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Interaction intensity and importance along two stress gradients: adding shape to the stress-gradient hypothesis

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Abstract The stress-gradient hypothesis (SGH) predicts that the community-wide prevalence of positive interactions, relative to negative interactions, is greater under more severe environmental conditions. Because the frequency of positive and negative interactions within a community is the aggregate of multiple pair-wise interactions, one approach to testing the SGH is to examine how pair-wise interactions vary along severity gradients. While the SGH suggests that the net outcome of an interaction should monotonically become more positive with increasing environmental severity, recent studies have suggested that the severity-interaction relationship (SIR) may rather be unimodal. We tested which of the proposed shapes of the SIR best fits the variation in the interaction between two species along two types of severity gradients on sub-Antarctic Marion Island. This was done by comparing the performance of the grass *Agrostis magellanica* in the presence and absence of the cushion plant *Azorella selago*, along both species' entire altitudinal ranges (transects spanning 4–8 km), and along a shorter (transect = 0.4 km) wind exposure gradient. Along the altitudinal transects the relative intensity, but not the absolute intensity or the importance, of the *Azorella selago–Agrostis magellanica* interaction increased with altitude, consistently forming a plateau-shaped SIR with a positive asymptote. Thus, while the performance of *Agrostis magellanica* was negatively affected by *Azorella selago* at low altitudes, the grass benefited from growing on the cushion plant under greater environmental severity. Along the wind exposure gradient the intensity of the interaction also became more positive with increasing environmental severity for most performance measures. This suggests that the switch from a net negative to a net positive interaction can occur across both short and long distances. Therefore, this study provides strong evidence for a plateau-shaped SIR, and confirms that the SIR is unimodal along the particular non-resource severity gradients of this study.

Keywords Biotic interactions · Environmental gradient · Facilitation · Nurse plant · Severity-interaction relationship

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Introduction

Positive and negative interspecific interactions occur throughout species ranges, with considerable broad- and fine-scale spatial variation in their prevalence and relative strength (Bertness and Callaway 1994; Bruno et al. 2003; Callaway et al. 2002; Pugnaire and Luque 2001). The stress-gradient hypothesis (SGH) attributes variability in the frequency of positive and negative interactions to

spatial heterogeneity in environmental severity. The SGH posits that plants benefit from the presence of neighbouring individuals in areas of high environmental severity because the positive effects of environmental modification by neighbours outweigh the negative effects of competition for resources (Bertness and Callaway 1994; Brooker and Callaghan 1998). By contrast, under more moderate conditions the SGH predicts a net negative impact of neighbouring plants since the effects of competition with nearby individuals will overwhelm any positive effects of environmental amelioration. Thus, across multiple species the prevalence of positive interactions is predicted to be higher under greater environmental severity (Bertness and Callaway 1994). An alternative view of the SGH focuses on variability in the nature of individual pair-wise species interactions (Brooker and Callaghan 1998), which in combination determine the community-level frequency of positive interactions (see e.g. Maestre et al. 2009). From this perspective, the SGH predicts that the net outcome of specific plant interactions gradually becomes more positive with increasing environmental severity [i.e. a monotonic severity-interaction relationship (SIR) (sensu Brooker et al. 2006)], due to changes in the strength of constituent positive and negative interactions.

Recent studies, however, show that the SIR may be unimodal rather than monotonic. Indeed, some studies have observed the net outcome of interspecific interactions to be most positive at intermediate levels of environmental severity (e.g. Anthelme et al. 2007). However, even among studies reporting unimodal SIRs, there has been considerable variation in the relationship. To date, there are four general forms of the curve that have been proposed to describe the relationship between competition and facilitation along gradients of abiotic stress (see e.g. Kawai and Tokeshi 2007; Maestre et al. 2009):

1. Linear. The relative strength of positive interactions increase across the complete range of environmental severity (Fig. 1a; Bertness and Callaway 1994; Brooker and Callaghan 1998). This model is supported by results from two meta-analyses (Gómez-Aparicio et al. 2004; Lortie and Callaway 2006) and numerous experimental and observational studies (e.g. Bertness and Ewanchuk 2002; Dullinger et al. 2007; Holzapfel et al. 2006; le Roux and McGeoch 2008c).
2. Symmetrical hump shape. The net outcome of interactions is most positive at moderate environmental severity, and negative under both low and high environmental severity (Fig. 1a). This model assumes that positive effects of neighbours cannot be sustained under high abiotic severity (e.g. species ameliorative capacity is overwhelmed under extreme severity), and that competition between neighbours does not decrease

with increasing severity (Maestre and Cortina 2004). Thus, under extreme abiotic severity individuals derive little benefit and still incur a cost from growing in close proximity to neighbouring individuals. Similarly, under extreme biotic severity (e.g. intense predation or grazing), plants compete strongly with neighbours but benefit little from associational defences (i.e. protection from herbivores; Brooker et al. 2006). There is some support for this model along both resource gradients (e.g. Anthelme et al. 2007) and consumer pressure gradients (Brooker et al. 2006; Smit et al. 2007).

3. Asymmetrical hump shape. As for the previous model, the net outcome of an interaction is most positive at moderate environmental severity, but the net interaction changes to neutral under more severe abiotic conditions (Fig. 1a). This model assumes a weakening of both positive (severe environmental conditions cannot be completely ameliorated) and negative interactions (plants are smaller and grow more slowly under extreme stress) beyond moderate abiotic environmental severity, with equally small costs and benefits from growing close to neighbours under the most extreme abiotic environmental severity (see e.g. Kawai and Tokeshi 2007; Michalet et al. 2006). No empirical studies have yet provided support for this model.
4. Plateau. This model suggests that the relative strength of positive interactions will increase with environmental severity until reaching an asymptote (Fig. 1a; Kawai and Tokeshi 2007). Therefore, under extreme abiotic environmental severity individuals have a more positive net interaction than at low environmental severity, although the strength of this net interaction is constrained. Three studies provide some evidence for the plateau model (Callaway et al. 2002; Graff et al. 2007; Kawai and Tokeshi 2007).

The shape of the SIR is important for understanding and predicting community properties along environmental gradients, and is therefore of central importance to ecology (Agrawal et al. 2007; Brooker et al. 2008; see also e.g. Hacker and Gaines 1997; Michalet et al. 2006). For example, when considering the role of interspecific interactions in determining species upper altitudinal distribution limits, different SIRs lead to contrasting predictions. A linear SIR predicts that a species will be able to establish at higher altitudes in the presence of species that ameliorate environmental conditions and not in their absence (e.g. Choler et al. 2001). However, a hump-shaped SIR would suggest that the presence of other species at more stressful, higher elevations could have little effect (or even a negative effect) on the upper altitude at which the species can establish. Thus, while there is a developing body of

Fig. 1 Hypothesized shapes of the **a** severity-interaction relationship (SIR) and **b** range of curves described by the Huisman-Olff-Fresco (HOF) models in response to environmental severity. **a** Based on figure from Kawai and Tokeshi (2007). HOF curves (in **b**) used to model the hypothesized shapes of the SIR (in **a**) share the same line style (i.e. HOF II and III were used to model the plateau shape)
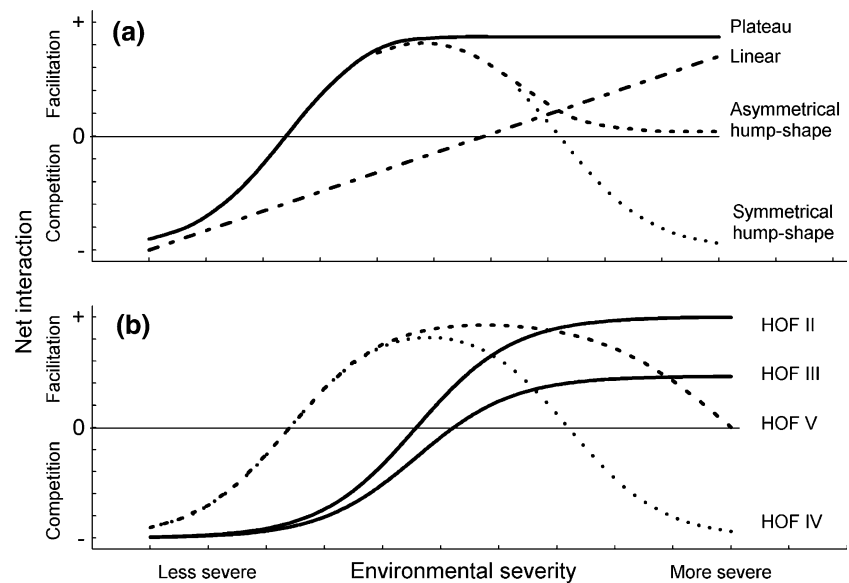
theoretical work dealing with the ecological consequences of positive interactions, the general form that the SIR may be expected to take across different stress gradients and plant communities has yet to be resolved.

Uncertainty about the shape of the SIR stems in part from four methodological issues. First, the net outcome of the interaction between species must be measured at multiple severity levels, because studies considering only one pair of sites (e.g. high and low altitude) cannot distinguish between linear and non-linear changes in interactions with increasing severity (Brooker et al. 2008; Holzapfel et al. 2006; Maestre and Cortina 2004). Second, studies need to investigate changes in interactions across a "complete" severity gradient (i.e. sites ranging from the most to the least severe environments where a species occurs; see Holzapfel et al. 2006; Kawai and Tokeshi 2007; Lortie and Callaway 2006). Studies covering a narrower range of existing severity cannot exclude the possibility of turning points or asymptotes in the relationship beyond the range of conditions investigated (Kawai and Tokeshi 2007). Third, shifts in the outcome of interspecific interactions across sites differing in environmental severity can be confounded by concurrent changes in species composition, since species traits are important determinants of the nature of interspecific interactions (Gómez-Aparicio et al. 2004; see also Elmendorf and Moore 2007; Pennings et al. 2003). Finally, investigations should simultaneously measure multiple species traits as some traits may be favoured by an interaction but not others (e.g. improved survival but lowered reproductive output: Choler et al. 2001; see also Brooker et al. 2008). Therefore, to effectively describe the shape of the SIR, changes in the net outcome of the interaction between the same set of species should be

documented at multiple sites along a complete severity gradient, examining multiple plant traits.

Further confusion about the shape of the SIR can also be attributed to the conceptual distinction between changes in the importance and the intensity of interactions along severity gradients (Grace 1993). While Brooker and Callaghan (1998) originally predicted that both the importance and intensity of facilitation should increase with increasing environmental severity, most studies only consider interaction intensity (Brooker et al. 2008). Interaction intensity describes the balance between the facilitative and competitive components of a pair-wise interaction, with absolute intensity measuring the difference in performance due to a second species, and relative intensity scaling the change in the species performance due to the second species relative to its performance in the absence of that species (Grace 1993; Weigelt and Jolliffe 2003). By contrast, interaction importance reflects the magnitude of the interaction's impact on individuals' fitness relative to all other factors. In other words, interaction importance describes the balance between the effect of the pair-wise interaction and the effect of the rest of the species' environment (Brooker and Kikvidze 2008; Brooker et al. 2008; Welden and Slauson 1986). Thus, the ecological interpretation of the SIR may differ depending on whether interaction intensity or importance is considered.

Here we test which of the proposed shapes of the SIR best fit the variation in the net interaction between two species along a complete altitudinal severity gradient on the species-poor and abiotically extreme sub-Antarctic Marion Island. Multiple performance measures of the grass *Agrostis magellanica* were compared in the presence and in the absence of the cushion plant *Azorella selago*, along the

entire altitudinal range of both species. Finer-scale variation in the *Azorella–Agrostis* interaction was also investigated along a wind exposure gradient to test if the same shape of the SIR would be observed along two types of stress gradients covering different distances (i.e. varying spatial extents). These analyses concurrently examined spatial variation in the absolute and relative intensity and the importance of the *Agrostis–Azorella* interaction to determine if the shape of the SIR varied for the different measures of interaction strength.

Materials and methods

Study site

Marion Island (46°54′S, 37°45′E; 290 km²) is the larger of the two islands comprising the Prince Edward Islands group, located in the southern Indian Ocean. The island has an oceanic climate, with cold but stable temperatures, and high winds, humidity and rainfall [although currently experiencing rapid climate change (le Roux and McGeoch 2008a)]. The island supports a relatively depauparate biota, with 40 vascular plant species and roughly 200 bryophyte and lichen species (Smith 1987).

Clear altitudinal abiotic severity gradients exist across Marion Island, as higher elevations experience lower mean temperatures, greater temperature extremes and stronger winds (le Roux 2008). The adiabatic lapse rate on the island averages 4.3°C per 1,000 m elevation (Schulze 1971), and mean and maximum wind speed increase rapidly with altitude (le Roux 2008; see also Blake 1996; le Roux and McGeoch 2008c). Soil stability also decreases with altitude, with a greater frequency and depth of freeze–thaw at higher elevations (Boelhouwers et al. 2003). Soil moisture probably also declines with elevation, due to enhanced evapotranspiration (associated with stronger winds) and more poorly developed soils (low organic matter content) at higher altitudes, further contributing to the elevational gradient in abiotic stress across the island. Therefore, with the exception of the lowest coastal areas with high salinities due to salt-spray (Huntley 1971), abiotic severity increases with altitude across Marion Island (le Roux and McGeoch 2008c). While altitude is an indirect gradient representing multiple proximate environmental factors, under "alpine" conditions it can be a useful surrogate for environmental severity (Austin 2002). In particular, on Marion Island this increasing abiotic severity with altitude is reflected in the progressive decline of species richness (le Roux and McGeoch 2008b), cover (Smith et al. 2001) and productivity [from more than 2,178 g/m² per year at the coast to less than 685 g/m² per year at higher altitudes (Smith 2008)] at higher elevations.

Only a small proportion of the island's primary productivity is consumed by herbivores (principally insects; Smith and Steenkamp 1990), and herbivory probably does not influence environmental severity across the altitudinal gradient.

Similar to elevation, wind exposure is also an important determinant of plant community composition on Marion Island (Smith and French 1988; Smith and Mucina 2006). Due to strong winds, exposed sites can be drier than sheltered equivalents (Smith and Mucina 2006), and plants growing there may experience accelerated moisture loss, enhanced cooling and wind-related physical damage (e.g. Bate and Smith 1983; Pammenter et al. 1986; see also Grace 1977). Due to the direct impact of the mechanical stresses and the indirect effects of microclimatic modification caused by strong winds, wind exposure is considered a strong measure of a site's abiotic severity (following, e.g. Eränen and Kozlov 2009; Eränen and Kozlov 2008).

Study species

Azorella selago (Apiaceae; referred to as "*Azorella*" from hereon) is a compact, low-growing, cushion-forming perennial plant (Huntley 1972). It is the most widespread plant on Marion Island, occurring from sea level to the upper altitudinal limit of vascular plant growth at 840 m a.s.l. (le Roux and McGeoch 2008b). *Azorella* is considered a keystone species on Marion Island due to its role in succession, its influence on geomorphological processes, and the high density and abundances of some invertebrate and plant species associated with it (Hugo et al. 2004; le Roux et al. 2005). The latter effect appears to be primarily due to the ability of *Azorella* cushions to function as nurse plants [i.e. *Azorella* facilitates the successful establishment of other species within its canopy (sensu e.g. Cavieres et al. 2002)], which results from its capacity to ameliorate local environment conditions by buffering soil temperatures, reducing wind speed, enhancing soil nutrient levels and providing a stable and moist substrate (Hugo et al. 2004; le Roux and McGeoch 2008c; le Roux et al. 2005; McGeoch et al. 2008; Nyakatya and McGeoch 2007).

Agrostis magellanica (Poaceae; referred to as "*Agrostis*" from hereon) is a perennial grass and the second most widespread vascular plant species on the island (Huntley 1971). This grass is dominant in mires on Marion Island, but also occurs in most other habitats (Huntley 1971), reaching altitudes exceeding 600 m a.s.l. *Agrostis* is the most common vascular plant growing on *Azorella* cushions (i.e. rooted within the cushion plant, rather than in the soil; Huntley 1972).

While our study only considered *Agrostis* and *Azorella*, they are the most widespread species on the island and contribute the majority of vascular plant biomass above

200 m a.s.l. Therefore, while our results do not describe the community-level SIR, it is likely that the net impact of the *Agrostis–Azorella* interaction will dominate an aggregated trend across all species pairs.

Data collection

Agrostis individuals were collected off *Azorella* plants and from the adjacent soil along exposed ridges from sea level to the upper altitudinal limit of vascular plant growth on Marion Island. Sixty-four pairs of *Azorella* cushions and adjacent soil (hereafter "paired samples") were sampled along two altitudinal transects on the north-eastern (NE; $n = 32$ pairs) and south-eastern (SE; $n = 32$) sides of the island at approximately 20-m altitudinal intervals (altitude measured using a barometric altimeter; Garmin Vista Mono, Garmin, USA). Medium-sized *Azorella* cushions [maximum diameter between 0.3 and 0.6 m (see le Roux and McGeoch 2004)] were randomly selected [using random bearing and distance values, following the methods of Badano and Cavieres (2006)]. Each sampled *Azorella* cushion was measured (maximum diameter) and the aerial cover of *Agrostis* on the cushion plant visually estimated. All *Agrostis* grasses rooted within the *Azorella* cushion were then carefully uprooted. A wire ring was moulded around the outer edge of each sampled *Azorella* cushion to reproduce the size and shape of the plant, and then placed 0.1 m from the cushion in a randomly selected direction. If this area overlapped with an *Azorella* cushion, another random direction was used. The aerial cover of *Agrostis* on the adjacent soil sample was visually estimated, before all *Agrostis* individuals rooted within the area were also collected. The proportion of the "soil" sample covered by large rocks (i.e. large enough to inhibit the growth of grasses) was estimated, and the performance of *Agrostis* at that site scaled to account for this area before analyses. Performance measures were scaled as:

$$X' = X / (1 - R) \tag{1}$$

where X represents the performance measure, X' the scaled performance measure and R the proportion of the sample area covered by rocks large enough to inhibit the growth of *Agrostis* seedlings. Performance measures were scaled by rock cover (i.e. areas unsuitable for *Agrostis* growth) to avoid confounding the effect of changes in abiotic stress with changes in suitable substrate availability.

In addition, variation in the performance of *Agrostis* on *Azorella* and on soil along a short exposure gradient was assessed by sampling eight pairs of *Azorella* cushions and adjacent soil at each of three sites on an exposed, coastal ridge. The three sites were within 400 m of each other, but differed considerably in environmental severity due to differing exposure to the prevailing north-westerly winds

(the sites were designated as high wind exposure, intermediate exposure, low exposure). Therefore, the spatial extent of the exposure gradient (i.e. the distance between the highly exposed and the sheltered sites was 0.4 km) was much shorter than that of the altitudinal transects (4–8 km). Differences in exposure (and therefore environmental severity) were reflected in declining species richness and total plant cover with increasing exposure across the three sites (dropping from more than eight species and >30% cover to three species and ± 10% cover). Following the same methodology as the altitudinal transects, all *Agrostis* individuals were collected from medium-sized *Azorella* cushions and from adjacent soil areas of the same size and shape.

All harvested *Agrostis* individuals were returned to the laboratory and dried at 60°C. The total mass (roots and shoots), leaf mass, basal diameter, number of inflorescences and number of inflorescence stalks were measured for each individual. These data provided four estimates of *Agrostis* performance: abundance, biomass (measured both as leaf biomass and total biomass), cover (measured both as canopy cover and basal cover) and reproductive output (numbers of inflorescences and inflorescence stems). Inflorescences and inflorescence stalks both measure reproductive effort, although the number of inflorescences represents more recent flowering events (i.e. within the last growing season), while the number of inflorescence stems provides an estimate of reproductive output over a long span. All seven performance variables were analysed, but due to the similarity of results for total mass and leaf mass, canopy cover and basal cover, and inflorescences and inflorescence stalks, results are only presented for total mass, canopy cover and inflorescence abundance (although full results are presented in the appendices).

Data analysis

The impact of *Azorella* on *Agrostis* was quantified using three distinct metrics, each measuring the impact of the cushion plant on the grass in a different way. First, the absolute interaction intensity [also known as absolute competition intensity (ACI)] was calculated as the difference between *Agrostis* performance in the presence and absence of *Azorella*:

$$\text{ACI} = P_{T+N} - P_{T-N} \tag{2}$$

where P_{T+N} and P_{T-N} represent the performance of *Agrostis* in the presence and absence of *Azorella*, respectively (Grace 1993; Weigelt and Jolliffe 2003).

Second, the relative intensity of the *Azorella-Agrostis* interaction (relative interaction intensity; RII) was assessed by calculating the relative interaction index:

$$\text{RII} = (P_{T+N} - P_{T-N})/(P_{T+N} + P_{T-N}) \qquad (3)$$

where the difference in *Agrostis* performance in the presence and absence of *Azorella* is scaled to the total *Agrostis* performance at that site (Armas et al. 2004). RII is bounded between −1 and 1, with positive (negative) values indicating net facilitative (competitive) interactions, and larger absolute values indicating stronger intensity of the interaction. This index has performed well in other studies testing the SIR (e.g. Elmendorf and Moore 2007; Tirado and Pugnaire 2005).

Finally, the importance of the *Azorella-Agrostis* interaction was calculated using the index of competitive importance (C_{imp}; following Brooker et al. 2005). This index scales the difference in *Agrostis* performance at a site in the presence and absence of *Azorella* (i.e. $P_{T+N} - P_{T-N}$) relative to the maximum performance difference that could be achieved at that site. Therefore,

$$C_{imp} = (P_{T+N} - P_{T-N})/(\text{Max}[P_{T-N}; P_{T+N}]$$
$$\text{across all samples} - \text{Min}[P_{T-N}; P_{T+N}]) \qquad (4)$$

where "Max[P_{T-N}; P_{T+N}] across all samples" refers to the largest value of P_{T-N} or P_{T+N} across all samples being considered, and Min[P_{T-N}; P_{T+N}] refers to the smallest value of either P_{T-N} or P_{T+N} at that site. In other words, the denominator of Eq. 4 calculates the difference between maximal performance across the entire gradient and the minimal performance at the site. The index was modified from Brooker et al. (2005) by changing "Max[P_{T-N}] across all samples" to "Max[P_{T-N}; P_{T+N}] across all samples" to ensure that the index scaled from −1 to 1 under extreme competition and facilitation, respectively (the original index approached infinity for strongly facilitative interactions). Thus, C_{imp} is also bounded between −1 and 1, with positive (negative) values indicating facilitative (competitive) interactions, and larger absolute values indicating greater importance of the interaction. Therefore, while ACI measures the absolute impact of a neighbour on a focal plant's performance, RII scales ACI relative to the average performance of the focal plant at that site and C_{imp} scales ACI relative to the maximum ACI possible at that site.

To distinguish which of the proposed shapes the *Agrostis–Azorella* severity-interaction most closely followed, the relationship between ACI (and RII and C_{imp}) and altitude was fitted to five different models (Fig. 1b). For analyses, RII and C_{imp} values were scaled to range between 0 and 1 (i.e. within the limits of the beta distribution; see below), and altitude was linearly scaled to range from 0 to 1 to simplify calculations (following recommendations and method of Smithson and Verkuilen 2006). ACI values were scaled to range between 0 and 1, assuming the maximum observed performance of *Agrostis*

(irrespective of the presence or absence of *Azorella*) across the whole study as an approximation of the maximum performance of the grass possible in the presence and absence of *Azorella*. First, a linear model was fitted to the data. Thereafter, four non-linear Huisman-Olff-Fresco (HOF) models were fitted. This set of nested models describes two forms of a logistic curve, a symmetrical unimodal curve, and an asymmetrical unimodal curve (Fig. 1b; Huisman et al. 1993). The models can be summarized as:

$$\mu = M \frac{1}{1 + \exp(a + bx)} \frac{1}{1 + \exp(c - dx)}. \qquad (5)$$

where μ is the expected value (i.e. ACI, RII or C_{imp}), M is the upper bound (set to 1 since that is the maximum value of the scaled indices) and a, b, c and d are the parameters to be estimated. These models form a hierarchical set, with nested models differing only by the number of parameters set to zero (Huisman et al. 1993; Oksanen and Minchin 2002). Estimating all four parameters (the most complex model, HOF V) models a skewed (i.e. asymmetrical) unimodal relationship, while setting $b = d$ (HOF IV) models a symmetrical unimodal relationship (see Fig. 1b). Setting c and $d = 0$ models a logistic (i.e. a plateau shape, HOF II) relationship with an upper bound of 1, while just setting $d = 0$ models a logistic curve with an upper bound of <1 (HOF III). The simplest relationship (where μ equals a constant, HOF I) is modelled by setting b, c, and $d = 0$, and represents our null hypothesis (i.e. expected if there is no effect of altitude on ACI, RII or C_{imp}).

Models were fitted to the data separately for the two transects as initial analyses revealed some differences between *Agrostis* performance on the transects. All models were repeated including the maximum diameter of the area sampled as a covariate. Models were fitted using maximum likelihood estimation, assuming a beta distribution of the response variables. The beta distribution is suitable for modelling our dependent variables since C_{imp} and RII both comprise bounded continuous data (Ferrari and Cribari-Neto 2004; Smithson and Verkuilen 2006). The proportion of variance explained by each model was calculated as a pseudo R^2 (Ferrari and Cribari-Neto 2004). Analysis of deviance [based on the change in the overall model likelihood for each additional parameter included in the model (McCullagh and Nelder 1989)] was used to distinguish the minimum adequate model where models' *df* differed. However, models with the same *df* (e.g. HOF III and IV; linear model and HOF II) were distinguished using pseudo R^2 values.

Therefore, we were able to test which of the five response shapes (linear, HOF II–HOF V) provided the best fit to the data, making it possible to distinguish among the proposed shapes of the SIR. A linear model (with a positive slope coefficient) would provide support for Brooker and

Callaghan's (1998) hypothesized relationship. In contrast, the HOF IV model would support Maestre and Cortina's (2004) symmetrical hump-shape model. HOF II and HOF III models suggest that Kawai and Tokeshi's (2007) plateau model provide the best fit to the SIR. Finally, a HOF V model would provide support for either the asymmetrical hump-shape model of Michalet et al. (2006) or the plateau model, depending if the interaction values continue to increase (or level off) or decrease respectively.

To compare the intensity and importance of the *Azorella–Agrostis* interaction between the three sites on the exposure gradient, ACI, RII and C_{imp} were again modelled with a beta distribution. Post hoc Tukey honest significant difference tests were used to determine which sites differed from each other where exposure level contributed significantly to explaining variation in ACI, RII and C_{imp}. These models were also repeated including the maximum diameter of the area sampled as a covariate. All models were fitted using the gnlm (Lindsey 2007) and betareg (de Bustamante Simas 2006) packages in R (R Development Core Team 2007).

Results

The abundance, cover and biomass of *Agrostis* growing in the soil declined linearly with altitude (square root-transformed abundance data, $F_{1,62} = 42.8$, $P < 0.001$, $R^2 = 39.9\%$; arcsine-square root-transformed canopy cover, $F_{1,62} = 46.26$, $P < 0.001$, $R^2 = 42.7\%$; square root-transformed total mass, $F_{1,62} = 31.96$, $P < 0.001$, $R^2 = 33.0\%$; data pooled across both transects), supporting the assumption that elevation is a strong proxy for abiotic severity on the island. A similar result was found along the exposure gradient, where *Agrostis* abundance, cover and total mass declined consistently with increasing wind exposure in the absence of *Azorella* (Fig. 3).

In the altitudinal transects the highest *Azorella* plants were found at 630 and 652 m a.s.l., and the lowest individuals just above the island's coastal cliffs (10 m a.s.l.). The distribution of *Agrostis* was nested within that of *Azorella*, with approximately coincident lower elevational limits but much lower upper limits than *Azorella* on both transects (446 and 465 m a.s.l.; details in Table 1).

The influence of *Azorella* on *Agrostis* performance differed considerably with position on the altitude and exposure gradients. In the NE transect ACI was not related to altitude for any performance measures. By contrast, ACI was significantly related to altitude for three performance measures in the SE transect: ACI peaked at mid altitudes for *Agrostis* cover, declining to zero at higher elevations. However, for total mass and inflorescence abundance ACI showed a plateau-shaped relationship with altitude, reaching a positive asymptote at high and mid altitudes (Table 2;

Fig. 2). The relationship between ACI and wind exposure was also variable. The difference in *Agrostis* inflorescence abundance was increasingly positive under greater wind exposure (the same trend was evident for total mass and canopy cover), while the difference in abundance was unaffected by exposure.

By contrast, the relative intensity of *Agrostis*'s interaction with *Azorella* increased with altitude for most measures of performance in the altitudinal transects, generally shifting from strongly negative (i.e. a net competitive effect) at low altitudes, to a positive plateau at higher altitudes (i.e. a net facilitative effect; Fig. 2; see also Fig. S1 in Electronic supplementary material). In these transects *Agrostis* performed better in the presence of *Azorella* than in the absence of the cushion plant in most samples. HOF III models provided the best fit to the data for most relationships, with a plateau at RII = 0.48–0.92 (Table 2; full results in Table S1). Where HOF V models performed significantly better than HOF III models, RII values at high altitudes all equalled 1 (Table 2).

Along the exposure gradient the relative intensity of the interaction increased from weakly positive to strongly positive with increasing exposure for all measures of *Agrostis* abundance, cover and biomass (Fig. 3, Table 3). However, for reproductive output, there was no difference in relative intensity between exposure levels (Table 3; full results in Table S2). Thus, RII and environmental severity were significantly related in most analyses, with a plateau-shaped relationship across the altitudinal gradient, and an approximately linear relationship over the shorter exposure gradient.

Similar to ACI, the importance of the *Azorella-Agrostis* interaction generally did not vary with altitude (Table 2; see e.g. Fig. 2), revealing that the difference in *Agrostis* performance due to *Azorella* relative to other environmental factors was not affected by altitude. Only in the SE transect were two of the performance measures significantly related to altitude; one formed a positive plateau and the other a unimodal relationship with altitude (Table 2). Similar results were observed along the exposure gradient, and the importance of the interaction was not related to exposure for *Agrostis* abundance, cover or biomass. However, the importance of the *Azorella–Agrostis* interaction increased significantly with exposure for reproductive output (Table 3; Fig. 3). These results suggest that interaction importance and environmental severity are generally not significantly related, but tend to be non-linear when they are.

Discussion

There was considerable variation in the strength of the *Azorella–Agrostis* interaction in this system, across both

Table 1 Summary of the *Azorella selago*-soil pairs sampled and *Agrostis magellanica* individuals harvested from these samples

	Altitudinal transects		Wind exposure gradient		
	NE	SE	High (i.e. exposed)	Intermediate	Low (i.e. sheltered)
All samples (irrespective of *Agrostis* presence)					
Number of samples	32	32	8	8	8
Highest altitude (m a.s.l.)	630	652	102	97	89
Lowest altitude	10	10	_[b]	_[b]	_[b]
Plant cover on all soil samples (%, mean ± SE)[a]					
Agrostis	4.1 ± 1.9	5.8 ± 1.4	0.6 ± 0.3 a	7.3 ± 2.7 ab	11.8 ± 3.7 b
Other vascular species	14.3 ± 4.7	16.5 ± 4.7	2.8 ± 2.5	11.3 ± 10.2	6.5 ± 3.9
Moss	7.8 ± 1.9	7.8 ± 1.9	0.3 ± 0.3	1.9 ± 0.9	5.0 ± 1.6
Epiphyte cover on all *Azorella* samples (%, mean ± SE)[a]					
Agrostis	8.7 ± 1.6	9.5 ± 1.7	14.4 ± 1.5	21.9 ± 4.5	19.4 ± 2.9
Other vascular species	4.3 ± 1.5	1.9 ± 0.7	1.5 ± 0.6	2.4 ± 1.8	2.1 ± 1.9
Moss	2.2 ± 0.7	0.7 ± 0.2	0 ± 0 a	0 ± 0 a	3.8 ± 1.8 b
Samples with *Agrostis* present on soil					
Number of samples	14	22	8	8	8
Highest altitude	465	423	102	97	89
Lowest altitude	50	10	_[b]	_[b]	_[b]
Total abundance	588	715	68	151	536
Total biomass (g)	29.8	61.8	1.2	38.6	47.5
Total number of inflorescences	47	125	4	12	8
Samples with *Agrostis* present on *Azorella*					
Number of samples	18	23	8	8	8
Highest altitude	465	446	102	97	89
Lowest altitude	50	10	_[b]	_[b]	_[b]
Total abundance	2,677	3,081	1,169	1,265	1,806
Total biomass (g)	250.7	197.7	127.7	125.4	94.2
Total number of inflorescences	588	352	240	148	51
Number of samples with *Agrostis* on soil and *Azorella*	14	22	8	8	8

NE North-east, *SE* south-east

[a] Sites not sharing a letter differ significantly ($P < 0.05$)

[b] All sites within close proximity

severity gradients and between transects. RII and altitude were most consistently and significantly related, showing a plateau shape in the altitudinal transects. By contrast, the ACI and the C_{imp} of the interaction varied independently of altitude (exceptions occurred in the SE transect, but the form of the relationship was inconsistent). Similar results were observed along the wind exposure gradient, with RII varying with exposure, and ACI and C_{imp} not differing significantly across the gradient. Therefore, the most consistent form of the SIR was a plateau shape, associated with the relative intensity of the *Azorella–Agrostis* interaction. The absolute intensity and importance of the interaction were generally unrelated to environmental severity.

These results support the general conceptual hypothesis of the SGH, i.e. facilitation increases with stress. However, in contrast to the general shape of the relationship first proposed, our data strongly support the plateau model for

the SIR (in agreement with Graff et al. 2007; Kawai and Tokeshi 2007; see also Callaway et al. 2002). The plateau-shaped SIR in the altitudinal transects showed that the impact of *Azorella* on *Agrostis* performance became more beneficial with increasing environmental severity before reaching a positive asymptote at high altitudes. Along the exposure gradient the intensity of the *Azorella-Agrostis* interaction also became more positive with increasing environmental severity (in agreement with, e.g. Choler et al. 2001). While the complete exposure gradient was not examined, the SIR increased monotonically over the range of exposure levels occurring on the landform that was sampled. Despite the large differences in the spatial extent of the two gradients the SIR was thus consistently mono-tonic across the altitudinal and exposure gradients. There-fore, the switch from net negative (or weakly positive) to strongly net positive *Azorella–Agrostis* interactions

Table 2 The shape of the minimum adequate models describing the relationship between the intensity and importance of the *Azorella selago–Agrostis magellanica* interaction along an altitudinal gradient

	SE transect		NE transect	
	Shape	Pseudo R^2	Shape	Pseudo R^2
Absolute interaction intensity (ACI)				
Abundance	–[a]		–[a]	
Canopy cover	Asymmetrical hump	0.49	–[a]	
Total mass	Plateau	0.22	–[a]	
Inflorescences	Plateau	0.26	–[a]	
Relative interaction intensity (RII)				
Abundance	Plateau	0.74	–[a]	
Canopy cover	Plateau	0.61	Plateau	0.72
Total mass	Plateau	0.63	Plateau[b]	0.80
Inflorescences	Plateau	0.70	Plateau	0.91
Interaction importance (C_{imp})				
Abundance	–[a]		–[a]	
Canopy cover	Asymmetrical hump	0.46	–[a]	
Total mass	–[a]		–[a]	
Inflorescences	Plateau	0.26	–[a]	

Only significant models ($P \leq 0.05$) are listed. Except where indicated, the plateau shape was best modelled by Huisman-Olff-Fresco (HOF) III models. Complete statistics are given in Table S1, and selected relationships illustrated in Figs. 2 and S1. For other abbreviations, see Table 1

[a] None of the models explained a significant proportion of the variance

[b] HOF V model gave the best fit, but showed a plateau shape

occurred along both severity gradients, although across different spatial extents. The observed monotonic SIR along the altitude and exposure gradients (i.e. non-resource gradients) agrees with suggestions that unimodal SIRs are only expected along resource gradients (Kawai and Tokeshi 2007; Maestre and Cortina 2004).

In contrast to the relative intensity of the *Azorella–Agrostis* interaction, both the absolute intensity and the importance of the interaction were weakly and inconsistently related to altitude. However, in the few significant cases, the impact of *Azorella* on *Agrostis* performance was always more positive at mid altitudes than at low altitudes (although the impact of the interaction varied between positive and neutral at the highest altitudes). For example, in the SE transect ACI and C_{imp} for canopy cover (asymmetrical hump shape) and reproductive output (plateau shape) were significantly related to altitude. Similarly along the exposure gradient, the absolute intensity and the importance of the *Azorella–Agrostis* interaction for reproductive output increased with wind exposure. This suggests that the positive impact of *Azorella* on *Agrostis* can, in some situations, increase with environmental severity

relative to the impact of other environmental factors on *Agrostis* performance (in agreement with, e.g. Gaucherand et al. 2006; Sammul et al. 2000; see also Brooker et al. 2005). In such a case, the performance of *Agrostis* under extreme environmental conditions depends primarily on whether a facilitator (e.g. *Azorella*) is present. By contrast, under more moderate conditions the grass's performance is determined by other environmental factors (i.e. the presence or absence of the facilitator has less of an impact on performance).

In most analyses, the absolute intensity and the importance of the *Azorella–Agrostis* interaction varied independently of altitude. The absence of a significant relationship between C_{imp} and altitude is of particular interest. It suggests that along the altitudinal gradient the increasing facilitative effect of *Azorella* was balanced by the increasingly negative effect of environmental severity. As a result, we cannot support the prediction of Brooker et al. (2008) that the importance of facilitative interactions will peak at high (but not extreme) environmental severity. Indeed, the presence of *Azorella* had a relatively constant proportional effect on the performance of *Agrostis*, suggesting that the impact of *Azorella* on the fitness of *Agrostis* is unrelated to environmental severity.

Variation in ACI, RII and C_{imp} along the severity gradients reflected some fundamental similarities and differences between these interaction indices. Most noticeably, variation in ACI and C_{imp} was similar across both types of severity gradients, with C_{imp} values approximating rescaled ACI values. This occurred because the best performance of *Agrostis* was much greater than the average performance of the grass along the gradients. In other words:

$$\text{Max}\ [P_{T-N};\ P_{T+N}]\ \text{across all samples}$$
$$\gg \text{Min}[P_{T-N};\ P_{T+N}]$$

As a result the denominator in Eq. 4 only varied slightly across most sites, effectively acting as a constant. This suggests that along environmental severity gradients where there is strong variation in the performance of the focal plant, the absolute intensity and importance of a pair-wise interaction can be strongly correlated.

Agrostis performed better when growing on *Azorella* than on soil in most samples (e.g. in the NE and SE transects), particularly at higher altitudes, providing evidence for a nurse effect. Indeed, other cushion plants in the same family (from the genera *Azorella*, *Laretia* and *Bolax*) are also known to act as nurse plants to other vascular species (Badano et al. 2007; Cavieres et al. 2002; Cavieres et al. 2007; Molina-Montenegro et al. 2000). Because *Agrostis* abundance and biomass are low on the soil at higher elevations, the grasses growing on *Azorella* represent the majority of the population. This is particularly pronounced
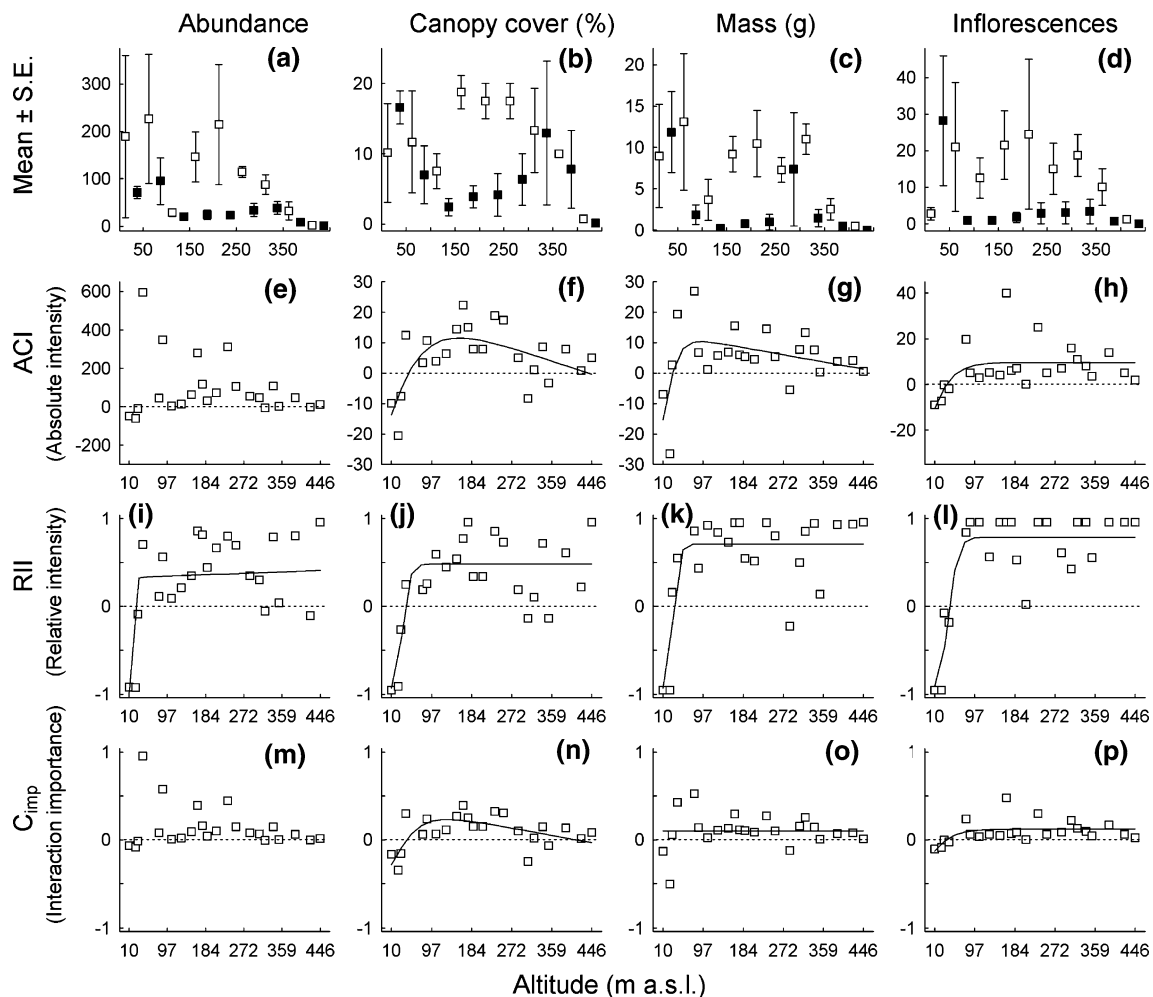
Fig. 2 Variation in the performance (mean ± SE) of *Agrostis magellanica* along the SE altitudinal gradient in the presence (*empty squares*) and absence (*filled squares*) of *Azorella selago*. Performance measures are **a** abundance, **b** canopy cover, **c** total mass, and **d** number of inflorescences. The absolute intensity (*ACI*; **e–h**), relative intensity (*RII*; **i–l**) and interaction importance (C_{imp}; **m–p**) of the *Azorella–Agrostis* interaction for these same variables. The *solid line* shows the best fit model to the data. Complete statistics in Table S1: see Fig. S1 for the equivalent data for the north-east transect

for the production of inflorescences at higher altitudes, with more than 90% of the total inflorescence crop borne by individuals growing on *Azorella*. Thus, since *Agrostis* growing on the cushion plant comprises the bulk of the population and produces the majority of inflorescences under severe environmental conditions, source-sink population dynamics may exist for *Agrostis* growing on *Azorella* (the source populations) and on the soil (the sink population) at higher elevations (see e.g. Tirado and Pugnaire 2003; although see also Kadmon and Tielbörger 1999). However, while the proportional increase in *Agrostis* performance due to *Azorella* is large at higher altitudes, the absolute increase can be small (i.e. ACI values). Nonetheless, the interaction appears sufficient to maintain *Agrostis* populations under abiotic environmental extremes.

Furthermore, it appears that the *Azorella–Agrostis* interaction may also extend the altitudinal limit of *Agrostis* beyond the range the grass would reach in the absence of *Azorella*. This was originally suggested by Huntley (1972), and has been reported for at least one species growing on *Azorella monantha* in the Andes (Badano et al. 2007; see also Bruno et al. 2003; Choler et al. 2001). Thus, it is possible that the positive influence of *Azorella* on *Agrostis* at fine spatial scales could affect the distribution of *Agrostis* at a much broader spatial scale. These results raise the question of what limits the facilitative interaction between *Azorella* and *Agrostis*, since the cushion plant's elevational distribution far exceeds that of the grass. There appears to be an abrupt limit to *Azorella*'s ability to facilitate *Agrostis*, but only at an altitude exceeding the elevational range of most soil-rooted grasses.
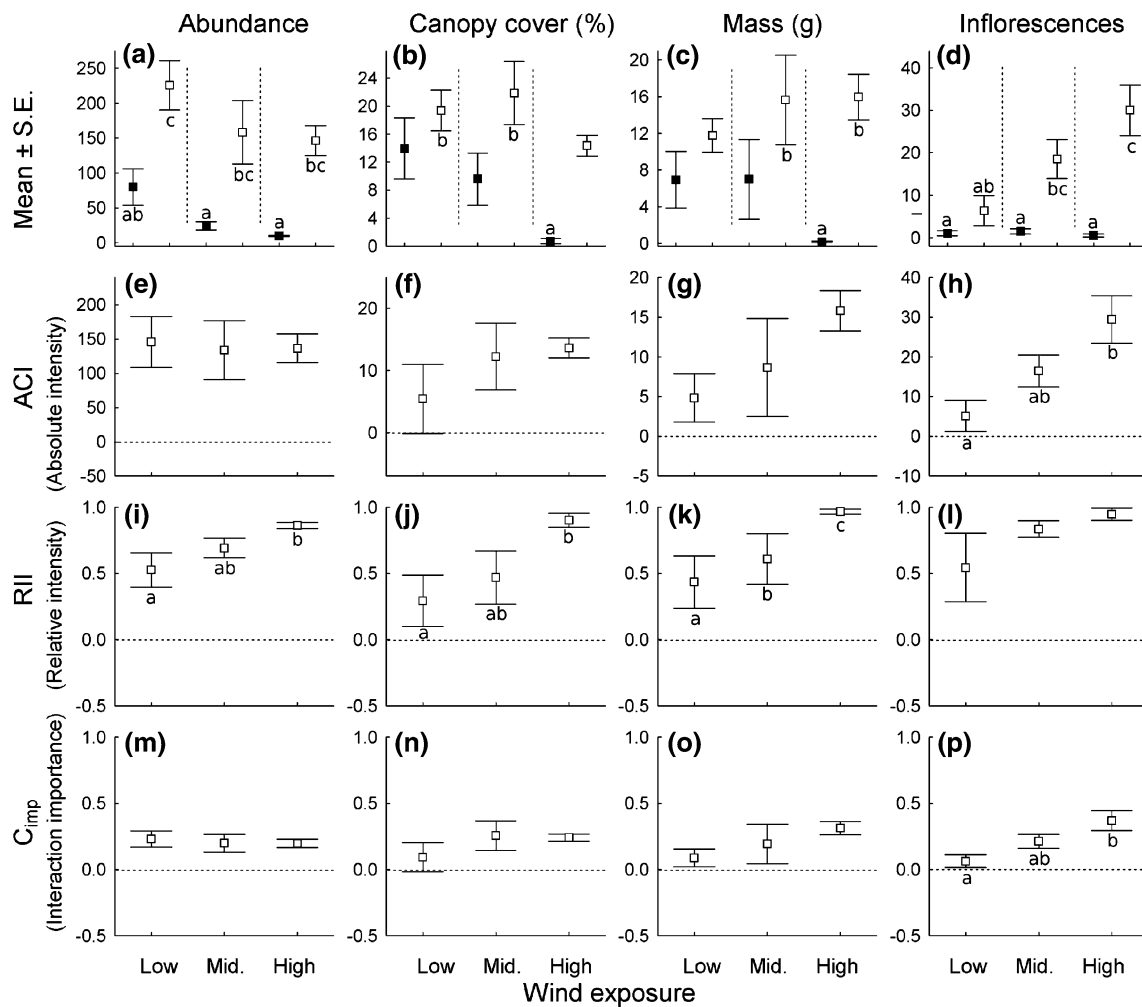
Fig. 3 Variation in the performance (mean ± SE) of *Agrostis magellanica* across a gradient of increasing wind exposure in the presence (*empty squares*) and absence (*filled squares*) of *Azorella selago*. Performance measures are: **a** abundance, **b** canopy cover, **c** total mass and **d** number of inflorescences. ACI (**e–h**), RII (**i–l**) and C_{imp} (**m–p**) of the *Azorella–Agrostis* interaction for these same variables. **a–p** Groups not sharing common letters differ significantly ($P < 0.05$). Complete statistical results in Table S2. *Low* Low wind exposure (i.e. sheltered), *Mid.* intermediate wind exposure, *High* high wind exposure; for other abbreviations, see Fig. 2

More generally, the existence of a plateau-shaped SIR adds to the evidence that positive interactions can be important under extreme environmental conditions (debate reviewed by Kawai and Tokeshi 2007). Predictions of community models that assume a linear SIR (e.g. Hacker and Gaines 1997) are in this case more appropriate than those that assume a hump-shaped relationship (e.g. Michalet et al. 2006). Indeed, the two predictions made by Hacker and Gaines (1997) are realized in our study. First, facilitation acts to increase the diversity of species at high altitudes through the facilitation of the occurrence of *Agrostis* at higher altitudes in the NE and SE transects (le Roux and McGeoch 2008b). Second, facilitation of *Agrostis* by *Azorella* at high altitudes also increases the diversity of interspecific interactions. Specifically, the

presence of *Agrostis* provides an additional niche for many species of microarthropods, increasing the abundance of this group of animals within *Azorella* (Hugo et al. 2004). Importantly, if only a portion of the altitudinal gradient had been examined, a qualitatively different shape for the SIR would have been documented. For example, if low altitude sites were not included, interaction intensity would have varied independently of altitude (or even show a negative correlation) in most analyses. Clearly, changes in species interactions must be considered along the full length of severity gradients to correctly identify the shape of the SIR.

This study demonstrates the variation that may be expected in the SIR, although net interspecific interactions generally became more positive with increasing environmental severity, levelling off to a positive asymptote at

Table 3 Differences in the net effect of *Azorella selago* on *Agrostis magellanica* at three sites along a wind exposure gradient

Index	P	Pseudo R^{2a}	Factor levels[b]
ACI			
Abundance	0.325		
Canopy cover	0.066	0.26	H > M > L
Total mass	0.268		
Inflorescences	0.005	0.40	H > M > L
RII			
Abundance	0.038	0.37	H > M > L
Canopy cover	0.021	0.37	H > M > L
Total mass	0.001	0.06	H > M > L
Inflorescences	0.431		
C_{imp}			
Abundance	0.294		
Canopy cover	0.123		
Total mass	0.393		
Inflorescences	0.005	0.40	H > M > L

Complete statistics are given in Table S2 and selected relationships illustrated in Fig. 3. *H* High wind exposure, *M* intermediate wind exposure, *L* low wind exposure (i.e. sheltered); for other abbreviations, see Table 2

[a] Pseudo R^2 estimated the proportion of the variance explained by significant models

[b] > indicates ranking of the effect of the different factor levels

intermediate and high altitudes. This sub-Antarctic system therefore provides clear support for the plateau-shaped SIR.

References

Agrawal AA et al (2007) Filling key gaps in population and community ecology. Front Ecol Environ 5:145–152

Anthelme F, Michalet R, Saadou M (2007) Positive associations involving the tussock grass *Panicum turgidum* Forssk. in the Air-Tenere Reserve, Niger. J Arid Environ 68:348–362

Armas C, Ordiales R, Pugnaire FI (2004) Measuring plant interactions: a new comparative index. Ecology 85:2682–2686

Austin MP (2002) Spatial prediction of species distribution: an interface between ecological theory and statistical modelling. Ecol Model 157:101–118

Badano EI, Cavieres LA (2006) Impacts of ecosystem engineers on community attributes: effects of cushion plants at different elevations of the Chilean Andes. Divers Distrib 12:388–396

Badano EI, Villarroel E, Bustamante RO, Marquet PA, Cavieres LA (2007) Ecosystem engineering facilitates invasions by exotic plants in high-Andean ecosystems. J Ecol 95:682–688

Bate GC, Smith VR (1983) Photosynthesis and respiration in the sub-Antarctic tussock grass *Poa cookii*. New Phytol 95:533–543

Bertness MD, Callaway RM (1994) Positive interactions in communities. Trends Ecol Evol 9:191–193

Bertness MD, Ewanchuk PJ (2002) Latitudinal and climate-driven variation in the strength and nature of biological interactions in New England salt marshes. Oecologia 132:392–401

Blake BJ (1996) Microclimate and prediction of photosynthesis at Marion Island. M.Sc. thesis, Department of Botany and Genetics, University of the Orange Free State, Bloemfontein, South Africa

Boelhouwers J, Holness S, Sumner P (2003) The maritime sub-Antarctic: a distinct periglacial environment. Geomorphology 52:39–55

Brooker RW, Callaghan TV (1998) The balance between positive and negative plant interactions and its relationship to environmental gradients: a model. Oikos 81:196–207

Brooker RW, Kikvidze Z (2008) Importance: an overlooked concept in plant interaction research. J Ecol 96:703–708

Brooker RW et al (2005) The importance of importance. Oikos 109:63–70

Brooker RW, Scott D, Palmer SCF, Swaine E (2006) Transient facilitative effects of heather on Scots pine along a grazing disturbance gradient in Scottish moorland. J Ecol 94:637–645

Brooker RW et al (2008) Facilitation in plant communities: the past, the present, and the future. J Ecol 96:18–34

Bruno JF, Stachowicz JJ, Bertness MD (2003) Inclusion of facilitation into ecological theory. Trends Ecol Evol 18:119–125

Callaway RM et al (2002) Positive interactions among alpine plants increase with stress. Nature 417:844–848

Cavieres LA, Arroyo MTK, Peñaloza A, Molina-Montenegro MA, Torres C (2002) Nurse effect of *Bolax gummifera* cushion plants in the alpine vegetation of the Chilean Patagonian Andes. J Veg Sci 13:547–554

Cavieres LA, Badano EI, Sierra-Almeida A, Molina-Montenegro MA (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. Arct Antarct Alp Res 39:229–236

Choler P, Michalet R, Callaway RM (2001) Facilitation and competition on gradients in alpine plant communities. Ecology 82:3295–3308

de Bustamante Simas A (2006) The betareg package: beta regression for modeling rates and proportions, version 1.2. Retrievable from http://www.cran.r-project.org

Dullinger S et al (2007) Weak and variable relationships between environmental severity and small-scale co-occurrence in alpine plant communities. J Ecol 95:1284–1295

Elmendorf SC, Moore KA (2007) Plant competition varies with community composition in an edaphically complex landscape. Ecology 88:2640–2650

Eränen JK, Kozlov MV (2008) Increasing intraspecific facilitation in exposed environments: consistent results from mountain birch populations in two subarctic stress gradients. Oikos 117:1569–1577

Eränen J, Kozlov M (2009) Interactions between mountain birch seedlings from differentiated populations in contrasting environments of subarctic Russia. Plant Ecol 200:167–177

Ferrari SLP, Cribari-Neto F (2004) Beta regression for modelling rates and proportions. J Appl Stat 31:799–815

Gaucherand S, Liancourt P, Lavorel S (2006) Importance and intensity of competition along a fertility gradient and across species. J Veg Sci 17:455–464

Gómez-Aparicio L, Zamora R, Gómez JM, Hódar JA, Castro J, Baraza E (2004) Applying plant facilitation to forest restoration:

A meta-analysis of the use of shrubs as nurse plants. Ecol Appl 14:1128–1138

Grace J (1977) Plant response to wind. Academic Press, London

Grace JB (1993) The effects of habitat productivity on competition intensity. Trends Ecol Evol 8:229–230

Graff P, Aguiar MR, Chaneton EJ (2007) Shifts in positive and negative plant interactions along a grazing intensity gradient. Ecology 88:188–199

Hacker SD, Gaines SD (1997) Some implications of direct positive interactions for community species diversity. Ecology 78:1990–2003

Holzapfel C, Tielbörger K, Parag HA, Kigel J, Sternberg M (2006) Annual plant-shrub interactions along an aridity gradient. Basic Appl Ecol 7:268–279

Hugo EA, McGeoch MA, Marshall DJ, Chown SL (2004) Fine scale variation in microarthropod communities inhabiting the keystone species Azorella selago on Marion Island. Polar Biol 27:466–473

Huisman J, Olff H, Fresco LFM (1993) A hierarchical set of models for species response analysis. J Veg Sci 4:37–46

Huntley BJ (1971) Vegetation. In: van Zinderen Bakker EM Sr, Winterbottom JM, Dyer RA (eds) Marion and Prince Edward Islands: report on the South African biological and geological expeditions, 1965–1966. Balkema, Cape Town, pp 98–160

Huntley BJ (1972) Notes on the ecology of Azorella selago Hook. f. S Afr J Bot 38:103–113

Kadmon R, Tielbörger K (1999) Testing for source-sink population dynamics: an experimental approach exemplified with desert annuals. Oikos 86:417–429

Kawai T, Tokeshi M (2007) Testing the facilitation–competition paradigm under the stress-gradient hypothesis: decoupling multiple stress factors. Proc R Soc B 274:2503–2508

le Roux PC (2008) Climate and climate change. In: Chown SL, Froneman PW (eds) The Prince Edward Islands: land-sea interactions in a changing ecosystem. African SunMedia, Stellenbosch, pp 39–64

le Roux PC, McGeoch MA (2004) The use of size as an estimator of age in the subantarctic cushion plant, Azorella selago (Apiaceae). Arct Antarct Alp Res 36:608–616

le Roux PC, McGeoch MA (2008a) Changes in climate extremes, variability and signature on sub-Antarctic Marion Island. Climatic Change 86:309–329

le Roux PC, McGeoch MA (2008b) Rapid range expansion and community reorganization in response to warming. Glob Change Biol 14:2950–2962

le Roux PC, McGeoch MA (2008c) Spatial variation in plant interactions across a severity gradient in the sub-Antarctic. Oecologia 155:831–844

le Roux PC, McGeoch MA, Nyakatya MJ, Chown SL (2005) Effects of simulated climate change on a keystone plant species in the sub-Antarctic. Glob Change Biol 11:1628–1639

Lindsey JK (2007) gnlm: generalized nonlinear regression models. Retrievable from http://popgen.unimaas.nl/~jlindsey/rcode.html

Lortie CJ, Callaway RM (2006) Re-analysis of meta-analysis: support for the stress-gradient hypothesis. J Ecol 94:7–16

Maestre FT, Cortina J (2004) Do positive interactions increase with abiotic stress? A test from a semi-arid steppe. Proc R Soc B 271:S331–S333

Maestre FT, Callaway RM, Valladares F, Lortie CJ (2009) Refining the stress-gradient hypothesis for competition and facilitation in plant communities. J Ecol 97:199–205

McCullagh P, Nelder JA (1989) Generalized linear models, 2nd edn. Chapman & Hall, London

McGeoch MA, le Roux PC, Hugo AE, Nyakatya MJ (2008) Spatial variation in the terrestrial biotic system. In: Chown SL, Froneman PW (eds) The Prince Edward Islands: land-sea interactions in a changing ecosystem. African SunMedia, Stellenbosch, pp 245–276

Michalet R et al (2006) Do biotic interactions shape both sides of the humped-back model of species richness in plant communities? Ecol Lett 9:767–773

Molina-Montenegro MA, Torres C, Parra MJ, Cavieres LA (2000) Species association with the cushion Azorella trifurcata (Gaertn.) Hook. (Apiaceae) in the high Andes of central Chile. Gayana Bot 57:161–168

Nyakatya MJ, McGeoch MA (2007) The microclimate associated with a keystone plant species (Azorella selago Hook. (Apiaceae)) on Marion Island. Polar Biol 31:139–151

Oksanen J, Minchin PR (2002) Continuum theory revisited: what shape are species responses along ecological gradients? Ecol Model 157:119–129

Pammenter NW, Drennan PM, Smith VR (1986) Physiological and anatomical aspects of photosynthesis of two Agrostis species at a sub-Antarctic island. New Phytol 102:143–160

Pennings SC, Selig ER, Houser LT, Bertness MD (2003) Geographic variation in positive and negative interactions among salt marsh plants. Ecology 84:1527–1538

Pugnaire FI, Luque MT (2001) Changes in plant interactions along a gradient of environmental stress. Oikos 93:42–49

R Development Core Team (2007) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna

Sammul M, Kull K, Oksanen L, Veromann P (2000) Competition intensity and its importance: results of field experiments with Anthoxanthum odoratum. Oecologia 125:18–25

Schulze BR (1971) The climate of Marion Island. In: van Zinderen Bakker EM Sr, Winterbottom JM, Dyer RA (eds) Marion and Prince Edward Islands: report on the South African biological and geological expeditions, 1965–1966. Balkema, Cape Town, pp 16–31

Smit C, Vandenberghe C, den Ouden J, Müller-Schärer H (2007) Nurse plants, tree saplings and grazing pressure: changes in facilitation along a biotic environmental gradient. Oecologia 152:265–273

Smith VR (1987) The environment and biota of Marion Island. S Afr J Sci 83:211–220

Smith VR (2008) Terrestrial and freshwater primary production and nutrient cycling. In: Chown SL, Froneman PW (eds) The Prince Edward Islands: land-sea interactions in a changing ecosystem. African SunMedia, Stellenbosch, pp 181–214

Smith VR, French DD (1988) Patterns of variation in the climates, soils and vegetation of some sub-Antarctic and Antarctic islands. S Afr J Bot 54:35–46

Smith VR, Mucina L (2006) Vegetation of Marion and Prince Edward Islands. In: Mucina L, Rutherford MC (eds) Vegetation of South Africa, Lesotho and Swaziland, Strelitzia 19. South African National Biodiversity Institute, Pretoria, pp 698–723

Smith VR, Steenkamp M (1990) Climatic change and its ecological implications at a sub-Antarctic island. Oecologia 85:14–24

Smith VR, Steenkamp M, Gremmen NJM (2001) Terrestrial habitats on sub-Antarctic Marion Island: their vegetation, edaphic attributes, distribution and response to climate change. S Afr J Bot 67:641–654

Smithson M, Verkuilen J (2006) A better lemon squeezer? Maximum-likelihood regression with beta-distributed dependent variables. Psychol Methods 11:54–71

Tirado R, Pugnaire FI (2003) Shrub spatial aggregation and consequences for reproductive success. Oecologia 136:296–301

Tirado R, Pugnaire FI (2005) Community structure and positive interactions in constraining environments. Oikos 111:437–444

Weigelt A, Jolliffe P (2003) Indices of plant competition. J Ecol 91:707–720

Welden CW, Slauson WL (1986) The intensity of competition versus its importance: an overlooked distinction and some implications. Q Rev Biol 61:23–44