

## RESEARCH ARTICLE

# Fine-scale variation in the effect of the cushion plant *Azorella selago* on vascular plants, mosses, hepatics and lichens in the sub-Antarctic

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## Abstract

**Question:** Plant–plant interactions can strongly influence community structure and composition. The outcome of these interactions can vary considerably across space and is often linked to environmental conditions, with, for example, a higher prevalence of facilitative interactions typically being observed under greater environmental severity. To date, most studies have documented shifts from competitive to facilitative (or neutral) plant–plant and plant–lichen interactions along gradients of increasing environmental severity from pairwise interspecific interactions. However, few studies have examined if the outcome of these interactions for different taxonomic groups is dependent on environmental conditions across multiple environmental stress gradients.

**Location:** Sub-Antarctic Marion Island.

**Methods:** We examine community-level variation in the response of four taxa (i.e., vascular plants, hepatics, mosses, and lichens) to an interaction with a long-lived cushion plant species (*Azorella selago*) that ameliorates microenvironmental conditions, testing how the effect of the cushion plant on the taxa varies along multiple stress gradients at the scale of a landform.

**Results:** Contrary to expectations, even when considering multiple proximate predictor variables, fine-scale spatial variation in the effect of *A. selago* on the taxa could not be explained. However, the outcome of the interaction with *A. selago* differed between taxonomic groups, with vascular plants benefitting and the non-vascular taxa experiencing neutral or negative impacts.

**Conclusions:** This study highlights that the impacts of biotic interactions cannot always be generalized across plant groups, and that it is necessary to consider taxon-specific responses when predicting community-level impacts of biotic interactions. More generally, we demonstrate how complex spatial variation in environmental stressors can be explicitly considered when modelling variation in the outcome of plant–plant interactions.

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## KEYWORDS

cushion plant, facilitation, fine-scale variation, plant–lichen communities, plant–lichen interactions, plant–plant interactions, proximal variables, stress gradient, sub-Antarctic

## 1 | INTRODUCTION

Community assembly can be strongly influenced by the outcomes of interactions between organisms at fine spatial scales (Kikvidze et al., 2015; Mod et al., 2015). Negative interactions (e.g., competition) were traditionally thought to be the most influential biotic interaction in communities, but positive interactions (e.g., facilitation) are now recognized as a key influence in some systems too (Bertness & Callaway, 1994). Irrespective of whether positive or negative biotic interactions have the largest impacts, the outcome of interactions can vary considerably through space and time, with this variation often strongly linked to environmental conditions (Mod et al., 2020). For example, a higher prevalence of net positive interactions is typically observed under greater environmental severity [as posited by the Stress Gradient Hypothesis (SGH); Bertness & Callaway, 1994; He et al., 2013]. However, under moderate or benign environmental conditions, negative interactions are predicted to generally dominate (Bertness & Callaway, 1994; Choler et al., 2001; Michalet et al., 2006). This shift towards plants benefitting more from the presence of neighbouring plants under increasingly severe conditions is hypothesized to occur because the strength of the positive impacts of neighbouring plants increases relative to their negative impacts with increasing environmental stress (Bertness & Callaway, 1994; Maestre et al., 2009a). To date, most studies have documented shifts from competitive to neutral or facilitative plant–plant (le Roux et al., 2013; Qi et al., 2018) and plant–lichen (Klanderud & Totland, 2004; see also Kjær et al., 2018) interactions (“plant–plant interactions” hereafter for brevity) along gradients of increasing environmental severity by examining, for example, the effects of benefactor plant species (i.e., plants that modify the local micro-environment for other species) on the performance of a target species, or individuals of the same species. However, a smaller number of studies have attempted to provide a broader context for the impact of plant–plant interactions by testing if the outcome of the interactions at the community level are also dependent on environmental conditions (e.g., Michalet et al., 2006; Anthelme et al., 2012; Bråthen & Lortie, 2016; Cavieres et al., 2016; Hupp et al., 2017).

Studies documenting relationships between the outcome of plant–plant interactions and environmental severity also generally only consider a single environmental factor (e.g., altitude, aspect or aridity; Cavieres et al., 2006; Anthelme et al., 2012; López et al., 2016; Liancourt et al., 2017; Guignabert et al., 2020). However, in ecological communities there are usually multiple co-occurring environmental stressors and disturbances (which differ in strength and orientation, creating complex, non-monotonic variation in severity across landscapes) that can operate independently and simultaneously on interacting species (Kawai & Tokeshi, 2007; He & Bertness, 2014; Mod et al., 2014; Halvorsen et al., 2020). These multiple

and complex co-occurring environmental factors can make it challenging to determine which environmental conditions drive variation in the outcome of species' interactions (Kawai & Tokeshi, 2007; Brooker et al., 2008; Maestre et al., 2009b; Anthelme et al., 2012; He & Bertness, 2014), therefore limiting the ability to predict how the outcome of plant–plant interactions will be affected by changing environmental conditions.

Elevation gradients and slope aspect are commonly used as proxies (i.e., ‘distal predictors’, *sensu* Austin, 2002) for environmental stressors due to large abiotic differences between high and low elevations or between north- and south-facing slopes (Choler et al., 2001). However, ‘proximal’ predictor variables (e.g., soil temperature and soil moisture; *sensu* Austin, 2002) may be better predictors than distal variables, since the latter represent a more direct, mechanistic effect on the performances of plant species (Bertness & Callaway, 1994; Austin, 2002; Kawai & Tokeshi, 2007). Therefore, to improve our understanding of how abiotic factors influence species' interactions with one another, there may be value, particularly at fine spatial scales, to explicitly consider proximal predictors which have direct effects on plant and lichen performance and, as a result, the outcome of interactions in comparison to more frequently studied distal predictors (Kawai & Tokeshi, 2007; Maestre et al., 2009b; Mod et al., 2014).

The net outcome of interactions is not only strongly determined by abiotic factors but also by the identity of the interacting species (Cavieres et al., 2006; Mod et al., 2014; Hupp et al., 2017). Different taxa may respond differently to similar biotic and abiotic conditions (Mod et al., 2016; Kjær et al., 2018; Asplund et al., 2022), and, as a result, examining multiple taxa with different combinations of traits is necessary to determine the generality of species' responses to neighbouring plants/taxa (Brooker et al., 2008; He & Bertness, 2014; Mod et al., 2014; Zhang & Tielbörger, 2019). For example, unlike vascular plant species, bryophyte species have a poikilohydric habit but are also ectohydric, the former allowing desiccation tolerance and the later permitting the absorption of water and solutes from the shoot surface (Buch, 1947; Hosokawa et al., 1964; Lindo & Gonzalez, 2010). Thus, one would expect bryophytes to respond differently to their environment and to interactions with other species compared to vascular plants and we could expect the outcomes of interactions to be taxon-specific. However, research on how vascular, hepatic, moss and lichen species vary simultaneously in their responses to plant–plant interactions along environmental stress gradients is limited (Löbel et al., 2006; but see Mod et al., 2016; Kjær et al., 2018), even despite these taxa all being integral components of high-latitude and high-elevation ecosystems (Lindo & Gonzalez, 2010; Asplund & Wardle, 2017; Asplund et al., 2022). Therefore, contrasting the responses of different taxonomic groups to an interaction with a single common species can provide insights into the



influence of broad trait differences on the outcome of interactions at the community level (Mod et al., 2015; Kjær et al., 2018).

This study examines fine-scale spatial variation in the outcome of the interactions between *Azorella selago*, a widespread cushion plant (i.e., a compact, hemispherical plant that can create favourable microhabitats by ameliorating abiotic stressors and disturbances for associated species; le Roux & McGeoch, 2008b; Nyakatya & McGeoch, 2008; Combrinck et al., 2020) and multiple co-occurring vascular plant, hepatic, moss, and lichen taxa, on sub-Antarctic Marion Island as a model system. We document the outcome of the interaction between *A. selago* and the different taxa across a landform characterized by pronounced variation in several ecologically important abiotic stress gradients (including substrate moisture, temperature and stability, and wind exposure). Two research questions are specifically addressed: (1) is the effect of *A. selago* on richness and cover consistent across four different taxonomic groups (vascular plants, hepatics, mosses, and lichens)? (2) Can variation in the impact of *A. selago* on the richness and cover of four taxa be related to environmental stress gradients, examining both distal and proximal environmental predictors? Accordingly, this study addresses key gaps in our understanding of fine-scale variation in the outcome of plant interactions across multiple taxonomic groups and abiotic stress gradients within plant and lichen communities.

## 2 | METHODS

### 2.1 | Study site

Marion Island (37°45' E; 46°54' S) is one of the two Prince Edward Islands, located in the southern Indian Ocean. The island occupies an area of approx. 290 km<sup>2</sup> and ranges in elevation from sea level to 1230 m a.s.l. (Chown & Froneman, 2008). The island experiences an oceanic climate with low annual and diurnal temperature ranges (mean annual temperature of 6°C), high relative humidity (average 83%), high rainfall and cloud cover (approx. 2500 mm per year), and frequent needle ice formation and strong winds (le Roux, 2008). The number of known indigenous species on the island is 21 for vascular species and approx. 44 for hepatics, 90 for mosses and 118 for lichens (Gremmen & Smith, 2008). An additional 18 alien terrestrial vascular plant species occur on the island (Greve et al., 2017).

Marion Island has approx. 130 pyroclastic scoria cones (i.e., cinder cones), which are geomorphically active sites because of their steep slopes and mobile substrate, particularly due to frost creep and frequent freeze–thaw cycles (Holness, 2004). This study was conducted at Junior's Kop, a large, partially vegetated scoria cone on the northeastern side of the island (37°50' E; 46°53' S; Appendix S1). Junior's Kop serves as a suitable study site for several reasons. First, Junior's Kop is a steep-sloped and large scoria cone covering approx. 0.4 km<sup>2</sup> in area and reaching 306 m a.s.l., that has a fairly homogeneous topography and is one of the only scoria cones on the island that goes from fully vegetated at the base to bare at the peak (see, e.g., Boelhouwers et al., 2000; Appendix S1). Second, on Junior's

Kop, *A. selago* occurs across almost the entire elevational gradient of the scoria cone at three different aspects, namely the west-, east-, and south-facing slopes. Lastly, abiotic conditions change strongly with elevation and aspect on Junior's Kop. For example, several abiotic conditions on Junior's Kop show a linear relationship with elevation, with an increase in scoria mobility and wind speed, and a decrease in temperature and scoria moisture, scoria particle size and scoria depth (Appendix S2; see also le Roux & McGeoch, 2008b). Additionally, variation in abiotic conditions with elevation is dependent on aspect for all variables (Appendix S2; see also le Roux & McGeoch, 2008b), likely reflecting that differences in exposure to the dominant winds and solar radiation mediate the impact of elevation on habitat conditions.

### 2.2 | Study species

*Azorella selago* is a hemispherical, cushion-forming plant species (Appendix S1). The species is the most widespread vascular plant on Marion Island, occurring from sea level to approx. 840 m a.s.l. (le Roux & McGeoch, 2008a). Due to its cushion growth form, *A. selago* strongly influences its immediate surroundings by stabilizing the substrate (Hausmann et al., 2009), decreasing temperature fluctuations, reducing leeward wind speeds (Nyakatya & McGeoch, 2008; le Roux & McGeoch, 2008b; Combrinck et al., 2020; see also Arroyo et al., 2003), and potentially increasing nutrient content (previously observed for the congeneric *Azorella monantha*; Cavieres et al., 2005). On Junior's Kop, a comparison of scoria moisture beneath *A. selago* plants and the adjacent open scoria indicates that the cushion plant significantly increases moisture on the west-facing aspect (with a similar trend on the east- and south-facing aspects; Appendix S3). Consequently, *A. selago* hosts an array of species, including other plant species and invertebrates (le Roux & McGeoch, 2010).

### 2.3 | Data collection

#### 2.3.1 | Variation in the effects of *Azorella selago* on different taxa

To assess if *A. selago* facilitates co-occurring plant species, we used species richness and cover as key measures of the impact of the cushion plant on the plant and lichen community's composition. The impact of *A. selago* on the cover and richness of other vascular plants, hepatics, mosses and lichens was assessed using a paired sampling approach (Badano & Cavieres, 2006). Sampling was restricted to *A. selago* individuals of a medium size (39–105 cm diameter perpendicular to the isoline of the scoria cone slope, mean  $\pm$  SE = 60.97  $\pm$  2.56 cm) to standardize sampling effort. This coincides with the majority of *A. selago* individuals on the island, which show diameters typically ranging from 40 to 115 cm (le Roux & McGeoch, 2004). Thirty-three paired samples were surveyed at approximately equal elevational intervals along the

south-, east- and west-facing aspects of Junior's Kop during April 2015 ( $n = 11$  pairs per aspect). A paired sample consisted of sampling an individual *A. selago* plant and an adjacent site of the same size without *A. selago* present. Transects ran from the base of the scoria cone to the highest elevation where *A. selago* occurred. For each pair of samples, a malleable metal wire was used to trace the outline of the *A. selago* plant, after which the wire-loop was placed 1 m away at approximately the same contour (i.e., the adjacent site) and avoiding sampling areas which could be affected by the *A. selago* plant blocking downslope movement of sediment (following the approach of le Roux & McGeoch, 2008b). The placement of the samples at the same contour 1 m apart minimizes variation in unmeasured environmental variables between the paired samples.

Cushion plants are often long-lived and some species can survive for several hundreds of years (Morris & Doak, 1998). However, given that it is impossible to study these plants over a lifetime, examining the performance of these plants from long-term data sets may provide deeper insights into the long-term balance of plant interactions (see, e.g., Raath-Krüger et al., 2022). For *A. selago* specifically, a very slow vertical growth rate of  $0.43 \pm 0.01$  cm/year (mean  $\pm$  SE) has been reported for Marion Island (see le Roux & McGeoch, 2004). In contrast, using a long-term data set of repeated measures to examine the outcome of plant-plant interactions, Raath-Krüger et al. (2022) reported that *A. selago* diameter increases more quickly (i.e., by  $1.98 \pm 0.07$  cm/year). Due to the longevity of *A. selago* plants (le Roux & McGeoch, 2004), the ability of the species to create a microhabitat unique from that of the surrounding matrix (e.g., Nyakaty & McGeoch, 2008; le Roux & McGeoch, 2008b; Haussmann et al., 2009), and with minimal variation in abiotic conditions at the scale of 1 m on the landform, a paired sampling approach was considered well suited for the study.

All vascular plant, hepatic, moss and lichen species rooted within, or growing on, the *A. selago* plant canopy and the adjacent site were identified, and the aerial cover of each species visually estimated by the same experienced observers. Where taxonomy was unclear, individuals were assigned to morphospecies (resulting in one hepatic, 14 moss and four lichen morphospecies), and cryptic species groups were identified to genus level (required for six hepatic, nine moss and seven lichen genera; see Appendix S4 for list of species names). The length (diameter perpendicular to isoline), width (diameter perpendicular to length) and height of all sampled *A. selago* plants were recorded to account for plant size. Since *A. selago* plant width was significantly correlated with length ( $r = 0.603$ ,  $p < 0.001$ ), this variable was subsequently excluded from analyses.

### 2.3.2 | Variation of abiotic variables across the elevational gradient

Spatial variation in environmental severity gradients was determined by quantifying several ecologically important abiotic variables across an elevational gradient and on different aspects of Junior's Kop. Scoria moisture was determined by recording the volumetric water

content (VWC, %) at 22 sites across each of the three transects. A FieldScout 300 TDR moisture meter (Spectrum Technologies, Plainfield, IL, USA) with 5-cm probes was used to record scoria moisture approx. 8 cm beneath the scoria surface, paired with readings of scoria moisture under *A. selago* canopies. Sampling was conducted on a rain-free day ( $< 1$  mm/h precipitation for the previous four days, with all recordings taken within 3 h on 5 October 2016) and the average of three recordings per site was used. Scoria particle size was classified as either fine (mean diameter  $< 3$  cm) or coarse (mean diameter  $> 3$  cm), and scoria depth was estimated using a metal rod pushed through the substrate until a change in resistance was felt. An organic layer was recorded where there was plant debris present on the scoria, as this layer may influence the microenvironmental conditions (i.e., moisture and nutrients; Suding & Goldberg, 1999). Whilst abiotic conditions were recorded over relatively short periods (e.g., one day to one month), the results are considered to be representative of conditions at the study site due to limited seasonal variation in climatic conditions on Marion Island (le Roux, 2008).

Data for three additional abiotic variables were available from previous research on Junior's Kop. Scoria temperature at 2 cm beneath the scoria surface was obtained from P.C. le Roux & M.A. McGeoch (unpublished data), where the temperature was logged every 15 min using ThermoChron iButton temperature loggers (Maxim Semiconductor Corporation, Dallas, US). Wind speed was logged hourly 1 m above the ground surface (during May 2009 and May 2010) using Pace WSD-100 sensor (Pace Scientific, Boone, USA) combined with either Pace XR5 or Campbell CR200 loggers (P.C. le Roux, M.A. McGeoch, B. Jansen van Vuuren & S.L. Chown, unpublished data). The sensors were placed at the scoria cone's summit (309 m a.s.l.) and at 220 m a.s.l. on the cone's eastern, western and southern slopes. Estimates of scoria movement rates (mm/year) were obtained from Holness (2004), who recorded scoria movement at an elevation of 200 m a.s.l. on different aspects of the landform.

## 2.4 | Statistical analysis

To assess whether species occurred solely or significantly more on *A. selago* or adjacent substrate, a  $\chi^2$  analysis was used to compare vascular plant, hepatic, moss and lichen species' occurrence between the two substrate types. We used total species cover and richness of each taxon only in the adjacent substrate as a proxy for how environmental severity changes with elevation. Change in the cover and species richness of each of the taxa with elevation were evaluated using general linear models.

The intensity and the importance (*sensu* Brooker et al., 2005) of the effect of *A. selago* on co-occurring species were calculated for the richness and cover of vascular plants, hepatic, moss and lichen species using:

- a. the relative interaction intensity index (RII: Armas et al., 2004). The intensity of an interaction is a measure of the net effect of one species on a second species (or a set of other species):



$$RII = \frac{A1 - A2}{A1 + A2}; \quad (1)$$

- b. the competitive importance index ( $C_{imp}$ ; Seifan et al., 2010). The importance of an interaction is the effect of one species on a second species (or a set of other species) expressed as a proportion of the effect of the whole environment on the second species (Brooker et al., 2005; Seifan et al., 2010):

$$C_{imp} = \frac{(A1 - A2)}{[\max(A2; A1) \text{ across all samples} - \min(A2; A1) \text{ across site}]}. \quad (2)$$

In this study, A1 and A2 are the species richness (or cover) occurring with the cushion plant and at the adjacent site respectively. RII (and  $C_{imp}$ ) values range from -1 to +1 with positive values indicating facilitation, negative values indicating competition, and larger absolute values indicating increasing strength of the interaction (Armas et al., 2004; Seifan et al., 2010). RII (and  $C_{imp}$ ) values for vascular plants, hepatic, moss and lichen species were calculated and tested for a significant difference from zero using a one sample *t*-test.

RII (and  $C_{imp}$ ) values for species richness and cover were transformed to a range between 0 and 1, and modelled as a function of environmental variables using generalized linear models (assuming a binomial distribution). First, it was tested if RII (and  $C_{imp}$ ) for richness and cover of vascular plants, hepatics, mosses and lichens was significantly related to the two distal variables, elevation and aspect, which are commonly used proxies for abiotic environmental severity (Austin, 2002):

Distal model: RII (or  $C_{imp}$ ) richness or cover = elevation + aspect

Initially the interaction term of elevation and aspect was included in these models, but subsequently excluded because the interaction term was not significant in any models. The subsequent proximal model, which included the distal and proximal measures of environmental severity (the majority of which were weakly correlated, with the strongest correlation between wind speed and altitude:  $r=0.7$ ), tested for an influence of all these predictor variables on RII (and  $C_{imp}$ ) for richness and cover of vascular plants, hepatics, mosses and lichens. Scoria movement was excluded from this analysis because it was only recorded at one elevation (see Holness, 2004):

Proximal model: RII (or  $C_{imp}$ ) for richness or cover =  
 elevation + aspect + scoria size + scoria depth  
 + organic layer presence + wind speed + scoria moisture  
 + scoria temperature + *A. selago* length + *A. selago* height.

All models were repeated for the cover and richness of vascular plant, hepatic, moss and lichen species separately. A best-subsets model-building approach was used to test for the best combination of predictor variables [as determined by having the lowest AIC (Akaike Information Criterion) value out of all possible predictor variable combinations], with all distal and proximal measures of environmental severity being considered in the models. However, since none of the models explained significant variation in RII (or  $C_{imp}$ ), only results from the full models are presented further on. Note that

RII (and  $C_{imp}$ ) values were rescaled to range from 0 to +1 for analysis; thus, model coefficients are for transformed data.

All analyses were conducted using R version 3.3.2 (R Development Core Team, 2014), using the *car* version 2.1-6 (Fox & Weisberg, 2011), *vegan* version 2.4-5 (Oksanen et al., 2017), *lme4* version 1.1-15 (Bates et al., 2015), *multcomp* version 1.4-8 (Hothorn et al., 2008), and *modEvA* version 1.3.2 (Barbosa et al., 2016) packages.

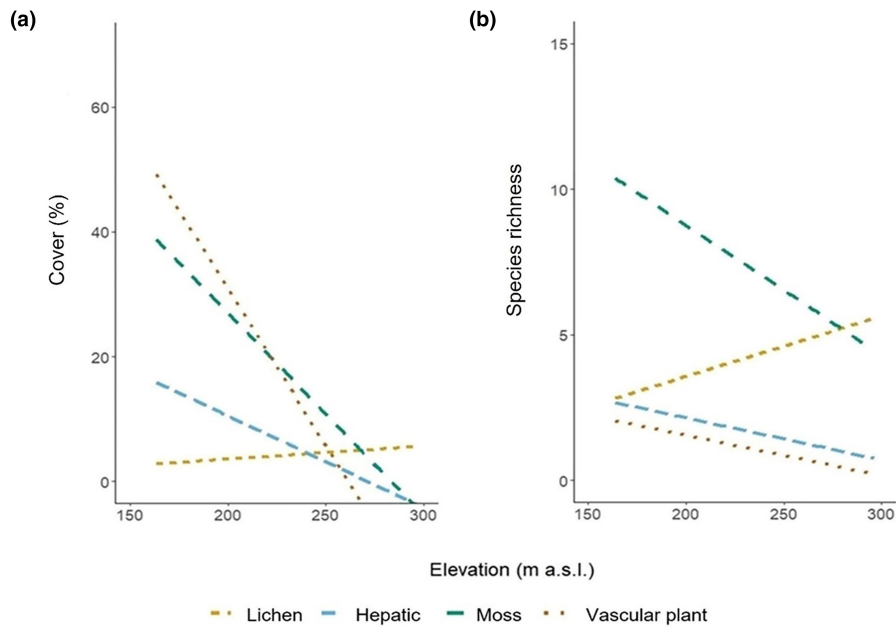
### 3 | RESULTS

A total of 82 species were recorded during sampling (see Appendix S4). Four rare species (i.e. species with a total of five occurrences or less) were recorded exclusively on cushion plants, whereas 28 rare species were recorded exclusively on the adjacent substrate. No rare lichen species occurred exclusively on cushion plants and no rare vascular plant species were recorded on the adjacent substrate (Appendix S4). Of the common species (species with a total of more than five occurrences), only two non-vascular species were found to occur exclusively only on cushion plants. In contrast, 12 non-vascular plant species occurred exclusively only on the adjacent substrate. These included one hepatic, six moss and five lichen species. No vascular plant species occurred only on the cushion plant or only on the adjacent substrate. Of the common species which occurred on both the cushion plant and adjacent substrate, the grass species *Agrostis magellanica* occurred significantly more frequently on the cushion plant, whereas the hepatic species, *Plagiochila heterodonta*, and two moss species, *Philonotis scabrifolia* and a *Bucklandiella* sp., occurred significantly more often on the adjacent substrate (Appendix S4).

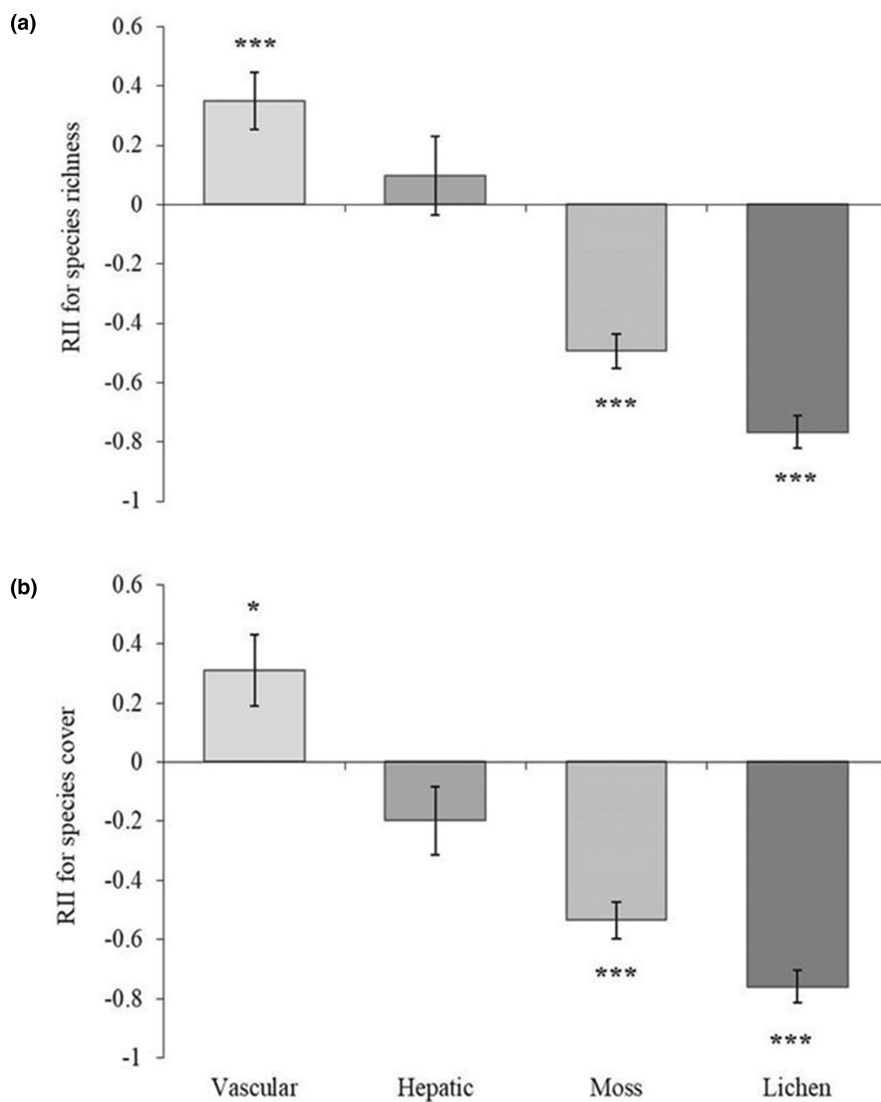
Total vascular plant species richness and cover decreased significantly with elevation (Figure 1:  $p < 0.05$  and  $p < 0.001$  respectively). The total cover and species richness of moss showed a significant decrease with elevation ( $p < 0.05$ ), while hepatic cover only showed a negative trend with elevation ( $p > 0.05$ ) and hepatic richness significantly decreased with elevation ( $p < 0.05$ ). In contrast, lichen species cover and richness showed a significant increase with elevation ( $p < 0.05$ ).

RII and  $C_{imp}$  were highly correlated for richness and cover within all taxa (Appendix S5), and  $C_{imp}$  cover and richness analyses gave very similar results to the RII cover and richness analyses (see also le Roux and McGeoch, 2010 for a comparable result). Thus, only RII richness and cover results are presented here (see Appendices S6–S8, S9 and S10 for results of the distal and proximal models of  $C_{imp}$  for richness and cover). RII values for richness and cover of vascular plant species were significantly larger than zero (Figure 2). In contrast, the mean RII for richness and cover of moss and lichen species were significantly smaller than zero, while values for hepatics were not significantly different from zero (Figure 2).

In all distal models, elevation and aspect were not significantly related to RII for richness and cover of any of the taxa (Table 1; Figures 3 and 4). Additionally, no proximal model performed better than expected by chance (all models  $p > 0.05$ , Table 2). Thus, the influence of *A. selago* on the richness and cover of other species across



**FIGURE 1** Variation in the (a) cover (%) and (b) richness of lichen, hepatic, moss and vascular plant species with elevation of Junior's Kop in only the adjacent plots. Note, cover and richness are of all aspects ( $n=33$  per taxa). Results for vascular plant, lichen and moss cover (%) were significant ( $p < 0.05$ ), while hepatic cover only showed a negative trend with elevation ( $p > 0.05$ ). Results for vascular, hepatic, lichen and moss richness were significant ( $p < 0.05$ )



**FIGURE 2** Mean ( $\pm$  SE) relative interaction intensity index (RII) for species (a) richness and (b) cover of vascular plant, hepatic, moss and lichen species. RII values range from -1 to 1, where positive values indicate net facilitation and negative values indicate net competition and larger absolute values indicating increasing strength of the interaction. \*,  $p < 0.05$ ; \*\*,  $p < 0.01$ ; \*\*\*,  $p < 0.001$  (one sample t-test)

**TABLE 1** Relative Interaction Intensity Index (RII) from distal models for the (a) richness and (b) cover of vascular plant, hepatic, moss and lichen species from  $n=33$  paired samples ( $n=11$  per aspect)

Response variable	Coefficient	Estimate $\pm$ SE	$p$ -Value
(a) RII for richness			
Vascular	(Intercept)	0.149 $\pm$ 3.309	0.964
$p=0.826$	Aspect	East > South > West	0.657
% DE=59.4	Elevation	0.005 $\pm$ 0.014	0.740
Hepatic	(Intercept)	-2.596 $\pm$ 3.291	0.430
$p=0.537$	Aspect	East > South > West	0.410
% DE=94.2	Elevation	0.015 $\pm$ 0.014	0.299
Moss	(Intercept)	-1.487 $\pm$ 3.750	0.692
$p=0.991$	Aspect	East > West > South	0.833
% DE=7.2	Elevation	0.003 $\pm$ 0.016	0.849
Lichen	(Intercept)	-3.474 $\pm$ 5.440	0.523
$p=0.957$	Aspect	East > South > West	0.588
% DE=14.4	Elevation	0.009 $\pm$ 0.024	0.708
(b) RII for cover			
Vascular	(Intercept)	-3.629 $\pm$ 3.467	0.295
$p=0.367$	Aspect	East > South > West	0.535
% DE=14.0	Elevation	0.021 $\pm$ 0.015	0.166
Hepatic	(Intercept)	-6.984 $\pm$ 4.011	0.082
$p=0.268$	Aspect	East > South > West	0.109
% DE=30.5	Elevation	0.032 $\pm$ 0.018	0.068
Moss	(Intercept)	-3.311 $\pm$ 4.013	0.409
$p=0.960$	Aspect	East > South > West	0.775
% DE=11.0	Elevation	0.011 $\pm$ 0.017	0.539
Lichen	(Intercept)	-3.102 $\pm$ 5.271	0.556
$p=0.961$	Aspect	East > South > West	0.610
% DE=13.3	Elevation	0.007 $\pm$ 0.023	0.753

Note: No individual predictor variables (far right column) or full models (far left column) significantly ( $p < 0.05$ ) explained variation in RII. Significance and percentage deviance explained (% DE) of full model are given in the first column. For categorical predictor variables the ranking of the factor levels is shown.

short distances varied independently of wind speed, scoria moisture, scoria temperature, aspect, elevation, *A. selago* size, scoria size, scoria depth or the presence of organic material (Table 2).

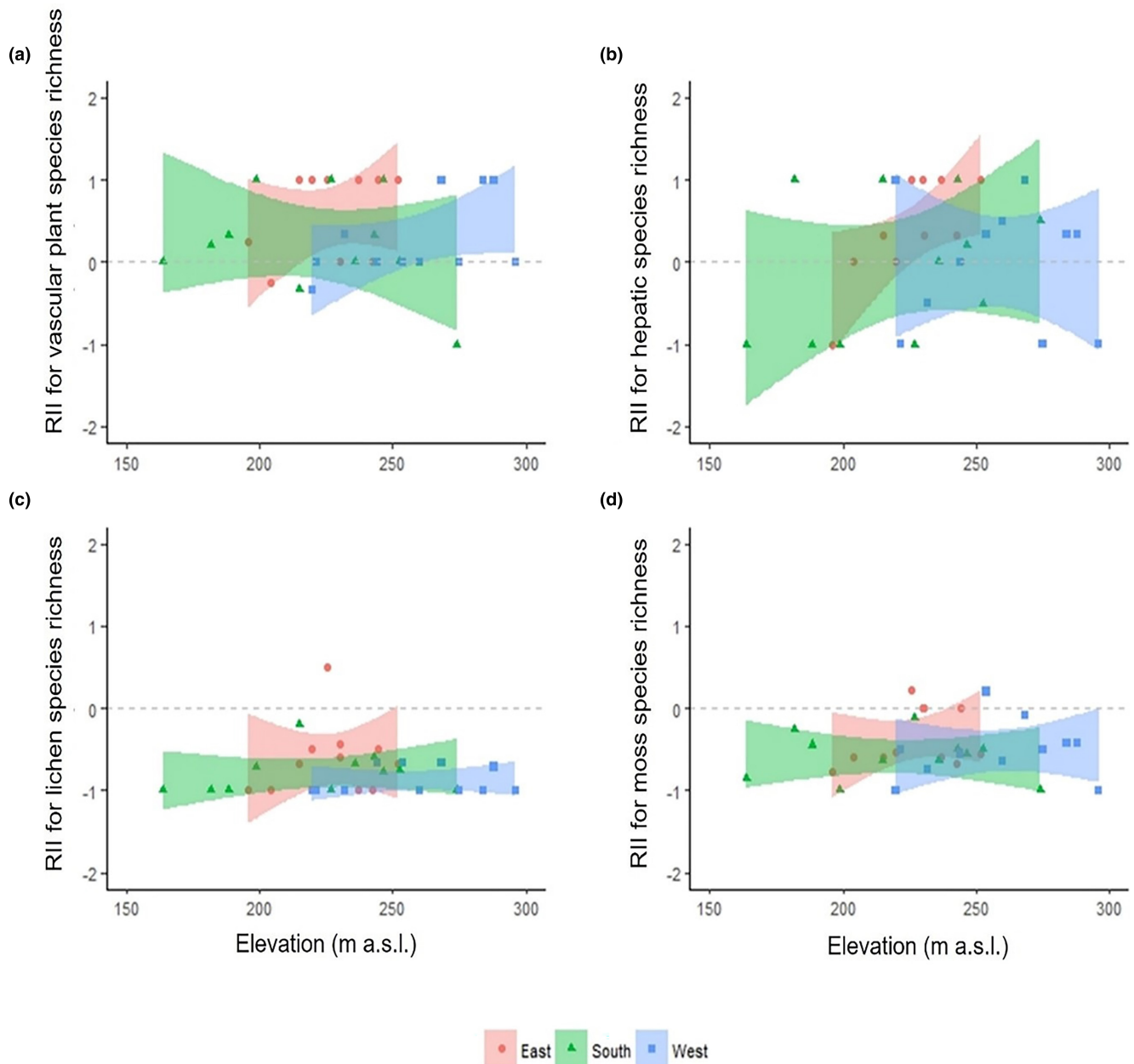
## 4 | DISCUSSION

A key finding from this study is that there was substantial variation in the outcome of interactions between *A. selago* and the four different taxonomic groups, with the positive response of vascular species contrasting strongly with those of the other taxa. The second key finding was that neither distal nor proximal predictor variables explained variation in the effect of *A. selago* on other species across a single landform. Thus, the outcomes of this community-level interaction could not be explained by fine-scale variation in abiotic conditions. These results were unexpected based on findings from other studies, both globally (Anthelme et al., 2012; Bråthen & Lortie, 2016; Cavieres et al., 2016; Hupp et al., 2017; although see

Callaway et al., 2002) and in the sub-Antarctic and similar habitats (e.g., Arroyo et al., 2003; le Roux & McGeoch, 2008b).

### 4.1 | The effect of *Azorella selago* differs between taxa

The variation in the effect of *A. selago* on the richness and cover between the taxonomic groups likely reflects the potential mechanisms by which *A. selago* interacts with the different species in the community, as well as variation in traits related to stress tolerance and competitive abilities between the four taxa (Choler et al., 2001; Liancourt et al., 2005; Anthelme et al., 2012; Zhang & Tielbörger, 2019). For example, the main mechanism behind interactions between some species and/or taxa could be thermal buffering (Arroyo et al., 2003; Cavieres et al., 2006), whereas for others, it could be nutrient and water provisioning (Anthelme et al., 2012; López et al., 2016) or protection from strong winds (Baumeister &



**FIGURE 3** Changes in the relative interaction intensity index (RII) for species richness (mean  $\pm$  SE) with elevation (m a.s.l.) for (a) vascular plants, (b) hepatics, (c) lichens and (d) mosses. RII values range from  $-1$  to  $1$ , where positive values indicate net facilitation and negative values indicate net competition and larger absolute values indicating increasing strength of the competitive importance

Callaway, 2006). We hypothesize that the type of microhabitat amelioration caused by the cushion plant (e.g., increase in substrate stability, moisture, wind sheltering, and potentially nutrient availability) may be of specific benefit to vascular plants due to their morphology and height (see Kjær et al., 2018 for comparable result). For instance, the deeper roots of vascular plants would be able to reach resources within and below the cushion plant canopy and the taller structure of these species may make them vulnerable to high wind stress, increasing the facilitative potential of cushion plants (le Roux & McGeoch, 2008b; Gouws et al., 2021). This idea is supported by the recent paper by Gouws et al. (2021), who found that *A. selago* improved the growth and survival of *Agrostis magellanica* grass of

later ontogenetic stages when the grasses are taller and roots are potentially longer.

In contrast to vascular plants, the overall effect of *A. selago* on hepatics was neutral, and negative for lichens and mosses. In agreement with our findings, Kjær et al. (2018) did not find evidence of facilitation at the community level between the cushion plant *Silene acaulis* and lichen and bryophyte species across a primary succession gradient. These results may reflect the habit of non-vascular taxa to grow along the substrate surface and their lack of deep root systems, with the non-vascular species being affected by temperature, moisture, and nutrient levels of their substrate surface (Kleier & Rundel, 2009; Mod et al., 2016). The growth habit of non-vascular



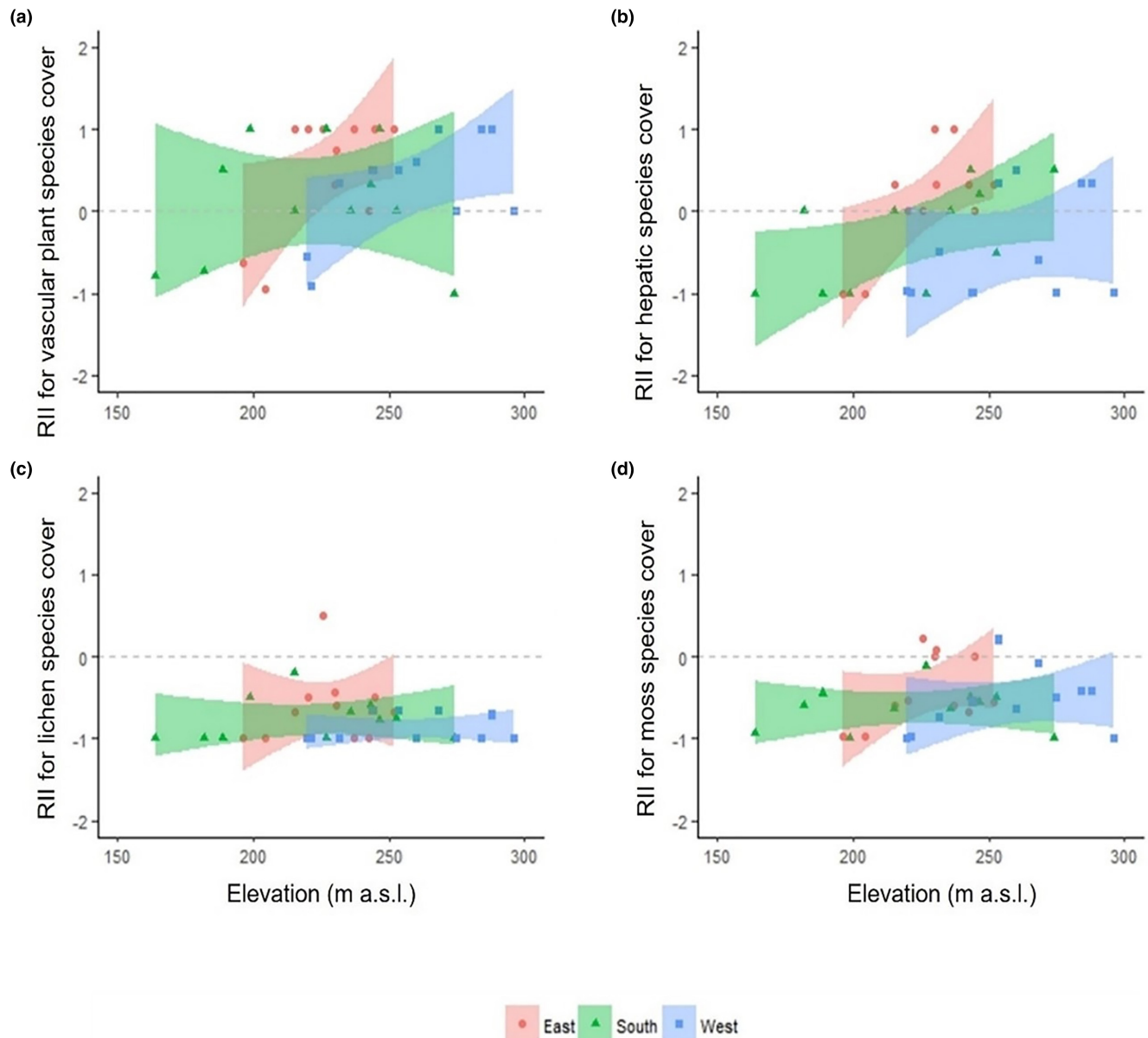


FIGURE 4 Changes in the relative interaction intensity index (RII) for species cover (mean  $\pm$  SE) with elevation (m a.s.l.) for (a) vascular plants, (b) hepatics, (c) lichens and (d) mosses. RII values range from  $-1$  to  $1$ , where positive values indicate net facilitation and negative values indicate net competition and larger absolute values indicating increasing strength of the competitive importance

taxa may, therefore, reduce the potential for positive effects from improvement in resource availability and microclimatic conditions deeper within the cushion plant canopy, such as buffered temperatures (Arroyo et al., 2003; Cavieres et al., 2007; Nyakatya & McGeoch, 2008; Kleier & Rundel, 2009) and increased moisture and nutrient levels (Cavieres et al., 2006, 2007). Indeed, Kleier and Rundel (2009) demonstrated that the surface temperatures of the cushion plant *Azorella compacta* reached sub-zero temperatures (up to  $-23^{\circ}\text{C}$ ) and exhibited large diurnal temperature ranges, in comparison to 5 cm within the species' canopy which showed warmer (e.g., consistently above  $0^{\circ}\text{C}$ ) and more buffered temperatures. Therefore, plants may potentially experience very different conditions at the surface of a cushion plant (e.g., thermal extremes for

non-vascular plants limited to the cushion plant surface) vs within the cushion plants canopy (e.g., increased resource availability for deep-rooted vascular species).

In addition to abiotic conditions, the negative effect of *A. selago* on lichens and mosses may result from mutually negative (i.e., competitive) interactions between the cushion plant and the mosses and lichens for space and/or light (Mod et al., 2015); particularly for lichens with a foliose growth form (e.g., *Cladonia* species) and mosses with a mat-forming habit (e.g., *Racomitrium lanuginosum*). For example, the space taken up by the large cushion plants (and the fact that these plants can form a compact continuous surface, leaving limited gaps for other organisms to colonize them; see, e.g., Michalet et al., 2011, and also Bonanomi et al., 2016), could hinder establishment of slow-growing

TABLE 2 Relative interaction intensity index (RII) from proximal models for the (a) richness and (b) cover of vascular plant, hepatic, lichen and moss species from  $n=33$  paired samples ( $n=11$  per aspect)

Response variable	Coefficient	Estimate $\pm$ SE	p-Value	
(a) RII for richness				
Vascular plant  $p=0.955$ % DE=30.4	(Intercept)	3.844 $\pm$ 26.164	0.883	
	Elevation	-0.008 $\pm$ 0.039	0.841	
	Aspect	West > East > South	0.831	
	Scoria particle size	Coarse > fine	0.366	
	Scoria depth	-0.004 $\pm$ 0.057	0.945	
	Organic material	Absent > present	0.699	
	Wind speed	-0.016 $\pm$ 0.298	0.956	
	Scoria moisture	0.008 $\pm$ 0.085	0.926	
	Scoria temperature	0.362 $\pm$ 3.028	0.905	
	<i>Azorella selago</i> length	0.032 $\pm$ 0.039	0.408	
	<i>Azorella selago</i> height	-0.008 $\pm$ 0.114	0.946	
	Hepatic  $p=0.634$ % DE=35.4	(Intercept)	-40.515 $\pm$ 32.011	0.206
		Elevation	0.028 $\pm$ 0.040	0.488
Aspect		South > East > West	0.135	
Scoria particle size		Fine > coarse	0.293	
Scoria depth		-0.110 $\pm$ 0.069	0.109	
Organic material		Present > absent	0.553	
Wind speed		-0.634 $\pm$ 0.492	0.198	
Scoria moisture		-0.053 $\pm$ 0.092	0.559	
Scoria temperature		3.698 $\pm$ 3.542	0.297	
<i>Azorella selago</i> length		0.054 $\pm$ 0.042	0.195	
<i>Azorella selago</i> height		0.061 $\pm$ 0.115	0.598	
Moss  $p=1.000$ % DE=45.2		(Intercept)	11.243 $\pm$ 28.910	0.697
		Elevation	-0.006 $\pm$ 0.041	0.883
	Aspect	West > East > South	0.691	
	Scoria particle size	Coarse > fine	0.919	
	Scoria depth	0.013 $\pm$ 0.061	0.837	
	Organic material	Absent > present	0.784	
	Wind speed	-0.123 $\pm$ 0.407	0.762	
	Scoria moisture	-0.015 $\pm$ 0.094	0.873	
	Scoria temperature	-1.179 $\pm$ 3.298	0.720	
	<i>Azorella selago</i> length	-0.029 $\pm$ 0.036	0.429	
	<i>Azorella selago</i> height	0.026 $\pm$ 0.119	0.826	
	Lichen  $p=0.986$ % DE=23.6	(Intercept)	3.361 $\pm$ 42.102	0.936
		Elevation	-0.025 $\pm$ 0.063	0.697
Aspect		East > South > West	0.670	
Scoria particle size		Fine > coarse	0.410	
Scoria depth		-0.085 $\pm$ 0.106	0.423	
Organic material		Absent > present	0.818	
Wind speed		-0.469 $\pm$ 0.684	0.493	
Scoria moisture		-0.110 $\pm$ 0.178	0.535	
Scoria temperature		-1.084 $\pm$ 5.136	0.833	
<i>Azorella selago</i> length		-0.015 $\pm$ 0.050	0.765	
<i>Azorella selago</i> height		0.079 $\pm$ 0.210	0.707	

TABLE 2 (Continued)

Response variable	Coefficient	Estimate $\pm$ SE	p-Value	
(b) RII for cover				
Vascular plant  $p=0.671$ % DE=40.0	(Intercept)	2.287 $\pm$ 26.062	0.930	
	Elevation	0.003 $\pm$ 0.038	0.934	
	Aspect	East > West > South	0.594	
	Scoria particle size	Coarse > fine	0.383	
	Scoria depth	-0.036 $\pm$ 0.057	0.533	
	Organic material	Absent > present	0.389	
	Wind speed	0.028 $\pm$ 0.304	0.926	
	Scoria moisture	-0.019 $\pm$ 0.093	0.835	
	Scoria temperature	-0.087 $\pm$ 3.075	0.977	
	<i>Azorella selago</i> length	-0.003 $\pm$ 0.037	0.939	
	<i>Azorella selago</i> height	-0.006 $\pm$ 0.115	0.959	
	Hepatic  $p=0.625$ % DE=46.9	(Intercept)	-23.519 $\pm$ 30.744	0.444
		Elevation	0.057 $\pm$ 0.043	0.184
Aspect		East > South > West	0.794	
Scoria particle size		Coarse > fine	0.767	
Scoria depth		-0.065 $\pm$ 0.064	0.314	
Organic material		Absent > present	0.391	
Wind speed		-0.086 $\pm$ 0.463	0.853	
Scoria moisture		0.049 $\pm$ 0.095	0.608	
Scoria temperature		2.143 $\pm$ 3.473	0.537	
<i>Azorella selago</i> length		0.013 $\pm$ 0.036	0.728	
<i>Azorella selago</i> height		0.019 $\pm$ 0.119	0.871	
Moss  $p=0.995$ % DE=39.1		(Intercept)	11.383 $\pm$ 31.112	0.714
		Elevation	-0.007 $\pm$ 0.046	0.882
	Aspect	East > West > South	0.584	
	Scoria particle size	Fine > coarse	0.895	
	Scoria depth	0.001 $\pm$ 0.065	0.985	
	Organic material	Absent > present	0.533	
	Wind speed	0.011 $\pm$ 0.452	0.981	
	Scoria moisture	-0.025 $\pm$ 0.102	0.806	
	Scoria temperature	-1.537 $\pm$ 3.649	0.674	
	<i>Azorella selago</i> length	-0.039 $\pm$ 0.039	0.319	
	<i>Azorella selago</i> height	0.059 $\pm$ 0.135	0.664	
	Lichen  $p=0.986$ % DE=43.6	(Intercept)	3.465 $\pm$ 40.515	0.932
		Elevation	-0.027 $\pm$ 0.061	0.664
Aspect		East > South > West	0.724	
Scoria particle size		Fine > coarse	0.424	
Scoria depth		-0.087 $\pm$ 0.105	0.405	
Organic material		Absent > present	0.827	
Wind speed		0.452 $\pm$ 0.672	0.501	
Scoria moisture		-0.114 $\pm$ 0.174	0.511	
Scoria temperature		-0.989 $\pm$ 4.953	0.842	
<i>Azorella selago</i> length		-0.009 $\pm$ 0.049	0.856	
<i>Azorella selago</i> height		0.059 $\pm$ 0.205	0.773	

Note: No individual predictor variables (far right column) or full models (far left column) significantly ( $p < 0.05$ ) explained variation in RII. Significance and percentage deviance explained (% DE) of full model given in first column. For categorical predictor variables the ranking of the factor levels is shown.

lichens and smaller, mat-forming mosses, potentially making the cushion plants an unfavourable substrate for regeneration of the cryptogams. In contrast, the growth of mosses and lichens on cushion plants will block sunlight and limit the photosynthetic capacity and growth of the cushion plants. This interaction between cushion plants and mosses and lichens may alternatively also be amensalistic, where the cushion plants are not directly benefitted or harmed by the presence of mosses and lichens, and the mosses and lichens are excluded by the growth of *A. selago*. Irrespective of the mechanisms, the similarity in growth form between cushion plants and lichens and mosses may contribute to the absence of facilitation observed in this study (see also, e.g., Fajardo et al., 2008). In contrast, hepatic species occurring in dark and damp areas may display a more filamentous growth form, allowing the species to grow between *A. selago* leaves (e.g., *Lepidozia* and *Metzgeria* species; N.J.M. Gremmen, personal observation), experiencing a net neutral interaction with the cushion plant.

#### 4.2 | Neither distal nor proximal predictor variables explain variation in the effect of *Azorella selago* on other species

We expected the intensity and importance of the interaction between *A. selago* and the four focal taxa to be dependent on elevation, given the observed increase in abiotic severity with elevation at our study site. However, the strength of the interaction with *A. selago* did not change with abiotic severity, contrary to the predictions of the SGH (for individual species; Bertness & Callaway, 1994; He et al., 2013) and as observed by other studies assessing facilitation by cushion plant species (Arroyo et al., 2003; le Roux & McGeoch, 2010; Anthelme et al., 2012; Cavieres et al., 2016; Hupp et al., 2017). We propose three potential explanations for the lack of correlation between the RII (and  $C_{imp}$ ) of the taxa with distal as well as proximal variables.

Firstly, this study site's elevational gradient potentially spans the range of abiotic conditions within which the outcome of an interaction may be relatively consistent. For example, our results contrast with previous findings from this system where the impact of *A. selago* on the grass *Agrostis magellanica* switched from negative to positive across the species' elevational range on the island (approx. 0m to 640 m a.s.l.; le Roux & McGeoch, 2010; Gouws et al., 2021). However, le Roux and McGeoch (2010) documented that the intensity and importance of facilitation by *A. selago* plateaued at moderate and high elevations. Thus, the lack of a significant relationship between the impact of *A. selago* on other species and abiotic conditions may reflect that the range of conditions on Junior's Kop chiefly falls within this 'plateau region' of the severity gradient, where the outcome of the interaction with *A. selago* is consistent across relatively large changes in habitat conditions. Indeed, the landform covers an elevational range of 164 m to 296 m a.s.l., with le Roux and McGeoch (2010) showing minimal changes in the interaction between *A. selago* and *Agrostis magellanica* at altitudes exceeding approx. 100 m a.s.l. (albeit on a very different type of substrate). Extending

sampling across the full length of the severity gradient and/or the complete distribution of *A. selago* may be necessary to identify the range of conditions under which the community-level impact of *A. selago* is dependent on environmental conditions (le Roux & McGeoch, 2010; Liancourt et al., 2017).

Secondly, unmeasured environmental factors may be driving variation in the outcome of interactions in this system. Our results can be compared to findings by Anthelme et al. (2012) who, contrary to expectations, observed stronger community-level facilitation by *Azorella aretioides* at 4400 m a.s.l. compared to 4550 m a.s.l. due to greater nutrient availability associated with cushion plants at lower altitudes, which appeared to overwhelm the other environmental conditions that became more stressful with increasing altitude. Indeed, other studies have also indicated that nutrient availability may more strongly influence the outcome of biotic interactions than the local microclimate (see, e.g., Maestre et al., 2009a; Dvorský et al., 2013; Michalet et al., 2014 from warm and dry environments). Therefore, in addition to the frequent focus on microclimatic conditions, the influence of resource availability on the outcome of plant–plant interactions (particularly for vascular plant species) likely requires more attention.

Thirdly, the lack of significant relationships between the impact of *A. selago* on other taxa and both distal and proximal abiotic variables may be a consequence of the fine spatial scale examined here. For example, propagule dispersal across short distances (despite also representing steep abiotic gradients) could allow for the persistence of species in relatively unfavourable sites. This form of sink–source dynamics, where populations growing in association with *A. selago* subsidize otherwise non-viable populations on the adjacent substrate (see e.g. Shmida & Ellner, 1984; however, see also Kadmon & Tielborger, 1999) could obscure some of the fine-scale facilitative impacts of *A. selago* that would be detected by a demographic approach (i.e., including plant fitness and ontogeny parameters; Miriti, 2006; Tielbörger & Kadmon, 2000; Gouws et al., 2021). This suggests that the predictability of plant–plant interactions, as well as the relative benefit of using distal vs proximal variables when predicting the outcome of plant–plant interactions, may be dependent on the spatial scale of the study. We hypothesize that proximal predictors may be superior to distal predictors at intermediate scales, i.e., scales larger than typical dispersal distances, but still small enough to represent environmental heterogeneity that affects plant performance.

## 5 | CONCLUSION

To improve our understanding of facilitation, we not only need to focus on the outcome of pairwise interactions along multiple stress gradients, but also need to consider the consequences of these interactions at the plant community level (see also Soliveres & Maestre, 2014; Soliveres et al., 2015; Kjær et al., 2018). Indeed, data collected at the individual and/or species level, and studies considering the impact of only one environmental stressor or

disturbance on the outcome of plant–plant interactions, may be insufficient to test the generality of predictions from the SGH (see, e.g., Kawai & Tokeshi, 2007; Mod et al., 2014; Soliveres et al., 2015; Kjær et al., 2018). For example, our community-level results contrast with findings from two studies focusing on a subset of the vascular flora in this same study system (le Roux & McGeoch, 2008b, 2010) that demonstrated that facilitative plant–plant interactions increase with elevation. Therefore, species- and community-level studies in this field can be considered as complementary approaches, offering the opportunity to understand both the generality of, and variability within, the impacts of plant–plant and plant–lichen interactions.

Natural communities display a wide variety of responses to variation in environmental severity which ecological theories are often unable to adequately predict (Brooker et al., 2008). Our data set enables us to examine the response of an entire plant and lichen community to an interaction with a widespread benefactor species that strongly ameliorates microenvironmental conditions. Hence, our study demonstrates how complex spatial variation in environmental stressors can be explicitly considered when modelling variation in the outcome of plant community interactions.

#### AUTHOR CONTRIBUTIONS

Isabelle Patricia Rita Buyens, William A. Haddad and Peter Christiaan le Roux developed the research questions and designed the methodology. William A. Haddad performed data collection. Isabelle Patricia Rita Buyens and Peter Christiaan le Roux conducted data analysis. Isabelle Patricia Rita Buyens, Morgan Jade Raath-Krüger and Peter Christiaan le Roux wrote the manuscript, with input from William A. Haddad.

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#### DATA AVAILABILITY STATEMENT

Accompanying data and R scripts can be accessed at <https://catalogue.saeon.ac.za/records/10.15493/SAPRI.08172023>.

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## SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

**Appendix S1.** Pictures of the study site and species on sub-Antarctic Marion Island.

**Appendix S2.** Variation of abiotic variables with elevation and aspect.

**Appendix S3.** Scoria volumetric water content below *Azorella selago*, and mean ( $\pm$ SE) scoria moisture beneath *A. selago* and adjacent sites.

**Appendix S4.** Vascular plant, hepatic, lichen and moss species occurrences on *Azorella selago* and adjacent sites.

**Appendix S5.** The correlation between the competitive importance index and the relative interaction intensity index for species richness and cover of vascular plants, hepatics, mosses and lichens.

**Appendix S6.** Competitive importance index from distal models for the richness and the cover of vascular plants, hepatics, mosses and lichens.

**Appendix S7.** Competitive importance index from proximal models for the richness and cover of vascular plants, hepatics, mosses and lichens.

**Appendix S8.** Mean ( $\pm$ SE) competitive importance index for the richness and cover of vascular plant, hepatic, moss and lichen species.

**Appendix S9.** Changes in the competitive importance index for species richness (mean  $\pm$  SE) with elevation (m a.s.l.) for vascular plants, hepatic lichens and mosses.

**Appendix S10.** Changes in the competitive importance index for species cover (mean  $\pm$  SE) with elevation (m a.s.l.) for vascular plants, hepatics, lichens and mosses.

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