

Interspecific facilitation mediates the outcome of intraspecific interactions across an elevational gradient

MORGAN J. RAATH-KRÜGER ^{1,2,5} CHRISTIAN SCHÖB ³ MELODIE A. MCGEOCH ⁴ AND PETER C. LE ROUX ¹

¹Department of Plant and Soil Sciences, University of Pretoria, Private Bag X20, Pretoria 0002 South Africa

²Department of Zoology, Centre for Ecological Genomics and Wildlife Conservation, University of Johannesburg, PO Box 524, Auckland Park 2006 South Africa

³Department of Environmental Systems Science, Swiss Federal Institute of Technology, ETH Zürich, Zürich 8092 Switzerland

⁴Department of Ecology, Environment and Evolution, School of Natural Sciences, La Trobe University, Bundoora, Victoria 3086 Australia

Citation: Raath-Krüger, M. J., C. Schöb, M. A. McGeoch, and P. C. le Roux. 2021. Inter-specific facilitation mediates the outcome of intra-specific interactions across an elevational gradient. *Ecology* 102(1): e03200. 10.1002/ecy.3200

Abstract. Where interspecific facilitation favors the establishment of high densities of a beneficiary species, strong intraspecific competition may subsequently impede beneficiary performance. Consequently, the negative influence of intraspecific competition between beneficiary individuals could potentially outweigh the positive influence of interspecific facilitation when, for example, higher densities of a beneficiary are negated by the negative effect of crowding on beneficiary reproduction. The aim of this study was, therefore, to examine the impact of an interspecific interaction on the outcome of intraspecific interactions within the context of plant–plant facilitation. We used the cushion-forming *Azorella selago* and a commonly co-occurring dominant perennial grass species, *Agrostis magellanica*, on sub-Antarctic Marion Island as a model system. We assessed the impact of an interspecific interaction (between *A. selago* and *A. magellanica*) on the outcome of intraspecific interactions (between *A. magellanica* individuals), by testing if the impact of *A. magellanica* density on *A. magellanica* performance is mediated by its interaction with *A. selago*. We observed evidence for competition among *A. magellanica* conspecifics, with a decreasing proportion of *A. magellanica* individuals being reproductive under higher conspecific density. This negative intraspecific effect was greater on *A. selago* than on the adjacent substrate, suggesting that the facilitative effect of *A. selago* changes the intensity of intraspecific interactions between *A. magellanica* individuals. However, experimentally reducing *A. magellanica* density did not affect the species' performance. We also observed that the effect of *A. selago* on *A. magellanica* was positive, and despite the negative effect of intraspecific density on the proportion of reproductive *A. magellanica* individuals, the net reproductive effort of *A. magellanica* (i.e., the density of reproductive individuals) was significantly greater on *A. selago* than on the adjacent substrate. These results highlight that, in abiotically severe environments, the positive effects of interspecific facilitation by a benefactor species may outweigh the negative effects of intraspecific competition among beneficiaries. More broadly, these results suggest that both positive inter- and intraspecific biotic interactions may be key to consider when examining spatial and temporal variation in species' performance.

Key words: abiotic severity; alpine; biotic interactions; facilitation; intraspecific density; plant communities; plant–plant interactions.

INTRODUCTION

Biotic interactions may strongly shape ecological communities by affecting plant fitness, abundance, cover, and survival (Cavieres et al. 2007, Kunstler et al. 2011, Schöb et al. 2013, Zhang and Wang 2016, Svanfeldt et al. 2017). The impact of these interactions can vary considerably with both extrinsic (e.g., environmental) and intrinsic (e.g., density dependent) factors (Olsen

et al. 2016, Svanfeldt et al. 2017, Kula et al. 2020, Zhang and Tielbörger 2020). For example, strong competition is generally expected between individuals of the same species because of greater niche overlap within species than between species (e.g., Adler et al. 2018). Therefore, if individuals of the same species are grown in high-density vs. low-density stands, individuals from the low-density stands may perform better than the individuals from high-density stands (e.g., Tilman and Cowan 1989, Kufel et al. 2018, Kula et al. 2020, but see in contrast, Leicht-Young et al. 2011, Svanfeldt et al. 2017). Thus, it is generally assumed that intraspecific interactions will have negative outcomes, with, for example, self-thinning

Manuscript received 18 June 2020; accepted 6 August 2020.
Corresponding Editor: Todd M. Palmer.

⁵E-mail: morganj.r@hotmail.com

reducing conspecific abundance. However, a switch from negative density dependence to positive density dependence (i.e., where survival and fecundity are enhanced at high densities) may be observed as environmental stress increases (see Goldenheim et al. 2008, Svanfeldt et al. 2017, Zhang and Tielbörger 2020). Indeed, facilitation can occur intraspecifically (Eränen and Kozlov 2008, Goldenheim et al. 2008, Fajardo and McIntire 2011, García-Cervigón et al. 2013, Zhang and Wang 2016, Svanfeldt et al. 2017), with, for example, individuals of the same plant species mitigating the impact of abiotic stress on one another (thereby benefitting each other) when growing in dense stands (e.g., Goldenheim et al. 2008, Zhang and Tielbörger 2019; see also Zhang and Tielbörger 2020). Although many studies have documented the impact of density-dependent effects on the survival and fecundity of individuals (e.g., Goldenheim et al. 2008, Dochtermann and Peacock 2013, Svanfeldt et al. 2017), few studies have documented density-dependent effects within the context of interspecific facilitation (but see, e.g., Tielbörger and Kadmon 2000, Zhang and Tielbörger 2020).

Interspecific facilitation is defined as an interaction where one species (i.e., a benefactor species) modifies the local microenvironment for another species (i.e., the beneficiary species) and either one or both of the species benefit from the interaction through enhanced growth, reproduction, and/or survival (Schöb et al. 2014). Where interspecific facilitation by a benefactor species increases beneficiary species' density, size and/or productivity (e.g., Tielbörger and Kadmon 2000, Maestre et al. 2004), it is possible that the negative influence of competition between beneficiary individuals could outweigh the positive influence of

interspecific facilitation (Tielbörger and Kadmon 2000, García-Cervigón et al. 2013, Schöb et al. 2013; see also Zhang and Tielbörger 2020). For example, if the facilitative effects of benefactor species change the composition of associated beneficiary species, this may have consequences for the interactions among the beneficiary species (e.g., Saccone et al. 2010, Zhang and Wang 2016, Llambí et al. 2018). The effects of interactions among beneficiaries appear to be mostly competitive, with negative impacts on plant growth and survival (Aguar and Sala 1994, Schöb et al. 2013). However, the outcome of these interactions can also be positive where beneficiaries facilitate one another. For example, beneficiary species can benefit from enhanced pollination by attracting shared pollinators (e.g., Molina-Montenegro et al. 2008), or from greater habitat amelioration at higher densities (e.g., Zhang and Tielbörger 2020). Therefore, facilitation among beneficiaries may be nested within facilitation by a benefactor in a facilitation cascade (Baumeister and Callaway 2006; see also Altieri et al. 2007 for the related concept of hierarchical organization through facilitation). Moreover, one species can facilitate other species through the competitive suppression of a third species (i.e., through indirect facilitation; Levine 1999, Llambí et al. 2018). For example, adult plants can also have a positive effect on conspecific seedlings through the reduction of herbaceous competitors (e.g., through intraspecific facilitation; see Saccone et al. 2010). Beneficiary survival and/or performance is therefore dependent on the effect of the benefactor species and the effect of interactions among beneficiary species (interspecific interactions) and/or conspecific individuals (intraspecific interactions) themselves.

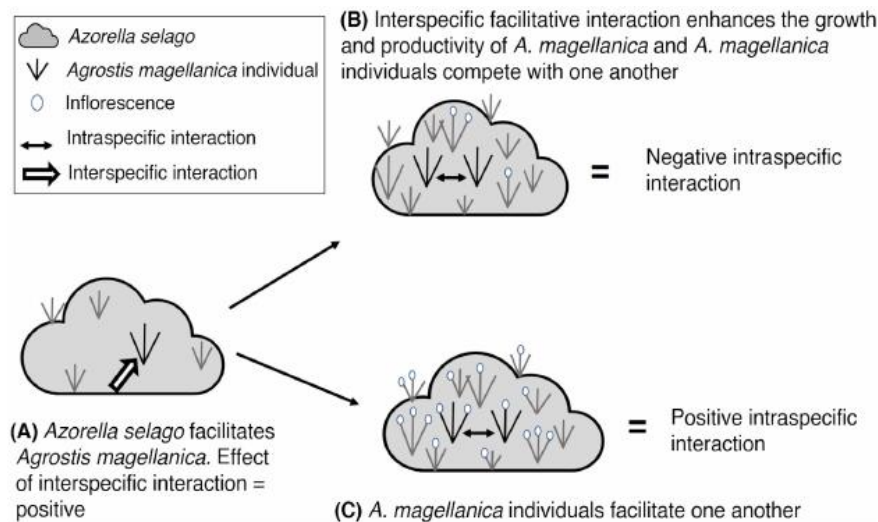


FIG. 1. Visual representation of the hypotheses considered in this study. (A, B) The facilitative effect of *Azorella selago* on *Agrostis magellanica* will result in competition among *A. magellanica* conspecifics, which will reduce *A. magellanica* reproductive performance (i.e., net reduction in fitness); or (A, C) the facilitative effect of *A. selago* on *A. magellanica* will indirectly result in increased intraspecific facilitation among *A. magellanica* conspecifics, improving *A. magellanica* reproductive performance. [Color figure can be viewed at wileyonlinelibrary.com]

When a benefactor facilitates beneficiaries (Fig. 1A; see also, e.g., Molenda et al. 2012, Schöb et al. 2013, Bonanomi et al. 2016, Hupp et al. 2017), the density of beneficiaries may be higher in the presence of a benefactor species, and consequently, beneficiaries may experience stronger intraspecific competition (Fig. 1B; Tielbörger and Kadmon 2000, García-Cervigón et al. 2013). Thus, by increasing the productivity and/or density of beneficiaries, interspecific interactions could potentially mediate the outcome of interactions among beneficiaries (see, e.g., Armas et al. 2008, García-Cervigón et al. 2013, Schöb et al. 2013, Llambi et al. 2018). For example, the positive effect that a benefactor has on the abundance of beneficiaries may be negated by the negative effect of high conspecific density on beneficiary reproduction. Thus, even if beneficiaries reach high densities as a result of facilitation by a benefactor, unless the beneficiaries are also able to reproduce, the net effect of the benefactor on the beneficiaries will not be positive. Alternatively, it is possible for interactions among beneficiaries to be facilitative (see, e.g., Goldenheim et al. 2008, Saccone et al. 2010), where, for example, beneficiary individuals could shield one another from strong winds (Zhang and Wang 2016) and/or low temperatures (Eränen and Kozlov 2008, Zhang and Wang 2016, Zhang and Tielbörger 2019), to a point where the positive effects of intraspecific facilitation outweigh the negative impacts of intraspecific competition (Fig. 1C; Fajardo and McIntire 2011, García-Cervigón et al. 2013). Moreover, facilitation by a benefactor could overwhelm the negative effects among beneficiaries, allowing beneficiaries a greater degree of coexistence (at the community level) and/or higher fitness (at the species level) than in the absence of the benefactor (Armas et al. 2008; see also, e.g., Feldman and Morris 2011). For example, when facilitation is absent, a stress-tolerant species may have a competitive advantage over another species (see Armas et al. 2008). However, where both species are facilitated by a benefactor, they may be more likely to coexist.

Here, we examine the impact of an interspecific interaction (Fig. 1A; between a benefactor and a beneficiary species) on the outcome of intraspecific interactions (Fig. 1B,C). We use *Azorella selago* (*Azorella* hereafter), a widespread cushion plant (i.e., compact, hemispherical plants that create favorable microhabitats by ameliorating abiotic disturbances and stresses), and a dominant perennial grass species, *Agrostis magellanica* (*Agrostis* hereafter) as a model system on sub-Antarctic Marion Island. Both experimental and observational approaches are used to assess the relationship between *Agrostis* density and *Agrostis* performance (i.e., intraspecific interactions), and how these interactions are modified by the interaction between *Azorella* and *Agrostis* (i.e., the interspecific interaction). We ask two broad questions: given that the outcome of the interspecific interaction between *Azorella* and *Agrostis* is typically positive (le Roux and McGeoch 2010, le Roux et al. 2013), (1) is higher

Agrostis density, due to the interaction with *Azorella*, correlated with poorer *Agrostis* performance?; and (2) will *Agrostis* performance increase if conspecific density is experimentally reduced? We hypothesize that the facilitative effect of *Azorella* on *Agrostis* (Fig. 1A) will increase the density of *Agrostis*, resulting in strong competition among *Agrostis* conspecifics. Consequently, *Agrostis* performance will be reduced (Fig. 1B), possibly even overwhelming the facilitative effect of *Azorella* on *Agrostis* (following, e.g., García-Cervigón et al. 2013). Additionally, we hypothesize that experimentally thinning *Agrostis* density will improve conspecific performance. Our alternative hypothesis is that interactions among *Agrostis* conspecifics on *Azorella* will be facilitative (e.g., Goldenheim et al. 2008, Saccone et al. 2010; or weak relative to the impact of the interspecific interaction), in which case, *Agrostis* performance may be improved by the interaction with *Azorella*, irrespective of the grass's density (Fig. 1C). Although interactions between beneficiaries that are a result of facilitation by benefactors are infrequently considered in empirical studies, they could have profound implications for communities (Schöb et al. 2013, Llambi et al. 2018).

METHODS

Study site and species

This study was conducted on sub-Antarctic Marion Island (46°54' S, 32°45' E; 290 km²), which is located in the southern Indian Ocean (Chown and Froneman 2008). Marion Island has a hyperoceanic climate, with low but very stable seasonal and daily temperatures, along with high precipitation and humidity, cloud cover on most days, and frequent strong winds (Smith and Steenkamp 1990, le Roux 2008). Altitude represents an important stress gradient on the island, as temperature and substrate stability decrease with elevation and wind speed increases (K. Goddard et al. *unpublished data*; Boelhouwers et al. 2003, le Roux and McGeoch 2010).

The island supports 22 indigenous vascular plant species and approximately 200 bryophyte and lichen species (Greve et al. 2019). Here, we examine the interaction between the two most widespread vascular plants on Marion Island, *Azorella selago* Hook. (Apiaceae) and *Agrostis magellanica* (Lam.) Vahl. (Poaceae). *Azorella selago* is a cushion plant species occurring on multiple sub-Antarctic islands and in many habitat types on those islands. Because of its cushion growth form, *Azorella* ameliorates stressful environmental conditions (see McGeoch et al. 2008, Nyakatya and McGeoch 2008), particularly in the cold, wind-exposed areas where the species is commonly found. Consequently, *Azorella* hosts an array of species, including invertebrates and other plant species (Huntley 1971, Huntley 1972, Barendse et al. 2002, Hugo et al. 2004), which makes the plant an important ecosystem engineer and keystone species (Hugo et al. 2004). Indeed, cushion plants elsewhere

have also been shown to impact other plant species positively (Badano and Cavieres 2006, Cavieres et al. 2007, Hupp et al. 2017, Yang et al. 2017).

Agrostis magellanica is a dominant perennial grass species on Marion Island and is the most common vascular plant species growing on *Azorella* (Huntley 1971). *Agrostis magellanica* is found in most habitats on Marion Island, occurring up to 600 m above sea level (a.s.l.; le Roux and McGeoch 2008). The *Azorella* (benefactor)–*Agrostis* (beneficiary) interaction on Marion Island is positive (except at the lowest altitudes), where *Azorella* presence has been shown to alter *Agrostis* population structure and increase *Agrostis* reproductive output, biomass, and abundance compared to surrounding areas where *Azorella* is absent (le Roux and McGeoch 2010, le Roux et al. 2013). *Agrostis* is the dominant plant growing on *Azorella* (mean cover \pm SE = $18.5 \pm 1.3\%$; this study), with all other vascular plants combined ($3.2 \pm 0.5\%$) and all bryophytes combined ($5.3 \pm 0.9\%$) having much lower cover on *Azorella*. On the adjacent substrate type, bryophytes, and mosses (mean cover \pm SE = $16.2 \pm 1.6\%$) and other vascular plants (excluding *Agrostis*; $13.0 \pm 2.2\%$) are more dominant, with cover of *Agrostis* ($8.6 \pm 0.8\%$) being lower than on *Azorella*.

Data collection

Observational study.—*Azorella* cushions and adjacent soil substrate were sampled using a paired approach at 20-m elevational intervals along six altitudinal transects (altitudes between 18 m a.s.l. and 650 m a.s.l.; data from two transects from le Roux and McGeoch 2010). A wire ring was molded around the outer edge of each sampled cushion plant to reproduce the size and shape of the plant. The wire ring was then placed 0.1 m in a random direction from the cushion to sample *Agrostis* from the adjacent substrate (following the methods of le Roux and McGeoch 2010). Another random direction was chosen if this area overlapped with, or was within 0.1 m of, another *Azorella* cushion. Cushion plant surface area was calculated from each cushion plant's maximum diameter and diameter perpendicular to its maximum diameter.

Agrostis abundance and cover (as a percentage of the sample area) were recorded. The percentage cover of other vascular plant species, bryophytes, and mosses on each *Azorella* cushion plant and on the adjacent substrate sample areas were also recorded. Additionally, the percentage rock cover on each cushion and adjacent substrate was also recorded. All *Agrostis* individuals were harvested and dried at 60°C for 48 h. For each *Agrostis* individual, size (i.e., maximum length of the longest leaf and basal diameter), biomass, and reproductive effort (i.e., the number of reproductive individuals) were recorded.

Experimental study.—For the experimental component of this study, three sites dominated by *Azorella* and

Agrostis were sampled on the eastern side of the island (at altitudes of 65–145 m a.s.l.; separated by 0.4–1.2 km). Three substrate types (i.e., cushion plant center, cushion plant edge, and soil) were sampled using 10 × 20 cm sampling quadrats (Appendix S1: Fig. S1). Data were collected separately from both the edges and the centers of cushion plants because there can be pronounced variation in facilitation within cushion plants (i.e., at the intraindividual level; see Anthelme et al. 2017). Data from cushion centers and cushion edges were collected from different cushion plant individuals, which were separated by ≥ 0.5 m. For the cushion plant edges, the sampling quadrat was placed to cover the cushion's edge and surrounding soil (representing the area immediately affected by the cushion plant) approximately equally. For all substrate types, the percentage rock cover within the plot was visually estimated, and the percentage cover of other vascular plant species and bryophytes recorded. Cushion plant size was recorded by measuring the height of the cushion plant, maximum diameter, and the diameter perpendicular to maximum diameter.

Prior to the implementation of the experimental treatment, *Agrostis* abundance was recorded within all sampling quadrats. *Agrostis* abundance was on average higher at the centers of *Azorella* (mean \pm SE = 33.02 ± 1.9) and on the edges of *Azorella* (30.2 ± 1.4) than on the adjacent substrate (14.1 ± 0.7). Then, for each substrate type, samples were split by *Agrostis* density: high density (i.e., the plots with the highest two-thirds of *Agrostis* abundance values) and low density (i.e., the plots with the lowest third of *Agrostis* abundance; Appendix S1: Table S1). Half of the high-density plots were randomly assigned to a thinned density *Agrostis* treatment (Appendix S1: Table S2), where *Agrostis* abundance was reduced to the average *Agrostis* abundance of the low-density treatment plots of that site and substrate type (Appendix S1: Table S1).

Up to three *Agrostis* individuals (termed “focal individuals” hereafter) per sampling quadrat were then randomly selected and monitored for a whole growing season (June 2016–March 2017) to determine their survival, growth, and reproductive effort. At the start of the growing season (September 2016) the maximum leaf height and number of inflorescences were recorded for each focal individual. All inflorescences were initially removed from these individuals to ensure that all new inflorescences could be identified (additionally, *A. magellanica* does not appear to preform flower buds). At the end of the 10-month period, the same measurements were repeated. All *Agrostis* individuals were harvested, dried at 60°C for 48 h, and weighed (obtaining shoot biomass). Only 4 focal individuals died during the monitoring period, and only 10 focal individuals produced inflorescences during the monitoring period. Therefore, analyses of survival and reproduction were not conducted.

Data analysis

Observational study.—A generalized linear mixed effects model (GLMM) was used to model the proportion of reproductive *Agrostis* individuals as a function of whether grasses were located on a cushion plant or the adjacent substrate (i.e., the interspecific interaction of interest), *Agrostis* density (the intraspecific interaction of interest; continuous density data), and altitude (m a.s.l.; a proxy for environmental severity), and the three pairwise interactions between these variables, because these predictors may mediate each other's effects on *Agrostis* performance. The combined cover of other vascular plants and mosses was included into these models to account for the effect of the other, subordinate species. To account for the spatial structure of the data, a random effect of “pair” (representing each pair of cushion and adjacent substrate samples) nested within “transect” (representing the different transects along which samples were collected) was included in all models. Therefore, data were analyzed using the following model:

$$\begin{aligned} \text{Proportion of reproductive } Agrostis \text{ individuals} &\sim \text{Altitude} + \text{Location} \\ &+ Agrostis \text{ density} + \text{cover of other plants} + (\text{Altitude} \times \text{Location}) \\ &+ (\text{Altitude} \times Agrostis \text{ density}) + (\text{Location} \times Agrostis \text{ density}) \\ &+ (1 | \text{Transect/Pair}). \end{aligned} \quad (1)$$

To determine the effect of these predictor variables on the net reproductive effort of *Agrostis*, a second, complementary GLMM was run using the number of reproductive *Agrostis* individuals as a response variable. In this model, the proportion of the sampled area covered by rock was additionally accounted for by including (1 – rock cover; i.e., sample area available for *Agrostis*) as an offset variable, because large rocks reduce the potentially suitable area for *Agrostis* to grow. The proportion and number of reproductive *Agrostis* individuals were used as the response variables instead of measures of *Agrostis* growth because reproduction is a more direct measure of fitness.

The first model (Eq. 1) was fitted using a binomial distribution and the logit-link function. When analyzing the number of reproductive *Agrostis* individuals as a response variable (i.e., in the second model), count data for number of reproductive individuals were zero-inflated but not overdispersed. Therefore, the second model was run as a generalized linear mixed effects hurdle model using a truncated negative binomial distribution with a log-link function. Hurdle models involve two separate analyses (Rose et al. 2006); one analysis assesses the positive (count) data with a linear model (conditional model), whereas the other compares samples with reproductive individuals to samples lacking reproductive individuals with a binary model (zero-inflation model).

Both models were implemented using the glmmTMB package (Brooks et al. 2017) in R version 4.0.2 (R Core Team 2018).

Experimental study.—Generalized linear mixed effects models (GLMMs) were used to test for differences in *Agrostis* performance measures (i.e., shoot mass, maximum leaf height, and basal diameter) taken at the end of the monitoring period in 2017 as a function of density treatments (representing the intraspecific interaction; categorical density data), whether grasses were located on the ‘cushion’ or ‘soil’ substrate types (representing the interspecific interaction of interest), the pairwise interaction between these two variables, and the corresponding initial *Agrostis* performance measure taken at the start of the experiment in 2016. Because up to three grass individuals were collected from each individual plot per site, plot identity nested within site was included into each model as a random effect. These models were built using the glmmTMB package in R, using a Gaussian distribution.

RESULTS

Observational study

A total of 12,109 *Agrostis* individuals were sampled from 125 pairs of cushion and soil plots along six altitudinal transects. The proportion of reproductive *Agrostis* individuals was significantly greater on *Azorella* (mean \pm SE = 0.25 ± 0.02) than on the adjacent substrate (mean \pm SE = 0.11 ± 0.02 ; Table 1). However, the proportion of reproductive *Agrostis* individuals was significantly negatively related to conspecific density, with this decrease in *Agrostis* performance with conspecific density being greater on *Azorella* than on the adjacent substrate, suggesting that the facilitative effect of the *Azorella* changes the intensity of intraspecific interactions between *Agrostis* individuals (Fig. 2).

The total reproductive effort of *Agrostis* (i.e., the density of reproductive *Agrostis* individuals per sample) was significantly greater on *Azorella* (mean \pm SE = 6.4 ± 0.6) than in the adjacent substrate plots (mean \pm SE = 1.3 ± 0.2 ; Appendix S1: Table S3, conditional model). The number of reproductive *Agrostis* individuals was also significantly positively related to conspecific density, with this increase in *Agrostis* performance with conspecific density being significantly greater on *Azorella* than on the adjacent substrate (Fig. 3).

TABLE 1. The proportion of reproductive *Agrostis magellanica* individuals (from observational data, $n = 250$ samples) in relation to fixed and random effects (model $P < 0.001$).

Fixed effects	Level	Estimate	SE	z	P
(Intercept)	–	–2.113	0.292	–7.250	<0.001
Altitude	–	0.003	0.001	3.830	<0.001
Location (Soil)	C > S	–1.008	0.351	–2.871	0.004
<i>Agrostis</i> density	–	–0.079	0.022	–3.558	<0.001
Cover of other plants	–	0.008	0.004	2.283	0.022
Altitude *	–	–0.002	0.001	–1.645	0.100
Location (Soil) *	–	0.000	0.000	–0.342	0.733
Altitude * <i>Agrostis</i> density	–	–0.021	0.043	–0.479	0.632
Location (Soil) * <i>Agrostis</i> density	–				
Random effect		Variance	SD		
Pair:Transect		0.3947	0.6282		
Transect		0.24	0.4899		

Note: C = cushion, S = soil. Asterisks indicate interactions. $P \leq 0.05$ indicated in bold.

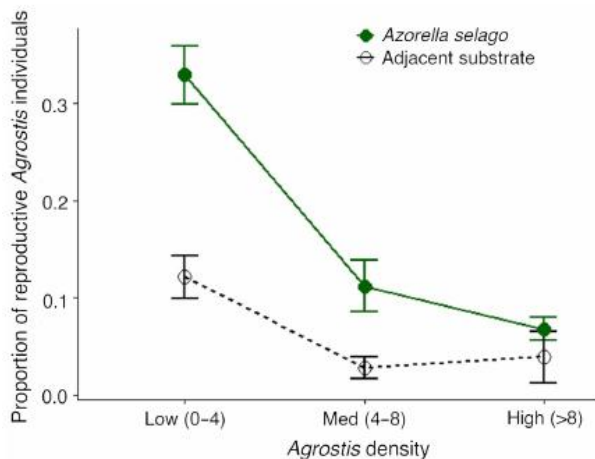


FIG. 2. Mean (\pm SE) proportion of reproductive *Agrostis magellanica* individuals in the observational study at low (0–4 individuals/cm²), medium (4–8 individuals/cm²), and high (>8 individuals/cm²) conspecific categorical densities on and away from *Azorella selago*. *Agrostis magellanica* density is represented here categorically for clarity, but in the associated statistical analyses was analyzed as a continuous variable. [Color figure can be viewed at wileyonlinelibrary.com]

The proportion of reproductive *Agrostis* individuals also increased significantly with altitude, and the effect of altitude on *Agrostis* performance was independent of *Agrostis* density (i.e., the intraspecific interaction; Table 1). The proportion of reproductive *Agrostis* individuals was, however, consistently higher at low conspecific densities compared to medium and high conspecific densities across the altitudinal range (Fig. 4).

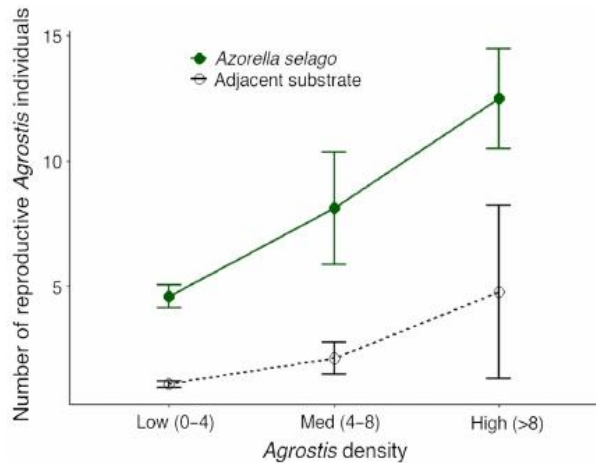


FIG. 3. Mean (\pm SE) number of reproductive *Agrostis magellanica* individuals in the observational study at low (0–4 individuals/cm²), medium (4–8 individuals/cm²), and high (>8 individuals/cm²) conspecific densities on and away from *Azorella selago*. [Color figure can be viewed at wileyonlinelibrary.com]

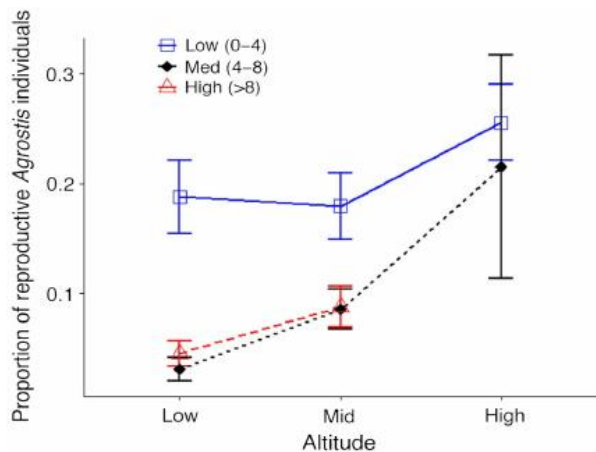


FIG. 4. Mean (\pm SE) proportion of reproductive *Agrostis magellanica* individuals in the observational study at low (0–4 individuals/cm²), medium (4–8 individuals/cm²), and high (>8 individuals/cm²) conspecific densities across the altitudinal range: low (18–160 m above sea level [a.s.l.]), medium (161–302 m a.s.l.), and high (307–535 m a.s.l.) altitudes. There were no reproductive *A. magellanica* individuals at high altitudes when *A. magellanica* density exceeded eight individuals per unit area. [Color figure can be viewed at wileyonlinelibrary.com]

Similarly, the effect of *Azorella* on the proportion of reproductive *Agrostis* individuals (i.e., the interspecific interaction) did not vary significantly across the altitudinal range (Table 1). However, the proportion of reproductive *Agrostis* individuals was greater on *Azorella* than on the adjacent substrate, with the highest proportion of reproductive *Agrostis* individuals occurring on *Azorella* at high altitudes (Fig. 5).

Experimental study.—In the experiment, a total of 520 *Agrostis* individuals were monitored for a growing

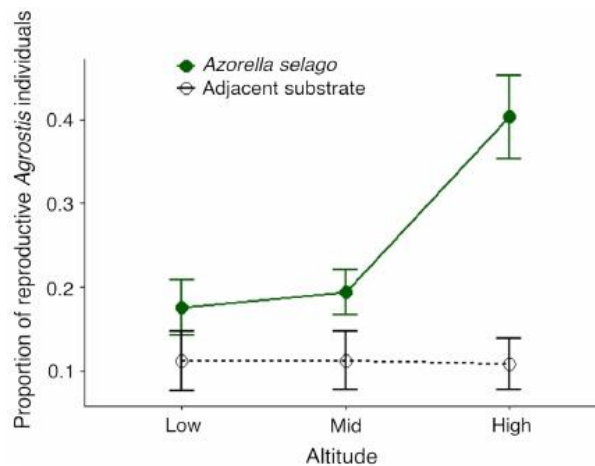


FIG. 5. Mean (\pm SE) proportion of reproductive *Agrostis magellanica* individuals in the observational study growing on *Azorella selago* cushion plants vs. on the adjacent substrate across an altitudinal gradient (low altitude: ≤ 160 m a.s.l., mid: 161–302 m a.s.l., high: > 307 m a.s.l.). [Color figure can be viewed at wileyonlinelibrary.com]

season. Experimentally reducing *Agrostis* density had no significant effect on *Agrostis* shoot mass, and the effect of *Agrostis* density on conspecific performance was not dependent on whether the grass was growing on vs away from *Azorella* (Table 2). *Agrostis* individuals growing on the edge of *Azorella* plants were significantly heavier than *Agrostis* individuals in the center of *Azorella* and on the adjacent substrate (Table 2; Fig. 6), and *Agrostis* shoot mass was greatest on the edges of *Azorella* at low conspecific densities (mean \pm SE = 0.23 ± 0.04) than any other density treatment per substrate type (Appendix S1: Table S4). The other two *Agrostis* characteristics examined, maximum leaf height and basal diameter, were both not significantly related to either intra- or interspecific interactions (Appendix S1: Tables S5, S6).

DISCUSSION

Where facilitation by a benefactor increases beneficiary species density (e.g., Tielbörger and Kadmon 2000), beneficiary species may experience strong

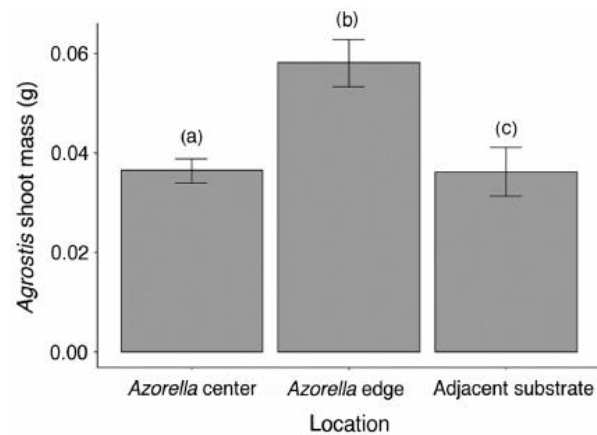


FIG. 6. Mean (\pm SE) total *Agrostis magellanica* shoot mass growing in the center of *Azorella selago* cushion plants, on the edges of cushion plants, and in the adjacent bare soil substrate in the experimental study.

competition, and because of crowding (i.e., negative density dependence) reproduction of the beneficiary species may be inhibited (e.g., as individuals may not be able to reach reproductive size; Tielbörger and Kadmon 2000, García-Cervigón et al. 2013, Schöb et al. 2013). Here, we tested this idea by examining the impact of *Agrostis* density on conspecific performance within the context of interspecific facilitation. Our results provide evidence for intraspecific competition because the proportion of reproductive *Agrostis* individuals was significantly lower at higher conspecific densities. However, in contrast to the results from the observational component of this research, experimentally thinning *Agrostis* density did not have an effect on conspecific performance.

The first key finding from this study is that, when examining the impact of *Agrostis* density on *Agrostis* performance (i.e., the impact of intraspecific interactions), we observed evidence for intraspecific competition among *Agrostis* conspecifics. Although some studies have demonstrated positive density-dependent effects (especially under stressful conditions, where low plant densities may be insufficient for habitat amelioration; e.g., Goldenheim et al. 2008, Zhang and Tielbörger

TABLE 2. *Agrostis magellanica* shoot mass at the end of the monitoring period (from experimental study, $n = 519$ samples) in relation to fixed and random effects (model $P < 0.001$; treatment = high density vs. low density vs. thinned density).

Fixed effects	Level	Estimate	SE	z	P
(Intercept)	–	–0.020	0.007	–2.854	0.004
Treatment	L = T = H	0.006	0.009	0.712	0.477
Location	E > C = S < E	0.007	0.009	0.794	0.06
Initial size	–	0.002	0.000	14.008	<0.01
Treatment:Location	–	0.016	0.012	1.302	0.08
Random effect		Variance	SD		
Plot identity: Site		<0.001	<0.001		
Site		<0.001	<0.001		

Note: L = low density, T = thinned density, H = high density, C = cushion, S = soil, and E = cushion edge. $P \leq 0.05$ indicated in bold.

2020), our results align with the more common pattern of negative interactions (i.e., negative density-dependent effects) among beneficiaries (Aguilar and Sala 1994, Maestre et al. 2004, Armas et al. 2008, Schöb et al. 2013) and can be explained by, at least in part, competition for space and/or resources supplied by benefactors (see, e.g., Armas et al. 2008, Schöb et al. 2013). Therefore, increased density and/or productivity of beneficiaries as a result of facilitation by a benefactor can cause a reduction in beneficiary reproductive output (Aguilar and Sala 1994, García-Cervigón et al. 2013, Schöb et al. 2013).

More interestingly, our results suggest that competition among beneficiaries may be strongly linked to (i.e., mediated by) the interaction with a benefactor (see, e.g., Schöb et al. 2013), as our observational data suggest that the facilitative effect of *Azorella* changes the intensity of intraspecific interactions between *Agrostis* individuals because the decrease in *Agrostis* performance with conspecific density was greater on *Azorella* than on the adjacent substrate. Therefore, facilitative interactions between species may alter the frequency and intensity of interactions among beneficiaries. We only consider a single benefactor species here, but the magnitude (or even the nature) of the impact of a benefactor on intraspecific beneficiary interactions may potentially vary depending on the strength of the facilitative interaction. For example, if one benefactor species (or benefactor individual) is able to modify limiting factors more positively than another (Hupp et al. 2017, Schöb et al. 2017, Yang et al. 2017), the former may result in a greater positive change in the composition, abundance, and performance of beneficiaries, which in turn may more negatively influence the outcome of interactions among beneficiaries.

Our second key finding is that, for both the experimental and observational components, the number of reproductive *Agrostis* individuals was on average higher on *Azorella* cushion plants than on the adjacent substrate, across the entire altitudinal range. Therefore, in agreement with previous findings, the interspecific *Azorella*–*Agrostis* interaction positively affected *Agrostis* performance (le Roux and McGeoch 2010, le Roux et al. 2013). These results also mirror the generally positive impact of vascular plants in abiotically severe environments from other studies, including the observed nurse effects of other cushion plant species in the same family as *Azorella*, that is, *Laretia* and *Bolax* spp. (Molina-Montenegro et al. 2000, Badano and Cavieres 2006, Bonanomi et al. 2016, Hupp et al. 2017, Yang et al. 2017). Specifically, the strongest positive effect on *Agrostis* performance was observed on the edges of cushion plants. This is in agreement with Anthelme et al. (2017), who showed that facilitation by the congeneric cushion plant, *Azorella compacta*, was higher at the periphery of the cushion plant than at the centers of the cushion plants (see also the Pescador et al. 2014 “facilitation in the halo” concept).

Our third key finding is that despite the negative effect of intraspecific density on the proportion of reproductive *Agrostis* individuals, the total reproductive effort of *Agrostis* (i.e., the density of reproductive individuals per sample) was significantly greater on *Azorella* than on the adjacent substrate. Therefore, even though high intraspecific *Agrostis* densities due to interspecific facilitation result in a lower proportion of individuals being reproductive, the total reproductive effort of *Agrostis* is still greater when *Agrostis* is facilitated by *Azorella*. This significant positive effect of *Azorella* on the density of reproductive *Agrostis* individuals may be driven by two mechanisms. First, these results may reflect both *Agrostis* abundance and net reproduction responding to an unmeasured variable. For example, *Agrostis* density and total inflorescence production may both be positively related to *Azorella* compactness, because compact cushion plants are typically associated with higher soil nutrient contents, more effective heat trapping, and greater stability than more lax cushion plants (Schöb et al. 2017, Yang et al. 2017). However, in this study system there are no a priori data to suggest that density and fecundity are responding in the same way to an unmeasured variable. Second, our results may reflect that the negative influence of intraspecific *Agrostis* density on the proportion of reproductive individuals is outweighed by the positive effect of interspecific facilitation by *Azorella* on the total reproductive effort of *Agrostis*. This explanation is in line with, for example, Armas et al. (2008), who found that although two beneficiary species competed for resources, the effect of facilitation by a benefactor exceeded competition among the beneficiary species, allowing the beneficiaries to coexist. This effect (i.e., of interspecific facilitation having a greater influence than intraspecific competition) may be greater as abiotic stress increases (i.e., along altitudinal gradients; see also, e.g., García-Cervigón et al. 2013). Therefore, our results suggest that the positive effects of interspecific facilitation (which increases total plant abundance/density) may outweigh the negative effects of intraspecific competition (which decrease the average performance of individual plants).

Our last finding is that the proportion of reproductive *Agrostis* individuals increased significantly with altitude, with a trend for a greater proportion of reproductive *Agrostis* individuals on *Azorella* at higher altitudes than on the adjacent substrate. Indeed, *Azorella* is known to facilitate *Agrostis* increasingly strongly along gradients of abiotic severity (i.e., in line with the stress gradient hypothesis: Bertness and Callaway 1994, le Roux and McGeoch 2010, He et al. 2013). Therefore, the significant increase in *Agrostis* performance with altitude may be reflective of an increase in the frequency and intensity of interspecific facilitation by *Azorella* along the altitudinal stress gradient. Alternatively, this result might just reflect that as a result of fewer *Agrostis* individuals at higher altitudes, the grasses experience less intraspecific

competition, resulting in more *Agrostis* individuals reaching reproductive size. Irrespective of the mechanism driving this pattern, our results show that benefactor–beneficiary systems are controlled by both the effect of benefactors on beneficiaries and by environmental conditions.

In this study we see that some of our key findings were not supported by the mensuration component of the study; for example, although we see that the impact of *Azorella* on *Agrostis* is positive, experimentally reducing *Agrostis* density had no significant effect on *Agrostis* performance, suggesting neither facilitation nor competition within species. This difference between the experimental and observational study may be due to the monitoring only being conducted for one season after the experimental reduction of *Agrostis* density, potentially reflecting that the species may respond slowly to changes in this biotic interaction or preallocate some resources in the previous season. Contradictions between experimental and observational approaches have been documented from other studies, with, for example, Metz and Tielbörger (2016) observing contradictory findings in the outcome of plant–plant interactions between spatial, temporal, and experimental approaches (see also Dormann and Brooker 2002). Despite our contradictory results, our findings still suggest that it is important to consider both intra- and interspecific interactions when examining plant–plant interactions in relation to abiotic stress (e.g., García-Cervigón et al. 2013).

More broadly, this study reveals four issues that could be considered to improve our understanding of the impact of interspecific interactions on the outcome of intraspecific interactions within the context of facilitation. First, the nature of the gradient being examined may be important (as suggested by Maestre et al. 2009, albeit in a different perspective). Specifically, we hypothesize that intraspecific competition between plants will more likely outweigh the effects interspecific facilitation along resource gradients, as opposed to along nonresource gradients (e.g., as in this study). Second, the outcome of biotic interactions could vary with individuals' ontogenetic stages (Eränen and Kozlov 2008, le Roux et al. 2013, Zhang and Tielbörger 2020). We hypothesize that as *Agrostis* individuals grow, the effects of intraspecific interactions are likely to become more negative, to the point where the effects of intraspecific competition surpass the positive effect of interspecific facilitation with decreasing space or resources. Third, the strength and/or outcome of interspecific facilitation might be related to the outcome of the intraspecific interaction. For example, different cushion plant species vary in their impact on associated beneficiary species (e.g., Hupp et al. 2017), and therefore, intraspecific competition may be greater on cushion plants that have stronger facilitative effects. Fourth, although this study focuses on intraspecific interactions, we expect the observed results to be general to plant species that grow

on cushion plants, especially in abiotically severe environments, with interspecific interactions between beneficiaries also potentially being negative (see, e.g., Llambi et al. 2018).

More generally, our results suggest that both inter- and intraspecific biotic interactions may be crucial for the performance and survival of plant species in extreme environments. Within the context of facilitation, the overall performance and abundance of beneficiary species may be dependent on the combined effects of the benefactor species on the beneficiaries, the indirect interactions among beneficiaries themselves, and the interaction of the benefactor and beneficiaries with their environment (e.g., Schöb et al. 2013, Llambi et al. 2018). Indeed, although other recent research (e.g., García-Cervigón et al. 2013, Zhang and Tielbörger 2020) has highlighted the importance of intraspecific interactions, this study emphasizes that there are several mechanisms that could drive the outcome of intraspecific interactions, and both inter- and intraspecific interactions could be important to consider when understanding variation in species' performance and community processes.

ACKNOWLEDGMENTS

The authors would like to thank the South African National Antarctic Program (SANAP; unique grant 110726), the National Research Foundation (NRF Scarce Skills Doctoral Scholarship, grant SFH150727131155), and the Swiss National Science Foundation (PPOOP3_170645) for funding. A special thanks to those who assisted with fieldwork, including Elana Mostert and Nothando Mhlongo. PEIMC1/2013 was issued by the Prince Edward Islands Management Committee. MJRK and PCLR designed the study with input from MAM and CS. MJRK collected the data, with additional data provided by PCLR and MAM. MJRK ran the analyses (with input from PCLR and CS), and MJRK and PCLR wrote the manuscript with input from CS and MAM.

LITERATURE CITED

- Adler, P. B., D. Smull, K. H. Beard, R. T. Choi, T. Furniss, A. Kulmatiski, J. M. Meiners, A. T. Tredennick, and K. E. Veblen. 2018. Competition and coexistence in plant communities: intraspecific competition is greater than interspecific competition. *Ecology Letters* 21:1319–1329.
- Aguiar, M. R., and O. E. Sala. 1994. Competition, facilitation, seed distribution and the origin of patches in a Patagonian steppe. *Oikos* 70:26–34.
- Altieri, A. H., B. R. Silliman, and M. D. Bertness. 2007. Hierarchical organization via a facilitation cascade in intertidal cordgrass bed communities. *American Naturalist* 169:195–206.
- Anthelme, F., R. I. Meneses, N. N. H. Valero, P. Pozo, and O. Dangles. 2017. Fine nurse variations explain discrepancies in the stress–interaction relationship in alpine regions. *Oikos* 126:1173–1183.
- Armas, C., F. I. Pugnaire, and O. E. Sala. 2008. Patch structure dynamics and mechanisms of cyclical succession in the Patagonian steppe (Argentina). *Journal of Arid Environments* 72:1552–1561.
- Badano, E. I., and L. A. Cavieres. 2006. Impacts of ecosystem engineers on community attributes: effects of cushion plants

- at different elevations of the Chilean Andes. *Diversity and Distributions* 12:388–396.
- Barendse, J., R. D. Mercer, D. J. Marshall, and S. L. Chown. 2002. Habitat specificity of mites on sub-Antarctic Marion Island. *Environmental Entomology* 31:612–625.
- Baumeister, D., and R. Callaway. 2006. Facilitation by *Pinus flexilis* during succession: A hierarchy of mechanisms benefits other plant species. *Ecology* 87:1816–1830.
- Bertness, M. D., and R. Callaway. 1994. Positive interactions in communities. *Trends in Ecology and Evolution* 9:191–193.
- Boelhouwers, J., S. Holness, and P. Sumner. 2003. The maritime sub-Antarctic: a distinct periglacial environment. *Geomorphology* 52:39–55.
- Bonomi, G., A. Stinca, G. B. Chirico, G. Ciaschetti, A. Saracino, and G. Incerti. 2016. Cushion plant morphology controls biogenic capability and facilitation effects of *Silene acaulis* along an elevation gradient. *Functional Ecology* 30:1216–1226.
- Brooks, M. E., K. Kristensen, K. J. van Benthem, A. Magnusson, C. W. Berg, A. Nielsen, H. J. Skaug, M. Machler, and B. J. Bolker. 2017. glmmTMB balances speed and flexibility among packages for zero-inflated generalized linear mixed modeling. *R Journal* 9:378–400.
- Cavieres, L. A., E. I. Badano, A. Sierra-Almeida, and A. Molina-Montenegro. 2007. Microclimatic modifications of cushion plants and their consequences for seedling survival of native and non-native herbaceous species in the high Andes of central Chile. *Arctic, Antarctic, and Alpine Research* 39:229–236.
- Chown, S. L., and P. W. Froneman. 2008. The Prince Edward Islands in a global context. Pages 1–15 in S. L. Chown and P. W. Froneman, editors. *The Prince Edward Islands: land-sea interactions in a changing ecosystem*. African SunMedia, Stellenbosch, South Africa.
- Dochtermann, N. A., and M. M. Peacock. 2013. Inter- and intra-specific patterns of density dependence and population size variability in Salmoniformes. *Oecologia* 171:153–162.
- Dormann, C. F., and R. W. Brooker. 2002. Facilitation and competition in the high Arctic: the importance of the experimental approach. *Acta Oecologia* 23:297–301.
- Eränen, J. K., and M. V. Kozlov. 2008. Increasing intraspecific facilitation in exposed environments: consistent results from mountain birch populations in two subarctic stress gradients. *Oikos* 117:1569–1577.
- Fajardo, A., and E. J. B. McIntire. 2011. Under strong niche overlap conspecifics do not compete but help each other to survive: facilitation at the intraspecific level. *Journal of Ecology* 99:642–650.
- Feldman, T. S., and W. F. Morris. 2011. Higher survival at low density counteracts lower fecundity to obviate Allee effects in a perennial plant. *Journal of Ecology* 99:1162–1170.
- García-Cervigón, A. I., A. Gazol, V. Sanz, J. J. Camarero, and J. M. Olano. 2013. Intraspecific competition replaces interspecific facilitation as abiotic stress decreases: The shifting nature of plant-plant interactions. *Perspectives in Plant Ecology, Evolution and Systematics* 15:226–236.
- Goldenheim, W. M., A. D. Irving, and M. D. Bertness. 2008. Switching from negative to positive density-dependence among populations of a cobble beach plant. *Oecologia* 158:473–483.
- Greve, M., C. E. O. von der Meden, and C. Janion-Scheepers. 2019. Biological invasions in South Africa's offshore sub-Antarctic territories. Pages 207–227 in B. W. van Wilgen, G. J. Measey, D. M. Richardson, J. R. Wilson, and T. Zengeya, editors. *Biological invasions in South Africa*. Springer, Berlin, Germany.
- He, Q., M. D. Bertness, and A. H. Altieri. 2013. Global shifts towards positive species interactions with increasing environmental stress. *Ecology Letters* 16:695–706.
- Hugo, E. A., M. A. McGeoch, D. J. Marshall, and S. L. Chown. 2004. Fine scale variation in microarthropod communities inhabiting the keystone species *Azorella selago* on Marion Island. *Polar Biology* 27:466–473.
- Huntley, B. J. 1971. Vegetation. Pages 98–160 in E. M. van Zinderen Bakker, J. M. Winterbottom, and R. A. Dyer, editors. *Marion and Prince Edward Islands: report on the South African biological and geological expeditions, 1965–1966*. A.A. Balkema, Cape Town, South Africa.
- Huntley, B. J. 1972. Notes on the ecology of *Azorella selago* Hook. f. *Journal of South African Botany* 38:103–113.
- Hupp, N., L. D. Llambí, L. Ramirez, and R. M. Callaway. 2017. Alpine cushion plants have species-specific effects on microhabitat and community structure in the tropical Andes. *Journal of Vegetation Science* 28:928–938.
- Kufel, L., M. Strzalek, and A. Przetakiewicz. 2018. Plant response to overcrowding—*Lemna minor* example. *Acta Oecologia* 91:73–80.
- Kula, A. A. R., M. H. Hey, J. J. Couture, P. A. Townsend, and H. J. Dalglish. 2020. Intraspecific competition reduces plant size and quality and damage severity increases defense responses in the herbaceous perennial, *Asclepias syriaca*. *Plant Ecology* 221:421–430.
- Kunstler, G., C. H. Albert, B. Courbaud, S. Lavergne, W. Thuiller, G. Vieilledent, N. E. Zimmermann, and D. A. Coomes. 2011. Effects of competition on tree radial-growth vary in importance but not in intensity along climatic gradients. *Journal of Ecology* 99:300–312.
- Leicht-Young, S., A. M. Latimer, and J. A. Silander, Jr. 2011. Lianas escape self-thinning: Experimental evidence of positive density dependence in temperate lianas *Celastrus orbiculatus* and *C. scandens*. *Perspectives in Plant Ecology, Evolution and Systematics* 13:163–172.
- le Roux, P. C. 2008. Climate and climate change. Pages 39–64 in S. L. Chown and P. W. Froneman, editors. *The Prince Edward Islands: land-sea interactions in a changing ecosystem*. African SunMedia, Stellenbosch, South Africa.
- le Roux, P. C., and M. A. McGeoch. 2008. Rapid range expansion and community reorganisation in response to warming. *Global Change Biology* 14:2950–2962.
- le Roux, P. C., and M. A. McGeoch. 2010. Interaction intensity and importance along two stress gradients: adding shape to the stress-gradient hypothesis. *Oecologia* 162:733–745.
- le Roux, P. C., J. D. Shaw, and S. L. Chown. 2013. Ontogenetic shifts in plant interactions vary with environmental severity and affect population structure. *New Phytologist* 200:241–250.
- Levine, J. M. 1999. Indirect facilitation: evidence and predictions from a riparian community. *Ecology* 80:1762–1769.
- Llambí, L. D., N. Hupp, A. Saez, and R. M. Callaway. 2018. Reciprocal interactions between a facilitator, natives, and exotics in tropical alpine plant communities. *Perspectives in Plant Ecology, Evolution and Systematics* 30:82–88.
- Maestre, F. T., R. M. Callaway, F. Valladares, and C. J. Lortie. 2009. Refining the stress-gradient hypothesis for competition and facilitation in plant communities. *Journal of Ecology* 97:199–205.
- Maestre, F. T., J. Cortina, and S. Bautista. 2004. Mechanisms underlying the interaction between *Pinus halepensis* and the native late-successional shrub *Pistacia lentiscus* in a semi-arid plantation. *Ecography* 27:776–786.
- McGeoch, M. A., P. C. le Roux, E. A. Hugo, and M. J. Nyakata. 2008. Spatial variation in the terrestrial biotic system. Pages 245–276 in S. L. Chown and P. W. Froneman, editors.

- The Prince Edward Islands: land–sea interactions in a changing ecosystem. African SunMedia, Stellenbosch, South Africa.
- Metz, J., and K. Tielbörger. 2016. Spatial and temporal aridity gradients provide poor proxies for plant–plant interactions under climate change: a large-scale experiment. *Functional Ecology* 30:20–29.
- Molenda, O., A. Reid, and C. J. Lortie. 2012. The alpine cushion plant *Silene acaulis* as foundation species: A bug's-eye view to facilitation and microclimate. *PLoS One* 7:1–10.
- Molina-Montenegro, M. A., E. I. Banano, and L. A. Cavieres. 2008. Positive interactions among plant species for pollinator service: assessing the 'magnet species' concept with invasive species. *Oikos* 117:1833–1839.
- Molina-Montenegro, M. A., C. Torres, M. J. Parra, and L. A. Cavieres. 2000. Species association with the cushion *Azorella trifurcata* (Gaertn.) Hook. (Apiaceae) in the high Andes of central Chile. *Gayana Botanica* 57:161–168.
- Nykatya, M. J., and M. A. McGeoch. 2008. Temperature variation across Marion Island associated with a keystone plant species (*Azorella selago* Hook. (Apiaceae)). *Polar Biology* 31:139–151.
- Olsen, S. L., J. P. Töpper, O. Skarpaas, V. Vandvik, and K. Klanderud. 2016. From facilitation to competition: temperature-driven shift in dominant plant interactions affects population dynamics in seminatural grasslands. *Global Change Biology* 22:1915–1926.
- Pescador, D. S., J. Chacón-Labela, M. de la Cruz, and A. Escudero. 2014. Maintaining distances with the engineer: patterns of coexistence in plant communities beyond the patch–bare dichotomy. *New Phytologist* 204:140–148.
- R Development Core Team. 2018. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. www.r-project.org
- Rose, C. E., S. W. Martin, K. A. Wannemuehler, and B. D. Pliskatis. 2006. On the use of zero-inflated and hurdle models for modeling vaccine adverse event count data. *Journal of Biopharmaceutical Statistics* 16:463–481.
- Saccone, P., J.-P. Pages, J. Girel, J.-J. Brun, and R. Michalet. 2010. *Acer negundo* invasion along a successional gradient: early direct facilitation by native pioneers and late indirect facilitation by conspecifics. *New Phytologist* 187:831–842.
- Schöb, C., C. Armas, and F. I. Pugnaire. 2013. Direct and indirect interactions co-determine species composition in nurse plant systems. *Oikos* 122:1371–1379.
- Schöb, C., 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.
- Schöb, C., P. Macek, N. Pistón, Z. Kikvidze, and F. I. Pugnaire. 2017. A trait-based approach to understand the consequences of specific plant interactions for community structure. *Journal of Vegetation Science* 28:696–704.
- Smith, V. R., and M. Steenkamp. 1990. Climate change and its ecological implications at a sub-Antarctic island. *Oecologia* 85:14–24.
- Svanfeldt, K., K. Monro, and D. J. Marshall. 2017. Field manipulations of resources mediate the transition from intraspecific competition to facilitation. *Journal of Animal Ecology* 86:654–661.
- Tielbörger, K., and R. Kadmon. 2000. Indirect effects in a desert plant community: is competition among annuals more intense under shrub canopies? *Plant Ecology* 150:53–63.
- Tilman, D., and M. L. Cowan. 1989. Growth of old field herbs on a nitrogen gradient. *Functional Ecology* 3:425–438.
- Yang, Y., J. G. Chen, C. Schöb, and H. Sun. 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* 8:465.
- Zhang, R. C., and K. Tielbörger. 2019. Facilitation from an intraspecific perspective—stress tolerance determines facilitative effect and response in plants. *New Phytologist* 221:2203–2212.
- Zhang, R. C., and K. Tielbörger. 2020. Density-dependence tips the change of plant–plant interactions under environmental stress. *Nature Communications* 11:2532.
- Zhang, L., and Wang, B. 2016. Intraspecific interactions shift from competitive to facilitative across a low to high disturbance gradient in a salt marsh. *Plant Ecology* 217 959–967.

SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article at <http://onlinelibrary.wiley.com/doi/10.1002/ecy.3200/supinfo>