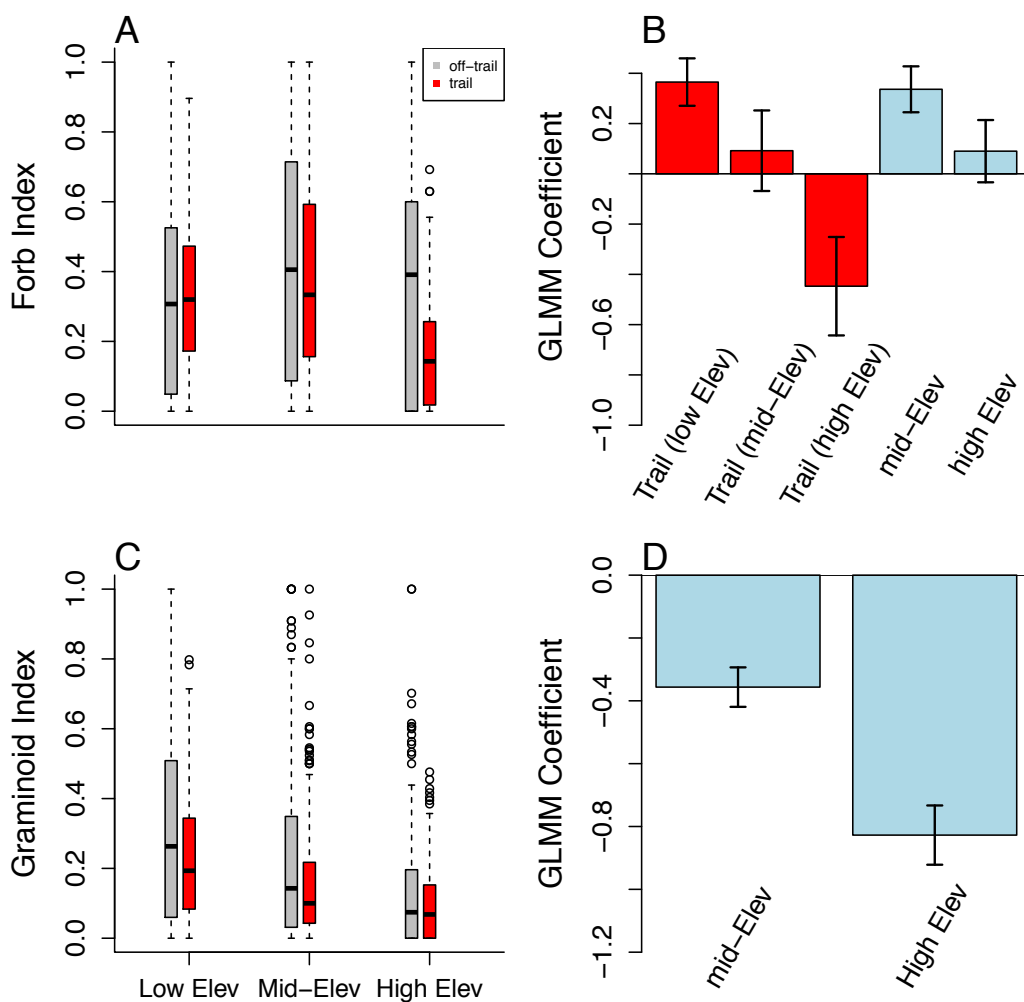


Figure A.A.5: Effect of trail disturbance and elevation on forbs and graminoids. Trail disturbance increases forbs (A) at lower elevations, an effect that switches to negative at higher elevations. In contrast, trail has no significant effect on graminoids (C), which decrease with elevation (D). Coefficients for Trail (mid-Elev) and Trail (high Elev) are the sum of the effects of trail and the respective by elevation interaction effect \pm adjusted standard error. All other coefficients are from raw model outputs \pm standard error. Colors in (C) are as in (A).

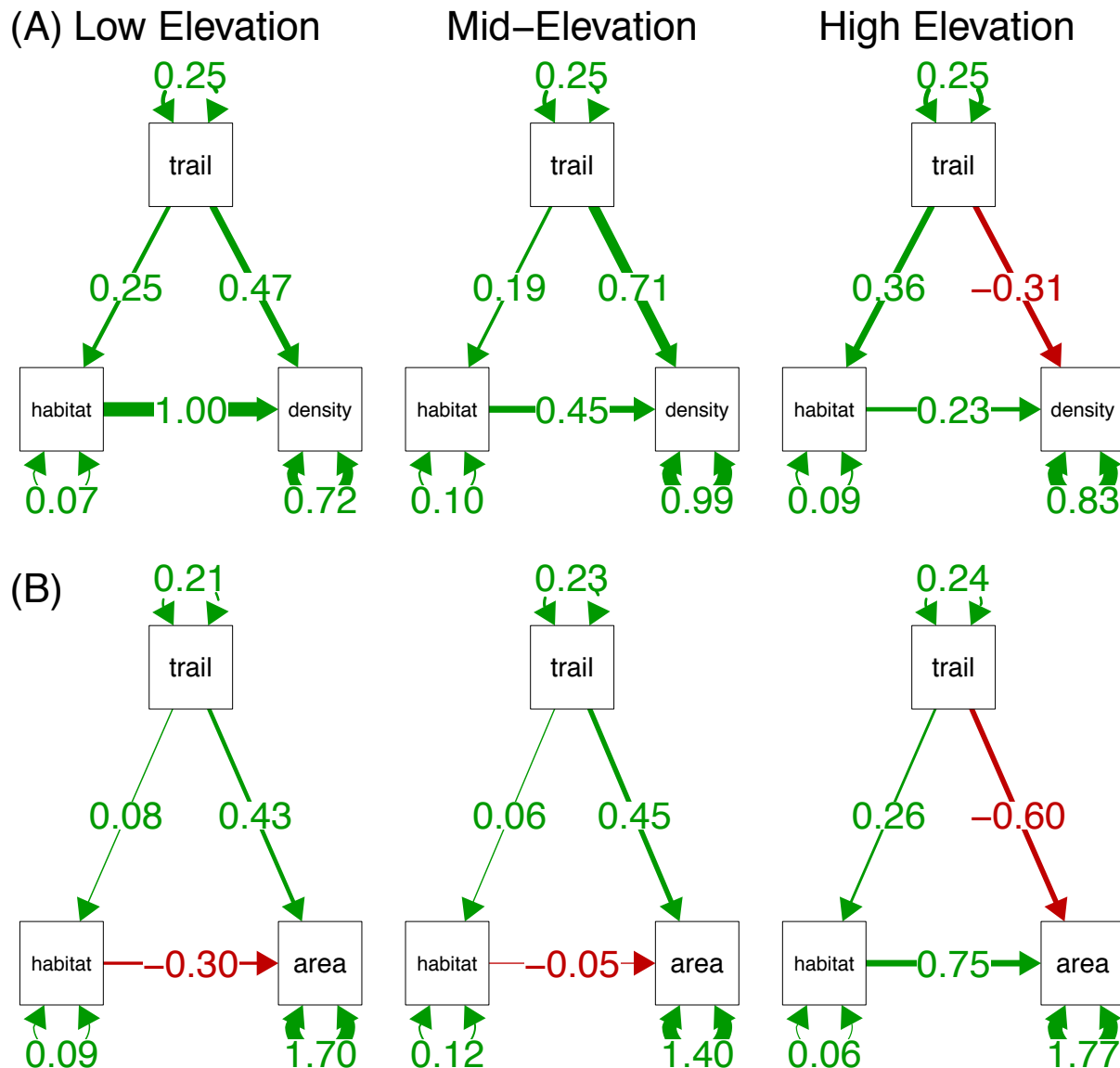


Figure A.A.6: Structural Equation Pathways for *Silene acaulis*. Structural Equation Models (SEMs) for *Silene acaulis* (A) density and (B) maximum cushion size for low, mid-, and high elevations. Habitat availability (habitat) is most important for *Silene* density at lowest elevations, and the positive effect of trail at lower elevations dominates with a negative effect at higher elevations. Habitat availability has a negative effect on maximum cushion area at lower elevations, but a positive effect at higher elevations. Area is positively influenced by trail disturbance at lowest elevations, but negatively at higher elevations. Model estimates are shown within each arrow, thickness of arrows reflect effect strength, and green and red colors indicate positive (+) and negative (-) effect, respectively. See Tables A.A5, A.A6 for details on model results.

Table A.A.1. List of all models testing the effect of trail disturbance (trail) and elevational level (level) on (A) *Silene acaulis* and *Minuartia obtusiloba* performance indicators and (B) all vegetation and habitat indices (see Materials & Methods for model details). Number of parameters (k), sample size (n), and Δ AICc with respect to most parsimonious model shown. All models tested with random intercept and random effect of site (1 | id).

A

type	y	model	k	n	Δ AICc
GLMM	Minuartia cover	trail * level + (1 id)	6	1561	0
GLMM	Minuartia cover	trail + level + (1 id)	4	1561	5.4
GLMM	Minuartia cover	trail + (1 id)	2	1561	56.7
GLMM	Minuartia cover	level + (1 id)	3	1561	66.76
LMM	Silene area	trail * level + (1 id)	6	3490	0
LMM	Silene area	trail + (1 id)	2	3490	20.99
LMM	Silene area	trail + level + (1 id)	4	3490	23.26
LMM	Silene area	(1 id)	1	3490	52.38
LMM	Silene area	level + (1 id)	3	3490	55.95
GLMM	Silene cover	trail * level + (1 id)	6	936	0
GLMM	Silene cover	trail + (1 id)	2	936	6.95
GLMM	Silene cover	trail + level + (1 id)	4	936	8.45
GLMM	Silene cover	level + (1 id)	3	936	20.94
LMM	Silene density	trail * level + (1 id)	6	1561	0
LMM	Silene density	trail + level + (1 id)	4	1561	53.85
LMM	Silene density	trail + (1 id)	2	1561	89.98
LMM	Silene density	level + (1 id)	3	1561	215.02
LMM	Silene density	(1 id)	1	1561	246.95

B

type	y	model	k	n	Δ AICc
GLMM	forb	trail * level + (1 id)	6	1561	0
GLMM	forb	trail + level + (1 id)	4	1561	18.27
GLMM	forb	level + (1 id)	3	1561	19.65
GLMM	forb	trail + (1 id)	2	1561	43.62
GLMM	graminoid	level + (1 id)	3	1561	0
GLMM	graminoid	trail + level + (1 id)	4	1561	1.24
GLMM	graminoid	trail * level + (1 id)	6	1561	3.38
GLMM	graminoid	trail + (1 id)	2	1561	81.26
GLMM	habitat availability	trail * level + (1 id)	6	1561	0
GLMM	habitat availability	trail + level + (1 id)	4	1561	3.24
GLMM	habitat availability	trail + (1 id)	2	1561	5.32
GLMM	habitat availability	level + (1 id)	3	1561	393.42
GLMM	vegetation	trail + level + (1 id)	4	1561	0
GLMM	vegetation	trail * level + (1 id)	6	1561	1.9
GLMM	vegetation	trail + (1 id)	2	1561	34.37
GLMM	vegetation	level + (1 id)	3	1561	46.68

Table A.A.2. List of all models testing the effect of all vegetation and habitat availability indices as well as elevational level on *Silene acaulis* and *Minuartia obtusiloba* performance indicators (see Materials & Methods for model details). Number of parameters (k), sample size (n), and Δ AICc with respect to most parsimonious model shown. All models tested with random effect of site (id).

type	y	model	k	n	Δ AICc
GLMM	Minuartia cover	habitat availability * level + (1 id)	6	1561	0
GLMM	Minuartia cover	habitat availability + level + (1 id)	4	1561	5.8
GLMM	Minuartia cover	level + (1 id)	3	1561	35.66
GLMM	Minuartia cover	graminoid * level + (1 id)	6	1561	36.62
GLMM	Minuartia cover	graminoid + level + (1 id)	4	1561	36.66
GLMM	Minuartia cover	vegetation + level + (1 id)	4	1561	36.78
GLMM	Minuartia cover	forb + level + (1 id)	4	1561	37
GLMM	Minuartia cover	vegetation * level + (1 id)	6	1561	37.64
GLMM	Minuartia cover	forb * level + (1 id)	6	1561	39.14
GLMM	Minuartia cover	habitat availability + (1 id)	2	1561	59.16
GLMM	Minuartia cover	forb + (1 id)	2	1561	77.96
GLMM	Minuartia cover	graminoid + (1 id)	2	1561	78.8
GLMM	Minuartia cover	vegetation + (1 id)	2	1561	79.38
LMM	Silene area	vegetation + (1 id)	2	3490	0
LMM	Silene area	vegetation + level + (1 id)	4	3490	3.16
LMM	Silene area	habitat availability + (1 id)	2	3490	5.34
LMM	Silene area	forb + (1 id)	2	3490	6.83
LMM	Silene area	habitat availability + level + (1 id)	4	3490	8.49
LMM	Silene area	vegetation * level + (1 id)	6	3490	9.4
LMM	Silene area	forb + level + (1 id)	4	3490	12.2
LMM	Silene area	(1 id)	1	3490	12.7
LMM	Silene area	graminoid + (1 id)	2	3490	12.89
LMM	Silene area	forb * level + (1 id)	6	3490	13.67
LMM	Silene area	graminoid + level + (1 id)	4	3490	14.18
LMM	Silene area	graminoid * level + (1 id)	6	3490	14.31
LMM	Silene area	habitat availability * level + (1 id)	6	3490	15.18
LMM	Silene area	level + (1 id)	3	3490	16.28
GLMM	Silene cover	habitat availability * level + (1 id)	6	1561	0
GLMM	Silene cover	habitat availability + level + (1 id)	4	1561	31.28
GLMM	Silene cover	habitat availability + (1 id)	2	1561	67.08
GLMM	Silene cover	graminoid * level + (1 id)	6	1561	81.56
GLMM	Silene cover	vegetation * level + (1 id)	6	1561	87.1
GLMM	Silene cover	level + (1 id)	3	1561	98.26
GLMM	Silene cover	graminoid + level + (1 id)	4	1561	99.48
GLMM	Silene cover	forb + level + (1 id)	4	1561	100.04
GLMM	Silene cover	forb * level + (1 id)	6	1561	100.12

GLMM	Silene cover	vegetation + level + (1 id)	4	1561	100.24
GLMM	Silene cover	forb + (1 id)	2	1561	121.28
GLMM	Silene cover	vegetation + (1 id)	2	1561	122.68
GLMM	Silene cover	graminoid + (1 id)	2	1561	123.08
LMM	Silene density	habitat availability * level + (1 id)	6	1561	0
LMM	Silene density	habitat availability + level + (1 id)	4	1561	48.22
LMM	Silene density	habitat availability + (1 id)	2	1561	85.09
LMM	Silene density	graminoid * level + (1 id)	6	1561	94.19
LMM	Silene density	vegetation * level + (1 id)	6	1561	102.87
LMM	Silene density	level + (1 id)	3	1561	120.11
LMM	Silene density	forb * level + (1 id)	6	1561	120.5
LMM	Silene density	forb + level + (1 id)	4	1561	124.44
LMM	Silene density	graminoid + level + (1 id)	4	1561	124.51
LMM	Silene density	vegetation + level + (1 id)	4	1561	125.21
LMM	Silene density	(1 id)	1	1561	152.03
LMM	Silene density	forb + (1 id)	2	1561	153.7
LMM	Silene density	vegetation + (1 id)	2	1561	156.07
LMM	Silene density	graminoid + (1 id)	2	1561	156.36

Table A.A.3. Structural Equation Model results for *Silene acaulis* percent cover. See Fig. 2.6a for visualization of results.

model			estimate	SE	p-value
<i>Low Elevation (chi-square = 1.59e-13 , RMSEA = 0 , DF = 3 , n = 359)</i>					
habitat availability	~	trail	0.087	0.031	0.005
Silene cover	~	habitat availability	0.298	0.204	0.145
Silene cover	~	trail	0.308	0.122	0.012
habitat availability	~~	habitat availability	0.075	0.006	0
Silene cover	~~	Silene cover	1.122	0.084	0
trail	~~	trail	0.214	0	NA
<i>Mid-Elevation (chi-square = 0 , RMSEA = 0 , DF = 3 , n = 479)</i>					
habitat availability	~	trail	0.093	0.03	0.002
Silene cover	~	habitat availability	0.269	0.14	0.055
Silene cover	~	trail	0.372	0.093	0
habitat availability	~~	habitat availability	0.1	0.006	0
Silene cover	~~	Silene cover	0.944	0.061	0
trail	~~	trail	0.234	0	NA
<i>High Elevation (chi-square = 0 , RMSEA = 0 , DF = 3 , n = 98)</i>					
habitat availability	~	trail	0.429	0.046	0
Silene cover	~	habitat availability	0.36	0.505	0.476
Silene cover	~	trail	-0.447	0.317	0.159
habitat availability	~~	habitat availability	0.052	0.007	0
Silene cover	~~	Silene cover	1.306	0.187	0
trail	~~	trail	0.249	0	NA

Table A.A.4. Structural Equation Model results for *Minuartia obtusiloba* percent cover. See Fig. 2.6b for visualization of results.

model			estimate	SE	p-value
<i>Low Elevation (chi-square = 2.13e-12 , RMSEA = 0 , DF = 3 , n = 600)</i>					
habitat availability	~	trail	0.254	0.021	0
Minuartia cover	~	habitat availability	0.517	0.17	0.002
Minuartia cover	~	trail	0.48	0.099	0
habitat availability	~~	habitat availability	0.069	0.004	0
Minuartia cover	~~	Minuartia cover	1.191	0.069	0
trail	~~	trail	0.25	0	NA
<i>Mid-Elevation (chi-square = 0 , RMSEA = 0 , DF = 3 , n = 721)</i>					
habitat availability	~	trail	0.186	0.024	0
Minuartia cover	~	habitat availability	0.311	0.102	0.002
Minuartia cover	~	trail	0.163	0.068	0.016
habitat availability	~~	habitat availability	0.101	0.005	0
Minuartia cover	~~	Minuartia cover	0.761	0.04	0
trail	~~	trail	0.25	0	NA
<i>High Elevation (chi-square = 1.07e-13 , RMSEA = 0 , DF = 3 , n = 240)</i>					
habitat availability	~	trail	0.365	0.038	0
Minuartia cover	~	habitat availability	0.049	0.174	0.778
Minuartia cover	~	trail	0.098	0.12	0.411
habitat availability	~~	habitat availability	0.085	0.008	0
Minuartia cover	~~	Minuartia cover	0.618	0.056	0
trail	~~	trail	0.25	0	NA

Table A.A.5. Structural Equation Model results for *Silene acaulis* density per 1m² quadrat. See Fig. A.A.6a for visualization of results.

model			estimate	SE	p-value
<i>Low Elevation (chi-square = 2.7e-13, RMSEA = 0, DF = 3, n = 600)</i>					
habitat	~	trail	0.254	0.021	0
density	~	habitat	0.996	0.132	0
density	~	trail	0.467	0.077	0
habitat	~~	habitat	0.069	0.004	0
density	~~	density	0.715	0.041	0
trail	~~	trail	0.25	0	NA
<i>Mid-Elevation (chi-square = 0, RMSEA = 0, DF = 3, n = 721)</i>					
habitat	~	trail	0.186	0.024	0
density	~	habitat	0.451	0.116	0
density	~	trail	0.708	0.077	0
habitat	~~	habitat	0.101	0.005	0
density	~~	density	0.988	0.052	0
trail	~~	trail	0.25	0	NA
<i>High Elevation (chi-square = 0, RMSEA = 0, DF = 3, n = 240)</i>					
habitat	~	trail	0.365	0.038	0
density	~	habitat	0.225	0.202	0.264
density	~	trail	-0.311	0.139	0.025
habitat	~~	habitat	0.085	0.008	0
density	~~	density	0.835	0.076	0
trail	~~	trail	0.25	0	NA

Table A.A.6. Structural Equation Model results for *Silene acaulis* cushion area. See Fig. A.A.6b for visualization of results.

model			estimate	SE	p-value
<i>Low Elevation (chi-square = 2.18e-12, RMSEA = 0, DF = 3, n = 1229)</i>					
habitat	~	trail	0.083	0.019	0
area	~	habitat	-0.303	0.124	0.015
area	~	trail	0.431	0.081	0
habitat	~~	habitat	0.09	0.004	0
area	~~	area	1.698	0.068	0
trail	~~	trail	0.213	0	NA
<i>Mid-Elevation (chi-square = 8.6e-13, RMSEA = 0, DF = 3, n = 1936)</i>					
habitat	~	trail	0.063	0.016	0
area	~	habitat	-0.055	0.079	0.488
area	~	trail	0.451	0.056	0
habitat	~~	habitat	0.117	0.004	0
area	~~	area	1.401	0.045	0
trail	~~	trail	0.229	0	NA
<i>High Elevation (chi-square = 0, RMSEA = 0, DF = 3, n = 325)</i>					
habitat	~	trail	0.255	0.027	0
area	~	habitat	0.745	0.313	0.017
area	~	trail	-0.601	0.17	0
habitat	~~	habitat	0.056	0.004	0
area	~~	area	1.769	0.139	0
trail	~~	trail	0.241	0	NA

A.B. Details on sampling and additional variables

A.B.1. Data collection

We established two to three 10x1 m² trailside transects at the lowest occurring *Silene* population found along each trail (median elevation = 3710 m), as well as 210-335 m (~700-1,100 ft) higher up (median elevation = 3983 m) for mid-range populations (n = 18; Fig. 2.2). At sites where *Silene* occurred at least 60 elevational m (200 ft) above the mid-range transects, we also established two trailside transects at the highest (median elevation = 4056 m) occurring population (n = 5). All trailside transects had to have a minimum of five 1 m² quadrats with *Silene* occurrence, in order to avoid transects that provided minimal data. Almost all (86%) trail-side transects also had *Minuartia* presence. We defined the edge of each transect by placing quadrats at the first occurring vegetation relative to the middle of the trail, which was usually the trail cut. We established off-trail transects at least 10 m away from their paired trailside transect and with no major visible signs of hiker or animal disturbance. Off-trail transects had similar slope and aspect to the trail transect. The transects were parallel to their paired trailside and followed a straight 10 m line.

Within each 1 m² quadrat of each transect, we quantified three *Silene* population performance indicators (Table 2.1). First, we measured the two-dimensional area of the five largest *Silene* cushions (following Doak & Morris 2010) within each quadrat. We also estimated both the total percent cover of *Silene* and counted number of individuals with > 20 rosettes as a measure of density. We also

estimated percent cover of *Minuartia*, but did not take other data on this species.

These cushion plant performance indicators are all positively correlated (Fig.

A.A.3). To estimate percent cover, we used a 1 m² quadrat gridded into 10 cm² for 1% grids (see photo insets in Fig. 2.2). If either species was present but at less than 1% cover, we recorded it as 1% to capture all occurrences.

To quantify competitive vegetation, we recorded percent cover of graminoids and of forbs (excluding *Silene* and *Minuartia*) within each quadrat. As an estimate of the unoccupied available habitat, we recorded percent cover of bare ground (soil particle diameter < 2 cm). We estimated all cover estimates to the nearest 5% and recorded cover less than 1% cover as 1%. As we were specifically interested in the effects of disturbance on these habitat availability and vegetation estimates, for our analyses we converted the raw percent cover values to account for uninhabitable areas of rock. We calculated vegetation, forb, graminoid, and habitat availability indices as follows: Vegetation Index = vegetation % cover / (vegetation % cover + bare ground % cover); Forb Index = forb % cover / (forb % cover + graminoid % cover + bare ground % cover); Graminoid Index = graminoid % cover / (graminoid % cover + forb % cover + bare ground % cover); Habitat availability Index = bare ground % cover / (bare ground % cover + vegetation % cover). We calculated all indices respective to *Silene* or *Minuartia*, excluding their percent cover where appropriate. A vegetation index of 0.5 would therefore indicate that half of the potentially habitable space for *Silene* is occupied by competitors, including *Minuartia*. Similarly, a habitat availability index of 0.25 would indicate that only a quarter of

potentially inhabitable space is available for cushion plant establishment. These indices effectively allowed us to control for variable rock cover along our sampled elevational gradient, while providing us with two negatively correlated (-0.62) indices of vegetation and habitat availability for our analyses.

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 (five sites with three sampled elevational range locations plus an additional site). At these six sites, also we recorded daily temperatures with temperature loggers (Maxim Integrated iButtons, CA, USA) buried 2-5 cm below ground between September 2016 – September 2017. This would allow us to understand if cushion plant populations are more responsive to polar growing season microclimate patterns or regional temperature by elevation. We deployed temperature buttons at two off-trail transects per elevational range location ($n = 2$ per elevation, $n = 4-6$ per site), to decrease the probability of discovery by hikers.

We quantified our elevational and climatic gradient with elevational levels based on *Silene*'s range limit (lower, middle, upper elevational range locations) and microscale temperature (Table 2.1). We used elevational level as a proxy for temperature, as it strongly predicts temperature (LMM with random effect of site: negative effect of level on temperature, $p\text{-value} < 0.0001$) and performed as a better predictor in our statistical models.

A.B.2.Data Analyses

To further test how all available disturbance and temperature variables affect cushion plant performance indicators, we fit a series of LMMs and GLMMs separate from those described in the main text. We tested the responses of *Silene* maximum size (LMM), density (LMM), and percent cover (GLMM) to elevational level, microscale temperature, trail disturbance, trail age, and yearly hikers (Table 2.1). We maintained the interaction effect between a disturbance measure (trail, trail age, yearly hikers) and temperature (elevational level, average summer temperature; Table A.B.2a). As there were no difference in variables with this model set, we did not run these additional analyses on *Minuartia*.

We also fit a separate set of LMMs and GLMMs to further test if disturbance mediates habitat availability and competitive vegetation. We tested the responses of vegetation, forb, graminoid, and habitat availability indices to the additional effects of microscale temperature, trail age, and yearly hikers, maintaining the interaction effect between a disturbance measure (trail, trail age, yearly hikers) and temperature (elevational level, average summer temperature; Table A.B.2b).

Table A.B.1. Model results of testing the effects of all disturbances (trail, trail age, yearly hikers), elevational level (level), and temperature (average summer temperature) on *Silene acaulis* performance indicators (area, density, and cover) as well as vegetation and habitat availability indices (see Materials & Methods for model details). Two most parsimonious models listed for each model set. Trail and elevational level are factor variables, with 2 and 3 levels, respectively. Parameter estimates for trail, yearly hikers, trail age, and average summer temperature (JJA) 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 Table A.B.2 for full list of models.

Type	Response Variable	Formula	Intercept	Trail	Level	Yearly Hikers	Trail Age	JJA	$\Delta AICc$	N	Goodness of fit
LMM	Silene area	trail * level	3.87	0.74*** +/- 0.2	unimodal (-)				0	1283	0.07, 0.08
LMM	Silene area	trail + level							27.49	1283	0.04, 0.05
LMM	Silene density	trail * level	0.18	1.13*** +/- 0.1	unimodal (+)				0	680	0.21, 0.29
LMM	Silene density	level							111.29	680	0.06, 0.15
GLMM	Silene cover	trail * level	-3.51	0.72*** +/- 0.18	(+)				0	371	0.27
GLMM	Silene cover	yearly hikers							13.45	371	0.12
GLMM	vegetation	trail age * JJA yearly hikers *	-12.01				0.67*** +/- 0.08	1.47*** +/- 0.15	0	680	0.53
GLMM	vegetation	JJA							7.08	680	0.52
GLMM	habitat availability	trail * JJA	0.64	0.37 +/- 0.45				-0.3*** +/- 0.05	0	680	0.64
GLMM	habitat availability	trail + JJA							1.05	680	0.64
GLMM	forb	trail age * level trail age	-0.35		unimodal (-)		-0.04 +/- 0.06		0	680	0.55
GLMM	forb	* JJA							0.04	680	0.51
GLMM	graminoid	trail age * JJA yearly hikers *	-11.17				0.47*** +/- 0.06	1.31*** +/- 0.13	0	680	0.54
GLMM	graminoid	JJA							15.21	680	0.5

Table A.B.2. List of all models testing the effect of all disturbances (trail, trail age, yearly hikers), elevational level (level), and temperature (average summer temperature) on (A) *Silene acaulis* performance indicators and (B) vegetation and habitat availability indices (see Materials & Methods for model details). Number of parameters (k), sample size (n), and ΔAICc with respect to most parsimonious model shown. All models tested with random intercept and random effect of site (1 | id).

A

type	y	model	k	n	ΔAICc
LMM	area	trail * level + (1 id)	6	1283	0
LMM	area	trail + level + (1 id)	4	1283	27.49
LMM	area	level + (1 id)	3	1283	32.94
LMM	area	yearly hikers + level + (1 id)	4	1283	38.67
LMM	area	trail age + level + (1 id)	4	1283	42.07
LMM	area	trail + (1 id)	2	1283	51.17
LMM	area	trail + average summer temperature + (1 id)	3	1283	52.61
LMM	area	yearly hikers * level + (1 id)	6	1283	53.79
LMM	area	trail * average summer temperature + (1 id)	4	1283	54.64
LMM	area	trail age * level + (1 id)	6	1283	55.81
LMM	area	average summer temperature + (1 id)	2	1283	60.93
LMM	area	(1 id)	1	1283	64.82
LMM	area	yearly hikers + average summer temperature + (1 id)	3	1283	67.36
LMM	area	age + average summer temperature + (1 id)	3	1283	68.46
LMM	area	yearly hikers + (1 id)	2	1283	70.76
LMM	area	trail age + (1 id)	2	1283	74.36
LMM	area	trail age * average summer temperature + (1 id)	4	1283	77.13
LMM	area	yearly hikers * average summer temperature + (1 id)	4	1283	77.41
LMM	area	yearly hikers + trail age + (1 id)	3	1283	80.58
LMM	area	yearly hikers * trail age + (1 id)	4	1283	89.68
GLMM	cover	trail * level + (1 id)	6	371	0
GLMM	cover	yearly hikers + (1 id)	2	371	13.45
GLMM	cover	trail + (1 id)	2	371	13.9
GLMM	cover	yearly hikers + average summer temperature + (1 id)	3	371	14.47
GLMM	cover	trail * average summer temperature + (1 id)	4	371	14.67
GLMM	cover	yearly hikers + trail age + (1 id)	3	371	14.89
GLMM	cover	trail + average summer temperature + (1 id)	3	371	14.9
GLMM	cover	yearly hikers + level + (1 id)	4	371	15.75
GLMM	cover	average summer temperature + (1 id)	2	371	16.36
GLMM	cover	yearly hikers * average summer temperature + (1 id)	4	371	16.55
GLMM	cover	trail + level + (1 id)	4	371	16.64
GLMM	cover	yearly hikers * level + (1 id)	6	371	16.67

GLMM	cover	yearly hikers * trail age + (1 id)	4	371	16.69
GLMM	cover	trail age * average summer temperature + (1 id)	4	371	17.72
GLMM	cover	trail age + (1 id)	2	371	17.83
GLMM	cover	level + (1 id)	3	371	17.94
GLMM	cover	age + average summer temperature + (1 id)	3	371	18.26
GLMM	cover	trail age + level + (1 id)	4	371	19.99
GLMM	cover	trail age * level + (1 id)	6	371	22.99
LMM	density	trail * level + (1 id)	6	371	0
LMM	density	level + (1 id)	3	371	5.71
LMM	density	trail + level + (1 id)	4	371	10.82
LMM	density	(1 id)	1	371	12.62
LMM	density	trail age + level + (1 id)	4	371	14.67
LMM	density	yearly hikers + level + (1 id)	4	371	14.88
LMM	density	trail + (1 id)	2	371	16.86
LMM	density	average summer temperature + (1 id)	2	371	17.77
LMM	density	yearly hikers * level + (1 id)	6	371	20.26
LMM	density	yearly hikers + (1 id)	2	371	21.21
LMM	density	trail age + (1 id)	2	371	21.22
LMM	density	trail + average summer temperature + (1 id)	3	371	22.43
LMM	density	yearly hikers * average summer temperature + (1 id)	4	371	24.88
LMM	density	trail * average summer temperature + (1 id)	4	371	25.9
LMM	density	yearly hikers + average summer temperature + (1 id)	3	371	26.37
LMM	density	age + average summer temperature + (1 id)	3	371	26.48
LMM	density	trail age * level + (1 id)	6	371	26.75
LMM	density	yearly hikers + trail age + (1 id)	3	371	29.46
LMM	density	trail age * average summer temperature + (1 id)	4	371	34.23
LMM	density	yearly hikers * trail age + (1 id)	4	371	38.29

B

type	y	model	k	n	$\Delta AICc$
GLMM	forb	trail age * level + (1 id)	6	680	0
GLMM	forb	trail age * average summer temperature + (1 id)	4	680	0.04
GLMM	forb	trail * average summer temperature + (1 id)	4	680	0.27
GLMM	forb	yearly hikers * average summer temperature + (1 id)	4	680	10.59
GLMM	forb	trail * level + (1 id)	6	680	23.76
GLMM	forb	yearly hikers * level + (1 id)	6	680	37.17
GLMM	forb	level + (1 id)	3	680	60.78
GLMM	forb	average summer temperature + (1 id)	2	680	60.99
GLMM	forb	trail + level + (1 id)	4	680	61.62
GLMM	forb	age + average summer temperature + (1 id)	3	680	61.77
GLMM	forb	trail age + level + (1 id)	4	680	62.06
GLMM	forb	trail + average summer temperature + (1 id)	3	680	62.71
GLMM	forb	yearly hikers + level + (1 id)	4	680	62.82
GLMM	forb	yearly hikers + average summer temperature + (1 id)	3	680	62.98
GLMM	forb	yearly hikers * trail age + (1 id)	4	680	64.69
GLMM	forb	trail age + (1 id)	2	680	66.48
GLMM	forb	trail + (1 id)	2	680	66.61
GLMM	forb	yearly hikers + (1 id)	2	680	67.3
GLMM	forb	yearly hikers + trail age + (1 id)	3	680	68.51
GLMM	graminoid	trail age * average summer temperature + (1 id)	4	680	0
GLMM	graminoid	yearly hikers * average summer temperature + (1 id)	4	680	15.21
GLMM	graminoid	yearly hikers * level + (1 id)	6	680	30.95
GLMM	graminoid	trail age * level + (1 id)	6	680	39.14
GLMM	graminoid	trail * average summer temperature + (1 id)	4	680	73.01
GLMM	graminoid	level + (1 id)	3	680	83.28
GLMM	graminoid	trail * level + (1 id)	6	680	83.34
GLMM	graminoid	trail + level + (1 id)	4	680	83.97
GLMM	graminoid	trail age + level + (1 id)	4	680	85.04
GLMM	graminoid	yearly hikers + level + (1 id)	4	680	85.06
GLMM	graminoid	average summer temperature + (1 id)	2	680	85.74
GLMM	graminoid	trail + average summer temperature + (1 id)	3	680	86.2
GLMM	graminoid	yearly hikers + average summer temperature + (1 id)	3	680	86.52
GLMM	graminoid	age + average summer temperature + (1 id)	3	680	87.6
GLMM	graminoid	yearly hikers * trail age + (1 id)	4	680	123.24
GLMM	graminoid	trail age + (1 id)	2	680	135.21
GLMM	graminoid	trail + (1 id)	2	680	135.61
GLMM	graminoid	yearly hikers + (1 id)	2	680	136.19
GLMM	graminoid	yearly hikers + trail age + (1 id)	3	680	137.24
GLMM	habitat				
GLMM	availability	trail * average summer temperature + (1 id)	4	680	0

	habitat				
GLMM	availability	trail + average summer temperature + (1 id)	3	680	3.09
	habitat				
GLMM	availability	trail * level + (1 id)	6	680	12.94
	habitat				
GLMM	availability	trail + level + (1 id)	4	680	16.87
	habitat				
GLMM	availability	trail + (1 id)	2	680	43.17
	habitat				
GLMM	availability	yearly hikers + average summer temperature + (1 id)	3	680	203.86
	habitat				
GLMM	availability	average summer temperature + (1 id)	2	680	204.08
	habitat				
GLMM	availability	yearly hikers * average summer temperature + (1 id)	4	680	205.9
	habitat				
GLMM	availability	age + average summer temperature + (1 id)	3	680	206.1
	habitat				
GLMM	availability	trail age * average summer temperature + (1 id)	4	680	208.06
	habitat				
GLMM	availability	level + (1 id)	3	680	215.24
	habitat				
GLMM	availability	trail age * level + (1 id)	6	680	215.42
	habitat				
GLMM	availability	yearly hikers + level + (1 id)	4	680	215.51
	habitat				
GLMM	availability	trail age + level + (1 id)	4	680	217.02
	habitat				
GLMM	availability	yearly hikers * level + (1 id)	6	680	219.46
	habitat				
GLMM	availability	yearly hikers * trail age + (1 id)	4	680	234.34
	habitat				
GLMM	availability	yearly hikers + (1 id)	2	680	239.41
	habitat				
GLMM	availability	trail age + (1 id)	2	680	240.99
	habitat				
GLMM	availability	yearly hikers + trail age + (1 id)	3	680	241.13
	habitat				
GLMM	vegetation	trail age * average summer temperature + (1 id)	4	680	0
	habitat				
GLMM	vegetation	yearly hikers * average summer temperature + (1 id)	4	680	7.08
	habitat				
GLMM	vegetation	yearly hikers * level + (1 id)	6	680	7.24
	habitat				
GLMM	vegetation	trail age * level + (1 id)	6	680	12.91
	habitat				
GLMM	vegetation	trail * level + (1 id)	6	680	54.17
	habitat				
GLMM	vegetation	trail + level + (1 id)	4	680	55.94
	habitat				
GLMM	vegetation	trail age + level + (1 id)	4	680	67.17
	habitat				
GLMM	vegetation	level + (1 id)	3	680	67.42
	habitat				
GLMM	vegetation	trail * average summer temperature + (1 id)	4	680	68.02
	habitat				
GLMM	vegetation	yearly hikers + level + (1 id)	4	680	69.37
	habitat				
GLMM	vegetation	trail + average summer temperature + (1 id)	3	680	73.87
	habitat				
GLMM	vegetation	trail + (1 id)	2	680	84.46
	habitat				
GLMM	vegetation	average summer temperature + (1 id)	2	680	85.53

GLMM	vegetation	age + average summer temperature + (1 id)	3	680	86.02
GLMM	vegetation	yearly hikers * trail age + (1 id)	4	680	86.49
GLMM	vegetation	yearly hikers + average summer temperature + (1 id)	3	680	87.36
GLMM	vegetation	trail age + (1 id)	2	680	94.92
GLMM	vegetation	yearly hikers + trail age + (1 id)	3	680	96.85
GLMM	vegetation	yearly hikers + (1 id)	2	680	96.95

A.C. Use of maximum size structure justification

A.C.1.Data

We conducted extensive *Silene acaulis* population surveys between May and August 2014 at North American southern (New Mexico), central (Colorado and Southern Alaska), and northern (Northern Alaska) portions of the species' range. At each site, we measured all *Silene* plant sizes (following Doak and Morris 2010) within 4 m² quadrats along elevational transects up an individual massif or summit, at least 2 m away from hiking trails and other major visible disturbances. This allowed us to sample slopes of various aspects within a concentrated area, as well as to capture population variation within the elevational range of *Silene* at each site. We recorded latitude, longitude, and elevation with a Garmin Oregon 550t device (Olathe, Kansas, USA), which we manually calibrated for elevation to ensure accuracy.

A.C.2.Data Analyses

To determine if size structure is a good measure of performance and if maximum plant sizes exhibit larger responses to environmental drivers within a population, we conducted two different analyses. First, to see which size classes of

Silene population structure respond strongest to external drivers, such as the climatic gradient along the species' latitudinal range, we fitted polynomial regression models with a quadratic latitude term on different descriptive statistics of population structure. Second, we calculated the coefficient of variation at each site for full population size structure and for the 90th percentile of cushion size.

A.C.3. Results

We found that the largest 90th percentile of *Silene* size at each site showed a significant relationship with latitude and quadratic latitude (p-value < 0.01), whereas mean size and median at each site did not (Fig. A.C.1). We found that the 90th percentile at each site accounts for 30-50% of coefficient of variation at that site. Combined, these analyses suggest that populations maximum plant size is a good indicator of population response to environmental drivers. A long-term, detailed demographic study of *Silene* has shown that larger plants have higher reproduction (Doak & Morris 2010), suggesting that populations with larger maximum plants are demographically better off in terms of overall performance. Data collected for this study also shows that largest *Silene* plants bear a disproportionate amount of fruits compared to smaller plants (*unpublished data*, D.F. Doak; Fig. A.C.2).

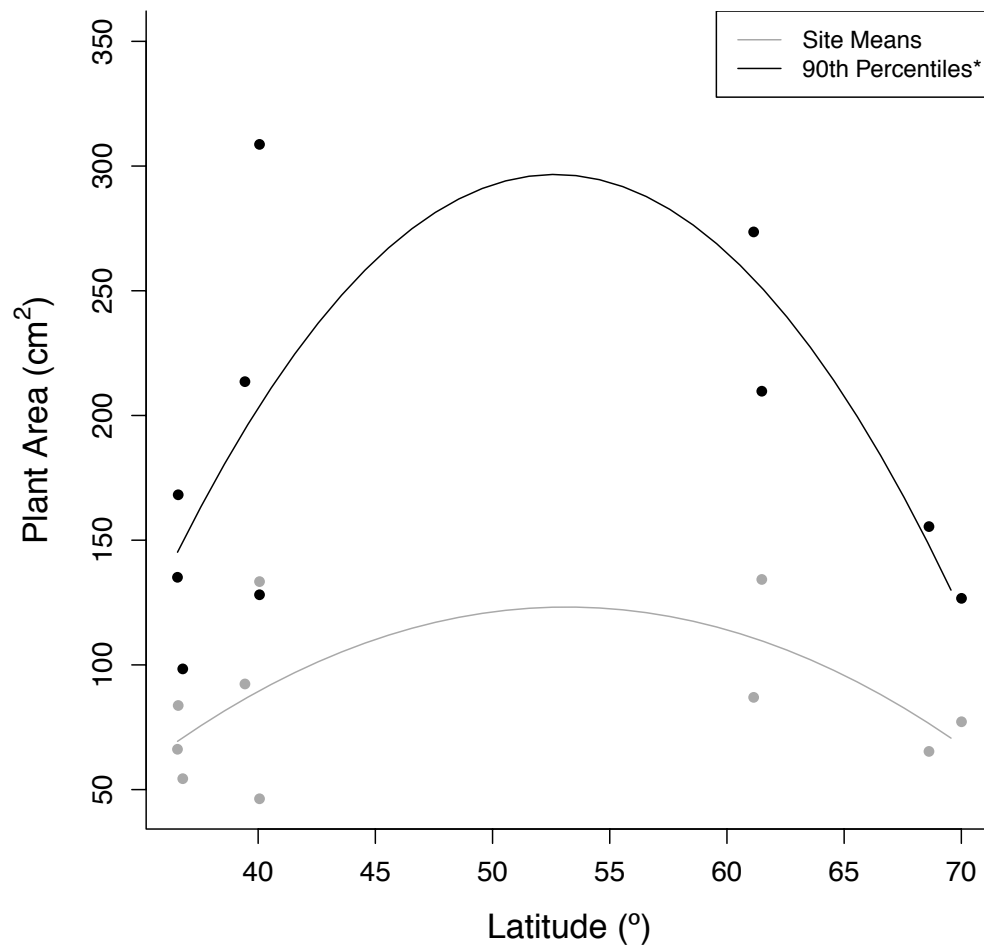


Figure A.C.1: Site mean and maximum sizes. The largest 90th percentile of *Silene acaulis* cushion size at each site is significantly related with quadratic latitude (simple linear regression; *p-value < 0.01), whereas mean and median size are not significant. Fitted lines shown for illustrative, not predictive, purposes.

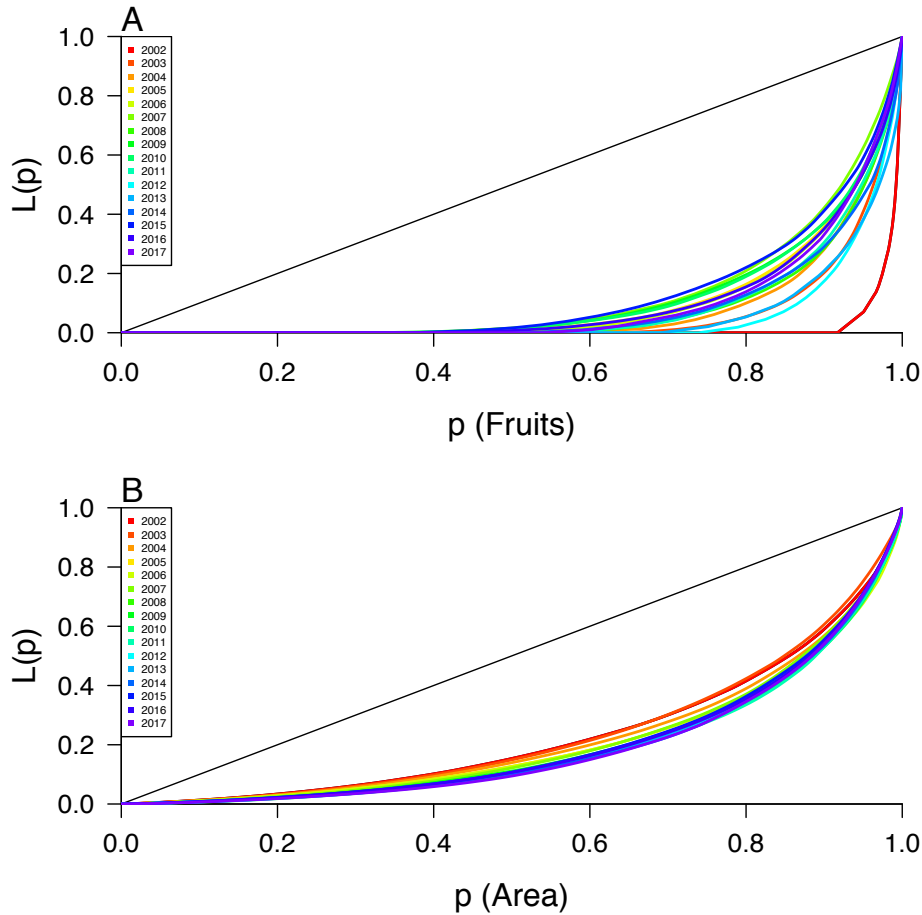


Figure A.C.2: Fruit & size inequalities. Lorenz curves show that largest *Silene acaulis* plants bear a disproportional higher amount of fruits (and therefore seeds) than smaller plants (A; Gini coefficient = 0.85), a higher inequality than for cushion plant size (B; Gini coefficient = 0.60). LMM (random intercept with random effect of year) results verify that larger plant size increases yearly fruit production (estimate = 0.13; standard error = 0.003; p-value < 0.0001). Data collected at Niwot Ridge, Colorado, USA between 2002 and 2017 (*unpublished data*, D.F. Doak).

APPENDIX B

Chapter 3 Appendix

B.A. Parameters, supplemental results, and supplemental figures

Table B.A.1. Parameters used to test the effects of A) disturbance and elevational level on cushion size and population density and B) disturbance, level, species community indices, and soil conditions on reproduction indicators. The second model set (B) replaces species community indices with soil condition. The full list of models tested is shown in Table B.B.1.

A

Parameter	Type	Variable
Disturbance	binary	explanatory
Elevational level	categorical (1:4)	explanatory
SOM	continuous	explanatory
SWC	continuous	explanatory
<i>Silene</i> size	continuous	response
<i>Silene</i> population density	continuous (calculated at plot level)	response

B

Parameter	Type	Variable
Disturbance	binary	explanatory
Elevational level	categorical (1:4)	explanatory
Species Richness	continuous	explanatory
Shannon Diversity Index	continuous	explanatory
% Vegetation Cover	continuous (0:100)	explanatory
Community competitiveness	continuous (1:3)	explanatory
SOM	continuous	explanatory
SWC	continuous	explanatory
<i>Silene</i> fruits per area	continuous	response
<i>Silene</i> relative reproduction	continuous	response

Table B.A.2. Parameters used in models testing the effects of disturbance, elevational level, *Silene acaulis* cushion presence, and sampling area on species community indices. A secondary model set replaces cushion presence with SOM and SWC. The full list of models tested is shown in Table B.B.2.

Parameter	Type	Variable
Disturbance	binary	explanatory
Elevational level	categorical (1:4)	explanatory
<i>Silene</i> presence (Cushion)	binary	explanatory
Sampling area	continuous	explanatory
Soil Organic Matter (SOM)	continuous	explanatory
Soil Water Content (SWC)	continuous	explanatory
Species richness	continuous	response
Shannon diversity	continuous	response
Species % cover	continuous	response

Table B.A.3. Parameters used in models testing effects of disturbance and elevation on Soil Organic Matter (SOM) and Soil Water Content (SWC). The full list of models tested is shown in Table B.B.4.

Parameter	Type	Variable
Disturbance	binary	explanatory
Elevational level	categorical (1:4)	explanatory
<i>Silene</i> presence (Cushion)	binary	explanatory
Soil Organic Matter	continuous	response
Soil Water Content	continuous	response

Table B.A.4. Parameters used in models testing the effects of disturbance and elevational level on Relative Interaction Indices (RII) and Bray-Curtis Dissimilarity indices. The full list of models tested is shown in Table B.B.5.

Parameter	Type	Variable
Disturbance	binary	explanatory
Elevational level	categorical (1:4)	explanatory
RII: species richness	continuous (-1:1)	response
RII: Shannon diversity	continuous (-1:1)	response
RII: species % cover	continuous (-1:1)	response
Bray-Curtis dissimilarity	continuous (0:1)	response

Table B.A.5. Results of most parsimonious models testing the additional effects of Soil Organic Matter (SOM) and Soil Water Content (SWC) on A) *Silene acaulis* cushion parameters and B) inside species community. Light green colors differentiate response variables tested using the same dataset. Interactions (Int(s)) are listed without the corresponding estimates. Elevational level and disturbance are factor variables, with 4 and 2 levels, respectively. Level coefficient values are hence summarized as follows: (+) positive trend, (-) negative trend, or unimodal with a maximum (+) or minimum (-) at levels 2 or 3. All models with Δ AICc values of less than 2 are shown for each response variable with marginal (marg) r^2 and conditional (cond) r^2 listed, and significant p-values ($< 0.001^{***}$, $< 0.01^{**}$, $< 0.05^*$) shown above the first listed model within each section. P-values for level indicate that at least one level was significant at < 0.05 . The full list of models tested and AICc weights are shown in Tables B.B.1, B.B.2.

A

Response variable	Intercept	SOM	SWC	Disturbance	Level	Int(s)	marg r^2	cond r^2	Δ AICc
Fruits per area	0.06		-0.012	-0.03	*	dist x level x SWC	0.69	0.69	0.00
Relative Reproduction	62.59	-159.39			-	SOM x level	0.27	0.29	0.00
Cushion size	200.92	-31.93	-95.49	-1918.19	-	SOM x SWC x dist x level	0.18	0.20	0.00

B

Response variable	Intercept	SOM	SWC	Disturbance	Level	Int(s)	marg r^2	cond r^2	Δ AICc
Species Richness _{inside}	5.64	-8.57	6.27	10.60	unimodal (+)	SOM x SWC x dist x level	0.30	0.77	0.00
Shannon Diversity _{inside}	1.33						0.00	0.60	0.00
Shannon Diversity _{inside}	1.33	0.15					0.05	0.63	1.36
Shannon Diversity _{inside}	1.45			-0.25			0.03	0.61	1.59
% Vegetation Cover _{inside}	26.95	-85.36	75.51	23.03	unimodal (+)	SOM x SWC x dist x level	0.36	0.52	0.00

Table B.A.6. Results of most parsimonious models testing effects of disturbance, elevational level, and *Silene acaulis* presence on community competitiveness within cushion and controls (inside) and within cushion rings and control rings (neighboring). Black bars differentiate different datasets. Interactions (Int(s)) are listed without the corresponding estimates. Elevational level and disturbance are factor variables, with 4 and 2 levels, respectively. Level coefficient values are hence summarized as follows: (+) positive trend, (-) negative trend, or unimodal with a maximum (+) or minimum (-) at levels 2 or 3. All models with Δ AICc values of less than 2 are shown for each response variable with marginal (marg) r^2 and conditional (cond) r^2 listed, and significant p-values ($< 0.001^{***}$, $< 0.01^{**}$, $< 0.05^*$) shown above the first listed model within each section. P-values for level indicate that at least one level was significant at < 0.05 . The full list of models tested is shown in Table B.B.3.

Response variable	Intercept	Disturbance	Level	Cushion	Int(s)	marg r^2	cond r^2	Δ AICc
			*					
Competitiveness _{inside}	1.22		-			0.38	0.38	0.00
Competitiveness _{inside}	1.18		-	0.08		0.40	0.40	0.34
			*					
Competitiveness _{neighboring}	1.21		unimodal (+)			0.52	0.53	0.00
Competitiveness _{neighboring}	1.24	-0.06	-			0.54	0.55	

Table B.A.7. Results of most parsimonious models testing effects of disturbance and elevation on Soil Organic Matter (SOM) and Soil Water Content (SWC). Light green colors differentiate response variables tested using the same dataset. Interactions (Int(s)) are listed without the corresponding estimates. Elevational level and disturbance are factor variables, with 4 and 2 levels, respectively. Level coefficient values are hence summarized as follows: (+) positive trend, (-) negative trend, or unimodal with a maximum (+) or minimum (-) at levels 2 or 3. All models with Δ AICc values of less than 2 are shown for each response variable with marginal (marg) r^2 and conditional (cond) r^2 listed, and significant p-values ($< 0.001^{***}$, $< 0.01^{**}$, $< 0.05^*$) shown above the first listed model within each section. P-values for level indicate that at least one level was significant at < 0.05 . The full list of models tested is shown in Table B.B.4.

Response variable	Intercept	Disturbance	Level	Cushion	Int(s)	marg r^2	cond r^2	Δ AICc
			*					
SOM _{inside}	25.08	-8.95	unimodal (+)	3.19	dist x level x cush	0.42	0.88	0.00
			*					
SWC _{inside}	37.96	-6.85	unimodal (+)	1.35	dist x level x cush	0.39	0.82	0.00

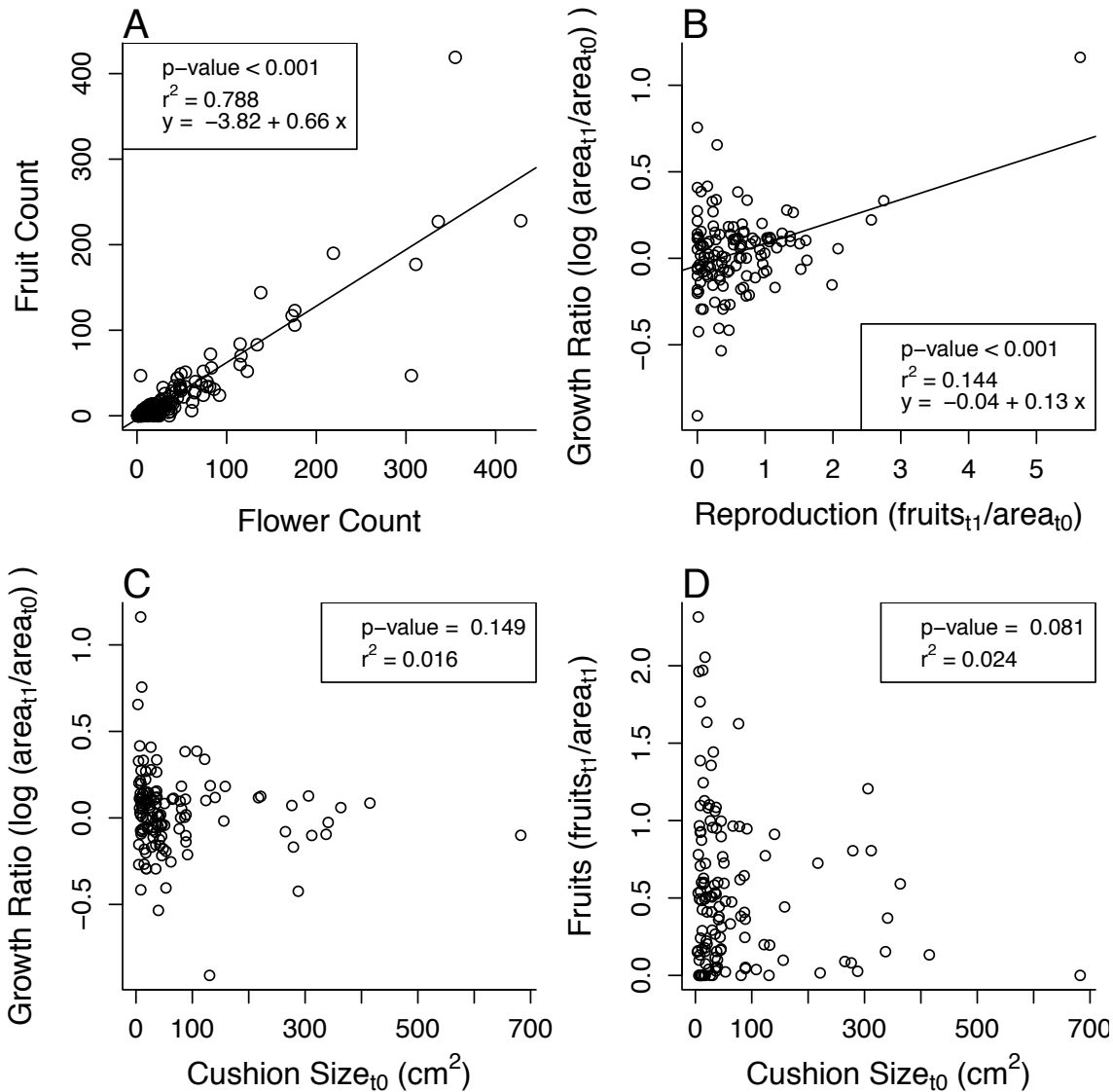


Figure B.A.1: Fruit production and growth rate. Females (A) as well as hermaphrodite (not shown) *Silene acaulis* individuals show a strong and significant correlation between the flowers observed at the beginning of the growing season to the fruits produced at the end of the growing season. Female growth is moderately-well predicted by fruits per area (B), making fruit count a good indicator to use of performance. Both female growth (C) and fruit production (D) have no significant relationship with cushion size of the previous growing season. Data collected (D.F. Doak, W.F. Morris, M.L. Peterson) at Niwot Ridge, Colorado, USA during growing seasons (June – August) in 2015 (t0) and 2016 (t1).

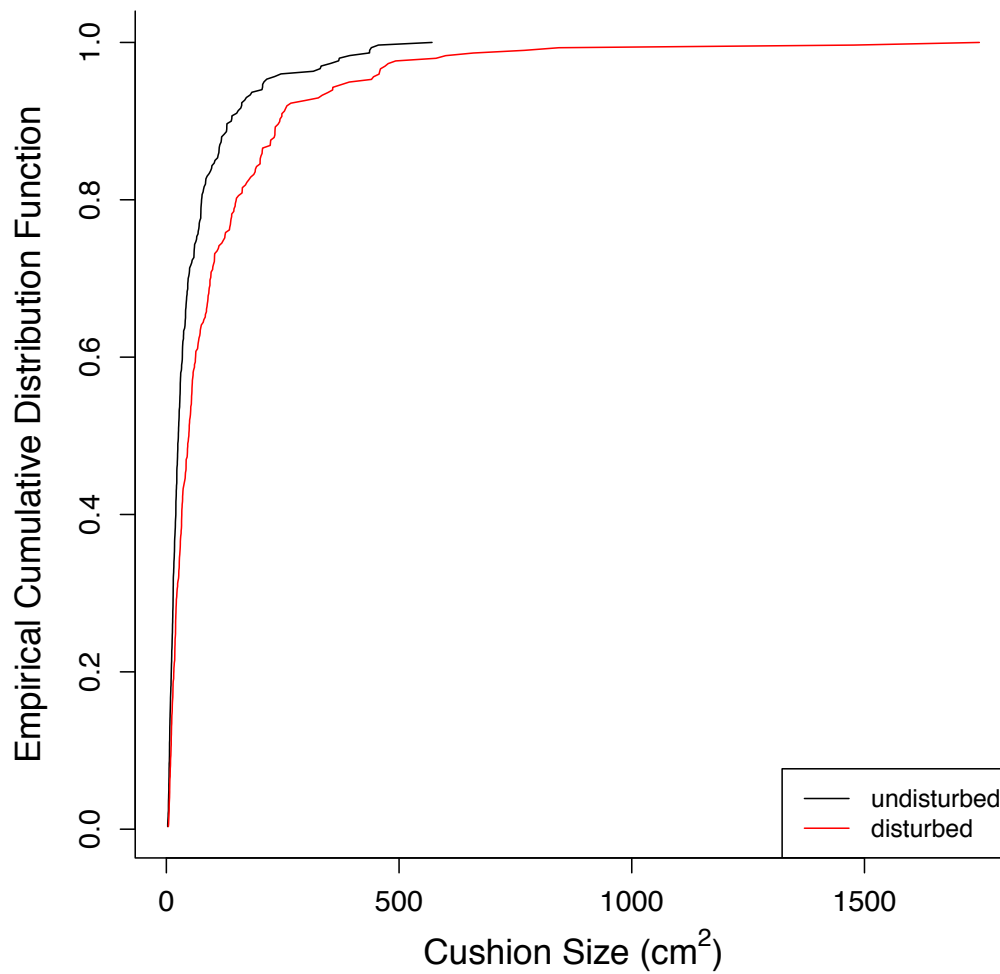


Figure B.A.2: Size distributions. *Silene acaulis* individuals have significantly different size distributions between disturbed and undisturbed areas, as tested with a Two-sample Kolmogorov-Smirnov test ($D = 0.21$, $p\text{-value} < 0.001$). Disturbed areas have fewer smaller individuals and disturbed cushions reach larger sizes.

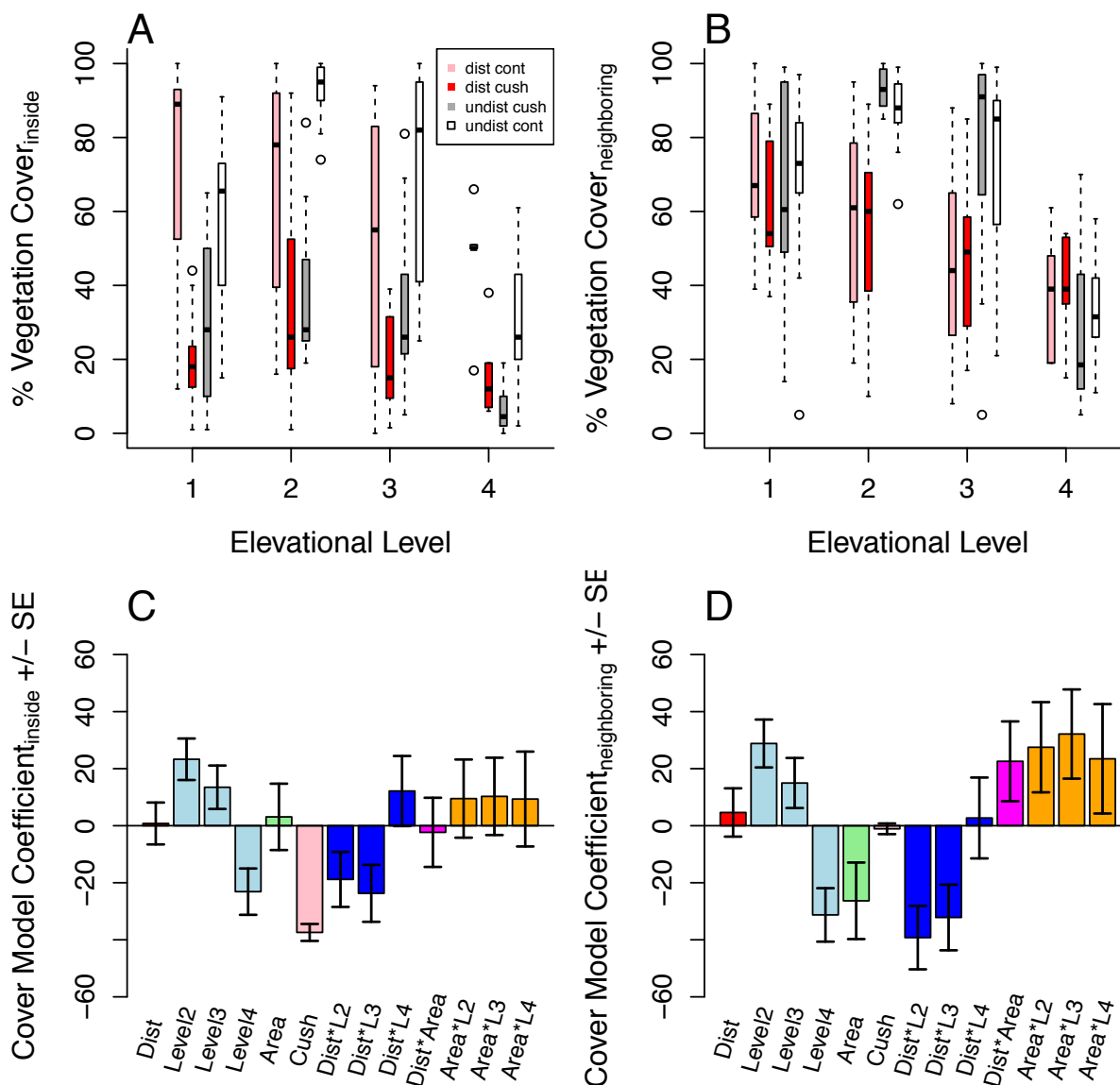


Figure B.A.3: Percent vegetation cover. Disturbance and cushion presence decrease both inside (A) and neighboring (B) species percent vegetation cover (colors for B as in (A)). Legend abbreviations are as follows: dist = disturbed, undist = undisturbed, cush = cushion, cont = control. The best supported model for inside species cover (C) highlights the importance of interactions between disturbance and elevation, which cause decreases in cover at middle elevations (levels 2 and 3), an effect partly mitigated by cushion area. The most parsimonious model for neighboring species cover (D) suggests the same. Both models have an interaction effects between disturbance, elevation, and area, which indicate weaker disturbance effects at low and high elevations and strong effects at middle elevations (see also Table B.B.6). Contrasting colors merely differentiate parameters.

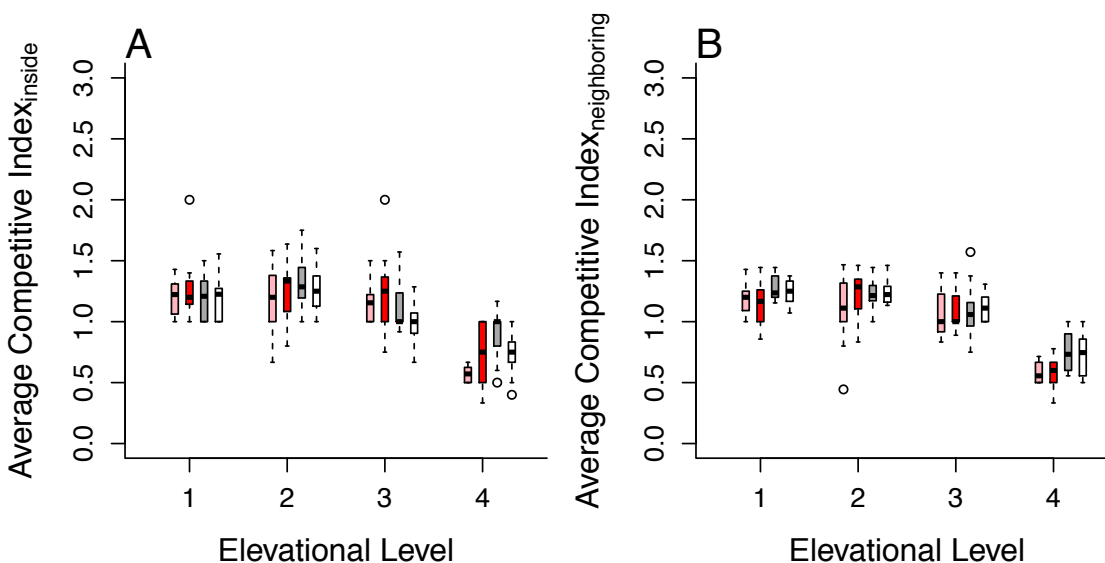


Figure B.A.4: Inside species competitiveness. Inside species community competitiveness (A) is highest at low elevations and neighboring community competitiveness (B) is highest at middle elevations. Colors same as in Fig. B.A.3a.

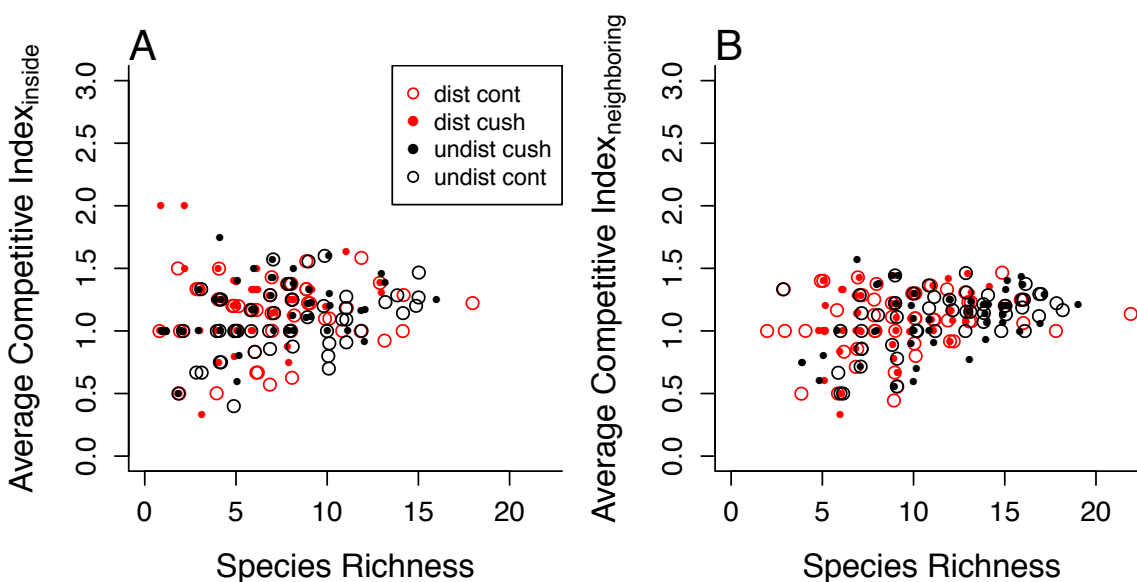


Figure B.A.5: Community competitiveness. Patterns in community competitiveness are mostly driven by sampling units of median species richness in both inside (A) and neighboring (B) communities, signifying that it is not just highly competitive individual species that drive the observed pattern. Points jittered for clarity. Legend abbreviations are as follows: dist = disturbed, undist = undisturbed, cush = cushion, cont = control.

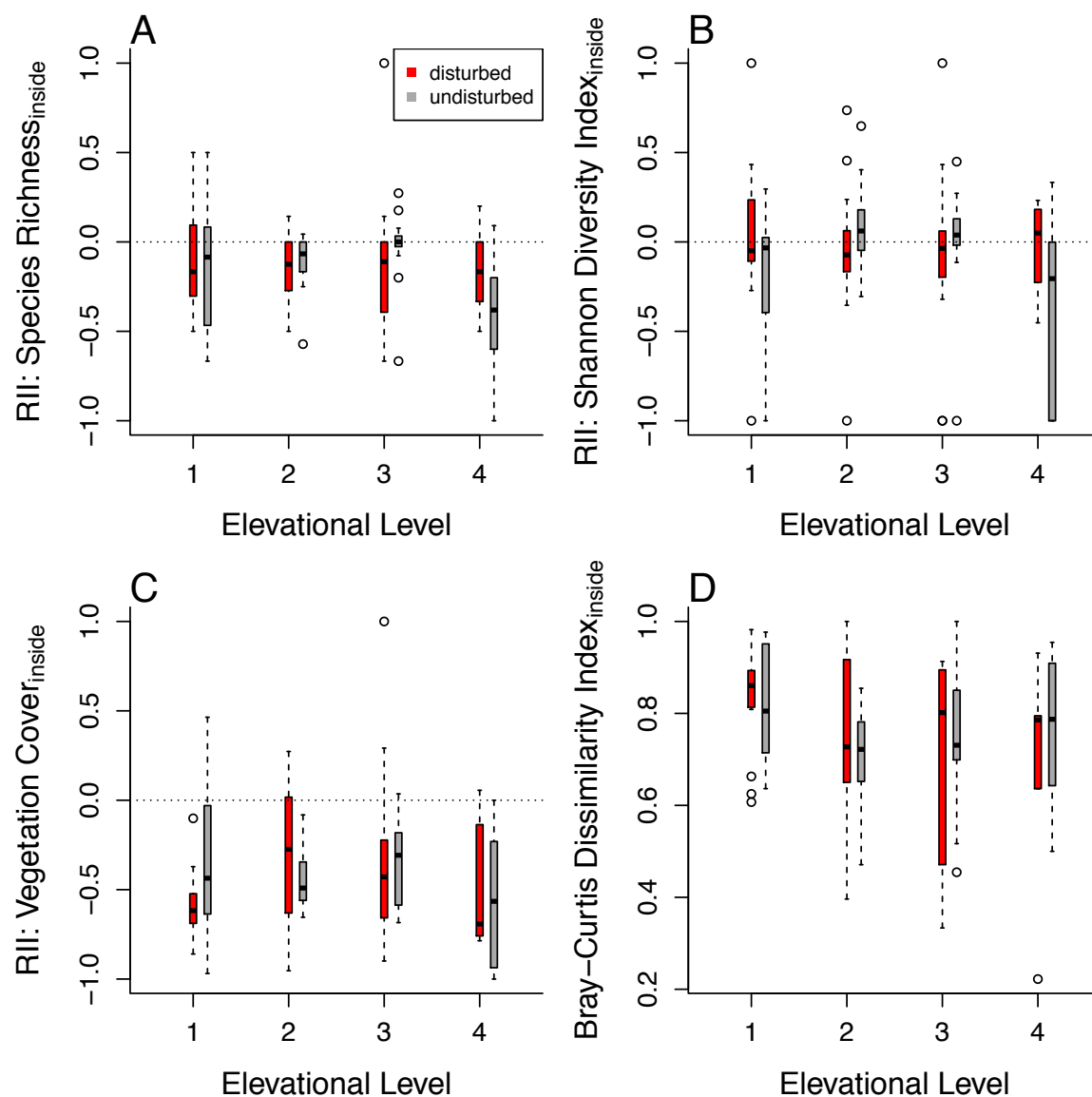


Figure B.A.6: Inside species interactions. The Relative Interaction Index for species richness (A), Shannon diversity (B), percent vegetation cover (C), and the Bray-Curtis Dissimilarity index (D) only include random effects and no effect of disturbance or elevation. Colors all as in (A).

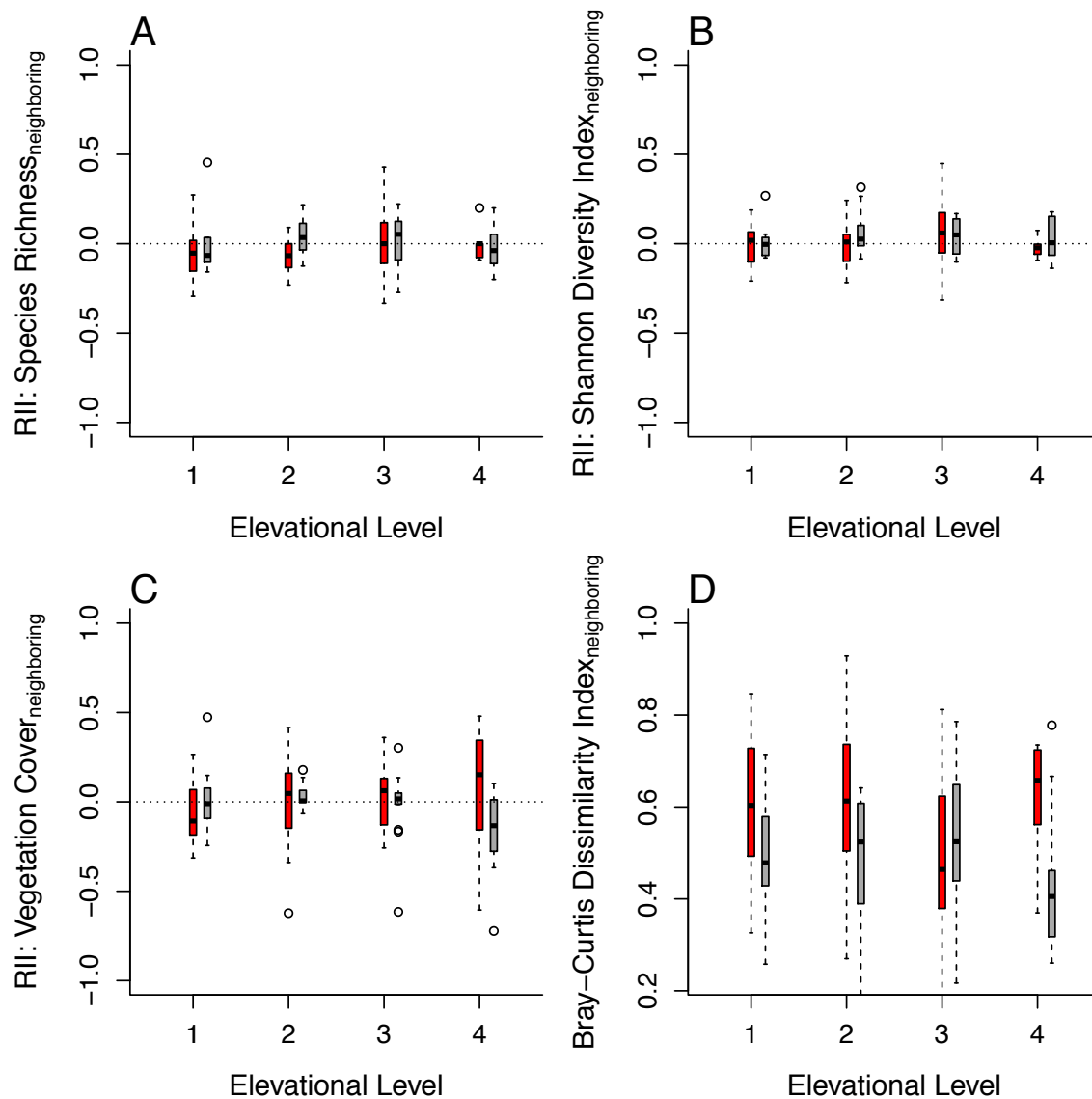


Figure B.A.7: Neighboring species interactions. The Relative Interaction Index for species richness (A), Shannon diversity (B), percent vegetation cover (C), and the Bray-Curtis Dissimilarity index (D) only include random effects and no effect of disturbance or elevation. Colors all as in Fig. B.A.6a.

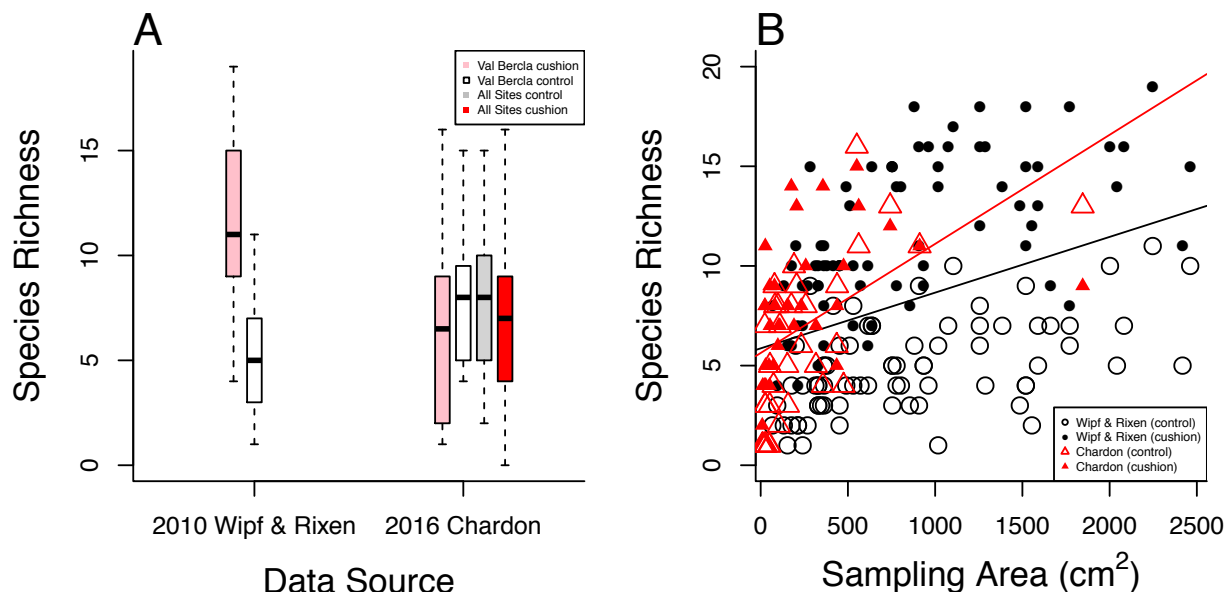


Figure B.A.8: Same-site data comparison. Data comparisons at the same site (Val Bercla at Fallerfurrga) between data we collected in 2016 and Wipf & Rixen collected in 2010 (used in Butterfield et al. 2013) show that (A) we had significantly lower species richness within cushions and significantly higher species richness in our controls than Wipf & Rixen. We suspect that differences in species richness within the controls are attributed to our careful selection of controls that differ from the methods of Wipf & Rixen. The differences in species richness within cushions are likely caused by (B) the discrepancy in the sampled cushion sizes, considering that cushion size increases species richness (see Results). Wipf & Rixen sampled much larger cushions, whereas we sampled proportional to the overall size structure. Linear regression lines including only the fixed effect of sampling area on species richness of both control and cushion shown for both our (p-value < 0.001) and the Wipf & Rixen (p-value < 0.001) data.

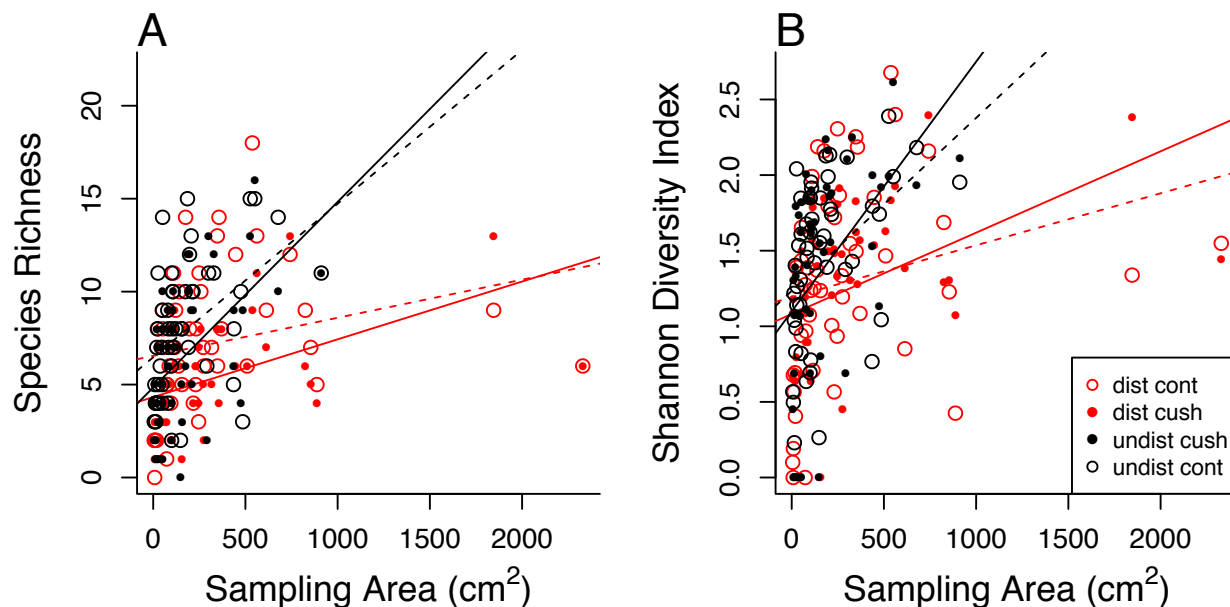


Figure B.A.9: Inside species richness and diversity. Disturbance changes the rate at which inside species richness (A) and diversity (B) accumulate with increasing total size of cushions (i.e. entire area of sampled cushion and not the area taken up by *Silene* itself) and controls. Linear regression lines including only the fixed effect of richness (A) and diversity (B) on cushion size shown and are all significant (p -values < 0.05). Colors in A are as in (B). Legend abbreviations are as follows: dist = disturbed, undist = undisturbed, cush = cushion, cont = control.

B.B. Full lists of models

Table B.B.1. Full list of LMMs to test the effects of disturbance and elevational level on A) cushion size and B) population density. We also tested the effects of C) disturbance, level, and species community indices, as well as D) disturbance, level, and soil conditions on reproduction indicators. Finally, we tested the effects of E) disturbance, level, SOM, and SWC on *Silene* cushion size. Black bars differentiate model sets, and k = number of parameters, n = sample size.

A

modeled parameter	model formula	k	n	AICc	Δ AICc	AICc weight
size	disturbance*level+(1 site)	10	598	7549.91	0.00	1.00
size	disturbance+level+(1 site)	7	598	7582.05	32.14	0.00
size	disturbance+(1 site)	4	598	7598.16	48.25	0.00
size	level+(1 site)	6	598	7605.34	55.43	0.00
size	(1 site)	3	598	7621.59	71.68	0.00

B

modeled parameter	model formula	k	n	AICc	Δ AICc	AICc weight
density	level+(1 site)	6	20	121.40	0.00	0.37
density	disturbance+level+(1 site)	7	20	122.04	0.64	0.27
density	disturbance*level+(1 site)	10	20	122.19	0.79	0.25
density	disturbance+(1 site)	4	20	124.57	3.17	0.08
density	(1 site)	3	20	125.93	4.53	0.04

C

modeled parameter	model formula	k	n	AICc	Δ AICc	AICc weight	species
fruits per area	(1 site)	3	99	223.80	0.00	0.32	inside
fruits per area	competition+(1 site)	4	98	224.48	0.68	0.23	inside
fruits per area	level+(1 site)	6	99	226.61	2.82	0.08	inside
fruits per area	disturbance+(1 site)	4	99	226.79	3.00	0.07	inside
fruits per area	shannon diversity+(1 site)	4	99	227.25	3.45	0.06	inside
fruits per area	disturbance*competition+(1 site)	6	98	227.47	3.67	0.05	inside
fruits per area	level+competition+(1 site)	7	98	227.54	3.74	0.05	inside
fruits per area	disturbance+competition+(1 site)	5	98	227.64	3.84	0.05	inside
fruits per area	level*competition+(1 site)	10	98	229.18	5.39	0.02	inside
fruits per area	species richness+(1 site)	4	99	229.88	6.09	0.02	inside
fruits per area	disturbance+shannon diversity+(1 site)	5	99	229.98	6.18	0.01	inside
fruits per area	disturbance+level+(1 site)	7	99	230.47	6.67	0.01	inside
fruits per area	level+shannon diversity+(1 site)	7	99	231.31	7.52	0.01	inside
fruits per area	disturbance+level+competition+(1 site)	8	98	231.39	7.59	0.01	inside

fruits per area	disturbance+species richness+(1 site)	5	99	232.15	8.35	0.00	inside
fruits per area	level+disturbance*competition+(1 site)	9	98	232.27	8.47	0.00	inside
fruits per area	disturbance*shannon diversity+(1 site)	6	99	232.42	8.62	0.00	inside
fruits per area	vegetation cover+(1 site)	4	99	232.80	9.01	0.00	inside
fruits per area	disturbance*level+(1 site)	10	99	232.88	9.08	0.00	inside
fruits per area	disturbance+level*competition+(1 site)	11	98	233.34	9.55	0.00	inside
fruits per area	disturbance*level+competition+(1 site)	11	98	233.51	9.71	0.00	inside
fruits per area	level+species richness+(1 site)	7	99	234.53	10.73	0.00	inside
fruits per area	disturbance+level+shannon diversity+(1 site)	8	99	235.12	11.33	0.00	inside
fruits per area	disturbance+vegetation cover+(1 site)	5	99	235.16	11.36	0.00	inside
fruits per area	disturbance*species richness+(1 site)	6	99	237.58	13.78	0.00	inside
fruits per area	level+vegetation cover+(1 site)	7	99	237.72	13.92	0.00	inside
fruits per area	disturbance*level+shannon diversity+(1 site)	11	99	237.77	13.98	0.00	inside
fruits per area	disturbance+level+species richness+(1 site)	8	99	238.15	14.35	0.00	inside
fruits per area	level+disturbance*shannon diversity+(1 site)	9	99	238.27	14.48	0.00	inside
fruits per area	disturbance*level*competition+(1 site)	18	98	238.35	14.56	0.00	inside
fruits per area	level*shannon diversity+(1 site)	10	99	239.73	15.94	0.00	inside
fruits per area	disturbance*level+species richness+(1 site)	11	99	241.03	17.24	0.00	inside
fruits per area	disturbance+level+vegetation cover+(1 site)	8	99	241.31	17.52	0.00	inside
fruits per area	disturbance+level*shannon diversity+(1 site)	11	99	243.67	19.87	0.00	inside
fruits per area	disturbance*vegetation cover+(1 site)	6	99	243.76	19.96	0.00	inside
fruits per area	level+disturbance*species richness+(1 site)	9	99	244.33	20.53	0.00	inside
fruits per area	disturbance*level+vegetation cover+(1 site)	11	99	244.42	20.63	0.00	inside
fruits per area	level+disturbance*vegetation cover+(1 site)	9	99	250.98	27.19	0.00	inside
fruits per area	level*species richness+(1 site)	10	99	251.10	27.30	0.00	inside
fruits per area	disturbance+level*species richness+(1 site)	11	99	255.03	31.24	0.00	inside
fruits per area	disturbance*level*shannon diversity+(1 site)	18	99	255.90	32.10	0.00	inside
fruits per area	level*vegetation cover+(1 site)	10	99	260.04	36.25	0.00	inside
fruits per area	disturbance+level*vegetation cover+(1 site)	11	99	264.39	40.60	0.00	inside
fruits per area	disturbance*level*species richness+(1 site)	18	99	280.49	56.69	0.00	inside
fruits per area	disturbance*level*vegetation cover+(1 site)	18	99	300.93	77.14	0.00	inside
relative reproduction	level*competition+(1 site)	10	37	138.83	0.00	0.40	inside
relative reproduction	disturbance+level*competition+(1 site)	11	37	140.32	1.49	0.19	inside
relative reproduction	shannon diversity+(1 site)	4	37	142.80	3.97	0.06	inside
relative reproduction	(1 site)	3	37	143.12	4.29	0.05	inside
relative reproduction	competition+(1 site)	4	37	143.47	4.64	0.04	inside
relative reproduction	disturbance*competition+(1 site)	6	37	143.70	4.87	0.04	inside
relative reproduction	level*shannon diversity+(1 site)	10	37	143.79	4.96	0.03	inside

relative reproduction	disturbance+(1 site)	4	37	144.19	5.36	0.03	inside
relative reproduction	disturbance+shannon diversity+(1 site)	5	37	144.70	5.87	0.02	inside
relative reproduction	disturbance+competition+(1 site)	5	37	144.74	5.91	0.02	inside
relative reproduction	level+shannon diversity+(1 site)	7	37	145.02	6.19	0.02	inside
relative reproduction	level+(1 site)	6	37	145.14	6.31	0.02	inside
relative reproduction	disturbance*shannon diversity+(1 site)	6	37	145.56	6.73	0.01	inside
relative reproduction	disturbance+level+(1 site)	7	37	145.69	6.86	0.01	inside
relative reproduction	disturbance+level*shannon diversity+(1 site)	11	37	145.87	7.04	0.01	inside
relative reproduction	level+competition+(1 site)	7	37	146.12	7.29	0.01	inside
relative reproduction	level+disturbance*competition+(1 site)	9	37	146.58	7.75	0.01	inside
relative reproduction	disturbance+level+shannon diversity+(1 site)	8	37	146.88	8.05	0.01	inside
relative reproduction	disturbance+level+competition+(1 site)	8	37	146.95	8.12	0.01	inside
relative reproduction	species richness+(1 site)	4	37	147.29	8.46	0.01	inside
relative reproduction	level+disturbance*shannon diversity+(1 site)	9	37	148.14	9.31	0.00	inside
relative reproduction	disturbance+species richness+(1 site)	5	37	149.04	10.21	0.00	inside
relative reproduction	level+species richness+(1 site)	7	37	149.86	11.03	0.00	inside
relative reproduction	vegetation cover+(1 site)	4	37	149.98	11.15	0.00	inside
relative reproduction	disturbance+level+species richness+(1 site)	8	37	151.32	12.49	0.00	inside
relative reproduction	disturbance+vegetation cover+(1 site)	5	37	151.81	12.98	0.00	inside
relative reproduction	disturbance*species richness+(1 site)	6	37	152.94	14.11	0.00	inside
relative reproduction	level+vegetation cover+(1 site)	7	37	153.31	14.48	0.00	inside
relative reproduction	disturbance+level+vegetation cover+(1 site)	8	37	154.83	16.00	0.00	inside
relative reproduction	level+disturbance*species richness+(1 site)	9	37	154.89	16.06	0.00	inside
relative reproduction	level*species richness+(1 site)	10	37	159.36	20.53	0.00	inside
relative reproduction	disturbance*vegetation cover+(1 site)	6	37	159.74	20.91	0.00	inside
relative reproduction	disturbance+level*species richness+(1 site)	11	37	161.23	22.40	0.00	inside
relative reproduction	level+disturbance*vegetation cover+(1 site)	9	37	162.80	23.97	0.00	inside
relative reproduction	level*vegetation cover+(1 site)	10	37	171.77	32.94	0.00	inside
relative reproduction	disturbance+level*vegetation cover+(1 site)	11	37	174.21	35.38	0.00	inside
fruits per area	disturbance*shannon diversity+(1 site)	6	99	218.30	0.00	0.66	neighboring
fruits per area	shannon diversity+(1 site)	4	99	223.64	5.34	0.05	neighboring
fruits per area	competition+(1 site)	4	99	223.71	5.41	0.04	neighboring

fruits per area	(1 site)	3	99	223.80	5.49	0.04	neighboring
fruits per area	disturbance+shannon diversity+(1 site)	5	99	223.80	5.50	0.04	neighboring
fruits per area	level*shannon diversity+(1 site)	10	99	223.94	5.63	0.04	neighboring
fruits per area	disturbance*level*shannon diversity+(1 site)	18	99	224.08	5.77	0.04	neighboring
fruits per area	disturbance*competition+(1 site)	6	99	225.41	7.10	0.02	neighboring
fruits per area	level+(1 site)	6	99	226.61	8.31	0.01	neighboring
fruits per area	disturbance+competition+(1 site)	5	99	226.71	8.41	0.01	neighboring
fruits per area	disturbance+(1 site)	4	99	226.79	8.49	0.01	neighboring
fruits per area	disturbance+level*shannon diversity+(1 site)	11	99	226.96	8.65	0.01	neighboring
fruits per area	disturbance+species richness+(1 site)	5	99	228.08	9.77	0.00	neighboring
fruits per area	level*competition+(1 site)	10	99	228.17	9.86	0.00	neighboring
fruits per area	species richness+(1 site)	4	99	228.19	9.89	0.00	neighboring
fruits per area	level+competition+(1 site)	7	99	228.47	10.16	0.00	neighboring
fruits per area	level+disturbance*shannon diversity+(1 site)	9	99	228.56	10.26	0.00	neighboring
fruits per area	level+shannon diversity+(1 site)	7	99	229.04	10.74	0.00	neighboring
fruits per area	disturbance+level+(1 site)	7	99	230.47	12.16	0.00	neighboring
fruits per area	disturbance+level+shannon diversity+(1 site)	8	99	231.30	12.99	0.00	neighboring
fruits per area	disturbance*species richness+(1 site)	6	99	231.48	13.17	0.00	neighboring
fruits per area	vegetation cover+(1 site)	4	99	231.81	13.50	0.00	neighboring
fruits per area	level+disturbance*competition+(1 site)	9	99	232.12	13.81	0.00	neighboring
fruits per area	disturbance+level*competition+(1 site)	11	99	232.40	14.10	0.00	neighboring
fruits per area	disturbance+level+competition+(1 site)	8	99	232.46	14.15	0.00	neighboring
fruits per area	disturbance+vegetation cover+(1 site)	5	99	232.62	14.31	0.00	neighboring
fruits per area	disturbance*level+(1 site)	10	99	232.88	14.57	0.00	neighboring
fruits per area	level+species richness+(1 site)	7	99	233.77	15.46	0.00	neighboring
fruits per area	disturbance*level*competition+(1 site)	18	99	234.74	16.43	0.00	neighboring
fruits per area	disturbance*level+shannon diversity+(1 site)	11	99	234.81	16.51	0.00	neighboring
fruits per area	disturbance*level+competition+(1 site)	11	99	235.20	16.89	0.00	neighboring
fruits per area	disturbance+level+species richness+(1 site)	8	99	235.97	17.67	0.00	neighboring
fruits per area	level+vegetation cover+(1 site)	7	99	238.03	19.73	0.00	neighboring
fruits per area	disturbance*level+species richness+(1 site)	11	99	239.54	21.24	0.00	neighboring
fruits per area	level+disturbance*species richness+(1 site)	9	99	240.27	21.96	0.00	neighboring
fruits per area	level*species richness+(1 site)	10	99	240.52	22.22	0.00	neighboring
fruits per area	disturbance+level+vegetation cover+(1 site)	8	99	240.85	22.54	0.00	neighboring
fruits per area	disturbance*vegetation cover+(1 site)	6	99	241.48	23.17	0.00	neighboring
fruits per area	disturbance+level*species richness+(1 site)	11	99	243.65	25.34	0.00	neighboring
fruits per area	disturbance*level+vegetation cover+(1 site)	11	99	244.49	26.18	0.00	neighboring
fruits per area	level+disturbance*vegetation cover+(1 site)	9	99	250.41	32.10	0.00	neighboring
fruits per area	disturbance*level*species richness+(1 site)	18	99	261.26	42.95	0.00	neighboring
fruits per area	level*vegetation cover+(1 site)	10	99	265.55	47.25	0.00	neighboring
fruits per area	disturbance+level*vegetation cover+(1 site)	11	99	269.26	50.95	0.00	neighboring

fruits per area	disturbance*level*vegetation cover+(1 site)	18	99	309.02	90.71	0.00	neighboring
relative reproduction	level*competition+(1 site)	10	37	127.60	0.00	0.73	neighboring
relative reproduction	disturbance+level*competition+(1 site)	11	37	129.61	2.01	0.27	neighboring
relative reproduction	level*shannon diversity+(1 site)	10	37	139.61	12.01	0.00	neighboring
relative reproduction	competition+(1 site)	4	37	140.64	13.04	0.00	neighboring
relative reproduction	disturbance*competition+(1 site)	6	37	141.05	13.45	0.00	neighboring
relative reproduction	disturbance+level*shannon diversity+(1 site)	11	37	141.54	13.94	0.00	neighboring
relative reproduction	disturbance+competition+(1 site)	5	37	141.90	14.29	0.00	neighboring
relative reproduction	(1 site)	3	37	143.12	15.52	0.00	neighboring
relative reproduction	level+competition+(1 site)	7	37	143.27	15.67	0.00	neighboring
relative reproduction	level+disturbance*competition+(1 site)	9	37	143.80	16.20	0.00	neighboring
relative reproduction	shannon diversity+(1 site)	4	37	144.05	16.45	0.00	neighboring
relative reproduction	disturbance+(1 site)	4	37	144.19	16.58	0.00	neighboring
relative reproduction	disturbance+level+competition+(1 site)	8	37	144.65	17.05	0.00	neighboring
relative reproduction	level+(1 site)	6	37	145.14	17.54	0.00	neighboring
relative reproduction	disturbance*shannon diversity+(1 site)	6	37	145.51	17.90	0.00	neighboring
relative reproduction	disturbance+shannon diversity+(1 site)	5	37	145.55	17.95	0.00	neighboring
relative reproduction	vegetation cover+(1 site)	4	37	145.58	17.98	0.00	neighboring
relative reproduction	disturbance+level+(1 site)	7	37	145.69	18.09	0.00	neighboring
relative reproduction	species richness+(1 site)	4	37	146.79	19.19	0.00	neighboring
relative reproduction	level+shannon diversity+(1 site)	7	37	146.85	19.25	0.00	neighboring
relative reproduction	disturbance+level+shannon diversity+(1 site)	8	37	147.47	19.87	0.00	neighboring
relative reproduction	level+disturbance*shannon diversity+(1 site)	9	37	147.61	20.01	0.00	neighboring
relative reproduction	disturbance+vegetation cover+(1 site)	5	37	147.76	20.16	0.00	neighboring
relative reproduction	disturbance+species richness+(1 site)	5	37	148.63	21.03	0.00	neighboring
relative reproduction	level+vegetation cover+(1 site)	7	37	148.85	21.25	0.00	neighboring
relative reproduction	level+species richness+(1 site)	7	37	149.98	22.38	0.00	neighboring
relative reproduction	disturbance+level+vegetation cover+(1 site)	8	37	151.36	23.75	0.00	neighboring
relative reproduction	disturbance+level+species richness+(1 site)	8	37	151.60	24.00	0.00	neighboring
relative reproduction	disturbance*species richness+(1 site)	6	37	152.50	24.90	0.00	neighboring
relative reproduction	disturbance*vegetation cover+(1 site)	6	37	154.69	27.09	0.00	neighboring

relative reproduction	level+disturbance*species richness+(1 site)	9	37	155.61	28.01	0.00	neighboring
relative reproduction	level*species richness+(1 site)	10	37	158.44	30.84	0.00	neighboring
relative reproduction	level+disturbance*vegetation cover+(1 site)	9	37	158.49	30.88	0.00	neighboring
relative reproduction	disturbance+level*species richness+(1 site)	11	37	161.32	33.72	0.00	neighboring
relative reproduction	level*vegetation cover+(1 site)	10	37	166.90	39.30	0.00	neighboring
relative reproduction	disturbance+level*vegetation cover+(1 site)	11	37	169.05	41.45	0.00	neighboring

D

modeled parameter	model formula	k	n	AICc	Δ AICc	AICc weight
fruits per area	disturbance*level*SWC+(1 site)	18	57	144.05	0.00	0.93
fruits per area	disturbance*level*SWC+SOM+(1 site)	19	57	149.12	5.08	0.07
fruits per area	(1 site)	3	57	162.66	18.61	0.00
fruits per area	level+(1 site)	6	57	163.78	19.73	0.00
fruits per area	disturbance+(1 site)	4	57	164.97	20.92	0.00
fruits per area	disturbance+SOM+(1 site)	5	57	165.82	21.77	0.00
fruits per area	SOM+(1 site)	4	57	165.93	21.89	0.00
fruits per area	SWC+(1 site)	4	57	166.76	22.72	0.00
fruits per area	disturbance+level+(1 site)	7	57	166.93	22.88	0.00
fruits per area	disturbance+SWC+(1 site)	5	57	168.18	24.13	0.00
fruits per area	disturbance*level+(1 site)	10	57	168.22	24.17	0.00
fruits per area	level+SOM+(1 site)	7	57	168.31	24.27	0.00
fruits per area	disturbance*SOM+(1 site)	6	57	168.48	24.43	0.00
fruits per area	disturbance+SOM+SWC+(1 site)	6	57	168.60	24.56	0.00
fruits per area	level+SWC+(1 site)	7	57	168.71	24.66	0.00
fruits per area	SOM+SWC+(1 site)	5	57	168.89	24.85	0.00
fruits per area	disturbance+level+SOM+(1 site)	8	57	170.47	26.42	0.00
fruits per area	disturbance*SWC+(1 site)	6	57	171.05	27.00	0.00
fruits per area	disturbance*SOM+SWC+(1 site)	7	57	171.39	27.35	0.00
fruits per area	disturbance*SOM+SWC*(1 site)	7	57	171.39	27.35	0.00
fruits per area	level+SOM+SWC+(1 site)	8	57	171.49	27.45	0.00
fruits per area	disturbance+level+SWC+(1 site)	8	57	171.58	27.53	0.00
fruits per area	SOM*SWC+(1 site)	6	57	172.15	28.11	0.00
fruits per area	disturbance*level+SWC+(1 site)	11	57	172.21	28.16	0.00
fruits per area	disturbance*level+SOM+(1 site)	11	57	172.86	28.82	0.00
fruits per area	level+disturbance*SOM+(1 site)	9	57	173.14	29.10	0.00
fruits per area	disturbance+level+SOM+SWC+(1 site)	9	57	173.33	29.29	0.00
fruits per area	level+disturbance*SWC+SOM+(1 site)	10	57	173.93	29.89	0.00
fruits per area	level+disturbance*SWC+(1 site)	9	57	173.94	29.90	0.00
fruits per area	disturbance*level+SOM+SWC+(1 site)	12	57	174.36	30.32	0.00

fruits per area	level*SOM+(1 site)	10	57	175.06	31.01	0.00
fruits per area	level+disturbance*SOM+SWC+(1 site)	10	57	175.41	31.36	0.00
fruits per area	disturbance*level*SOM+(1 site)	18	57	176.70	32.65	0.00
fruits per area	disturbance+level+SOM*SWC+(1 site)	10	57	176.91	32.86	0.00
fruits per area	level+disturbance+SOM*SWC+(1 site)	10	57	176.91	32.86	0.00
fruits per area	level*SOM+SWC+(1 site)	11	57	177.12	33.08	0.00
fruits per area	level*SOM+SWC+(1 site)	11	57	177.12	33.08	0.00
fruits per area	disturbance*level*SOM+SWC+(1 site)	19	57	177.72	33.68	0.00
fruits per area	disturbance+level*SOM+(1 site)	11	57	178.20	34.15	0.00
fruits per area	level*SWC+(1 site)	10	57	178.44	34.39	0.00
fruits per area	disturbance*level+SOM*SWC+(1 site)	13	57	178.72	34.67	0.00
fruits per area	disturbance+level*SOM+SWC+(1 site)	12	57	180.25	36.20	0.00
fruits per area	disturbance+level*SWC+(1 site)	11	57	181.16	37.11	0.00
fruits per area	disturbance+level*SWC+SOM+(1 site)	12	57	182.59	38.55	0.00
fruits per area	level*SOM*SWC+(1 site)	18	57	184.51	40.47	0.00
relative reproduction	disturbance*SOM+(1 site)	6	17	62.74	0.00	0.37
relative reproduction	SWC+(1 site)	4	17	65.62	2.88	0.09
relative reproduction	SOM*SWC+(1 site)	6	17	65.83	3.10	0.08
relative reproduction	SOM+(1 site)	4	17	65.97	3.23	0.07
relative reproduction	disturbance*SOM+SWC+(1 site)	7	17	66.29	3.56	0.06
relative reproduction	disturbance*SOM+SWC*(1 site)	7	17	66.29	3.56	0.06
relative reproduction	level*SOM+(1 site)	8	17	66.79	4.05	0.05
relative reproduction	disturbance+SOM+(1 site)	5	17	67.00	4.27	0.04
relative reproduction	disturbance+(1 site)	4	17	67.64	4.90	0.03
relative reproduction	disturbance+SWC+(1 site)	5	17	67.69	4.96	0.03
relative reproduction	SOM+SWC+(1 site)	5	17	68.08	5.35	0.03
relative reproduction	(1 site)	3	17	68.34	5.60	0.02
relative reproduction	disturbance*SWC+(1 site)	6	17	68.98	6.24	0.02
relative reproduction	disturbance+SOM+SWC+(1 site)	6	17	69.86	7.12	0.01
relative reproduction	level+SWC+(1 site)	6	17	70.30	7.57	0.01
relative reproduction	level+SOM+(1 site)	6	17	71.23	8.49	0.01
relative reproduction	disturbance+level+(1 site)	6	17	71.47	8.73	0.00
relative reproduction	level+(1 site)	5	17	72.29	9.56	0.00
relative reproduction	level+disturbance*SOM+(1 site)	8	17	72.70	9.97	0.00
relative reproduction	disturbance+level*SOM+(1 site)	9	17	73.30	10.57	0.00
relative reproduction	level*SOM+SWC+(1 site)	9	17	73.62	10.88	0.00
relative reproduction	level*SOM+SWC+(1 site)	9	17	73.62	10.88	0.00
relative reproduction	disturbance+level+SWC+(1 site)	7	17	74.17	11.43	0.00
relative reproduction	disturbance+level+SOM+(1 site)	7	17	74.26	11.53	0.00
relative reproduction	level+SOM+SWC+(1 site)	7	17	74.61	11.87	0.00

relative reproduction	level*SWC+(1 site)	8	17	75.95	13.21	0.00
relative reproduction	level+disturbance*SWC+(1 site)	8	17	78.04	15.30	0.00
relative reproduction	disturbance+level+SOM+SWC+(1 site)	8	17	79.17	16.43	0.00
relative reproduction	disturbance+level+SOM*SWC+(1 site)	9	17	80.11	17.37	0.00
relative reproduction	level+disturbance+SOM*SWC+(1 site)	9	17	80.11	17.37	0.00
relative reproduction	level+disturbance*SOM+SWC+(1 site)	9	17	80.11	17.37	0.00
relative reproduction	disturbance+level*SWC+(1 site)	9	17	83.24	20.51	0.00
relative reproduction	disturbance+level*SOM+SWC+(1 site)	10	17	83.41	20.68	0.00
relative reproduction	level+disturbance*SWC+SOM+(1 site)	9	17	83.46	20.72	0.00
relative reproduction	disturbance+level*SWC+SOM+(1 site)	10	17	93.47	30.73	0.00

E

modeled parameter	model formula	k	n	AICc	Δ AICc	AICc weight
size	disturbance*level*SOM+SWC+(1 site)	19	57	654.80	0.00	0.89
size	disturbance*level*SWC+SOM+(1 site)	19	57	659.55	4.74	0.08
size	disturbance*level*SOM+(1 site)	18	57	662.47	7.67	0.02
size	disturbance*level*SWC+(1 site)	18	57	667.59	12.79	0.00
size	level*SOM*SWC+(1 site)	18	57	668.89	14.09	0.00
size	disturbance*level+SOM*SWC+(1 site)	13	57	720.29	65.48	0.00
size	disturbance*level+SOM+SWC+(1 site)	12	57	727.66	72.85	0.00
size	disturbance+level*SWC+SOM+(1 site)	12	57	730.38	75.58	0.00
size	disturbance+level*SOM+SWC+(1 site)	12	57	730.91	76.11	0.00
size	disturbance*level+SWC+(1 site)	11	57	736.36	81.55	0.00
size	disturbance*level+SOM+(1 site)	11	57	737.81	83.01	0.00
size	disturbance+level*SWC+(1 site)	11	57	738.90	84.10	0.00
size	level*SOM+SWC+(1 site)	11	57	740.02	85.21	0.00
size	level*SOM+SWC+(1 site)	11	57	740.02	85.21	0.00
size	disturbance+level*SOM+(1 site)	11	57	740.87	86.07	0.00
size	disturbance*level+(1 site)	10	57	745.21	90.41	0.00
size	level*SWC+(1 site)	10	57	748.10	93.29	0.00
size	level+disturbance*SOM+SWC+(1 site)	10	57	749.49	94.69	0.00
size	level+disturbance*SWC+SOM+(1 site)	10	57	749.64	94.84	0.00
size	level*SOM+(1 site)	10	57	749.91	95.10	0.00
size	disturbance+level+SOM*SWC+(1 site)	10	57	750.61	95.80	0.00
size	level+disturbance+SOM*SWC+(1 site)	10	57	750.61	95.80	0.00
size	disturbance+level+SOM+SWC+(1 site)	9	57	758.35	103.55	0.00
size	level+disturbance*SWC+(1 site)	9	57	758.96	104.15	0.00
size	level+disturbance*SOM+(1 site)	9	57	760.06	105.26	0.00
size	disturbance+level+SWC+(1 site)	8	57	768.28	113.48	0.00
size	disturbance+level+SOM+(1 site)	8	57	769.68	114.88	0.00
size	level+SOM+SWC+(1 site)	8	57	769.70	114.90	0.00

size	disturbance*SOM+SWC+(1 site)	7	57	776.34	121.54	0.00
size	disturbance*SOM+SWC*(1 site)	7	57	776.34	121.54	0.00
size	disturbance+level+(1 site)	7	57	777.15	122.34	0.00
size	level+SWC+(1 site)	7	57	778.21	123.41	0.00
size	level+SOM+(1 site)	7	57	779.97	125.17	0.00
size	disturbance*SWC+(1 site)	6	57	785.34	130.53	0.00
size	disturbance+SOM+SWC+(1 site)	6	57	785.62	130.82	0.00
size	disturbance*SOM+(1 site)	6	57	786.40	131.59	0.00
size	SOM*SWC+(1 site)	6	57	789.11	134.31	0.00
size	level+(1 site)	6	57	789.46	134.66	0.00
size	disturbance+SWC+(1 site)	5	57	795.33	140.52	0.00
size	disturbance+SOM+(1 site)	5	57	796.63	141.83	0.00
size	SOM+SWC+(1 site)	5	57	797.56	142.75	0.00
size	disturbance+(1 site)	4	57	804.29	149.48	0.00
size	SWC+(1 site)	4	57	806.28	151.48	0.00
size	SOM+(1 site)	4	57	807.74	152.94	0.00
size	(1 site)	3	57	817.31	162.51	0.00

Table B.B.2. Full list of LMMs to test effects of A) disturbance, elevational level, *Silene acaulis* cushion presence, and sampling area on species community indices. B) A secondary model set replaces cushion presence with SOM and SWC, and could only be tested on inside species. Black bars differentiate model sets, and k = number of parameters, n = sample size.

A

modeled parameter	model formula	k	n	AICc	Δ AICc	AICc weight	species
species richness	disturbance*level*area+cushion+(1 site/cushion ID)	20	198	947.01	0.00	1.00	inside
species richness	disturbance+level*area+cushion+(1 site/cushion ID)	13	198	960.89	13.88	0.00	inside
species richness	disturbance*level+area+cushion+(1 site/cushion ID)	13	198	966.23	19.22	0.00	inside
species richness	level+disturbance*area+cushion+(1 site/cushion ID)	11	198	967.42	20.41	0.00	inside
species richness	cushion+area*level+(1 site/cushion ID)	12	198	970.79	23.78	0.00	inside
species richness	disturbance+level+area+cushion+(1 site/cushion ID)	10	198	974.30	27.29	0.00	inside
species richness	cushion+area+level+(1 site/cushion ID)	9	198	983.60	36.59	0.00	inside
species richness	cushion*level+area+(1 site/cushion ID)	12	198	983.98	36.97	0.00	inside
species richness	disturbance*area+cushion+(1 site/cushion ID)	8	198	990.02	43.01	0.00	inside
species richness	disturbance*level*cushion+(1 site/cushion ID)	19	200	992.19	45.18	0.00	inside
species richness	disturbance*level+cushion+(1 site/cushion ID)	12	200	995.16	48.15	0.00	inside
species richness	disturbance+cushion+area+(1 site/cushion ID)	7	198	996.95	49.94	0.00	inside
species richness	disturbance*cushion+area+(1 site/cushion ID)	8	198	997.45	50.44	0.00	inside
species richness	disturbance+level+cushion+(1 site/cushion ID)	9	200	1001.00	53.99	0.00	inside
species richness	disturbance+level*cushion+(1 site/cushion ID)	12	200	1001.41	54.41	0.00	inside
species richness	cushion+area+(1 site/cushion ID)	6	198	1001.79	54.78	0.00	inside
species richness	level+disturbance*cushion+(1 site/cushion ID)	10	200	1001.80	54.79	0.00	inside
species richness	cushion+level+(1 site/cushion ID)	8	200	1004.37	57.36	0.00	inside
species richness	cushion*level+(1 site/cushion ID)	11	200	1004.71	57.70	0.00	inside
species richness	disturbance*level+(1 site/cushion ID)	11	200	1018.92	71.91	0.00	inside
species richness	disturbance+cushion+(1 site/cushion ID)	6	200	1020.31	73.30	0.00	inside
species richness	disturbance*cushion+(1 site/cushion ID)	7	200	1021.04	74.03	0.00	inside
species richness	cushion+(1 site/cushion ID)	5	200	1021.35	74.34	0.00	inside
species richness	disturbance+level+(1 site/cushion ID)	8	200	1024.84	77.83	0.00	inside
species richness	level+(1 site/cushion ID)	7	200	1028.22	81.21	0.00	inside
species richness	disturbance+(1 site/cushion ID)	5	200	1044.21	97.21	0.00	inside

species richness	(1 site/cushion ID)	4	200	1045.27	98.26	0.00	inside
shannon diversity	level+disturbance*area+cushion+(1 site/cushion ID)	11	198	342.07	0.00	0.33	inside
shannon diversity	disturbance+level+area+cushion+(1 site/cushion ID)	10	198	343.24	1.16	0.18	inside
shannon diversity	disturbance*area+cushion+(1 site/cushion ID)	8	198	343.57	1.50	0.16	inside
shannon diversity	cushion+area+(1 site/cushion ID)	6	198	344.75	2.68	0.09	inside
shannon diversity	disturbance+cushion+area+(1 site/cushion ID)	7	198	345.01	2.94	0.08	inside
shannon diversity	disturbance+level*area+cushion+(1 site/cushion ID)	13	198	345.44	3.36	0.06	inside
shannon diversity	cushion+area+level+(1 site/cushion ID)	9	198	345.64	3.57	0.06	inside
shannon diversity	cushion+area*level+(1 site/cushion ID)	12	198	347.89	5.82	0.02	inside
shannon diversity	disturbance*level+area+cushion+(1 site/cushion ID)	13	198	348.79	6.72	0.01	inside
shannon diversity	(1 site/cushion ID)	4	200	349.25	7.18	0.01	inside
shannon diversity	disturbance*cushion+area+(1 site/cushion ID)	8	198	349.63	7.56	0.01	inside
shannon diversity	level+(1 site/cushion ID)	7	200	350.54	8.47	0.00	inside
shannon diversity	disturbance+level+(1 site/cushion ID)	8	200	352.15	10.08	0.00	inside
shannon diversity	disturbance+(1 site/cushion ID)	5	200	352.37	10.29	0.00	inside
shannon diversity	cushion+(1 site/cushion ID)	5	200	354.80	12.72	0.00	inside
shannon diversity	cushion*level+area+(1 site/cushion ID)	12	198	354.89	12.82	0.00	inside
shannon diversity	cushion+level+(1 site/cushion ID)	8	200	356.15	14.08	0.00	inside
shannon diversity	disturbance+level+cushion+(1 site/cushion ID)	9	200	357.78	15.71	0.00	inside
shannon diversity	disturbance+cushion+(1 site/cushion ID)	6	200	357.93	15.86	0.00	inside
shannon diversity	disturbance*level+(1 site/cushion ID)	11	200	359.23	17.16	0.00	inside
shannon diversity	disturbance*level*area+cushion+(1 site/cushion ID)	20	198	359.69	17.61	0.00	inside
shannon diversity	level+disturbance*cushion+(1 site/cushion ID)	10	200	362.42	20.34	0.00	inside
shannon diversity	disturbance*cushion+(1 site/cushion ID)	7	200	362.50	20.42	0.00	inside
shannon diversity	disturbance*level+cushion+(1 site/cushion ID)	12	200	364.94	22.86	0.00	inside
shannon diversity	cushion*level+(1 site/cushion ID)	11	200	365.71	23.64	0.00	inside
shannon diversity	disturbance+level*cushion+(1 site/cushion ID)	12	200	367.42	25.34	0.00	inside
shannon diversity	disturbance*level*cushion+(1 site/cushion ID)	19	200	381.76	39.68	0.00	inside
vegetation cover	disturbance*level*area+cushion+(1 site/cushion ID)	20	198	1729.72	0.00	1.00	inside
vegetation cover	disturbance*level*cushion+(1 site/cushion ID)	19	200	1744.12	14.41	0.00	inside

vegetation cover	disturbance*level+area+cushion+(1 site/cushion ID)	13	198	1763.99	34.27	0.00	inside
vegetation cover	disturbance+level*area+cushion+(1 site/cushion ID)	13	198	1773.71	44.00	0.00	inside
vegetation cover	cushion*level+area+(1 site/cushion ID)	12	198	1781.20	51.48	0.00	inside
vegetation cover	level+disturbance*area+cushion+(1 site/cushion ID)	11	198	1781.56	51.84	0.00	inside
vegetation cover	cushion+area*level+(1 site/cushion ID)	12	198	1782.32	52.60	0.00	inside
vegetation cover	disturbance*level+cushion+(1 site/cushion ID)	12	200	1787.83	58.11	0.00	inside
vegetation cover	disturbance+level+area+cushion+(1 site/cushion ID)	10	198	1787.86	58.14	0.00	inside
vegetation cover	disturbance+level*cushion+(1 site/cushion ID)	12	200	1795.31	65.60	0.00	inside
vegetation cover	cushion+area+level+(1 site/cushion ID)	9	198	1796.57	66.85	0.00	inside
vegetation cover	cushion*level+(1 site/cushion ID)	11	200	1801.84	72.12	0.00	inside
vegetation cover	level+disturbance*cushion+(1 site/cushion ID)	10	200	1807.62	77.90	0.00	inside
vegetation cover	disturbance+level+cushion+(1 site/cushion ID)	9	200	1810.81	81.09	0.00	inside
vegetation cover	cushion+level+(1 site/cushion ID)	8	200	1817.40	87.68	0.00	inside
vegetation cover	disturbance*area+cushion+(1 site/cushion ID)	8	198	1824.57	94.85	0.00	inside
vegetation cover	disturbance*cushion+area+(1 site/cushion ID)	8	198	1827.35	97.64	0.00	inside
vegetation cover	disturbance+cushion+area+(1 site/cushion ID)	7	198	1830.60	100.88	0.00	inside
vegetation cover	cushion+area+(1 site/cushion ID)	6	198	1836.04	106.32	0.00	inside
vegetation cover	disturbance*cushion+(1 site/cushion ID)	7	200	1849.56	119.84	0.00	inside
vegetation cover	disturbance+cushion+(1 site/cushion ID)	6	200	1852.81	123.10	0.00	inside
vegetation cover	cushion+(1 site/cushion ID)	5	200	1856.98	127.26	0.00	inside
vegetation cover	disturbance*level+(1 site/cushion ID)	11	200	1895.86	166.15	0.00	inside
vegetation cover	disturbance+level+(1 site/cushion ID)	8	200	1916.83	187.11	0.00	inside
vegetation cover	level+(1 site/cushion ID)	7	200	1922.62	192.90	0.00	inside
vegetation cover	disturbance+(1 site/cushion ID)	5	200	1953.17	223.45	0.00	inside
vegetation cover	(1 site/cushion ID)	4	200	1957.29	227.58	0.00	inside
species richness	disturbance*level*area+cushion+(1 site/cushion ID)	20	198	972.41	0.00	0.79	neighboring
species richness	disturbance*level+area+cushion+(1 site/cushion ID)	13	198	975.13	2.72	0.20	neighboring
species richness	disturbance*level*cushion+(1 site/cushion ID)	19	200	981.45	9.04	0.01	neighboring
species richness	disturbance*level+(1 site/cushion ID)	11	200	984.86	12.45	0.00	neighboring
species richness	disturbance*level+cushion+(1 site/cushion ID)	12	200	985.59	13.18	0.00	neighboring
species richness	level+disturbance*area+cushion+(1 site/cushion ID)	11	198	986.74	14.33	0.00	neighboring

species richness	disturbance+level+area+cushion+(1 site/cushion ID)	10	198	986.79	14.38	0.00	neighboring
species richness	disturbance+level*area+cushion+(1 site/cushion ID)	13	198	987.71	15.30	0.00	neighboring
species richness	level+disturbance*cushion+(1 site/cushion ID)	10	200	994.20	21.79	0.00	neighboring
species richness	disturbance+level+(1 site/cushion ID)	8	200	995.76	23.35	0.00	neighboring
species richness	disturbance+level*cushion+(1 site/cushion ID)	12	200	995.80	23.39	0.00	neighboring
species richness	disturbance+level+cushion+(1 site/cushion ID)	9	200	996.42	24.01	0.00	neighboring
species richness	cushion*level+area+(1 site/cushion ID)	12	198	1005.93	33.52	0.00	neighboring
species richness	cushion+area*level+(1 site/cushion ID)	12	198	1006.31	33.90	0.00	neighboring
species richness	cushion+area+level+(1 site/cushion ID)	9	198	1006.78	34.37	0.00	neighboring
species richness	cushion*level+(1 site/cushion ID)	11	200	1012.52	40.11	0.00	neighboring
species richness	level+(1 site/cushion ID)	7	200	1012.57	40.16	0.00	neighboring
species richness	disturbance*cushion+area+(1 site/cushion ID)	8	198	1012.84	40.43	0.00	neighboring
species richness	cushion+level+(1 site/cushion ID)	8	200	1013.20	40.79	0.00	neighboring
species richness	disturbance*area+cushion+(1 site/cushion ID)	8	198	1014.50	42.09	0.00	neighboring
species richness	disturbance+cushion+area+(1 site/cushion ID)	7	198	1015.19	42.78	0.00	neighboring
species richness	disturbance*cushion+(1 site/cushion ID)	7	200	1023.56	51.15	0.00	neighboring
species richness	disturbance+(1 site/cushion ID)	5	200	1025.26	52.84	0.00	neighboring
species richness	disturbance+cushion+(1 site/cushion ID)	6	200	1025.85	53.44	0.00	neighboring
species richness	cushion+area+(1 site/cushion ID)	6	198	1026.92	54.51	0.00	neighboring
species richness	(1 site/cushion ID)	4	200	1033.99	61.58	0.00	neighboring
species richness	cushion+(1 site/cushion ID)	5	200	1034.56	62.15	0.00	neighboring
shannon diversity	disturbance+level+(1 site/cushion ID)	8	200	203.42	0.00	0.77	neighboring
shannon diversity	disturbance+level+cushion+(1 site/cushion ID)	9	200	206.91	3.49	0.13	neighboring
shannon diversity	disturbance*level+(1 site/cushion ID)	11	200	209.69	6.26	0.03	neighboring
shannon diversity	level+disturbance*cushion+(1 site/cushion ID)	10	200	210.67	7.25	0.02	neighboring
shannon diversity	disturbance+level+area+cushion+(1 site/cushion ID)	10	198	211.07	7.65	0.02	neighboring
shannon diversity	level+(1 site/cushion ID)	7	200	212.29	8.87	0.01	neighboring
shannon diversity	disturbance*level+cushion+(1 site/cushion ID)	12	200	213.24	9.82	0.01	neighboring
shannon diversity	disturbance+(1 site/cushion ID)	5	200	213.92	10.50	0.00	neighboring
shannon diversity	cushion+level+(1 site/cushion ID)	8	200	215.76	12.34	0.00	neighboring
shannon diversity	level+disturbance*area+cushion+(1 site/cushion ID)	11	198	216.07	12.65	0.00	neighboring

shannon diversity	disturbance*level+area+cushion+(1 site/cushion ID)	13	198	216.74	13.32	0.00	neighboring
shannon diversity	(1 site/cushion ID)	4	200	216.85	13.43	0.00	neighboring
shannon diversity	disturbance+cushion+(1 site/cushion ID)	6	200	217.34	13.92	0.00	neighboring
shannon diversity	disturbance+level*cushion+(1 site/cushion ID)	12	200	219.13	15.71	0.00	neighboring
shannon diversity	disturbance+cushion+area+(1 site/cushion ID)	7	198	220.09	16.67	0.00	neighboring
shannon diversity	cushion+(1 site/cushion ID)	5	200	220.24	16.82	0.00	neighboring
shannon diversity	disturbance*cushion+(1 site/cushion ID)	7	200	221.04	17.62	0.00	neighboring
shannon diversity	cushion+area+level+(1 site/cushion ID)	9	198	221.58	18.16	0.00	neighboring
shannon diversity	disturbance+level*area+cushion+(1 site/cushion ID)	13	198	222.54	19.11	0.00	neighboring
shannon diversity	disturbance*cushion+area+(1 site/cushion ID)	8	198	223.62	20.20	0.00	neighboring
shannon diversity	disturbance*area+cushion+(1 site/cushion ID)	8	198	224.42	21.00	0.00	neighboring
shannon diversity	cushion+area+(1 site/cushion ID)	6	198	224.90	21.48	0.00	neighboring
shannon diversity	cushion*level+(1 site/cushion ID)	11	200	227.91	24.49	0.00	neighboring
shannon diversity	cushion+area*level+(1 site/cushion ID)	12	198	231.69	28.27	0.00	neighboring
shannon diversity	cushion*level+area+(1 site/cushion ID)	12	198	233.44	30.02	0.00	neighboring
shannon diversity	disturbance*level*cushion+(1 site/cushion ID)	19	200	239.14	35.72	0.00	neighboring
shannon diversity	disturbance*level*area+cushion+(1 site/cushion ID)	20	198	243.52	40.10	0.00	neighboring
vegetation cover	disturbance*level*area+cushion+(1 site/cushion ID)	20	198	1670.06	0.00	1.00	neighboring
vegetation cover	disturbance*level*cushion+(1 site/cushion ID)	19	200	1689.52	19.46	0.00	neighboring
vegetation cover	disturbance*level+area+cushion+(1 site/cushion ID)	13	198	1698.80	28.74	0.00	neighboring
vegetation cover	disturbance+level*area+cushion+(1 site/cushion ID)	13	198	1716.65	46.59	0.00	neighboring
vegetation cover	disturbance*level+cushion+(1 site/cushion ID)	12	200	1717.66	47.60	0.00	neighboring
vegetation cover	disturbance*level+(1 site/cushion ID)	11	200	1718.74	48.68	0.00	neighboring
vegetation cover	level+disturbance*area+cushion+(1 site/cushion ID)	11	198	1724.56	54.50	0.00	neighboring
vegetation cover	disturbance+level+area+cushion+(1 site/cushion ID)	10	198	1727.29	57.23	0.00	neighboring
vegetation cover	cushion*level+area+(1 site/cushion ID)	12	198	1732.33	62.27	0.00	neighboring
vegetation cover	cushion+area*level+(1 site/cushion ID)	12	198	1732.95	62.89	0.00	neighboring
vegetation cover	disturbance+level*cushion+(1 site/cushion ID)	12	200	1735.79	65.73	0.00	neighboring
vegetation cover	level+disturbance*cushion+(1 site/cushion ID)	10	200	1743.92	73.86	0.00	neighboring
vegetation cover	cushion+area+level+(1 site/cushion ID)	9	198	1744.42	74.36	0.00	neighboring
vegetation cover	disturbance+level+cushion+(1 site/cushion ID)	9	200	1747.36	77.30	0.00	neighboring

vegetation cover	disturbance+level+(1 site/cushion ID)	8	200	1748.50	78.44	0.00	neighboring
vegetation cover	cushion*level+(1 site/cushion ID)	11	200	1754.92	84.86	0.00	neighboring
vegetation cover	cushion+level+(1 site/cushion ID)	8	200	1766.57	96.51	0.00	neighboring
vegetation cover	level+(1 site/cushion ID)	7	200	1767.73	97.67	0.00	neighboring
vegetation cover	disturbance*cushion+area+(1 site/cushion ID)	8	198	1769.14	99.08	0.00	neighboring
vegetation cover	disturbance*area+cushion+(1 site/cushion ID)	8	198	1769.70	99.64	0.00	neighboring
vegetation cover	disturbance+cushion+area+(1 site/cushion ID)	7	198	1772.80	102.74	0.00	neighboring
vegetation cover	cushion+area+(1 site/cushion ID)	6	198	1783.17	113.11	0.00	neighboring
vegetation cover	disturbance*cushion+(1 site/cushion ID)	7	200	1789.54	119.48	0.00	neighboring
vegetation cover	disturbance+cushion+(1 site/cushion ID)	6	200	1793.05	122.99	0.00	neighboring
vegetation cover	disturbance+(1 site/cushion ID)	5	200	1794.26	124.20	0.00	neighboring
vegetation cover	cushion+(1 site/cushion ID)	5	200	1804.31	134.25	0.00	neighboring
vegetation cover	(1 site/cushion ID)	4	200	1805.54	135.48	0.00	neighboring

B

modeled parameter	model formula	k	n	AICc	Δ AICc	AICc weight
species richness	disturbance*level*SWC*SOM+(1 site/cushion ID)	35	114	543.41	0.00	1.00
species richness	disturbance*level*SOM+(1 site/cushion ID)	19	114	586.99	43.58	0.00
species richness	disturbance*level*SOM+SWC+(1 site/cushion ID)	20	114	587.79	44.38	0.00
species richness	disturbance*level*SWC+(1 site/cushion ID)	19	114	588.13	44.72	0.00
species richness	disturbance*level*SWC+SOM+(1 site/cushion ID)	20	114	588.58	45.17	0.00
species richness	level*SOM*SWC+(1 site/cushion ID)	19	114	592.29	48.88	0.00
species richness	disturbance*level+(1 site/cushion ID)	11	114	594.19	50.78	0.00
species richness	disturbance*level+SOM+(1 site/cushion ID)	12	114	596.14	52.73	0.00
species richness	disturbance*level+SWC+(1 site/cushion ID)	12	114	596.19	52.78	0.00
species richness	disturbance*level+SOM+SWC+(1 site/cushion ID)	13	114	596.89	53.48	0.00
species richness	disturbance*level+SOM*SWC+(1 site/cushion ID)	14	114	598.47	55.06	0.00
species richness	disturbance+level+(1 site/cushion ID)	8	114	599.95	56.54	0.00
species richness	disturbance+level*SOM+(1 site/cushion ID)	12	114	601.24	57.83	0.00
species richness	disturbance+level+SWC+(1 site/cushion ID)	9	114	601.55	58.14	0.00
species richness	disturbance+level+SOM+(1 site/cushion ID)	9	114	601.62	58.20	0.00
species richness	level+disturbance*SOM+(1 site/cushion ID)	10	114	601.73	58.31	0.00
species richness	disturbance+level*SWC+(1 site/cushion ID)	12	114	601.87	58.46	0.00
species richness	disturbance+level*SOM+SWC+(1 site/cushion ID)	13	114	601.99	58.58	0.00
species richness	level+disturbance*SOM+SWC+(1 site/cushion ID)	11	114	602.03	58.61	0.00
species richness	level+disturbance*SWC+(1 site/cushion ID)	10	114	602.10	58.69	0.00
species richness	disturbance+level+SOM+SWC+(1 site/cushion ID)	10	114	602.17	58.76	0.00

species richness	disturbance+level*SWC+SOM+(1 site/cushion ID)	13	114	602.46	59.05	0.00
species richness	level+disturbance*SWC+SOM+(1 site/cushion ID)	11	114	602.50	59.09	0.00
species richness	level*SOM+(1 site/cushion ID)	11	114	602.63	59.22	0.00
species richness	level+(1 site/cushion ID)	7	114	602.96	59.54	0.00
species richness	level+SOM+(1 site/cushion ID)	8	114	603.31	59.90	0.00
species richness	level*SOM+SWC+(1 site/cushion ID)	12	114	603.48	60.07	0.00
species richness	level*SOM+SWC+(1 site/cushion ID)	12	114	603.48	60.07	0.00
species richness	level+SWC+(1 site/cushion ID)	8	114	603.58	60.17	0.00
species richness	disturbance+level+SOM*SWC+(1 site/cushion ID)	11	114	603.68	60.27	0.00
species richness	level+disturbance+SOM*SWC+(1 site/cushion ID)	11	114	603.68	60.27	0.00
species richness	level*SWC+(1 site/cushion ID)	11	114	603.77	60.35	0.00
species richness	level+SOM+SWC+(1 site/cushion ID)	9	114	604.15	60.73	0.00
species richness	disturbance*SOM+(1 site/cushion ID)	7	114	609.73	66.32	0.00
species richness	disturbance*SOM+SWC+(1 site/cushion ID)	8	114	609.78	66.36	0.00
species richness	disturbance*SOM+SWC*(1 site/cushion ID)	8	114	609.78	66.36	0.00
species richness	disturbance*SWC+(1 site/cushion ID)	7	114	609.91	66.50	0.00
species richness	disturbance+(1 site/cushion ID)	5	114	610.28	66.86	0.00
species richness	disturbance+SWC+(1 site/cushion ID)	6	114	610.32	66.90	0.00
species richness	disturbance+SOM+(1 site/cushion ID)	6	114	610.36	66.94	0.00
species richness	disturbance+SOM+SWC+(1 site/cushion ID)	7	114	610.83	67.42	0.00
species richness	SOM+(1 site/cushion ID)	5	114	610.91	67.50	0.00
species richness	SWC+(1 site/cushion ID)	5	114	611.26	67.85	0.00
species richness	SOM+SWC+(1 site/cushion ID)	6	114	611.54	68.13	0.00
species richness	(1 site/cushion ID)	4	114	612.21	68.80	0.00
species richness	SOM*SWC+(1 site/cushion ID)	7	114	612.83	69.41	0.00
shannon diversity	(1 site/cushion ID)	4	114	217.75	0.00	0.34
shannon diversity	SOM+(1 site/cushion ID)	5	114	219.10	1.36	0.17
shannon diversity	disturbance+(1 site/cushion ID)	5	114	219.34	1.59	0.15
shannon diversity	SWC+(1 site/cushion ID)	5	114	220.11	2.36	0.10
shannon diversity	level+(1 site/cushion ID)	7	114	221.58	3.83	0.05
shannon diversity	disturbance+SOM+(1 site/cushion ID)	6	114	222.34	4.59	0.03
shannon diversity	disturbance+level+(1 site/cushion ID)	8	114	222.40	4.66	0.03
shannon diversity	disturbance+SWC+(1 site/cushion ID)	6	114	222.87	5.12	0.03
shannon diversity	SOM+SWC+(1 site/cushion ID)	6	114	223.32	5.58	0.02
shannon diversity	level+SOM+(1 site/cushion ID)	8	114	224.23	6.48	0.01
shannon diversity	disturbance*SOM+(1 site/cushion ID)	7	114	224.65	6.91	0.01
shannon diversity	level+SWC+(1 site/cushion ID)	8	114	225.29	7.54	0.01
shannon diversity	disturbance*SWC+(1 site/cushion ID)	7	114	225.80	8.05	0.01
shannon diversity	disturbance+SOM+SWC+(1 site/cushion ID)	7	114	226.55	8.80	0.00
shannon diversity	disturbance+level+SOM+(1 site/cushion ID)	9	114	226.81	9.07	0.00

shannon diversity	disturbance+level+SWC+(1 site/cushion ID)	9	114	227.23	9.49	0.00
shannon diversity	SOM*SWC+(1 site/cushion ID)	7	114	228.04	10.29	0.00
shannon diversity	disturbance*SOM+SWC+(1 site/cushion ID)	8	114	228.53	10.78	0.00
shannon diversity	disturbance*SOM+SWC*(1 site/cushion ID)	8	114	228.53	10.78	0.00
shannon diversity	level+SOM+SWC+(1 site/cushion ID)	9	114	228.54	10.79	0.00
shannon diversity	disturbance*level+(1 site/cushion ID)	11	114	228.64	10.90	0.00
shannon diversity	level+disturbance*SOM+(1 site/cushion ID)	10	114	230.02	12.28	0.00
shannon diversity	level+disturbance*SWC+(1 site/cushion ID)	10	114	231.08	13.33	0.00
shannon diversity	disturbance+level+SOM+SWC+(1 site/cushion ID)	10	114	231.19	13.44	0.00
shannon diversity	disturbance*level+SOM+(1 site/cushion ID)	12	114	233.36	15.61	0.00
shannon diversity	disturbance*level+SWC+(1 site/cushion ID)	12	114	233.74	16.00	0.00
shannon diversity	level+disturbance*SOM+SWC+(1 site/cushion ID)	11	114	234.23	16.48	0.00
shannon diversity	level*SOM+(1 site/cushion ID)	11	114	234.48	16.73	0.00
shannon diversity	level+disturbance*SWC+SOM+(1 site/cushion ID)	11	114	235.05	17.30	0.00
shannon diversity	disturbance+level+SOM*SWC+(1 site/cushion ID)	11	114	235.91	18.17	0.00
shannon diversity	level+disturbance+SOM*SWC+(1 site/cushion ID)	11	114	235.91	18.17	0.00
shannon diversity	level*SWC+(1 site/cushion ID)	11	114	236.64	18.89	0.00
shannon diversity	disturbance+level*SOM+(1 site/cushion ID)	12	114	236.86	19.12	0.00
shannon diversity	disturbance*level+SOM+SWC+(1 site/cushion ID)	13	114	237.77	20.02	0.00
shannon diversity	disturbance+level*SWC+(1 site/cushion ID)	12	114	238.40	20.65	0.00
shannon diversity	level*SOM+SWC+(1 site/cushion ID)	12	114	238.75	21.00	0.00
shannon diversity	level*SOM+SWC+(1 site/cushion ID)	12	114	238.75	21.00	0.00
shannon diversity	disturbance+level*SOM+SWC+(1 site/cushion ID)	13	114	241.21	23.46	0.00
shannon diversity	disturbance+level*SWC+SOM+(1 site/cushion ID)	13	114	242.42	24.68	0.00
shannon diversity	disturbance*level+SOM*SWC+(1 site/cushion ID)	14	114	242.54	24.80	0.00
shannon diversity	disturbance*level*SOM+(1 site/cushion ID)	19	114	248.72	30.98	0.00
shannon diversity	level*SOM*SWC+(1 site/cushion ID)	19	114	251.50	33.76	0.00
shannon diversity	disturbance*level*SWC+(1 site/cushion ID)	19	114	252.55	34.81	0.00
shannon diversity	disturbance*level*SOM+SWC+(1 site/cushion ID)	20	114	252.98	35.24	0.00
shannon diversity	disturbance*level*SWC+SOM+(1 site/cushion ID)	20	114	256.57	38.83	0.00
shannon diversity	disturbance*level*SWC*SOM+(1 site/cushion ID)	35	114	264.46	46.72	0.00
vegetation cover	disturbance*level*SWC*SOM+(1 site/cushion ID)	35	114	912.47	0.00	1.00
vegetation cover	disturbance*level*SOM+SWC+(1 site/cushion ID)	20	114	1016.11	103.64	0.00
vegetation cover	disturbance*level*SOM+(1 site/cushion ID)	19	114	1019.68	107.21	0.00
vegetation cover	disturbance*level*SWC+SOM+(1 site/cushion ID)	20	114	1019.71	107.24	0.00
vegetation cover	level*SOM*SWC+(1 site/cushion ID)	19	114	1022.08	109.61	0.00
vegetation cover	disturbance*level*SWC+(1 site/cushion ID)	19	114	1023.33	110.86	0.00
vegetation cover	disturbance*level+SOM*SWC+(1 site/cushion ID)	14	114	1053.92	141.45	0.00
vegetation cover	disturbance*level+SOM+SWC+(1 site/cushion ID)	13	114	1056.61	144.14	0.00
vegetation cover	disturbance+level*SOM+SWC+(1 site/cushion ID)	13	114	1058.94	146.47	0.00

vegetation cover	disturbance*level+SWC+(1 site/cushion ID)	12	114	1060.18	147.71	0.00
vegetation cover	disturbance+level*SWC+SOM+(1 site/cushion ID)	13	114	1061.40	148.93	0.00
vegetation cover	disturbance*level+SOM+(1 site/cushion ID)	12	114	1062.08	149.61	0.00
vegetation cover	level*SOM+SWC+(1 site/cushion ID)	12	114	1063.37	150.90	0.00
vegetation cover	level*SOM+SWC+(1 site/cushion ID)	12	114	1063.37	150.90	0.00
vegetation cover	disturbance+level*SOM+(1 site/cushion ID)	12	114	1063.49	151.02	0.00
vegetation cover	disturbance+level*SWC+(1 site/cushion ID)	12	114	1064.92	152.45	0.00
vegetation cover	disturbance*level+(1 site/cushion ID)	11	114	1066.02	153.55	0.00
vegetation cover	level*SOM+(1 site/cushion ID)	11	114	1067.60	155.13	0.00
vegetation cover	level*SWC+(1 site/cushion ID)	11	114	1069.03	156.56	0.00
vegetation cover	level+disturbance*SOM+SWC+(1 site/cushion ID)	11	114	1069.21	156.74	0.00
vegetation cover	level+disturbance*SWC+SOM+(1 site/cushion ID)	11	114	1069.62	157.15	0.00
vegetation cover	disturbance+level+SOM*SWC+(1 site/cushion ID)	11	114	1070.44	157.97	0.00
vegetation cover	level+disturbance+SOM*SWC+(1 site/cushion ID)	11	114	1070.44	157.97	0.00
vegetation cover	disturbance+level+SOM+SWC+(1 site/cushion ID)	10	114	1073.25	160.79	0.00
vegetation cover	level+disturbance*SWC+(1 site/cushion ID)	10	114	1073.46	160.99	0.00
vegetation cover	level+disturbance*SOM+(1 site/cushion ID)	10	114	1075.44	162.97	0.00
vegetation cover	disturbance+level+SWC+(1 site/cushion ID)	9	114	1077.16	164.69	0.00
vegetation cover	level+SOM+SWC+(1 site/cushion ID)	9	114	1078.98	166.51	0.00
vegetation cover	disturbance+level+SOM+(1 site/cushion ID)	9	114	1080.35	167.88	0.00
vegetation cover	level+SWC+(1 site/cushion ID)	8	114	1082.20	169.73	0.00
vegetation cover	level+SOM+(1 site/cushion ID)	8	114	1084.85	172.38	0.00
vegetation cover	disturbance+level+(1 site/cushion ID)	8	114	1086.70	174.23	0.00
vegetation cover	disturbance*SOM+SWC+(1 site/cushion ID)	8	114	1090.08	177.61	0.00
vegetation cover	disturbance*SOM+SWC*(1 site/cushion ID)	8	114	1090.08	177.61	0.00
vegetation cover	disturbance*SWC+(1 site/cushion ID)	7	114	1093.61	181.14	0.00
vegetation cover	SOM*SWC+(1 site/cushion ID)	7	114	1093.79	181.33	0.00
vegetation cover	disturbance+SOM+SWC+(1 site/cushion ID)	7	114	1094.12	181.65	0.00
vegetation cover	level+(1 site/cushion ID)	7	114	1095.30	182.83	0.00
vegetation cover	disturbance*SOM+(1 site/cushion ID)	7	114	1097.09	184.62	0.00
vegetation cover	SOM+SWC+(1 site/cushion ID)	6	114	1097.60	185.13	0.00
vegetation cover	disturbance+SWC+(1 site/cushion ID)	6	114	1097.68	185.21	0.00
vegetation cover	disturbance+SOM+(1 site/cushion ID)	6	114	1100.98	188.51	0.00
vegetation cover	SWC+(1 site/cushion ID)	5	114	1101.23	188.76	0.00
vegetation cover	SOM+(1 site/cushion ID)	5	114	1104.29	191.82	0.00
vegetation cover	disturbance+(1 site/cushion ID)	5	114	1116.87	204.40	0.00
vegetation cover	(1 site/cushion ID)	4	114	1123.21	210.74	0.00

Table B.B.3. Full list of LMMs to test how species community competitiveness is influenced by disturbance, elevation, and cushion presence. Black bars differentiate model sets, k = number of parameters, n = sample size.

modeled parameter	model formula	k	n	AICc	Δ AICc	AICc weight	species
competition	level+(1 site)	6	198	-20.07	0.00	0.53	inside
competition	cushion+level+(1 site)	7	198	-19.73	0.34	0.44	inside
competition	disturbance+level+(1 site)	7	198	-12.81	7.26	0.01	inside
competition	disturbance+level+cushion+(1 site)	8	198	-12.42	7.65	0.01	inside
competition	disturbance*level+(1 site)	10	198	-7.87	12.19	0.00	inside
competition	disturbance*level+cushion+(1 site)	11	198	-7.67	12.39	0.00	inside
competition	level+disturbance*cushion+(1 site)	9	198	-6.50	13.57	0.00	inside
competition	cushion*level+(1 site)	10	198	-4.95	15.12	0.00	inside
competition	disturbance+level*cushion+(1 site)	11	198	2.42	22.49	0.00	inside
competition	disturbance*level*cushion+(1 site)	18	198	25.53	45.60	0.00	inside
competition	(1 site)	3	198	51.12	71.19	0.00	inside
competition	cushion+(1 site)	4	198	53.12	73.19	0.00	inside
competition	disturbance+(1 site)	4	198	56.95	77.02	0.00	inside
competition	cushion+disturbance+(1 site)	5	198	59.01	79.08	0.00	inside
competition	cushion*disturbance+(1 site)	6	198	64.40	84.46	0.00	inside
competition	level+(1 site)	6	200	-122.69	0.00	0.50	neighboring
competition	cushion+level+(1 site)	7	200	-122.57	0.12	0.47	neighboring
competition	disturbance+level+(1 site)	7	200	-115.09	7.60	0.01	neighboring
competition	disturbance+level+cushion+(1 site)	8	200	-114.92	7.78	0.01	neighboring
competition	disturbance*level+(1 site)	10	200	-109.58	13.11	0.00	neighboring
competition	disturbance*level+cushion+(1 site)	9	200	-108.69	14.00	0.00	neighboring
competition	level+disturbance*cushion+(1 site)	11	200	-101.85	20.84	0.00	neighboring
competition	cushion*level+(1 site)	10	200	-98.32	24.37	0.00	neighboring
competition	disturbance+level*cushion+(1 site)	11	200	-98.02	24.67	0.00	neighboring
competition	disturbance*level*cushion+(1 site)	18	200	-66.55	56.14	0.00	neighboring
competition	(1 site)	3	200	0.51	123.20	0.00	neighboring
competition	cushion+(1 site)	4	200	7.29	129.98	0.00	neighboring
competition	disturbance+(1 site)	4	200	7.46	130.15	0.00	neighboring
competition	cushion+disturbance+(1 site)	5	200	14.26	136.95	0.00	neighboring
competition	cushion*disturbance+(1 site)	6	200	19.83	142.52	0.00	neighboring

Table B.B.4. LMMs used to test the effects of disturbance and elevation on soil parameters. Black bars differentiate model sets, and k = number of parameters, n = sample size.

modeled parameter	model formula	k	n	AICc	Δ AICc	AICc weight
SOM	disturbance*level*cushion+(1 site/cushion ID)	19	114	810.86	0.00	1.00
SOM	disturbance*level+cushion+(1 site/cushion ID)	12	114	836.90	26.04	0.00
SOM	disturbance*level+(1 site/cushion ID)	11	114	837.83	26.97	0.00
SOM	disturbance+level*cushion+(1 site/cushion ID)	12	114	856.43	45.57	0.00
SOM	level+disturbance*cushion+(1 site/cushion ID)	10	114	860.92	50.06	0.00
SOM	disturbance+level+cushion+(1 site/cushion ID)	9	114	863.61	52.75	0.00
SOM	disturbance+level+(1 site/cushion ID)	8	114	864.69	53.83	0.00
SOM	cushion*level+(1 site/cushion ID)	11	114	878.42	67.56	0.00
SOM	cushion+level+(1 site/cushion ID)	8	114	885.74	74.88	0.00
SOM	level+(1 site/cushion ID)	7	114	886.86	76.00	0.00
SOM	cushion*disturbance+(1 site/cushion ID)	7	114	892.96	82.10	0.00
SOM	cushion+disturbance+(1 site/cushion ID)	6	114	895.79	84.94	0.00
SOM	disturbance+(1 site/cushion ID)	5	114	897.00	86.14	0.00
SOM	cushion+(1 site/cushion ID)	5	114	910.54	99.68	0.00
SOM	(1 site/cushion ID)	4	114	911.79	100.93	0.00
SWC	disturbance*level*cushion+(1 site/cushion ID)	19	114	801.49	0.00	1.00
SWC	disturbance*level+cushion+(1 site/cushion ID)	12	114	828.54	27.06	0.00
SWC	disturbance*level+(1 site/cushion ID)	11	114	829.27	27.79	0.00
SWC	disturbance+level*cushion+(1 site/cushion ID)	12	114	854.76	53.27	0.00
SWC	level+disturbance*cushion+(1 site/cushion ID)	10	114	858.32	56.84	0.00
SWC	disturbance+level+cushion+(1 site/cushion ID)	9	114	862.16	60.67	0.00
SWC	disturbance+level+(1 site/cushion ID)	8	114	863.03	61.54	0.00
SWC	cushion*level+(1 site/cushion ID)	11	114	865.62	64.13	0.00
SWC	cushion+level+(1 site/cushion ID)	8	114	873.16	71.67	0.00
SWC	level+(1 site/cushion ID)	7	114	874.07	72.59	0.00
SWC	cushion*disturbance+(1 site/cushion ID)	7	114	882.33	80.84	0.00
SWC	cushion+disturbance+(1 site/cushion ID)	6	114	886.30	84.81	0.00
SWC	disturbance+(1 site/cushion ID)	5	114	887.30	85.81	0.00
SWC	cushion+(1 site/cushion ID)	5	114	894.26	92.77	0.00
SWC	(1 site/cushion ID)	4	114	895.30	93.81	0.00

Table B.B.5. Full list of LMMs testing the effects of disturbance and elevational level on Relative Interaction Indices (RII) and Bray-Curtis Dissimilarity indices. Black bars differentiate model sets, and k = number of parameters, n = sample size.

modeled parameter	model formula	k	n	AICc	Δ AICc	AICc weight	species
RII: species richness	(1 site)	3	100	39.41	0.00	0.95	inside
RII: species richness	disturbance+(1 site)	4	100	45.53	6.11	0.04	inside
RII: species richness	level+(1 site)	6	100	50.35	10.93	0.00	inside
RII: species richness	disturbance+level+(1 site)	7	100	56.53	17.12	0.00	inside
RII: species richness	disturbance*level+(1 site)	10	100	67.05	27.63	0.00	inside
RII: shannon diversity	(1 site)	3	100	103.55	0.00	0.93	inside
RII: shannon diversity	disturbance+(1 site)	4	100	108.92	5.38	0.06	inside
RII: shannon diversity	level+(1 site)	6	100	114.79	11.24	0.00	inside
RII: shannon diversity	disturbance+level+(1 site)	7	100	120.36	16.82	0.00	inside
RII: shannon diversity	disturbance*level+(1 site)	10	100	127.72	24.18	0.00	inside
RII: % vegetation cover	(1 site)	3	100	86.07	0.00	0.94	inside
RII: % vegetation cover	disturbance+(1 site)	4	100	91.70	5.63	0.06	inside
RII: % vegetation cover	level+(1 site)	6	100	97.77	11.70	0.00	inside
RII: % vegetation cover	disturbance+level+(1 site)	7	100	103.51	17.44	0.00	inside
RII: % vegetation cover	disturbance*level+(1 site)	10	100	111.23	25.16	0.00	inside
RII: species richness	(1 site)	3	100	-82.52	0.00	0.95	neighboring
RII: species richness	disturbance+(1 site)	4	100	-76.55	5.97	0.05	neighboring
RII: species richness	level+(1 site)	6	100	-63.94	18.58	0.00	neighboring
RII: species richness	disturbance+level+(1 site)	7	100	-57.71	24.81	0.00	neighboring
RII: species richness	disturbance*level+(1 site)	10	100	-44.13	38.39	0.00	neighboring
RII: shannon diversity	(1 site)	3	100	-110.56	0.00	0.96	neighboring
RII: shannon diversity	disturbance+(1 site)	4	100	-103.98	6.58	0.04	neighboring
RII: shannon diversity	level+(1 site)	6	100	-92.41	18.16	0.00	neighboring
RII: shannon diversity	disturbance+level+(1 site)	7	100	-85.63	24.93	0.00	neighboring
RII: shannon diversity	disturbance*level+(1 site)	10	100	-70.24	40.32	0.00	neighboring
RII: % vegetation cover	(1 site)	3	100	-15.11	0.00	0.97	neighboring
RII: % vegetation cover	disturbance+(1 site)	4	100	-8.45	6.66	0.03	neighboring
RII: % vegetation cover	level+(1 site)	6	100	1.06	16.17	0.00	neighboring
RII: % vegetation cover	disturbance+level+(1 site)	7	100	7.83	22.94	0.00	neighboring
RII: % vegetation cover	disturbance*level+(1 site)	10	100	17.85	32.96	0.00	neighboring

Table B.B.6. Predicted values modeled using the parameter estimates and simulated data (shown in table) from the most parsimonious models for inside species vegetation cover, neighboring species vegetation cover, and neighboring species richness, which all include a three-way interaction between disturbance, cushion area, and level. Differences between disturbed and undisturbed predicted values suggest that disturbance effects are strongest at middle elevations (levels 2 and 3). Black bars differentiate models.

predicted parameter	species	disturbance	cushion area	level	cushion presence	prediction	difference = disturbed - undisturbed
vegetation cover	inside	0	-0.58	1	1	23.11	
vegetation cover	inside	1	-0.58	1	1	25.24	2.13
vegetation cover	inside	0	0.19	1	1	25.50	
vegetation cover	inside	1	0.19	1	1	25.83	0.33
vegetation cover	inside	0	-0.58	2	1	40.91	
vegetation cover	inside	1	-0.58	2	1	23.00	-17.91
vegetation cover	inside	0	0.19	2	1	50.65	
vegetation cover	inside	1	0.19	2	1	32.55	-18.10
vegetation cover	inside	0	-0.58	3	1	30.65	
vegetation cover	inside	1	-0.58	3	1	14.65	-15.99
vegetation cover	inside	0	0.19	3	1	40.99	
vegetation cover	inside	1	0.19	3	1	15.72	-25.26
vegetation cover	inside	0	-0.58	4	1	-5.42	
vegetation cover	inside	1	-0.58	4	1	6.76	12.18
vegetation cover	inside	0	0.19	4	1	4.20	
vegetation cover	inside	1	0.19	4	1	17.40	13.20
vegetation cover	neighboring	0	-0.76	1	1	75.91	
vegetation cover	neighboring	1	-0.76	1	1	68.29	-7.62
vegetation cover	neighboring	0	0.51	1	1	55.57	
vegetation cover	neighboring	1	0.51	1	1	63.88	8.31
vegetation cover	neighboring	0	-0.76	2	1	88.87	
vegetation cover	neighboring	1	-0.76	2	1	53.90	-34.97
vegetation cover	neighboring	0	0.51	2	1	90.47	
vegetation cover	neighboring	1	0.51	2	1	56.40	-34.08

vegetation cover	neighboring	0	-0.76	3	1	73.62	
vegetation cover	neighboring	1	-0.76	3	1	51.07	-22.55
vegetation cover	neighboring	0	0.51	3	1	75.33	
vegetation cover	neighboring	1	0.51	3	1	45.64	-29.69
vegetation cover	neighboring	0	-0.76	4	1	30.32	
vegetation cover	neighboring	1	-0.76	4	1	39.08	8.76
vegetation cover	neighboring	0	0.51	4	1	30.20	
vegetation cover	neighboring	1	0.51	4	1	36.69	6.49
species richness	neighboring	0	-0.76	1	1	11.61	
species richness	neighboring	1	-0.76	1	1	10.48	-1.14
species richness	neighboring	0	0.51	1	1	11.60	
species richness	neighboring	1	0.51	1	1	11.17	-0.43
species richness	neighboring	0	-0.76	2	1	12.93	
species richness	neighboring	1	-0.76	2	1	8.84	-4.09
species richness	neighboring	0	0.51	2	1	14.60	
species richness	neighboring	1	0.51	2	1	9.97	-4.63
species richness	neighboring	0	-0.76	3	1	10.57	
species richness	neighboring	1	-0.76	3	1	7.44	-3.13
species richness	neighboring	0	0.51	3	1	13.04	
species richness	neighboring	1	0.51	3	1	7.35	-5.69
species richness	neighboring	0	-0.76	4	1	6.97	
species richness	neighboring	1	-0.76	4	1	5.71	-1.26
species richness	neighboring	0	0.51	4	1	7.66	
species richness	neighboring	1	0.51	4	1	8.15	0.49

APPENDIX C

Chapter 4 Appendix

C.A. Supplemental tables & figures

Table C.A.1. Summary of all sites with *Silene acaulis* trait data. Site names retained from original data sets (with indication of relative position or replication for identical site names). Elevation estimates are from GoogleEarth (2009). Cavieres et al. (2013) sites contain data on both *Silene* cushion sizes as well as beneficiary species, and Peterson et al. (2018) sites contain data on only *Silene* cushion sizes.

Site	Country	Latitude (°)	Longitude (°)	Elevation (m)	Source
Ny-Ålesund	Svalbard, Norway	78.9122611	12.01742778	21	Cavieres et al.
Latnja	Sweden	68.35748	18.49861	1050	Cavieres et al.
Hlupy Peak	Slovakia	49.2358333	20.21916667	1974	Cavieres et al.
Dolomites (High)	Italy	46.529639	12.016326	2481	Cavieres et al.
Dolomites (Low)	Italy	46.506363	12.019999	2343	Cavieres et al.
Val Bercla	Switzerland	46.477778	9.582778	2490	Cavieres et al.
Gemmi	Switzerland	46.42502	7.6292	2301	Cavieres et al.
Benasque	Spain	42.6894722	0.646013889	2298	Cavieres et al.
Pink Mountains (High)	Canada	57.0610071	-122.865635	1764	Cavieres et al.
Pink Mountains (Middle)	Canada	57.0606464	-122.864367	1760	Cavieres et al.
Pink Mountains (Low)	Canada	57.0633692	-122.865099	1749	Cavieres et al.
Red Mountain	Canada	51.209385	-122.561666	2185	Cavieres et al.
Ptarmigan Cirque	Canada	50.610646	-114.975924	2519	Cavieres et al.
Whistler (North)	Canada	50.032482	-122.571218	1271	Cavieres et al.
Whistler (South)	Canada	50.032425	-122.571316	1281	Cavieres et al.
Cathedral Lake (High)	Canada	49.0505155	-120.218209	2513	Cavieres et al.
Cathedral Lake (Low)	Canada	49.0571346	-120.220331	2478	Cavieres et al.
Swiftcurrent (High)	USA	48.78443	-113.766932	2515	Cavieres et al.
Swiftcurrent (Low)	USA	48.780317	-113.766637	2285	Cavieres et al.
Piegán Pass	USA	48.724819	-113.681581	2497	Cavieres et al.
Windy Pass	USA	48.479221	-113.329427	2272	Cavieres et al.
Abisko (High)	Sweden	68.40511	18.35701	1120	Peterson et al.
Abisko (Low)	Sweden	68.36552	18.67874	1053	Peterson et al.
Jamtland (High)	Sweden	63.2044	12.3298	1187	Peterson et al.

Jamtland (Low)	Sweden	63.20552	12.33841	1163	Peterson et al.
ValBercla (High)	Switzerland	46.47379	9.58758	2576	Peterson et al.
ValBercla (Low)	Switzerland	46.475752	9.582989	2492	Peterson et al.
Pyrenees (High)	Spain	42.6723	0.0225	2681	Peterson et al.
Pyrenees (Low)	Spain	42.6039	0.0282	1991	Peterson et al.
Pingo	Alaska, USA	70.005488	-148.76348	59	Peterson et al.
Toolik (1)	Alaska, USA	68.72102	-149.04736	737	Peterson et al.
Toolik (2)	Alaska, USA	68.61435	-149.65048	779	Peterson et al.
Toolik (3)	Alaska, USA	68.61825	-149.68735	912	Peterson et al.
Toolik (4)	Alaska, USA	68.71893	-149.05435	809	Peterson et al.
Wrangells (1)	Alaska, USA	61.52666	-142.86337	1616	Peterson et al.
Wrangells (2)	Alaska, USA	61.48848	-142.81171	1514	Peterson et al.
Wrangells (3)	Alaska, USA	61.48746	-142.84068	1240	Peterson et al.
Wrangells (4)	Alaska, USA	61.48917	-142.8215	1436	Peterson et al.
Wrangells (5)	Alaska, USA	61.49036	-142.81453	1521	Peterson et al.
Wrangells (6)	Alaska, USA	61.48722	-142.84708	1208	Peterson et al.
Banff (1)	Canda	52.18089	-117.12188	2335	Peterson et al.
Banff (2)	Canda	52.18243	-117.13224	2350	Peterson et al.
Banff (3)	Canda	52.19353	-117.1556	2370	Peterson et al.
Banff (4)	Canda	52.19466	-117.1534	2314	Peterson et al.
Niwot (1)	USA	40.05523	-105.58654	3552	Peterson et al.
Niwot (2)	USA	40.05648	-105.59731	3618	Peterson et al.
Niwot (3)	USA	40.05514	-105.59736	3597	Peterson et al.
Niwot (4)	USA	40.05638	-105.58373	3539	Peterson et al.
Latir	USA	36.78601	-105.46595	3744	Peterson et al.
Latir	USA	36.79603	-105.4827	3775	Peterson et al.
SantaFe	USA	35.79273	-105.7757	3731	Peterson et al.

Table C.A.2. Results from quadratic LMMs fitting suitability values from each SDM type to beneficiary species percent cover, richness, and Shannon diversity. All but the intercept-only model test the effects of suitability + suitability² per SDM with a random effect of population (n = 21). Model estimates for suitability and suitability² effects are given by estimate and estimate_{sq}, respectively, and p-values by p-value and p-value_{sq}, respectively. R² values are marginal R² values. See Methods for model details.

parameter	SDM	intercept	estimate	estimate _{sq}	p-value	p-value _{sq}	n	R ²	Δ AICc
	suitability								
cover	global	0.1	4.26	4.13	0.002	0.183	1669	0.151	0
	habitat	0.13	5.31	5.18	0.48	0.088	1669	0.058	6.924
	genetic	0.14	5.35	5.18	0.721	0.784	1669	0.003	10.502
	intercept only	2.75	-	-	-	-	1669	0	16.875
diversity	global	0.08	3.37	3.26	0.144	0.773	1669	0.045	0
	genetic	0.08	3.23	3.12	0.183	0.76	1669	0.035	0.714
	habitat	0.09	3.62	3.54	0.528	0.683	1669	0.012	1.616
	intercept only	1.09	-	-	-	-	1669	0	6.898
richness	global	0.47	19.08	18.5	0.076	0.944	1669	0.078	0
	genetic	0.51	19.38	18.76	0.427	0.83	1669	0.016	2.83
	habitat	0.51	21.26	20.75	0.716	0.733	1669	0.007	2.865
	intercept only	4.64	-	-	-	-	1669	0	14.878

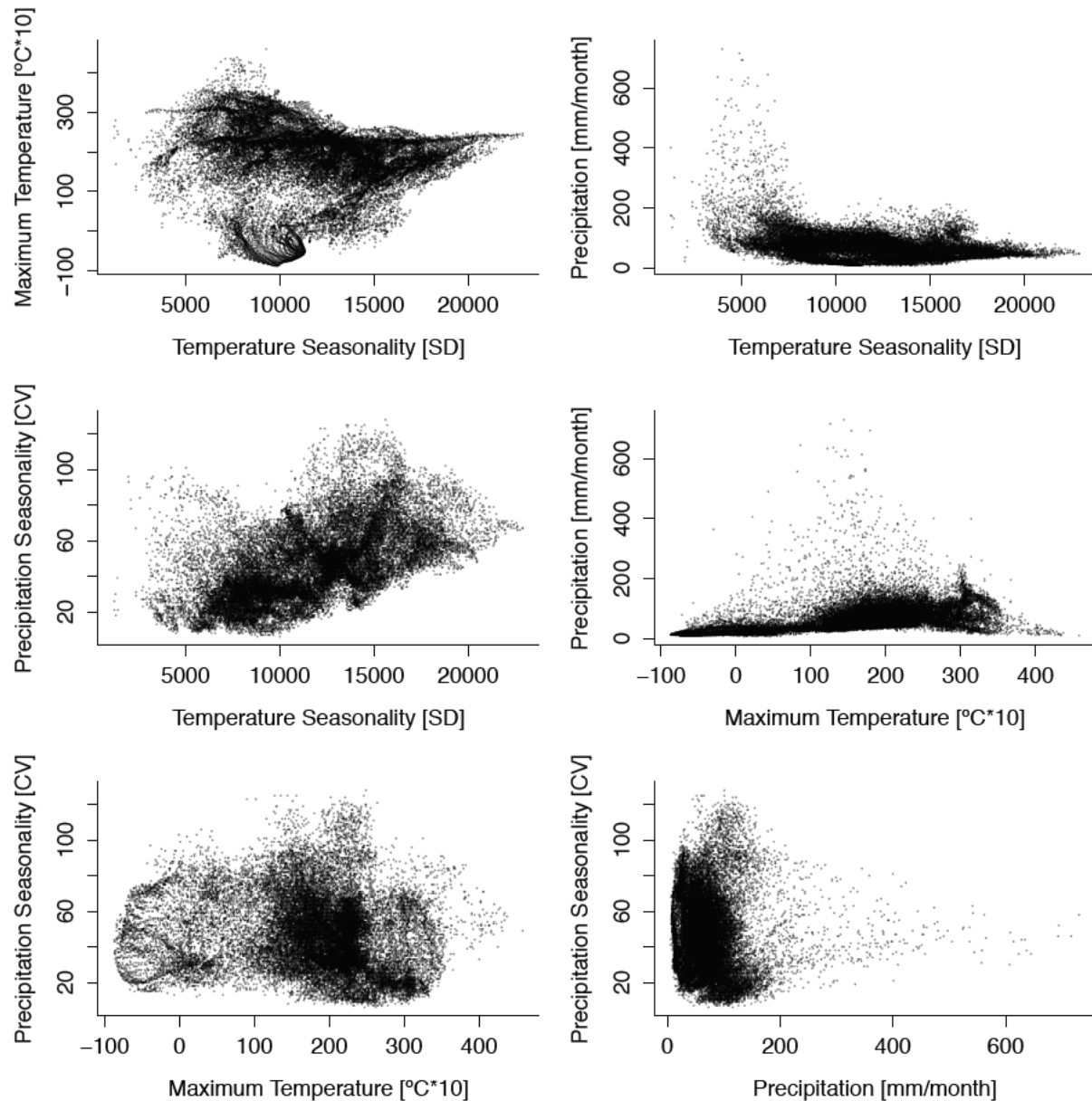


Figure C.A.1: Bioclimatic variables. We used four non-correlated bioclimatic variables from the CHELSA climatology data set (Karger et al. 2017) to construct our Species Distribution Models (SDMs). Less than 1% of the data is shown for figure clarity.

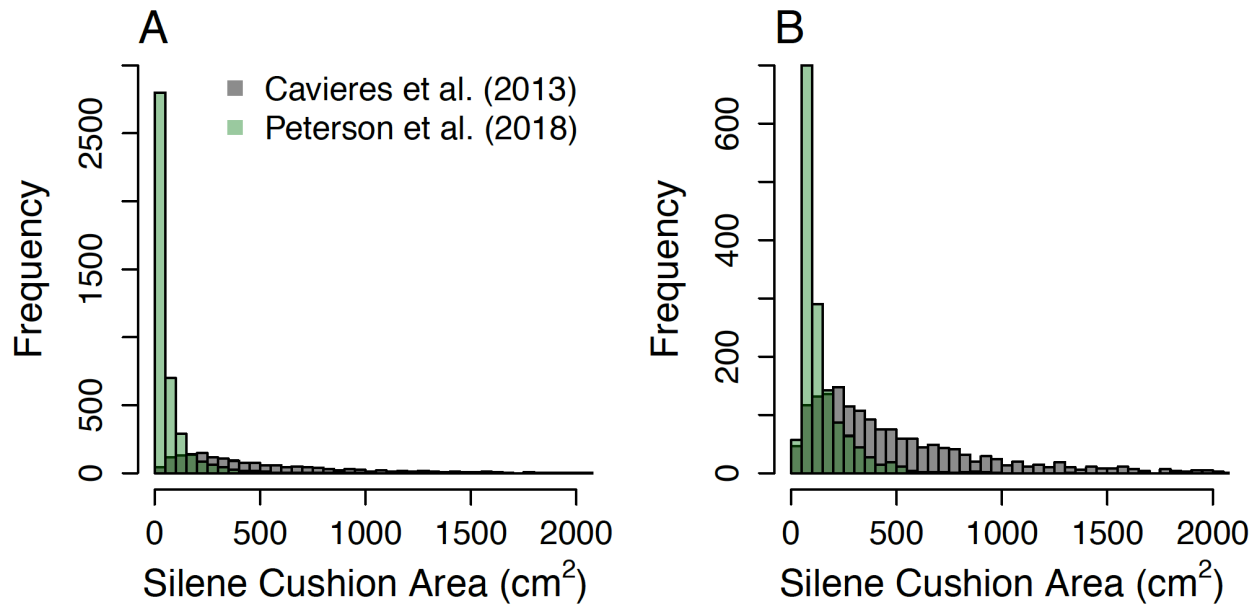


Figure C.A.2: Cushion plant sizes. The data collection method inconsistencies between the two data sets on *Silene acaulis* sizes yield large differences in cushion areas (A). We therefore only retained the 65th percentile of cushion areas from the Peterson et al. data to minimize these differences (B). Note that outliers > 2000 cm² are removed (n = 52, all from Cavieres et al.) and y-axes are on different scales.

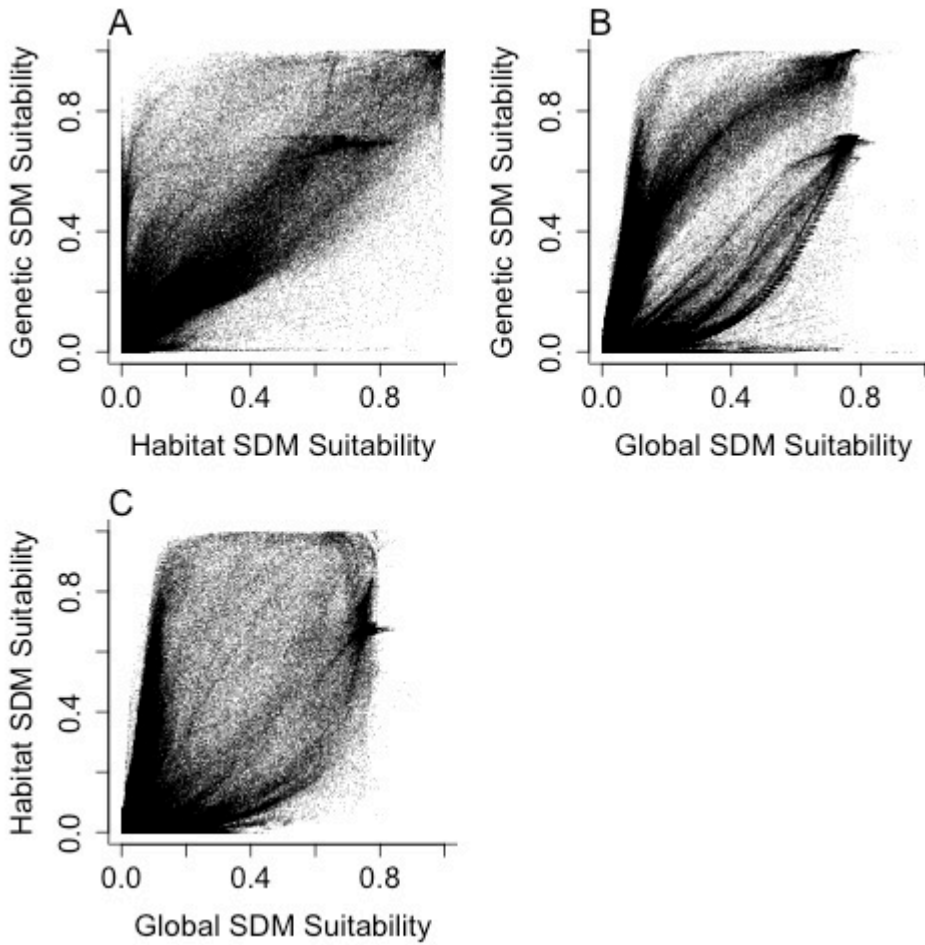


Figure C.A.3: Suitability values between SDM types. The best two SDM types yield similar suitability predictions (A), whereas the global SDM type yields markedly different suitability predictions from both the genetic (B) and habitat (C) SDM types. Shown are 1% of data for figure clarity.

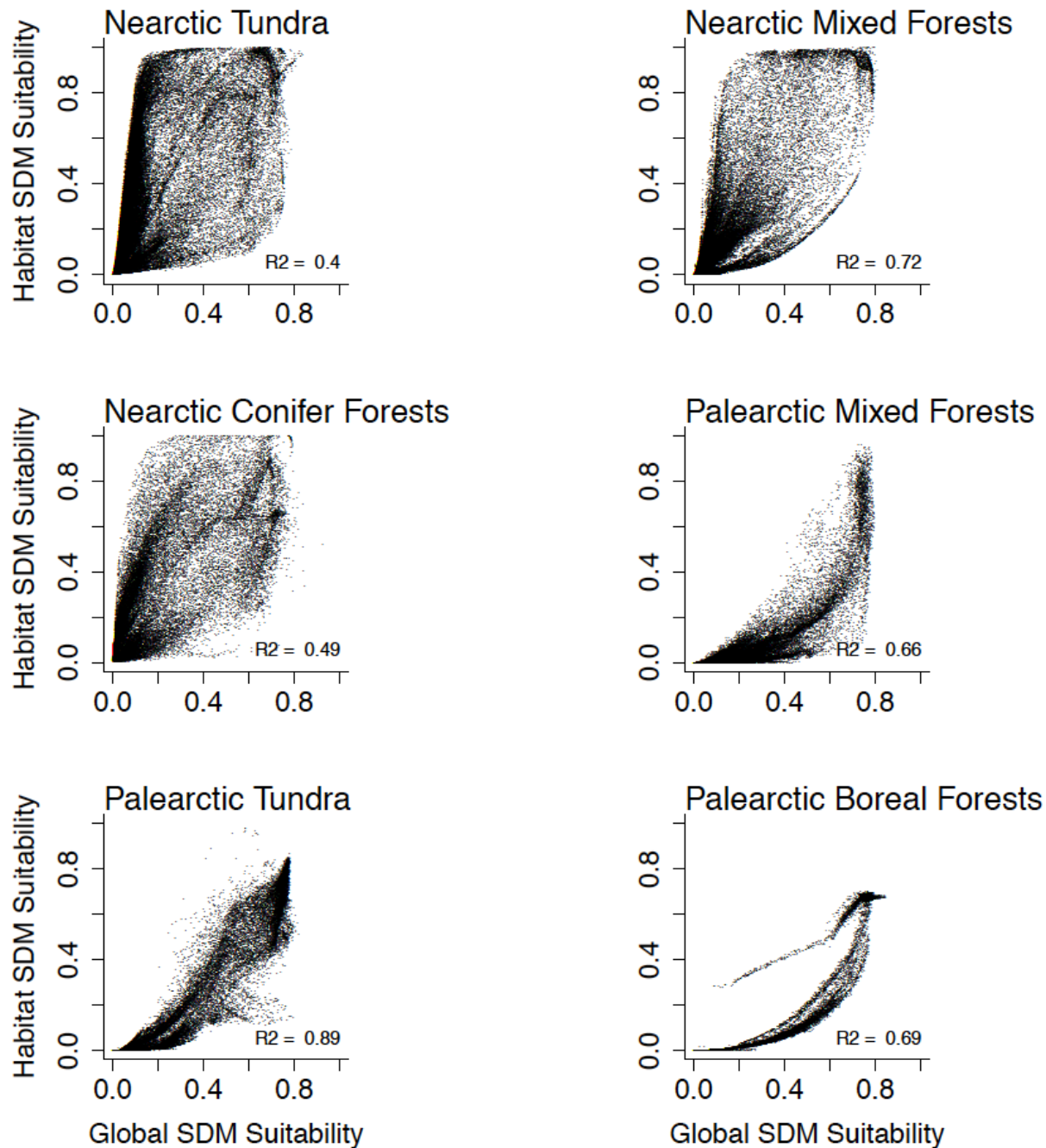


Figure C.A.4: SDM suitability by habitat group. SDM suitability predictions between the habitat and global SDM vary between habitat groups. Overall, predictions are more similar in the Palearctic than Nearctic, corresponding to differences in sampling intensity (see Fig. 4.1). The global SDM tends to overpredict suitability in the Palearctic and underpredict in the Nearctic. Shown are 1% of data per habitat group for figure clarity, and R^2 values are from linear regressions. See Fig. 4.1 for distribution of biomes (Ecoregions2017).

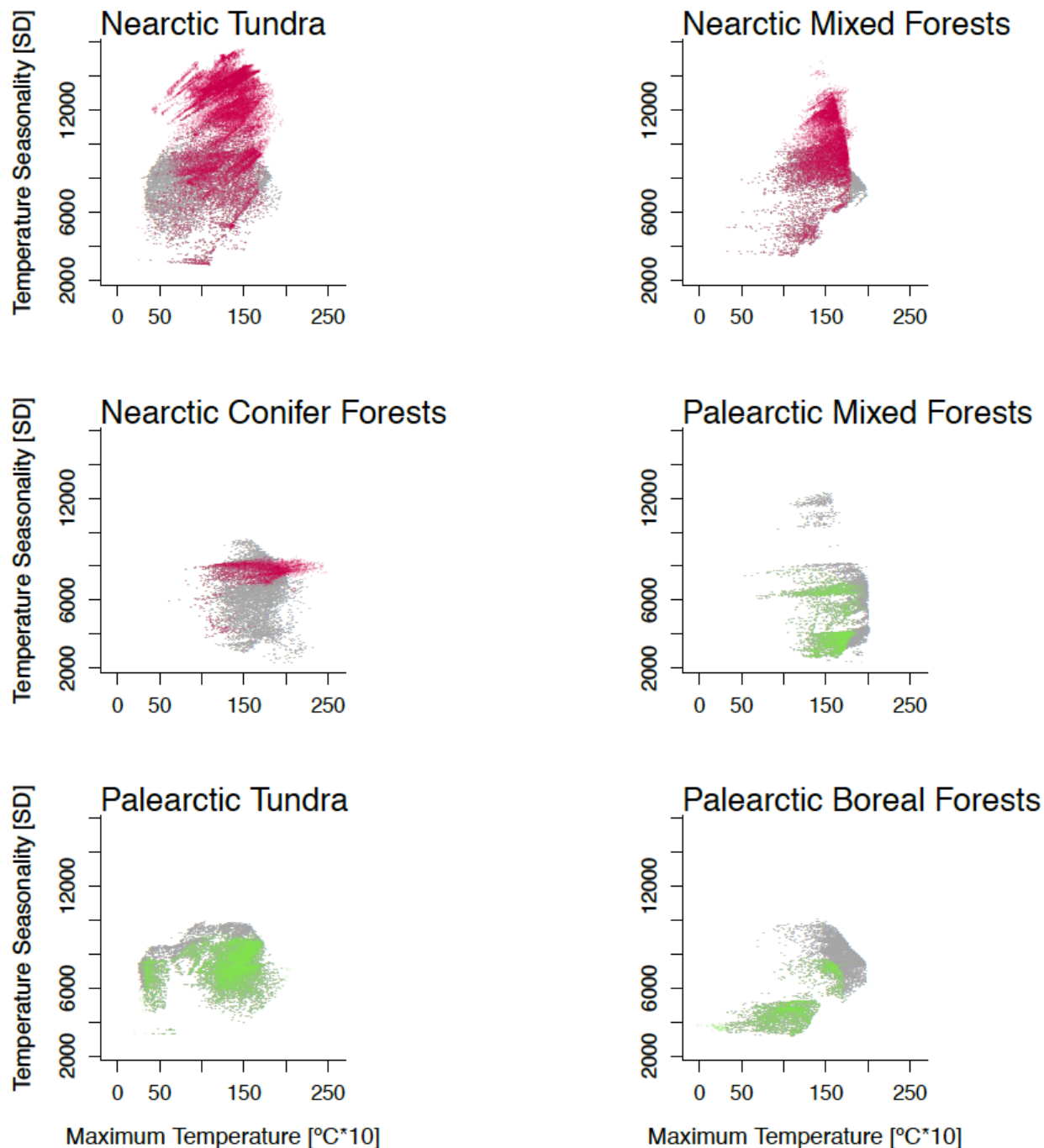


Figure C.A.5: Predicted climate niches. The type of error in the global SDM (shown in grey) compared to the habitat SDM (shown in pink for Nearctic and green for Palearctic biomes) varies by habitat group. Shown are 1% of data per habitat group for figure clarity, and the predicted presence (determined by equal testing sensitivity plus specificity threshold) cells plotted are the same as in Fig. C.A.6.

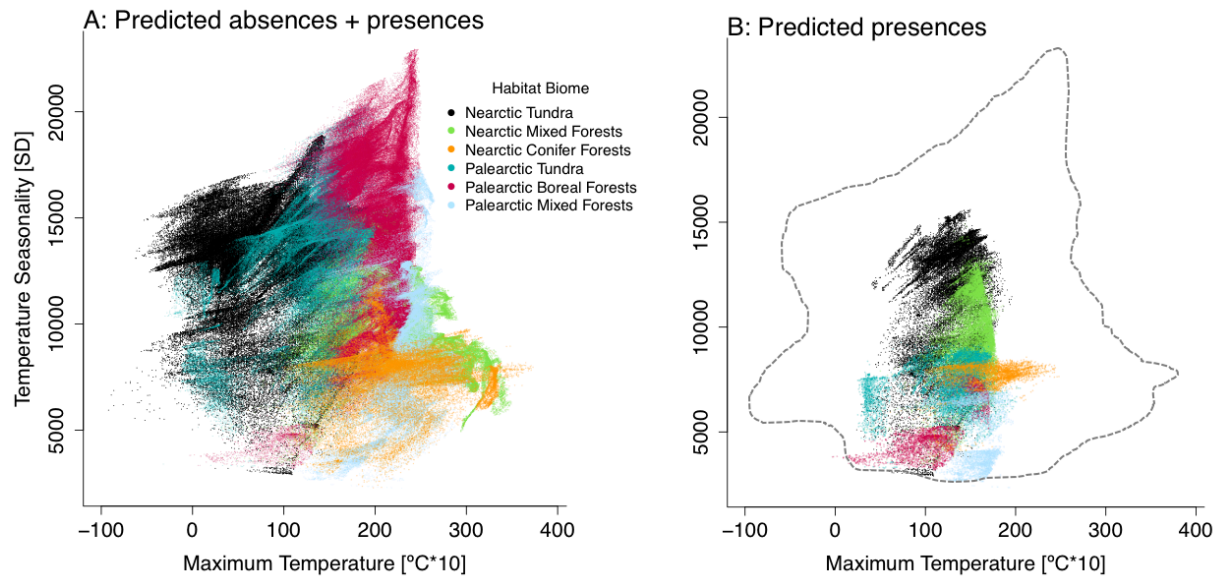


Figure C.A.6: Habitat subpopulation climate niches. The climate niche for all 1 km² cells used to calibrate SDMs (A) illustrate some overlap between each biome. The predicted presence cells (B) occupy a narrower climate niche and have greater total climate overlap between habitat groups. Shown are 1% of data per habitat group for figure clarity, colors in (B) are as in (A), and the temperature niche in (A) is outlined in (B). Note that we constructed SDMs with the additional variables precipitation seasonality and precipitation of the wettest month, but plot only the two most important climate variables as identified by MaxEnt.

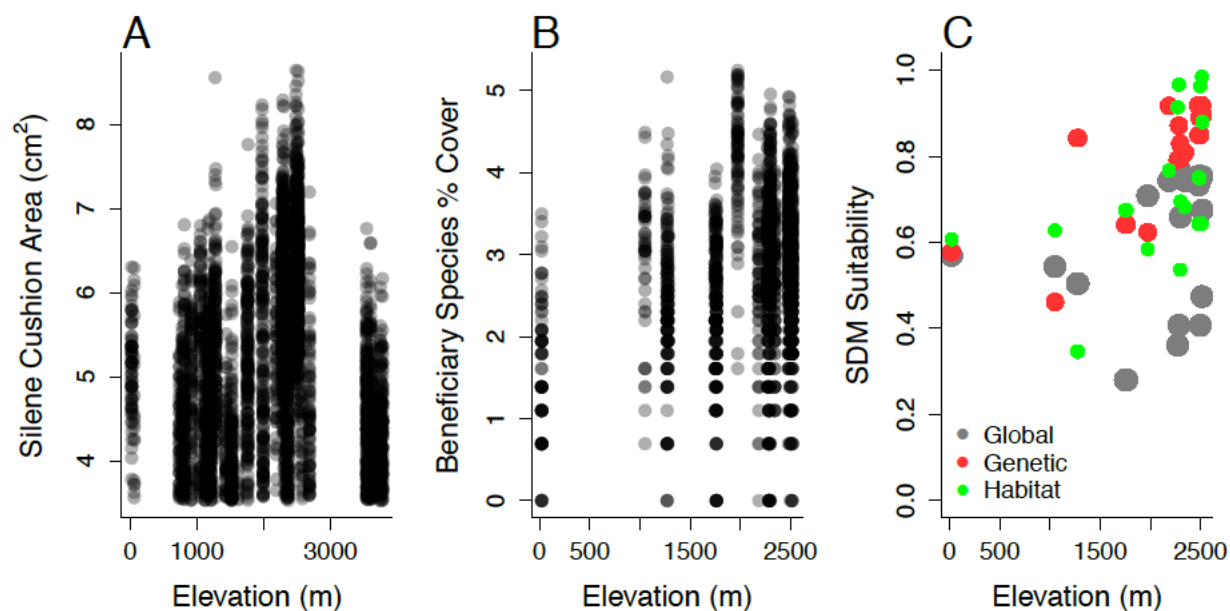


Figure C.A.7: Traits follow an elevational pattern. *Silene acaulis* cushion area (A) and its beneficiary species percent cover (B) peak at approximately mid-elevation, whereas suitability values generally peak at high elevations (C). Shown are the log-transformed data above the 40th percentile used to fit the models for (A) and log-transformed data for (B).

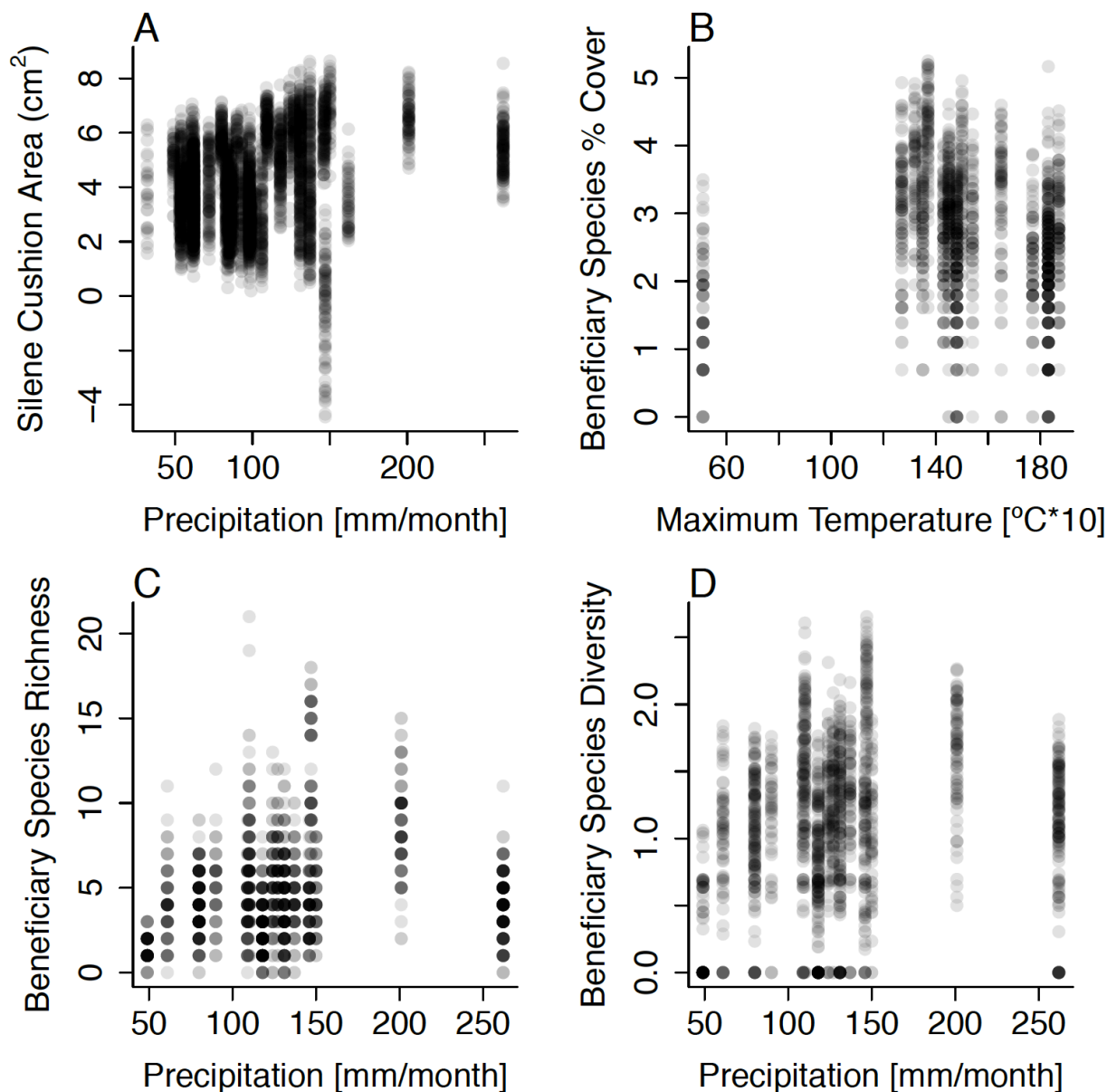


Figure C.A.8: Species traits only weakly correlated to climate. *Silene acaulis* cushion area (A; log-transformed) and its beneficiary species percent cover (B; log-transformed), richness (C), and diversity (D) do not only have a poor relationship with SDM suitability values (see Fig. 4.7) but also with climate. Shown are the relationships from LMMs with lowest AICc, and note that both (C) and (D) have a second model within 2 AICc points of the best model shown (see Table A.C.3).