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Positive interactions in temperate and tropical alpine plant communities: the role of facilitation in species-specific interactions, invasion, and landscape-scale distribution

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Positive interactions in temperate and tropical alpine plant communities: the role

of facilitation in species-specific interactions, invasion, and landscape-scale

distribution

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Chapter 1

Species-specific relationships between cushion plants and community

composition in the alpine tropical Andes

Nicole Hupp

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Abstract

Question: Species-specific interactions can connect particular species to others, which has important ramifications for community and landscape diversity. We investigated the impacts of facilitation on species diversity in a tropical alpine pant community and explored species-specific patterns related to two morphologically similar foundation species. We asked whether these foundation species differed in their effects on landscape species accumulation, local species richness, community composition, and effects on a widespread exotic species (*Rumex acetosella*).

Location: Piedras Blancas páramo, La Culata National Park, northern Andes Mountains, Venezuela

Methods: We recorded the presence and abundance of plant species growing within two similar cushion species, *Azorella julianii* and *Arenaria venezuelana*, and paired "open" samples. For both cushion species, we compared species richness, total species abundance, and the abundance of the exotic *Rumex acetosella* within cushions and outside using relative interactions indices (RII), and community composition with non-metric multidimensional scaling (NMDS) ordination. We also compared species accumulation curves at the landscape scale between the cushion species.

Results: *Arenaria* and *Azorella* did not differ in total species accumulation across the landscape, but *Azorella* cushions had a more positive association with other species than *Arenaria* at the scale of the cushion plants. Community composition differed among the two cushion species, and *Azorella* was more positively associated with the exotic *Rumex* than *Arenaria* was. *Rumex* density was not associated with a decline in the diversity of native species.

Conclusions: We found evidence for species-specific facilitation in the alpine tropical Andes. The two cushion species, based on their associations with a large number of different species at the local and landscape scale, were not fully interchangeable in their effects on community diversity and composition.

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Introduction

Facilitation, the positive effects of species on other species, occurs in virtually all biomes (Hunter & Aarssen 1988; Callaway 2007) and is recognized as an important process that shapes natural communities (Bruno et al. 2003; Brooker et al. 2007). However, not all facilitators are equal; some species have much stronger positive or negative effects on their neighbors than others (Callaway 2007; Cavieres & Badano 2009; Butterfield et al. 2013). In other words, facilitation can be highly species-specific, with some benefactor species having stronger facilitative effects than others (Hutto et al. 1986; Callaway 1998; Cavieres et al. 2008). This is important because species-specificity in interactions among plants suggest greater interdependence of species within communities when some species are more strongly associated with one nurse than another (Callaway 2007; Martorell & Freckleton 2014). Understanding the effects of species-specific interactions on community diversity also informs the efforts to conserve biodiversity, emphasizing the intertwined relationships between diversity and ecosystem functions (Tilman 1996; Tilman et al. 1997; Loreau et al. 2001). Several studies have investigated species-specific interactions among selected species (Hutto et al. 1986) but very few studies have explicitly explored species-specific facilitation at the scale of whole communities.

Facilitation can increase native community diversity, but can also increase the abundance of exotic species (Cavieres et al. 2005; Bulleri et al. 2008; Saccone et al. 2010). In alpine systems, exotic invasion is relatively rare, yet facilitation appears to increase the potential for invasion (Badano et al. 2007; Cavieres et al. 2008). For example, Cavieres et al. (2005, 2008) found that *Taraxacum officinale* (dandelion), a native of Eurasia, was much more common and grew larger in alpine cushion species than on open substrates in the Chilean Andes. This aspect of facilitation has the potential to further increase total diversity (exotics plus natives), or decrease native and total diversity if particular exotic species suppress natives, as is common in many invaded systems (Vilà et al. 2011; Besaw et al. 2011; Shah et al. 2014). Biological invasion is a major driver of local biodiversity decline, but to our knowledge there have

been no explicit studies of species-specific facilitative effects on exotic, potentially invasive, plant species.

Alpine ecosystems provide good opportunities to explore species-specific facilitative interactions because stress-tolerant cushion nurse plants that are common in alpine communities often ameliorate harsh conditions in ways that increase species and phylogenetic diversity (Michalet 2006; Cavieres & Badano 2009; Anthelme & Dangles 2012; Butterfield et al. 2013; Cavieres et al. 2014) and influence natural selection (Michalet et al. 2011). Also, different species of similar cushion plants often co-occur at the same sites.

There have been studies of facilitation in temperate alpine systems, but far fewer in tropical alpine systems (Körner 2003; Anthelme & Dangles 2012; Cavieres et al. 2014). There is reason to suspect that fundamental interactions between potential nurse species and neighbors may differ between temperate and tropical alpine communities. Many environmental stressors in tropical and temperate alpine systems are similar, such as low temperatures, high ultraviolet radiation, exposure to wind, and drought. However, some stressors differ greatly, and in ways that might affect the intensity of nurse-neighbor interactions. Tropical systems lack seasonality, a salient feature of temperate alpine systems. Tropical alpine communities experience a year-round growing season with very similar mean high and low temperatures during the year, whereas alpine plants in temperate climates may have growing seasons of less than two months. Additionally, the daily temperature extremes in some tropical alpine ecosystems, such as the northern Andes, lead to very frequent freeze-thaw cycles in the soil that lift and separate layers (Pérez 1987). This form of natural erosion creates unstable substrate and a constant natural disturbance which may in turn promote facilitation and exotic species.

Tropical alpine ecosystems are also hotspots of biodiversity, and locally endemic species are common (Jacobsen & Dangles 2012; Anthelme et al. 2014). A small number of studies have integrated results from a very small number of tropical sites with temperate sites in global syntheses (Butterfield et

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al. 2013; Cavieres et al. 2014), and a smaller number have focused specifically on facilitation in the tropics (Anthelme & Dangles 2012). But to our knowledge, few studies have focused on the northern Andes (Sklenar 2009, Anthelme et al 2011, Caceres et al 2015, Ramirez and Llambi 2015), which according to Jacobsen (2008) comprise 90% or more of the global tropical alpine biome. We explored species specificity in facilitative interactions in the "páramo" of the Venezuelan Andes. The Venezuelan páramo is a tropical alpine ecosystem that occupies the upper belt of the Northern Andes (3000 to 4800 m) where species with cushion morphologies are common.

We investigated species-specificity in the spatial relationships between two morphologically similar foundation species, *Azorella julianii* Mathias & Constance (Asteraceae) and *Arenaria venezuelana* Briq. (Caryophyllaceae), as well as whole-community diversity and composition. We also measured spatial relationships between the cushions and the abundance of a widespread exotic species in the region, *Rumex acetosella* L. (Chenopodiaceae). We asked the questions: 1) Do tropical cushion species increase local species richness and the density of other species, 2) do different cushion species produce species-specific relationships with local species richness and the abundance of other species, 3) do different cushion species produce species-specific effects on the invader, *Rumex*, and 4) is *Rumex* abundance correlated with decreasing native species diversity?

Methods

 STUDY SITE

Our study was conducted in the northern-most reaches of the Andes Mountains in the Piedras Blancas páramo, Sierra de La Culata National Park, Venezuela, during January 2014 (dry season). Sites were in the páramo between 4200m-4400m, with slopes of approximately 25°, and on northeast facing aspects. We sampled three sites in a 5 km area: Rio Azul (8.8866, -70.8685), Avenida (8.8847,-70.8666), and Gloria (8.8928,-70.8714). Life in this region is subject to exceptionally harsh and dynamic alpine

conditions. Mean annual temperature is relatively constant (3°C ± 2.7), daily temperature near the soil

surface can range between 40°C to less than -5 °C at night (Cáceres 2011).   This region is the driest in

Venezuela's high alpine, with precipitation ranging from 688 mm (Mucuchies station, 2,980 m) to 860

mm (Pico El Águila weather station, 4,118 m) annually. The soils at the study sites are coarse, shallow,

and importantly, subject to constant disturbance by needle-ice formation due to frequent freeze-thaw

cycles in the soil (Perez 1995).

The plant community in our study sites sparsely covers the landscape with generally less than

50% cover and the vegetation is highly clustered. The cover is partitioned into two strata, one of which

is primarily giant rosettes and shrubs, and the other consists of grasses, forbs, cushions, and acaulescent

rosettes (Perez 1995).

We studied two of the four most abundant cushion species in the area, *Azorella julianii* and

Arenaria venezuelana. *Azorella julianii* is commonly found in the Andes Mountains from northern Chile

to Venezuela and *A. venezuelana* is a cushion species endemic to the northern Andes Mountains

(Briceño & Morillo 2002). We also measured the spatial relationships between the two cushion species

and an exotic species that was introduced to lower elevations in the eighteen century (Salgado-

Labouriau and Schubert 1977, Sarmiento et al 2003) and has recently moved into alpine systems, *Rumex*

acetosella. Rumex is native to Eurasia, and at elevations between 3300-3900 m in the Venezuelan

Andes it can be a dominant early successional species in abandoned fields. In the first two years after

abandonment, *Rumex* can comprise c. 50% of the total above-ground biomass (Sarmiento et al. 2003).

In our study area, *Rumex* cover ranges from 5% to 15% on mountain summits at 4200 and 4400m and is

among the 5 most abundant species in the community (Llambi, unpublished data from long term

monitoring GLORIA sites). There are several reasons why *Rumex* might be a threat to the native species

diversity in the high Andean páramo: 1) it has been introduced at lower elevations where it is now very

abundant in disturbed areas, 2) the open vegetation at these elevations and the constant soil

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disturbance from soil freeze-thaw cycles might promote recruitment, 3) there is cattle grazing activity in these high páramo and increased disturbance might promote colonization, 4) facilitation by cushion species might increase *Rumex* establishment.

SAMPLING

At each of the three sites we haphazardly selected individual cushions within a 200m by 200m area. For each individual cushion, we placed a wire ring, 315 cm^2 in area, on the cushion and recorded the presence of all vascular plant species within the ring. We also recorded the total number of all individuals of each plant species to provide a measure of density. Importantly, in our research and throughout this paper, we define individuals as ramets, as many species in the páramo are interconnected underground. Then we randomly sampled open substrate 1 m from the cushion and measured richness and density within the wire rings in the same way we did in the cushion.

We surveyed 35 individuals of each cushion species at each of the three sites for a total of 105 paired samples for each cushion species. We also established line intersect transects to quantify cover (e.g. Greig-Smith 1983) parallel to the elevational contours (2-4 1000m long transects per site at each of the three sites) and quantified the cover of all cushion species. Whenever a cushion fell directly on our transect line, we measured the length of the plant that touched the line.

SPECIES RICHNESS

Comparisons of species richness between habitats are best made with a data set that represents the majority of species present. To estimate whether our sampling was representative we created species accumulation curves for each cushion species and their associated open samples across all three study sites combined. In these curves, the ideal amount of sampling effort is the point where the sample size (x axis) reaches or nears an asymptote with the number of species sampled (y axis), or the

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point at which few new species are discovered by increasing the sampling effort. These models and 95%

confidence intervals around the mean values of species richness were calculated following Gotelli &

Colwell (2011). We also used these curves to compare total diversity patterns at the landscape scale

between cushion species.   All values for the accumulation curves were calculated with the *vegan*

package (Osaken et al. 2013) in R version 3.0.2 (R Core Team 2014).

To compare the richness of plant species, and the total density of all individuals of all species,

inside of cushions to that of open substrate outside of the cushion, we used the mean Relative

Interaction Index (RII) for cushion species and open samples at each site (Armas et al. 2004). The RII is

an index that measures interaction "intensity" (Brooker et al. 2005) computed with the formula $RII=$

$N_{cushion} - N_{open}/N_{cushion} + N_{open}$ where N represents the variable of interest, such as the number of

individuals of a species or species richness, in a sample, e.g. one cushion and its paired open sample

(Butterfield et al. 2013). In our case, this metric can be used to quantify the magnitude of the

interaction between cushions plants and other species. RII values range from 1 to -1, where positive

values suggest facilitation and negative values indicate inhibitory effects of cushions (Armas et al. 2004).

We compared the RII values of each paired sample for total species richness and the total number of

individuals, between the two cushion species, *Azorella* and *Arenaria,* to explore species-specific

differences. We compared RII's for the two cushion species across sites with two-way ANOVA's with site

as a random effect and cushion species as a fixed effect in R version 3.0.2.

COMMUNITY COMPOSITION

We conducted Non-metric Multidimensional Scaling (NMDS) ordination with the *vegan* package (see

methods in Osaken 2015; R version 3.0.2.) to compare the composition of species assemblages, based

on the density of species, inside of the cushion plants to those outside of cushions. We also conducted

NMDS to compare assemblages of all species in *Azorella* cushions to those inside *Arenaria* cushions.

INVASION

We compared the RII values for the density of *R. acetosella* individuals between the two cushion

species, *Azorella* and *Arenaria,* to explore species-specific differences. We used RII's to quantify the

intensity of the spatial relationship between cushion plants and *Rumex.* We also estimated the possible

impact of the exotic *Rumex* on native diversity within the cushions, and how that impact differed

between the two cushion species, by regressing *Rumex* density against native species richness in each

plot for each cushion species. The slopes and intercepts for each cushion species were compared with

ANCOVA using cushion species as a fixed variable, *Rumex* density as a covariate, and native species

richness as the dependent variable.

Results

A total of 52 species were identified in our study system, including the exotic species *Rumex*

acetosella. There were several species of cushion plants at each site, but of these *Arenaria venezuelana*

and *Azorella julianii* were the most abundant. At the *Rio Azul* site, all cushion species comprised 13% of

the total landscape cover, with *Azorella* and *Arenaria* comprising 10% and 2%, respectively. At the

Avenida site total landscape cushion cover was 7%, with *Azorella* and *Arenaria* comprising 3% and 2%

respectively. Finally, at the *Gloria* site total cushion cover was 11%, with *Azorella* and *Arenaria* each

comprising 5% of the cover.

SPECIES RICHNESS

Species accumulation curves approached asymptotes indicating that our sampling represented

most of the local species pool (Figure 1). Across the sampled landscape, more plant and non-vascular

species accumulated in *Arenaria* cushions than in the associated open samples, but for *Azorella* the

pattern was the opposite with open sites accumulating more species than *Azorella* cushions. Based on

overlaps of 95% confidence intervals, species accumulation curves for *Arenaria* and *Azorella* did not differ (results not shown).

RII for local species richness differed between the two cushion species, with a positive RII for *Azorella* cushions and a RII not different than zero for *Arenaria* ($F_{species}$ = 5.369, p=0.0211; Figure 2). The average RII for local species richness in *Azorella* cushions were positive at all three sites, the means and 95% confidence intervals for species richness in *Azorella* were 0.26±0.14 at Rio Azul, 0.18±0.13 at Avenida, and 0.36±0.16 at Gloria. The mean RII for species richness in *Arenaria* cushions was significantly greater than zero only at the Avenida site (mean RII for species richness in *Arenaria* was 0.06 ± 0.16 at Rio Azul, 0.26±0.21 at Avenida, and 0.09±0.21 at Gloria). RII for local species density strongly differed between the two cushion species, with greater RII for *Azorella* than *Arenaria* for all sites tested together ($F_{species}$ = 15.815, p < 0.0001; Figure 2). Average RII's for local plant density in *Azorella* cushions were positive at all three sites (mean RII for species density in *Azorella* was 0.41± 0.13 at Rio Azul, 0.33±0.15 at Avenida, and 0.42±0.15 at Gloria). Mean RII for plant density of *Arenaria* was only greater than zero at one site, Avenida (mean RII for species density in *Arenaria* was 0.26± 0.22 at Rio Azul, 0.06±0.19 at Avenida, and 0.09±0.22 at Gloria).

COMMUNITY COMPOSITION

NMDS ordination indicated that the plant communities inside of cushion species were compositionally different than those in the open (Figure 3A). Similarly the ordination comparing the two cushion species indicated that community assemblages were different in *Azorella* cushions than in *Arenaria* cushions (Figure 3B).

INVASION

RII for *Rumex* abundance also differed between the two cushions, with higher RII's for *Azorella* than for *Arenaria* cushions (F = 5.36, p=0.021; Figure 4). Across the study area, *Azorella* had positive interactions with *Rumex* (mean RII and 95% confidence interval= 0.160 ± 0.125) while *Arenaria* had no significant association with *Rumex* (mean RII and 95% confidence interval= 0.028 ± 0.110; Figure 1 supplemental materials). However, the mean RII for the number of *Rumex* individuals in *Azorella* cushions was only significantly above zero at the Avenida site. The mean RII for *Rumex* abundance in *Azorella* was 0.16± 0.19 at Rio Azul, 0.32±0.23 at Avenida site, and 0.01±0.22 at Gloria. Mean RII for *Rumex* abundance in *Arenaria* was not significantly above zero at any of the three sites. Mean RII for *Rumex* abundance in *Arenaria* was 0.04± 0.23 at Rio Azul, 0.04±0.18 at Avenida site, and 0.09±0.15 at Gloria. For both cushion species we found a positive relationship between the density of *Rumex* inside of cushions and the species richness of native species (Supplementary Information; Figure 1), indicating that *Rumex* abundance does not suppress native species richness. On the contrary, high *Rumex* density was associated with higher native species richness within cushions.

Discussion

We found evidence for species-specific effects of foundation species on community structure. Interestingly, *Arenaria* cushions accumulated more species than their paired open samples while *Azorella* cushions accumulated fewer species than their paired open samples. This finding suggests species-specific differences in relationships between these foundation species and beneficiaries at the landscape scale of the species pool (Cavieres et al. 2014). However, for most other metrics of facilitation, *Azorella* was the superior foundation species. *Azorella* cushions had higher local beneficiary species richness and higher associated plant densities than *Arenaria*. *Azorella* was also a stronger facilitator of the exotic *Rumex* than *Arenaria* was. Finally, the composition of species assemblages differed among foundation species. The degree of species-specificity in positive and negative

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interactions among plants is important for understanding the general role of these interactions in plant communities. If foundation species are not fully interchangeable - if foundation species with similar functional traits alter the realized niches of beneficiaries in different ways - then plant communities lean more towards functional interdependence than if foundation species or other kinds of nurse species simply altered the biophysical environment in ways similar to inanimate objects (Callaway 1998; Bruno et al. 2003). We do not know why our foundation species showed species-specificity in their effects, but variation in the particular mechanisms of facilitation may contribute to species-specific effects. For example, facilitators can vary in their effects on shade, soil resources, water retention, or protection from wind or other forms of disturbance (Callaway 2007). If *Azorella* and *Arenaria* vary substantially in these or other facilitative mechanisms, or if they occupy different environments at a landscape scale, then this may drive species-specific effects. Furthermore, strong net facilitative effects of nurse species do not mean that competitive effects are absent. *Net* effects are often products of the relative intensity of facilitative and competitive effects (Callaway et al. 1991; Callaway 2007; Atwater et al. 2011). Variation in the competitive effects of net facilitators has the potential to drive strong species-specificity.

Despite the similar morphology of *Arenaria* and *Azorella*, species-specific facilitative effects may have been related to subtle trait differences between the species (Butterfield 2009; Butterfield & Callaway 2013). For example, *Azorella* plants were 180% larger on average than *Arenaria* plants, potentially contributing to stronger local facilitative effects. *Arenaria* has shorter thinner leaves whereas *Azorella* has broader and more rigid leaves, and these physical trait differences, among others, might contribute to the dissimilarities in the mechanisms for facilitation.

We focused on the *effects* of foundation cushion species on other species; however, a substantial component of general species interactions involve the *responses* of foundation species to the beneficiaries they facilitate. For example, Schöb et al. (2014) assessed the context dependence of how

variation in the abiotic environment altered the "feedback effects" of cushion-associated beneficiary species on their cushion benefactors. They found that the effect of beneficiaries on cushions became negative when beneficiary diversity increased and when facilitative effects were more intense. Since interactions among species are necessarily determined by ongoing feedbacks between effects and responses, variation in the response of different cushions species to beneficiaries could also contribute to net species-specific effects.

We found interesting differences in cushion effects at local and landscape scales. *Azorella* cushions accumulated fewer species than the associated open samples overall, but appeared to be a better facilitator in terms of RII. At the local micro-habitat scale, the paired open samples for *Arenaria* had fewer species than the paired open samples for *Azorella* even though these two species were sampled in the same study sites (open samples were monitored 1 m away from cushion samples). One explanation for this could be that *Arenaria* may occupy less favorable local micro-habitats. In other words, the two species may exist in different local habitats. This could help to explain why at a landscape scale *Arenaria* showed comparatively *higher* richness within cushions than *Azorella*. Similar differences between local and community effects of ecosystem engineers on richness were found by Cáceres et al. (2015) with shrubs associated with increased local, but not landscape, richness. Conversely Badano et al. (2006) found landscape scale effects of cushions on richness, but no significant local effects. Further on larger scales, Kikvidze et al. (2015) found that between-site diversity was higher outside of cushions than inside of cushions.

It is important to note that our measurements were correlative, not experimental, thus we cannot separate microsite effects from the biological effects of cushions (see Cáceres et al. 2015). Yet our cushion species were highly intermixed, and thus any microsite effect would have to be quite micro indeed. Also, experiments with dozens of species around the world in high alpine habitats have shown

facilitation to be very common (Callaway et al. 2002) and experimental evidence for facilitation has been

shown to correspond well with positive spatial associations (Choler et al. 2001).

To our knowledge, there have been no studies of species-specific foundation species effects at

the scale of whole communities, but numerous studies have measured the effects of several species of

nurses on targeted beneficiaries and demonstrating species-specific effects (Hutto et al. 1986; McAuliffe

1988). Other studies have compared the effects of several nurse species on large numbers of other

species. For example, Suzán et al. (1996) reported that *Olneya tesota* was a "keystone" facilitator in

some Sonoran Desert communities but noted that some beneficiary species were much more highly

correlated with other nurse species. Valiente-Banuet and Ezcurra (1991) found similar correlations

between potential nurse plants and different species of cacti in central Mexico. Quantified networks of

facilitating species showed that spatial relationships are not random, and demonstrated a high degree of

species-specificity (Verdú & Valiente-Banuet 2008). In these desert networks species-specificity shows a

phylogenetic signal with more phylogenetically distant species showing the strongest associations

(Verdú et al. 2010; Verdú & Valiente-Banuet 2011).

Facilitation has been shown to promote exotic invasion in a number of systems, including alpine

communities (Badano et al. 2007; Bulleri et al. 2008; Cavieres et al. 2008; Johnson et al. 2009; Saccone

et al. 2010) and others. For example, Siemann and Rodgers (2003) found that facilitation promoted the

exotic tree species *Sapium sebiferum* to outcompete a native tree and establish itself in North American

grasslands. Similarly in Australia, an invasive stem succulent, *Orbea variegata*, had higher growth and

establishment when in the shade of a native shrub than in exposed sites (Lenz & Facelli 2003). Our

results show a degree of specifies-specificity in such facilitative effects of nurses on an exotic, with more

positive associations with *Azorella* than *Arenaria* in an alpine setting. Importantly, we found no

evidence that *Rumex* was impacting native species inside of the cushions. Other studies in this region

found that shrubs, which also act as foundation species, have negative interactions with *Rumex* (Caceres

et al 2015, Ramirez and Llambi 2015). This difference could be due to morphological differences between cushions and shrubs or difference in the habitats the shrubs occupy.

Our results contribute to a growing body of evidence for species-specificity in foundation species effects and facilitative interactions among plants. The two cushion species we studied varied in their landscape and local scale association with diversity, local scale spatial associations with the abundances of other species, community composition, and their spatial associations with a common exotic species. Such specificity indicates a relatively high degree of functional interdependence among plant species in the high tropical Andes.

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Figure Legends

Figure 1. Species accumulation curves for cushions (black lines) and open areas (white lines) in Venezuelan high páramo (4200-4400 m) showing means ± 95% confidence levels for the mean at each sampling interval. Three study sites were combined for each cushion species and associated open areas.

Figure 2. Mean relative interaction intensities (RII) and ± 95% confidence levels for local plant species richness in *Azorella julianii* and *Arenaria venezuelana* cushion plants in three sites (data combined) in Venezuelan páramo (A). Mean relative interaction intensities (RII) and ± 95% confidence levels for total plant density in *Azorella* and *Arenaria* cushion plants at the three sites combined in Venezuela. We excluded from this analysis the exotic species *Rumex acetosella*.

Figure 3. Nonmetric multidimensional scaling ordination comparing community similarity (indicate index) for all within-cushion to all open samples in a high Venezuelan páramo. Small triangle and circle symbols represent individual samples (indicate number of samples). Larger square symbols represent means ± 95% confidence levels (A). Nonmetric multidimensional scaling ordination comparing all within-Azorella cushions to all within *Arenaria* samples. *Rumex* was not included. Small triangle and circle symbols represent individual samples. Larger square symbols represent means ± 95% confidence levels (B). We excluded from these analyses the exotic species *Rumex acetosella*.

Figure 4. Mean relative interaction intensities (RII) and 95% confidence levels for the density of *Rumex acetosella* individuals in *Azorella julianii* cushions vs. in *Arenaria venezuelana* cushions across the study area in a high Venezuelan páramo (4200-4400 m).
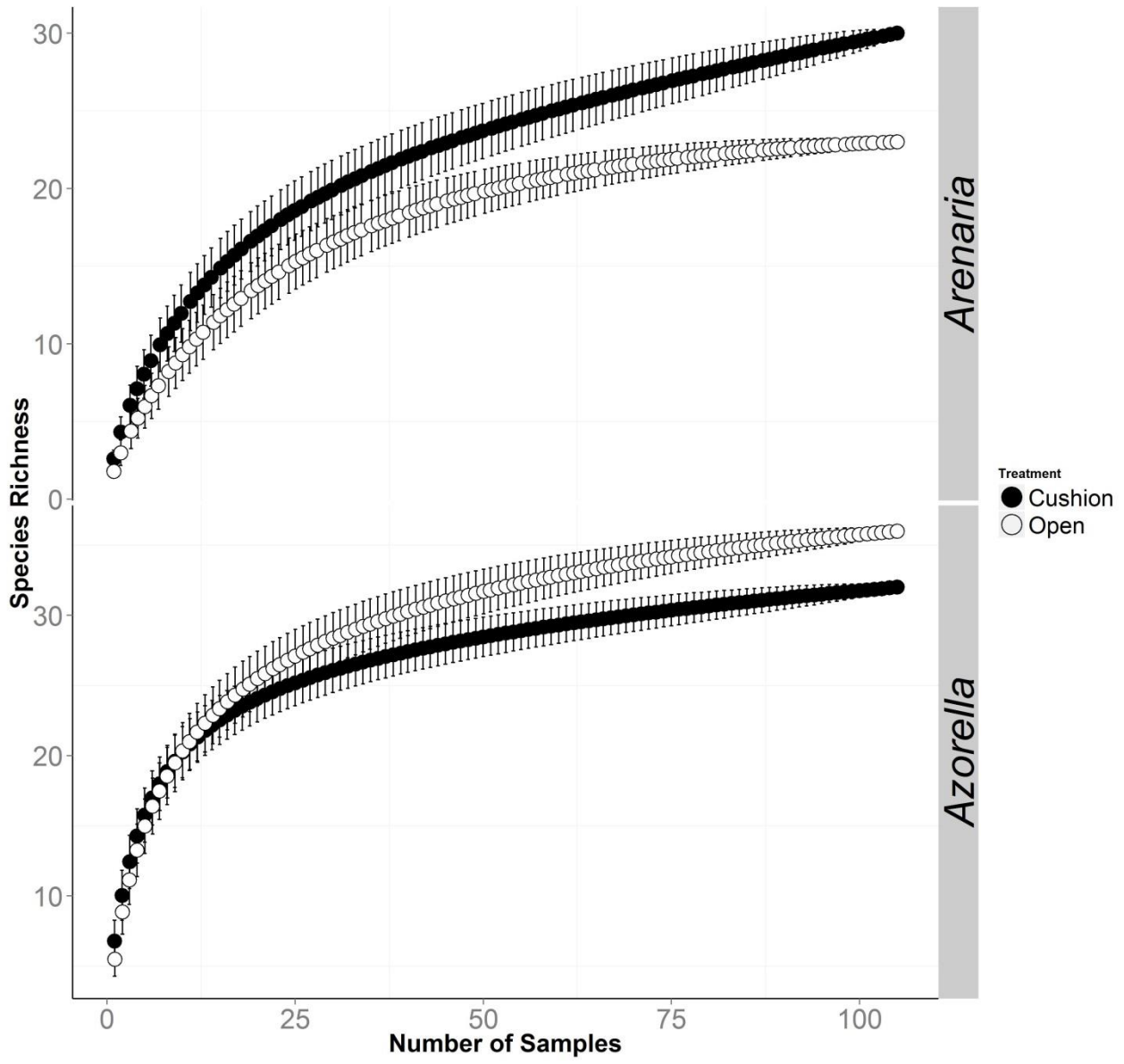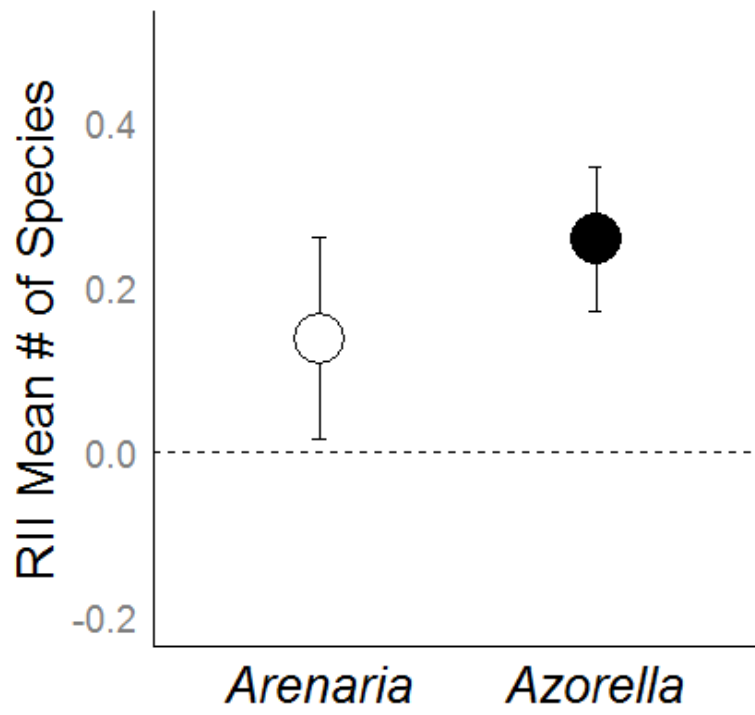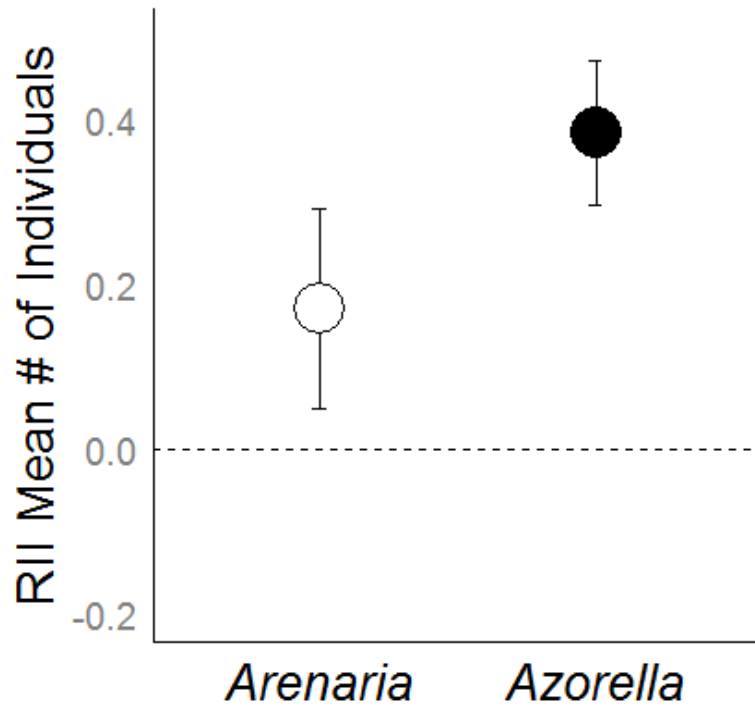
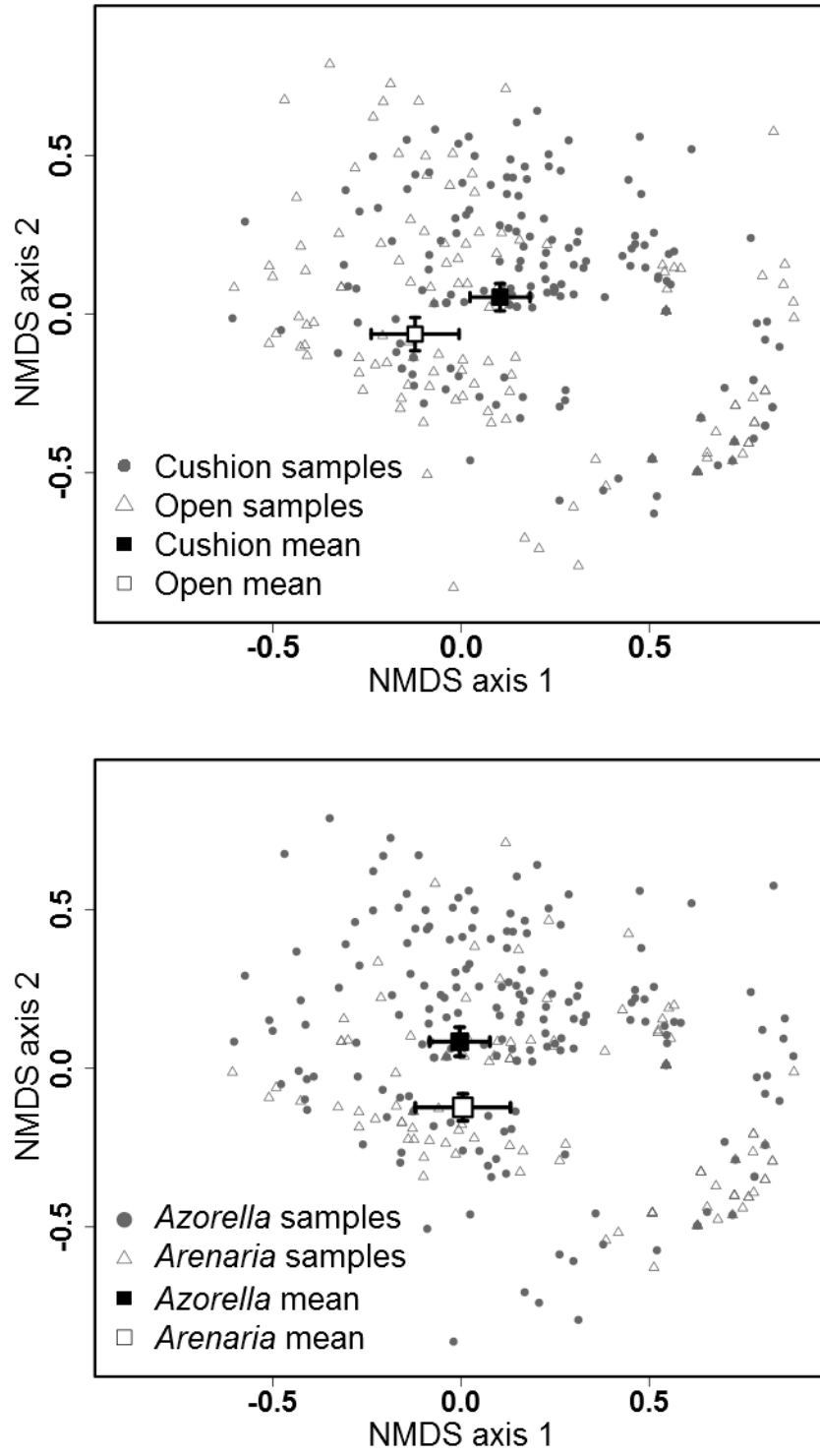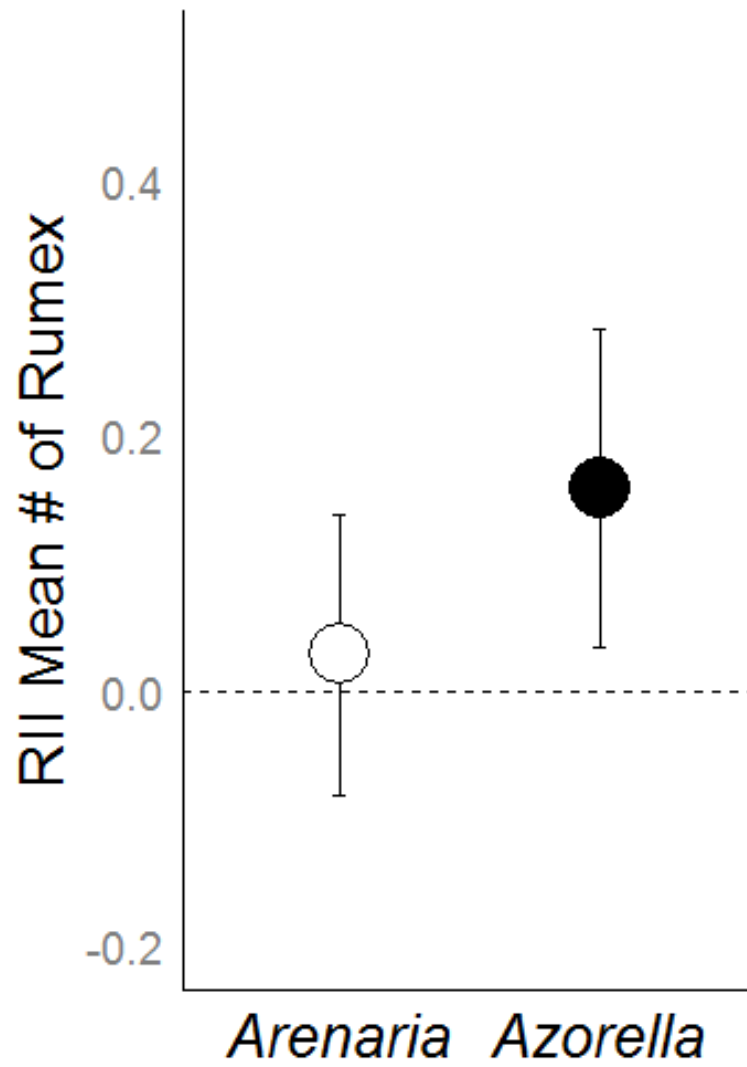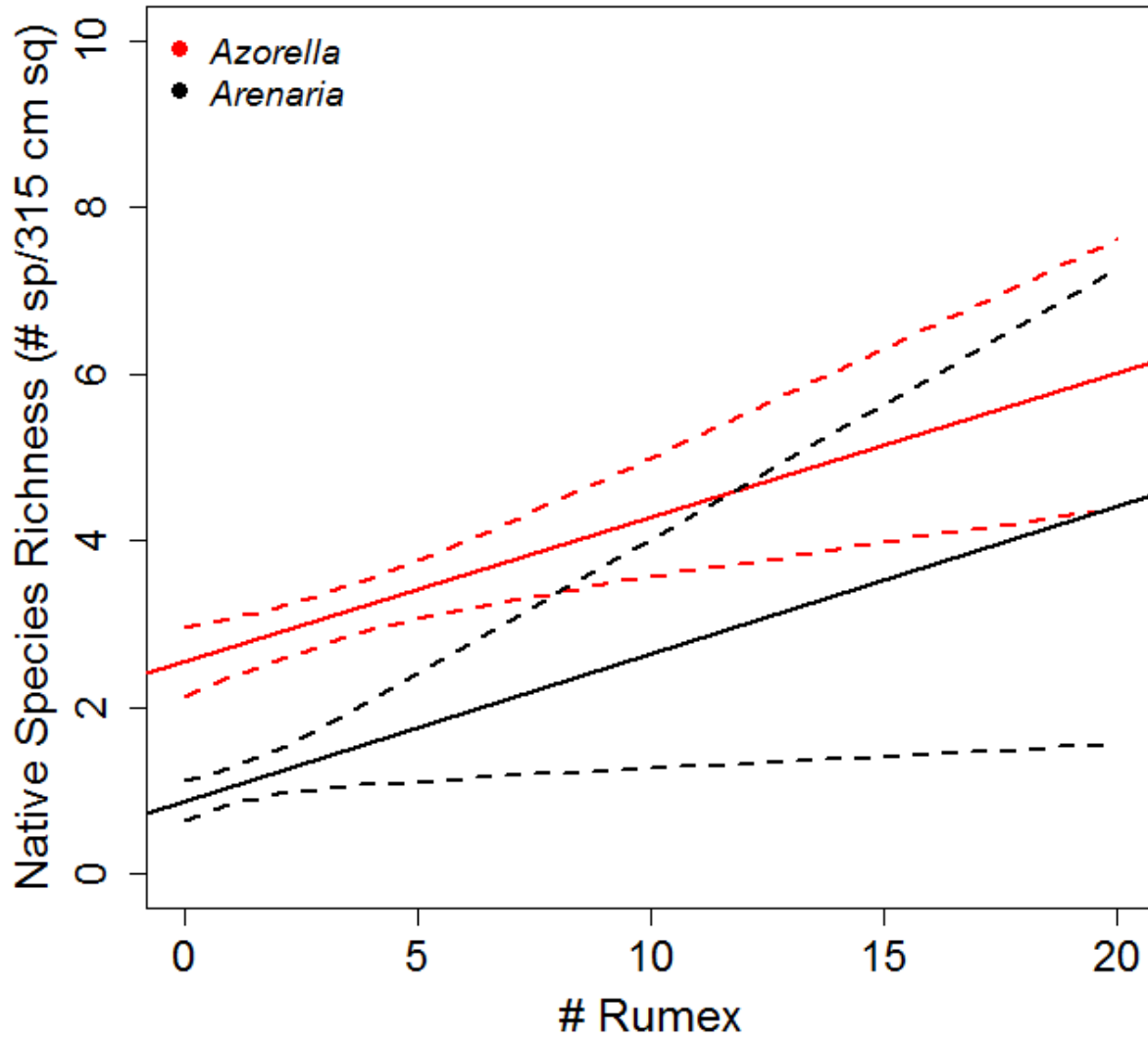Figure 1.

Figure 2.

Figure 3.

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Supplemental Information Figure 1. Regressions for the relationship between native richness vs. *Rumex* density in *Azorella* and *Arenaria* cushions.

Chapter 2

Facilitation and the regional-scale distribution of alpine plants

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INTRODUCTION

In systems characterized by abiotic stress such as deserts and high mountains, facilitation can play an important role in the structure of plant communities and increase the local abundance of many species (Hutto et al. 1986; Callaway 1998; Valiente-Banuet & Verdú 2007; Fajardo et al. 2008; Cavieres et al. 2014). Facilitation can also affect the smaller scale distributions of plant species. Choler et al. (2001) found that subalpine and alpine species were generally facilitated at the upper ends of their elevational distributions, suggesting that facilitative interactions might extend the ranges of some species to higher elevations. In contrast, competition appeared to restrict species from occupying lower elevations. Similarly, Bertness and Shumway (1993) found that neighbors increased the abundance of *Juncus gerardii* in highly saline conditions that occurred at the end of a gradient where inundation was common, but when salt stress was alleviated, the presence of neighbors decreased the abundance of *J. gerardii* at the end of the gradient where inundation was less frequent. In other words, facilitation expanded the distribution of *J. gerardii* at one end of the gradient while competition restricted its distribution at the other end (also see Bertness & Ewanchuk 2002). Such evidence that positive interactions can increase the distributions of species at relatively small scales is conceptualized as expansion of the realized niche (see Bruno et al. 2003).

The realized niche can be altered by other biotic interactions (Jankowski et al. 2010). Bullock et al. (2000) demonstrated that the distributions of two species of evergreen shrubs (*Ulex minor* and *Ulex gallii*) were limited to a large degree by competition with each other. Stanton-Geddes and Anderson (2011) found that the availability of appropriate mutualists outside of a plant species range can limit the expansion of that species range. Moeller et al. (2011) reported that pollinator availability declined from the center of the range of *Clarkia xantiana* to the outer limits of that distribution, and therefore pollination limitation restricted reproduction of *Clarkia* and checked range expansion (also see Eckhart et al. 2011). These studies have helped us understand the effects of biotic interactions on large-scale

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distributions of plant species; however, there is still a pressing need to explore how interactions among plant species might affect landscape or regional scale distributions of species; for example how facilitation might expand the range limits of species.

Climate change appears to be altering the distributions and range limits of species (Grabherr et al. 1994, Gottfried et al. 2012; Brusca et al. 2013), particularly in alpine ecosystems (Cannone et al. 2007; Smith et al. 2009; Rixen et al. 2014). However, climate change impacts species distributions in ways than can be diminished or amplified by other ecological processes (Walther et al. 2002), which makes changes in distributions challenging to predict (Thuiller et al. 2008). Gilman et al. (2010) suggest that this unpredictability is due in part to a lack of understanding interactions among specie at these scales, and they propose interdisciplinary integration of global-change biology and community ecology to better understand how plant distributions and range limits might respond to climate change.

In this context, interactions with other species have a substantial potential to ameliorate or exacerbate the effects of climate change on species distribution (Davis et al. 1998; Gilman et al. 2010). However, "the complexity of ecological interactions renders it difficult to extrapolate from studies of individuals and populations to the community or ecosystem level" (Davis et al. 1998; see also Walther et al. 2002; Klanderud 2005). To make such extrapolations, "macroecological" studies are essential because they provide the synthetic power crucial for landscape-scale and regional scale predictions (Maurer 2000; Swihart et al. 2002; Beck et al. 2012). Such large scale studies link local biotic data and environmental variables to understand large scale processes and might improve our ability to understand current distributions and predict future distributions and abundances.

The lack of landscape-scale investigations of biotic interactions is due in part to the challenges of sampling at large scales, which requires integrating large datasets that are often collected at multiple scales (Araújo & Guisan 2006; Sexton et al. 2009). For example, scaling from local experiments conducted to quantify interactions among species to the much larger scale of the distributions of

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interacting species is problematic (Sexton et al. 2009). Guisan & Thuiller (2005)and Randin et al. (2009)

reviewed species distribution models and observed that failure to accurately quantify interactions

among species has the potential to downplay the importance of biotic interactions relative to the effects

of climate and historical processes, as drivers of large-scale ecological patterns (see Ricklefs 2008). But

not all distribution models have discounted biotic interactions. Carlson (2013) found gradient-

dependent species interactions, along with abiotic drivers and disturbance, were strong drivers of the

distributions of alpine plant species. Furthermore, recent reviews of state-of-the-art modeling of the

distributions of alpine plants note that understanding how interactions, such as facilitation, affect large

scale distributions is a significant and under-addressed issue (Araújo & Luoto 2007; Van der Putten et al.

2010; Carlson et al. 2013). Such reviews indicate that the combination of fine-grain biotic data collected

along environmental gradients and combined with climate data might help understand how biotic

interactions affect the large-scale distributions of species, their range limits, and how these limits might

be modified by climate change (Gilman et al. 2010; Wisz et al. 2013).

We tackled this knowledge gap by combining local scale spatial correlations among species that

infer interactions with large-scale distributions of species and climate patterns throughout the central

and northern Rocky Mountains. We measured patterns of spatial associations among cushion species

and species without such morphologies. We then created generalized linear models to explore the

relative importance of cushion plant/non-cushion plants interactions, climate, and latitude on the

abundances of species across the region. Next, we built climate based niche envelopes to compare

abundances of species when grown in cushions and when grown in the open matrix. We then compared

niche *breadth* for selected non-cushion species based on temperature, precipitation, and latitude by

comparing distributions derived from within-cushion patterns to distributions derived from outside-

cushion patterns.

METHODS

Location

We sampled a total of 35 sites in alpine communities containing species with "cushion" morphologies from southern Colorado to southern Canada. Data were obtained for 16 of these sites from a collaborative cushion sampling database (sampled from 2003-2012) and 19 of these sites were sampled in the summer of 2014 (Figure 1). Sites were located between 1117 and 4153 meters (mean elevation = 2896 m ± 841m). Mean summer temperatures ranged from 4.4 to 16.1°C (mean summer temperature = 8°C ± 2.5°C). Mean total summer precipitation ranged from 113 to 353 mm (mean summer precipitation = 232 ± 58 mm). Sites were located from 35.3°N to 57.1°N. Growing seasons at our sites are roughly from mid-June to September.

Sampling

At each site we haphazardly sampled the most dominant cushion species in a 500-1000 m^2 area. Since the sample locations were spread widely throughout the Rockies, the dominant cushion species at a given site varied. We sampled one cushion species per site, and sampled a total of 13 cushion species. For each individual cushion, we placed a wire ring around the perimeter of the cushion, using the size of the cushion as the sample size, and recorded the presence of all vascular plant species within the ring. We also recorded the total number of all individuals of each plant species to provide a measure of density. Then we sampled the same area in open substrate 100 cm from the cushion in a random direction and measured richness and density within the wire rings in the same way we did in the cushion. At each site, we collected between 50 and 150 paired cushion/open samples (the mean sample size for all study sites was 78 paired samples). Throughout, we compare abundances across environmental gradients in the cushion samples to those in the open, and refer to these paired samples as the cushion vs open microhabitat "treatment".

We sampled 239 non-cushion species across all sites. However, most of these species were found in very few of our 35 sites, and some were locally endemic; over 40 species were found at just 1 location. Consequently, we did not sample high numbers of sites for any single non-cushion species. Thus for all of the distributions of non-cushion species the sample sizes are small. *Poa alpina* was found in the largest number of sites, which was present in 24 sites across the study area. There were only 4 species that were exclusively present outside of the cushions, and we found 21 species that were found exclusively inside of cushions. Therefore, we focused on the 5 most abundant species across all sites, these "focal species" were present in at least 14 sites across the study region (Table 1). For some of our analyses we expanded the focal species subset to include more species from the dataset. In these cases, we selected the species that were present in a cushion, in the open, or both in at least 6 sample locations, which included 30 species.

Environmental Variables

Climate data for each site were obtained from the Worldclim database (http://www.worldclim.org; Hijmans et al. 2005) with a spatial resolution of c. 1 km^2. For our analyses we used total precipitation during the summer months (June–August) and mean temperature at the onset of the growing season (June; T_{max} June), because these two variables have shown to be the best predictors of cushion-based spatial relationships many in studies similar to ours (Cavieres et al. 2014). We also used latitude at each study site for some analyses of niche space, though this variable was not used in other statistical tests because it was highly correlated with precipitation and temperature.

Species Abundance

We first determined the overall strength of associations or disassociations between non-cushion and cushion alpine species, prior to examining distributions. We modeled how microhabitat (cushion vs.

open), temperature, precipitation, and latitude, correlated with the abundance of all 239 species combined across all sites using a generalized linear model (Guisan et al. 2002). Models were fit using a Poisson distribution and selected through backwards elimination, AIC (Akaike's Information Criterion), and BIC (Bayesian Information Criterion). We then tested correlations between the abundance of all non-cushion species and microhabitat, temperature, precipitation, and latitude. We used generalized linear models (using the *glmm* function in the *lme4* package in R version 3.0.1) to correlate species abundances (the response variable) with the presence or absence of a cushion (the "microhabitat"), temperature, precipitation, and latitude. In these models, how microhabitat affected species' responses to climate was key thus we focused on interactions between microhabitat and temperature and precipitation.

We ran GLM's, using the same explanatory and response variables as above, for the 5 species that were found the most often across all of our sites. We also modeled two pooled samples, the most abundant 10 species and all 239 species. As above, models were fit using a Poisson distribution and selected through backwards elimination, AIC (Akaike's Information Criterion), and BIC (Bayesian Information Criterion). Again, we were interested in the correlations between the abundance individual non-cushion species and microhabitat, temperature, precipitation, and latitude.

Climate Envelopes

We then compared two climate envelopes for each of the 5 non-cushion focal species. For each species, one envelope was constructed using all individuals occurring in cushions, and a comparable envelope was constructed using all individuals in the open. These climate envelopes are contour plots based on species abundance along gradients of temperature and precipitation. Put another way, for each species, we created two niche envelopes and projected the abundance of species over the gradients of

temperature (on the x axis) and precipitation (on the y axis). These climate envelopes were not tested

statistically, but provide a way to visualize the output from the generalized linear models.

Niche Differences

We used this same two-group approach (cushion compared to open samples) for each species to

investigate how cushions might modify niche space. Here, we define "niche space" as the range of

latitude, precipitation, and temperature for sites where a species was present. In other words, we asked

if the climate-based niche space displayed for a species in cushions differed from such niche space

displayed in the open.   We built histograms of frequency distributions based on the number of sites at

which a species occurred (based roughly on Dobrowski et al. 2015), and graphed frequencies of sites

along axes of temperature, precipitation, and latitude. In these histograms, we plotted two

distributions, one for sites where a focal species was found in cushions and one where a focal species

was in the open treatment. If a species was found inside cushions and outside cushions at every site

where it occurred, then histograms are identical. It is important to re-emphasize that these analyses

were based on the *presence* of a species in a given microhabitat at a given site, and not on abundance as

used for climate envelopes. Thus comparing histograms is limited by small sample sizes much more

than the climate envelopes. Following Dobrowski et al. (2015), we considered frequency distributions of

species along climate gradients as proxies for niche breadth. We statistically compared the center of

climate niches using the means, and compared them between cushion and open using Welch's two-

sample and one-sided paired t tests for each species.

To statistically compare the climate ranges of a species in cushions versus in the open, or "niche

tolerance" (Dobrowski et al. 2015), we measured the distance between the 5th and 95th percentiles from

each pair of histograms. Niche boundaries can be thought of as simply the range occupied by a species

along an environmental variable, such as precipitation. First, we statistically compared the mean niche

tolerance for the 5 most abundant species across the sample sites in cushions to mean niche tolerance

outside of cushions using Welch's two-sample, one-way paired t-tests for precipitation, temperature, latitude, and elevation. We also conducted the same analyses on an expanded subset of species - the 36 most abundant species across our sites (each species was present in cushions and/or in the open in at least 6 sites).

RESULTS

Abundance and Climate Envelopes

The best GLM for all non-cushion species pooled (239 species total) was the full model, which included microhabitat (cushion vs. open), precipitation, temperature, and latitude. All terms were significant, indicating that temperature, precipitation, and the effect of cushions were highly predictive of these alpine species abundances. The abundance of all non-cushion species was positively correlated with cushions. More importantly for our purposes, there were significant interactions between temperature and microhabitat (z= -5.2, p<0.001), precipitation and microhabitat (z= -2.5, p<0.01), and latitude and microhabitat (z= 28.5, and p<0.001). In other words, when all species abundances were pooled together, the effect of cushion species on the abundances of non-cushion specie varied with changes in temperature, precipitation, and latitude.

GLMs also indicated that microhabitat (cushion vs. open) was highly predictive of the abundance for all five focal species (Table 2) examined independently.   Of these five, four species were facilitated by cushions and one preferred open microhabitat (*Geum rossii)*; however these effects did not always show an interaction with temperature or precipitation, meaning the effect of microhabitat did not vary across environmental gradients for all species.   For example, *Poa alpina* was more abundant in cushions than in the open, but its distributions on climate axes were similar in both microhabitats; there were no interactions between climate variables and microhabitat for this species. However, four species had significant climate by microhabitat (in versus out of cushions) interactions, indicating that the effect of

either temperature or precipitation on these species was changed by microhabitat. Four focal species demonstrated significant interactions between cushions and temperature. For example, the abundance of *Antennaria alpina* and *Erigeron compositus* had significant cushion by temperature interactions (Table 2), and these corresponded with contour plots suggesting that cushions might promote the expansion of these species into colder temperatures. *Achillea millefolium* was the only focal species with a significant cushion by precipitation interaction (Table 2), and the climate envelopes depicted in contour plots indicated that *A. millefolium* occupied drier sites when in cushions.

The one species that was more common in the open than in cushions, *Geum rossii*, there was also a strong cushion by temperature interaction for *G. rossii*. However, the contour plots did not show clear shifts in distributions along the temperature axis, but instead a substantial increase in abundance within the same dimensional space.

Niche differences

In the analysis of niche breadth, which is depicted with histograms of frequency distributions, we found no differences in the center point of distributions between cushion versus open frequencies for any species along gradients of precipitation, temperature, or latitude (Figures 5-6). Neither did we find any significant differences between the means of the 5th and means for 95th percentiles in cushions compared to the open for the 10 focal species that were pooled. When we expanded the number of species to include species that were much less common (36 species) we still detected no difference in 5th or 95th percentiles in cushions vs. the open for precipitation, temperature, or latitude. However, several histograms suggest the potential for cushions to modify habitat in ways that could expand species' niches. For example, cushion microhabitats were associated with a trend in the frequency of sites occupied by *Antennaria alpina* to shift towards wetter climates and more southern latitudes. *Geum rossii* showed a tendency towards higher site frequency at warmer climates and more northern

latitudes. *Poa alpina* showed a slight tendency to shift its distribution to wetter temperatures in cushion microhabitats.

Niche Tolerance

We compared niche tolerances (the occupied niches along axes, measured as the distance between the 95th percentile and the 5th percentile) for mean temperature, precipitation, and latitude using the expanded sample of 36 species in cushions verse the open and again found no differences (temperature t = 0.670, df = 67.64, p-value = 0.253; precipitation t = 1.038, df = 67.99, p-value = 0.151; latitude t = 0.936, df = 66.49, p-value = 0.176). However, several histograms suggest that there is potential for cushions to increase species' niche tolerances. Overall, 9 out of 15 histograms tended towards cushions expanding niches, with four of the 15 showing very weak trends toward niche contraction. For 2 of the comparisons niche tolerances were very similar in cushions vs. the open.

DISCUSSION

We found evidence that facilitation may expand the ranges of some species, based on contour plots of species abundances and generalized linear models. All of the species showed strong preferences for one of the microhabitats, and four out of five preferred cushions. For 4 of the 5 focal species and for the pooled samples, linear models indicated that the effect of cushions on species abundance is moderated by climate (at least one microhabitat by climate interaction term was significant). These interactions are particularly relevant because they indicate that biotic interactions among plant species have the potential to change species distributions along climate gradients. Also, for each microhabitat by climate interaction, the cushion microhabitat was correlated with an *increase* in species abundances along climate gradients. In other words, the climate envelopes and GLMs suggest that facilitation may increases the large scale distribution of some alpine species. However, in our niche breadth and niche

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tolerance analyses we found no statistically significant patterns indicating either a compressed or expanded realized regional climatic or latitudinal niche. There were no significant shifts in the means, niche breadths, or niche tolerances of species inside cushions compared to outside of cushions.

One potential reason for why frequency-based niche diagram analysis did not detect any significant shifts in occupied site frequency (histograms) may have been because they were highly limited by sample size. Since very few species were found at more than 15 sites across our study system, and site was the dependent variable in this analysis, our ability to make histograms with enough replication as to represent our large-scale study system was difficult. In contrast, the calculation of climate envelopes and the corresponding GLMs was based on the abundances of individuals either across or within species, and thus replication was greater. A second drawback to our analytics of niche comparisons was the use of presence-absence results to calculate frequencies. In other words, if 1000 individuals of a species occurred within cushions at a site, and one individual of the species occurred outside of cushions, then this site was counted in both frequency diagrams for a species. Placing each target species into abundance classes might provide a clearer picture of niche patterns.

Bruno et al. (2003) noted that because foundation species expand the range of habitats in which an organism can live, "including positive interactions in niche theory leads to a paradox" where the realized niche is larger than the fundamental niche. Some species in our study demonstrate patterns that offer some empirical insight to this theoretical paradox. Species such as *Achillea millefolium* and *Antennaria alpina* were not only more abundant in cushions they were disproportionately more abundant in cushions at sites with lower precipitation levels and lower temperatures when compared to the open. Though higher abundance does not confirm that the ranges are expanding due to facilitation, higher abundance could be associated with niche expansion in indirect ways or a result of species persisting in cushions and repopulating open sites.

There has been much speculation about the role of biotic interactions in landscape scale distributions (Svenning et al 2014), and while studies have shown that biotic interactions shape species distributions on local scales (Bertness & Shumway 1993, Bullock et al 2000), to our knowledge this study is among the first to empirically, but not experimentally, test this at a regional scale. Recent reviews on species distribution modeling point out that biotic interactions are indeed relevant for understanding the distribution of a species, but explain that to study these interactions on a large scale requires large amounts of fine grain large scale data that is lacking (Wisz et al. 2013; Carlson et al. 2013). Our approach was regional in scope and represents a large number of sites and species sampled throughout the Rockies, but sample sizes still limited some of our analyses and interpretations. This was because we could not know if a targeted non-cushion species might occupy a particular site, as our sampling was based on where we could find cushion species. Therefore our sample sizes for the frequency-based niche diagrams were very low. For example, the species with the largest sample size (number of sites at which it occurred) was *Poa alpina*, which occurred at 24 sites. The focal species with the smallest sample size number was *Achillea millefoium*, which occurred at 14 sites. We estimate that this approach would likely require expanding the number of sites sampled, or a more targeted approach to locating specific non-cushion species.

How microclimate affects the distribution and abundance of a species across environmental gradients could be informed by trait-based analyses of focal species. Accounting for species functional traits can help predict distributions of species (Choler 2005), and may moderate the strength of interactions with facilitators (Schöb et al. 2012). Additionally, traits offer insights into the realized niches of species (McGill 2006). Traits are relevant for community assembly and as for biotic interactions, can affect where species are found in nature (Spasojevic & Suding 2012). Within our subset of focal species, there is a wide variety of plant function traits that we did not analyze. For example, many species we studied are alpine specialists, such as *Tetraneuris acaulis* and *Smelowskia*

calycina. Such alpine and arctic specialists often share traits that are well adapted for harsh, high light intensity scenarios like light color leaves, hairy structures, and low stature habits (Körner 2003). Two other species also are common in alpine communities, and can form loose cushion forms, *Trifolium dasyphyllum* and *Geum rossii.* This may offer insight into why *G. rossii* showed reduced abundance in the GLMs when the species was grown in cushion plants compared to the open. We also sampled species that are more common at lower, drier sites, and have very different life history strategies than other targeted species, such as *Sedum lanceolatum*.

Our study used relatively coarse grain climate data and did not measure aspects of the microclimate at sites, and this likely limited the strength of correlations between climate and species abundances. Alpine plant community composition and interactions among species can be strongly influenced by topographic microclimate (Choler et al. 2001). Opedal et al. (2015) found that small- scale topography in alpine ecosystems in Norway creates microclimatic differences within sites that contributed to higher species richness and diversity than comparatively flat sites. We do not know if such micro-topographical differences among our sites affected our results. Future research should include finer grain climate data and other fine scale environmental variables, as greater resolution could more accurately depict the relationship between environmental variables and microclimate for predicting the abundances of species.

Our research investigated positive interactions at the landscape scale by quantifying correlations between cushion foundation species and the distribution of other members of the plant community in a large region of the northern Rocky Mountains. Our exploration of the effects of facilitators on large scale species distributions through alpine sampling in North America is a start to an empirical understanding.

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TABLES

Table 1. Information on the 5 species occurring at a minimum of 15 sites, enough to conduct analyses of climate envelopes and niche tolerances.

Table 2. The generalized linear model output for 5 of the most abundant species, the top 10 species pooled, and all species (239 pooled). The table includes model estimates from a generalized linear model. Model estimate is followed by asterisks to denote significant p values. Sample size for all species is 80 (40 sites total, with 1 cushion and 1 open sample for each site).

Table 1.

Species	Mean Open Density	Mean Cushion Density	# Open Sites Where Sp. Was Present	# Cushion Sites Where Sp. Was Present
Achillea millefolium	0.032	0.262	12	11
Antennaria alpina	0.088	0.086	9	14
Erigeron compositus	0.054	0.202	18	17
Geum rossii	0.354	0.599	11	14
Poa alpina	0.106	0.593	17	24

Table 2.

Species	Model Estimates for terms in GLM				
	Cushion	**Temp.**	**Precip.**	**Cushion* Temp.**	**Cushion* Precip.**
Poa alpina	2.70 **	-0.03 **	-0.001	-0.003	-0.0012
Erigeron compositus	2.19 **	0.02 **	0.008 **	-0.014 **	-0.0006
Geum rossii	-0.91 **	-0.34 **	-0.049 **	0.025 **	-0.0006
Achillea millefolium	5.61 **	-0.13 **	-0.045**	-0.007	-0.0114 **
Antennaria alpina	1.56 **	-0.07 **	-0.053 **	-0.012 **	-0.0001
10 Species Pooled	0.92 **	0.0001 **	0.007 **	0.006**	-0.0001
All Species Pooled	1.32 **	0.00001**	0.001 **	-0.003**	-4.0101 *

 * Denotes p values < 0.01 ** Denotes p values < 0.001; n= 80 for each species (40 cushion samples & 40 open samples)

Figure Legends

Figure 1. Locations of all sample sites.

Figure 2. Contour plots depicting climate envelopes for focal species that occurred at relatively low densities across all sites (displayed on a scale of 0-0.8 individuals /m^2). Contour plots should be evaluated in conjunction with the results from GLMs shown in Table 2.

Figure 3. Contour plots depicting climate envelopes for focal species that occurred at high densities across all sites (displayed on a scale of 0-2.0 individuals /m^2). Contour plots should be evaluated in conjunction with the results from GLMs shown in Table 2.

Figure 4. Histograms of the frequencies of sites at which five focal species occurred, either in cushions or in the open, on gradients of precipitation, temperature, and latitude. Black lines represent sites where a focal species was present in cushions, and the gray dotted lines represent sites where a focal species was present in the open. The solid vertical black lines represent the 5th percentile, the mean, and the 95th percentile of the climate variables in cushion samples. The gray dotted vertical lines represent the 5th percentile, mean, and the 95th percentile of the climate variables in the open samples.
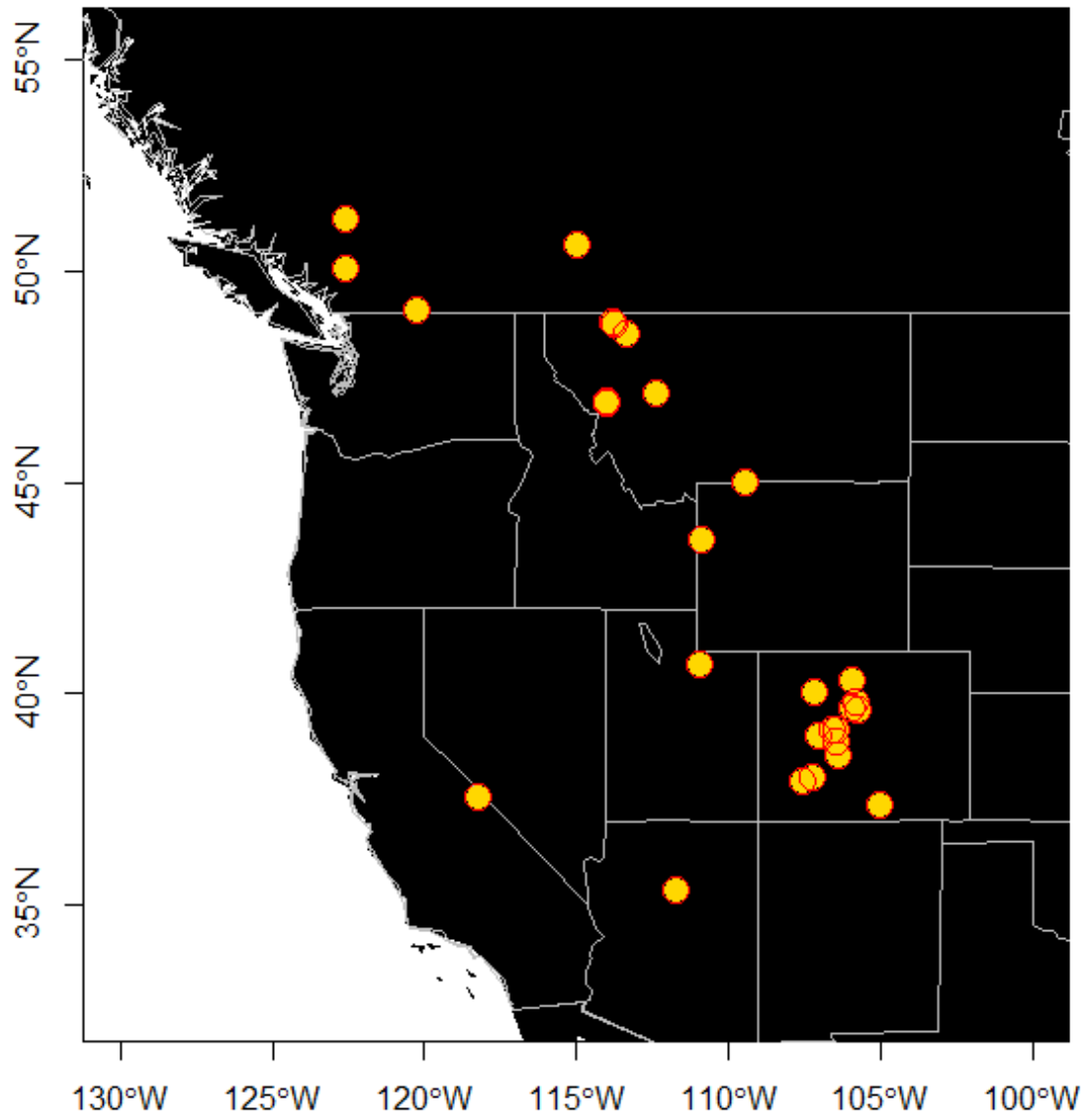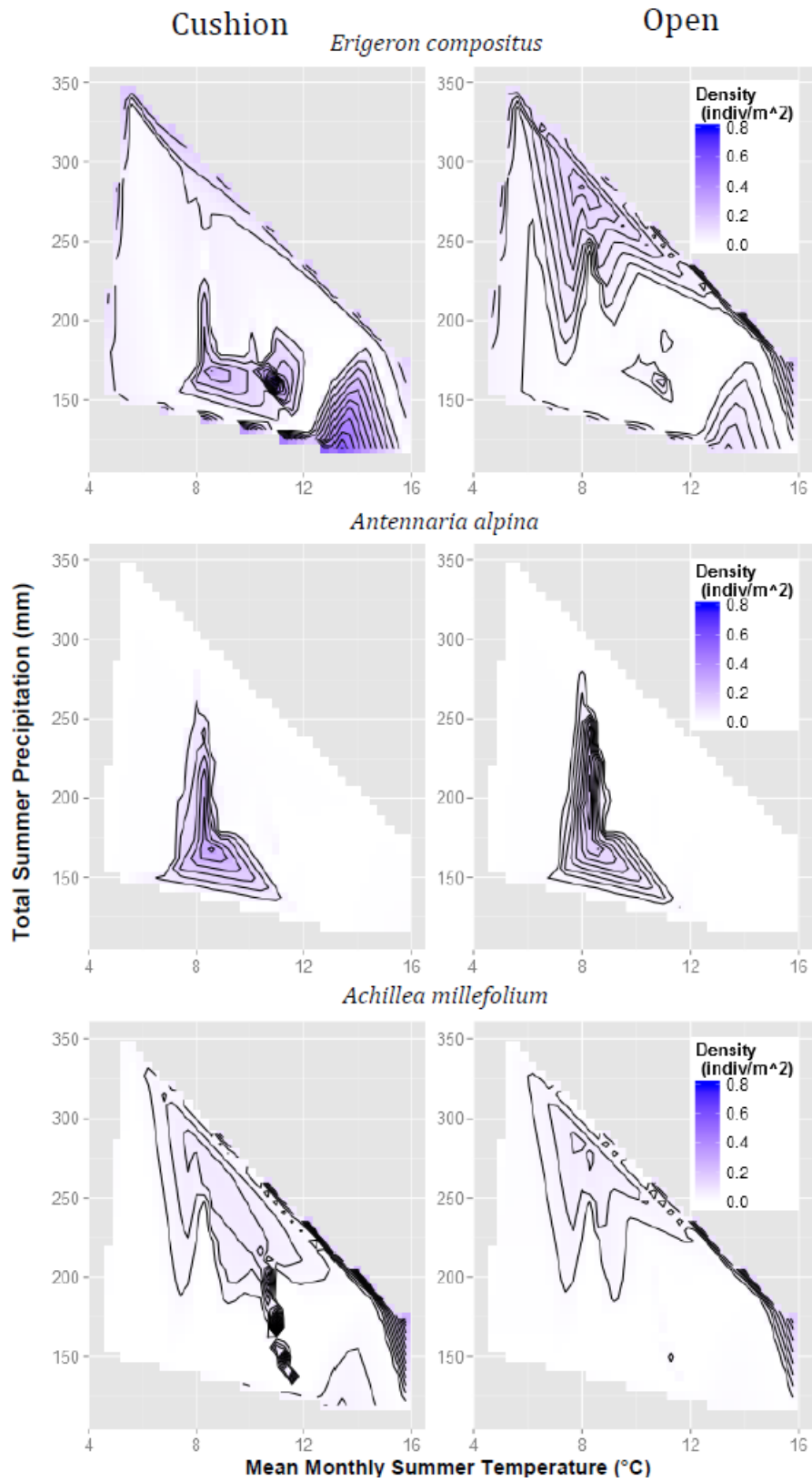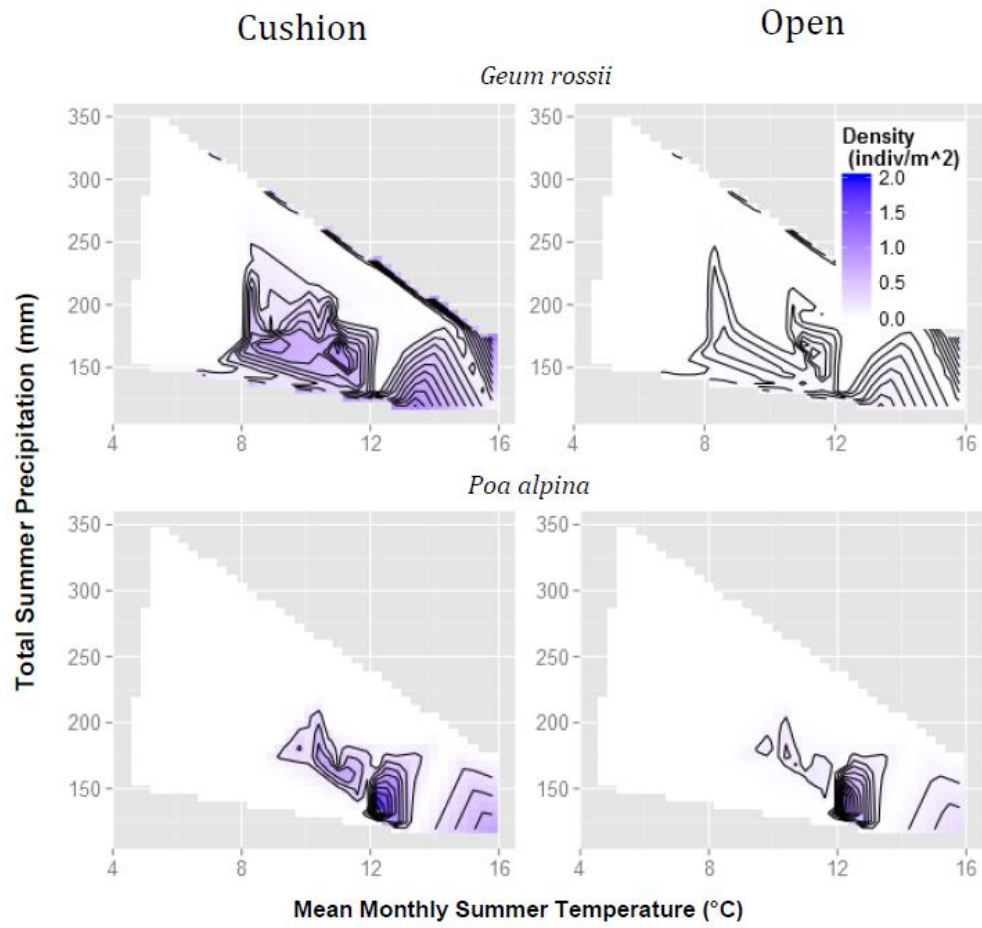
Figure 1.

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