Ontogenetic shifts in plant interactions vary with environmental severity and affect population structure

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Summary

- Environmental conditions and plant size may both alter the outcome of inter-specific plant–plant interactions, with seedlings generally facilitated more strongly than larger individuals in stressful habitats. However, the combined impact of plant size and environmental severity on interactions is poorly understood.
- Here, we tested explicitly for the first time the hypothesis that ontogenetic shifts in interactions are delayed under increasingly severe conditions by examining the interaction between a grass, *Agrostis magellanica*, and a cushion plant, *Azorella selago*, along two severity gradients.
- The impact of *A. selago* on *A. magellanica* abundance, but not reproductive effort, was related to *A. magellanica* size, with a trend for delayed shifts towards more negative interactions under greater environmental severity. Intermediate-sized individuals were most strongly facilitated, leading to differences in the size-class distribution of *A. magellanica* on the soil and on *A. selago*. The *A. magellanica* size-class distribution was more strongly affected by *A. selago* than by environmental severity, demonstrating that the plant–plant interaction impacts *A. magellanica* population structure more strongly than habitat conditions.
- As ontogenetic shifts in plant–plant interactions cannot be assumed to be constant across severity gradients and may impact species population structure, studies examining the outcome of interactions need to consider the potential for size- or age-related variation in competition and facilitation.

Introduction

The net outcome of interactions between plants varies through space and time, ranging from facilitation and mutualism (i.e. positive) to competition and parasitism (i.e. negative). Spatial variation in the net outcome of plant interactions is strongly linked to environmental conditions, with facilitative interactions generally dominating under conditions of abiotic extremes, low resource availability, high herbivory or intense disturbance (i.e. high environmental severity; *sensu* Brooker & Callaghan, 1998), and competition being more common in milder environments (Bertness & Callaway, 1994; although see also e.g. Maestre *et al.*, 2009). The outcome of plant–plant interactions can also vary within and between years as environmental conditions fluctuate, with the strength of positive interactions increasing relative to negative interactions during more stressful periods (Tielbörger & Kadmon, 2000; Kikvidze *et al.*, 2006; Sthultz *et al.*, 2007). This spatial and temporal variation in the balance of positive and negative interactions is predicted to be related to environmental severity by the stress-gradient hypothesis (SGH; Bertness & Callaway, 1994; Brooker & Callaghan, 1998), an assumption

that is well supported by the majority of studies that have tested the hypothesis (He *et al.*, 2013).

Changes in individuals' size, age or life stage may also influence the outcome of interactions, although this source of temporal variation is less frequently studied (Callaway & Walker, 1997; Soliveres *et al.*, 2010). As plants germinate, establish and grow, their physiological tolerances and resource requirements change, as does their influence on the surrounding environment (Parish & Bazzaz, 1985; Miriti, 2006). In consequence, the balance between the positive and negative components of plant–plant interactions often shifts as plants age, giving rise to ontogenetic shifts in the outcome of interactions (i.e. a change in the nature and/or strength of an interaction related to an individual's ontogeny). The majority of studies show a transition from facilitation during establishment (i.e. neighbouring plants benefit seedling survival) to the inhibition of, or a neutral effect on, adult plant growth and reproduction (Miriti, 2006; Reisman-Berman, 2007; Lortie & Turkington, 2008; Valiente-Banuet & Verdú, 2008; Armas & Pugnaire, 2009). This probably reflects the fact that larger plants often have greater resource requirements which increase their competitive impacts, and also usually have lower

sensitivity to climatic extremes, reducing the benefits of environmental amelioration by neighbouring plants.

Schiffers & Tielbörger (2006) hypothesized that the timing of ontogenetic shifts could vary with environmental severity, with the net outcome of interactions remaining positive for longer under more stressful conditions. Thus, under greater environmental severity an ontogenetic shift in the interaction (from facilitation to competition) should be delayed. Sthultz *et al.* (2007) supported this hypothesis by demonstrating that at low altitudes *Fallugia paradoxa* facilitates the survival of *Pinus edulis* seedlings but increases the mortality of adult *P. edulis* (i.e. a negative ontogenetic shift). By contrast, at a more stressful high-altitude site, all life stages of *P. edulis* were facilitated by *F. paradoxa*, illustrating a marked change in the nature of the ontogenetic shift in this interaction with increasing environmental severity. Few other studies have determined whether ontogenetic shifts in plant interactions are affected by environmental conditions (Eränen & Kozlov, 2008; Soliveres *et al.*, 2010), with none explicitly testing Schiffers & Tielbörger's (2006) hypothesis or examining any consequences of the ontogenetic shifts. Ignoring ontogenetic shifts in interactions could lead to incorrect interpretation of variation in the outcome of plant–plant interactions and to inaccurate broad generalizations, which may be especially critical for areas showing rapid changes in environmental severity (see e.g. Hansen *et al.*, 2012). Specifically, the SGH's failure to incorporate ontogenetic shifts in interactions may account for some of the discrepancies between the model's predictions and observed patterns (He *et al.*, 2013). Ontogenetic shifts therefore need to be examined more critically and incorporated more explicitly into plant–plant interaction models.

One potential impact of plant interactions and their associated ontogenetic shifts may be on species population structure, acting through altered survival and reproduction rates. However, studies of plant–plant interactions have generally focused either on the impact of neighbouring individuals on the performance of focal plants (e.g. survival, growth rate or photosynthetic efficiency; Cavieres *et al.*, 2005; Sthultz *et al.*, 2007; Armas & Pugnaire, 2009) or on the composition of the entire flora associated with benefactor species (including biomass, species richness and diversity; Tewksbury & Lloyd, 2001; Holzapfel *et al.*, 2006; see also Gross *et al.*, 2009). Use of these methods has yielded important insights into the effect of plant interactions at the individual and community levels (Brooker *et al.*, 2008; Butterfield *et al.*, 2013). However, effects on individuals result in variation at the community level only insofar as the former alter population-level parameters such as stage-specific survival or age-specific reproduction. The balance between mortality (including success of immigration), reproduction and emigration for each species largely determines community diversity (richness, abundance structure and size structure; e.g. Andrewartha & Birch, 1954; Ricklefs, 2008). In consequence, investigations at the population level are essential for understanding how the outcome of individual plant–plant interactions scales up to affect communities.

In this study, we investigated whether there was an ontogenetic shift in the impact of the sub-Antarctic cushion plant *Azorella selago* (benefactor) on the grass *Agrostis magellanica* (beneficiary),

whether the nature and timing of the ontogenetic shift varied with environmental severity (examined along two different stress gradients), and the extent to which the interaction affected the population structure and reproductive output of *A. magellanica*.

Materials and Methods

Study site

Fieldwork was conducted on sub-Antarctic Marion Island ($46°54'S$, $32°45'E$; $290 km^2$), located in the southern Indian Ocean (details in Chown & Froneman, 2008). This island has a hyper-oceanic climate, with cold but stable temperatures, strong winds, and high humidity, precipitation and cloud cover (Smith, 2002; although the island's climate is changing rapidly; le Roux & McGeoch, 2008a). The island supports a relatively depauperate vascular flora, with 38 vascular plants (Chown *et al.*, 2013).

Altitude and wind exposure represent two important stress gradients on the island. At higher elevations, temperatures are lower and the temperature range more extreme, wind speeds are higher and the soil is more unstable and has a greater frequency and depth of freezing than at lower elevations (Lee *et al.*, 2009; le Roux & McGeoch, 2010). While altitude is an indirect gradient representing multiple proximate environmental factors, under the alpine conditions of Marion Island it can be a useful surrogate for environmental severity (see Austin, 2002). Similarly, as a result of strong winds, exposed sites can be drier than sheltered equivalents, and plants growing there may experience accelerated moisture loss, enhanced cooling and wind-related physical damage (Bate & Smith, 1983; Pammenter *et al.*, 1986; le Roux & McGeoch, 2010). Therefore, because of the direct impact of the mechanical stresses and the indirect effects of microclimatic modification caused by strong winds, wind exposure also provides a measure of a site's abiotic severity (Eränen & Kozlov, 2008).

Study species

We examined the interaction between the two most widespread vascular plant species on Marion Island: *Azorella selago* Hook. (Apiaceae) and *Agrostis magellanica* Lam. (Poaceae) (Huntley, 1971). *Azorella selago* has a compact, prostrate cushion growth form and is a slow-growing, long-lived and stress-tolerant species (Frenot *et al.*, 1993; le Roux & McGeoch, 2004). As a result of the species' compact nature, individual plants retain their dead leaves, developing a rich humus-filled core below a thin surface of green leaves. This organic substrate is thermally buffered relative to the adjacent soil (Nyakatya & McGeoch, 2007), and probably also has higher nutrient and moisture content (observed for other species in this genus; e.g. Cavieres *et al.*, 2005) (see also Hugo *et al.*, 2004; McGeoch *et al.*, 2008). As a result, *A. selago* provides a more favourable substrate than the surrounding mineral soil for many plants (le Roux & McGeoch, 2008c, 2010) and invertebrates (Barendse & Chown, 2001; Hugo *et al.*, 2004). *Agrostis magellanica* is the most common species to grow on *A. selago* plants on Marion Island (Huntley, 1971). It is a perennial grass that occurs in most of Marion Island's habitats and it has the

second largest altitudinal range of the island's vascular plants after *A. selago* (Huntley, 1971; le Roux & McGeoch, 2008b). As a consequence of the extreme longevity of some *A. selago* individuals (le Roux & McGeoch, 2004), multiple generations of *A. magellanica* may interact with a single *A. selago* plant. At low altitudes and in wind-sheltered sites, *A. magellanica*'s performance is negatively impacted by growing on *A. selago*, but above 150 m elevation and at wind-exposed sites the grass is strongly facilitated by the cushion plant (le Roux & McGeoch, 2010).

Data collection

Agrostis magellanica individuals were collected off *A. selago* plants and from the adjacent soil along two exposed ridges from sea level to the upper altitudinal limit of vascular plant growth on Marion Island, at *c.* 20 m altitudinal intervals. In these habitats *A. magellanica* is the dominant vascular plant growing on *A. selago*, with the species average cover six times greater than the cover of all other plants combined (le Roux & McGeoch, 2010). In view of the compact canopy of *A. selago* plants and the rocky, rugose nature of the adjacent substrate in this habitat, *A. selago* plants are unlikely to trap a disproportionate abundance of seeds (Cavieres *et al.*, 2005; Haussmann *et al.*, 2010). Medium-sized *A. selago* cushion plants (maximum diameter between 0.3 and 0.6 m) were randomly selected, and all *A. magellanica* grasses rooted within the *A. selago* plants were carefully uprooted. A wire ring was moulded around the outer edge of each sampled *A. selago* cushion plant to reproduce the size and shape of the plant, and then placed 0.1 m from the cushion plant in a randomly selected direction. All *A. magellanica* individuals rooted within the adjacent soil sample were then 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 measurements of *A. magellanica* abundance, size, mass and reproductive effort at each site were scaled to account for variation in the area available to the grass before calculating interaction intensity (see 'Data analysis') (methodology detailed in le Roux & McGeoch, 2010).

In addition, variation in *A. magellanica* abundance, size, mass and reproductive effort on *A. selago* and on the adjacent soil was assessed along a wind exposure gradient by sampling eight pairs of *A. selago* cushions and adjacent soil at each of three sites on an exposed, low-altitude (*c.* 90 m above sea level (asl)) coastal ridge. The three sites were within 400 m of each other, but differed considerably in environmental severity as a result of differing exposure to the prevailing north-westerly winds (the sites were designated as high wind exposure, intermediate exposure, and low exposure; see le Roux & McGeoch, 2010 for further site details). Following the same methodology as for the altitudinal transects, all *A. magellanica* individuals were collected from medium-sized *A. selago* cushions and from adjacent paired soil areas of the same size. Decreasing biomass of soil-rooted *A. magellanica* with increasing altitude and exposure confirmed that our sampling designs represent ecologically relevant severity gradients (le Roux & McGeoch, 2010).

All harvested *A. magellanica* individuals ($n = 12 155$) were returned to the laboratory and dried at 60°C for 48 h. Mass

(0.5 mg precision; AE260 Delta Range Balance; Mettler-Toledo, Columbus, OH, USA), number of inflorescences (i.e. current reproductive effort) and number of inflorescence stalks (i.e. an estimate of recent reproductive effort) were recorded for each individual. As *A. magellanica* abundance and mass, and the number of inflorescences and the number of inflorescence stalks, showed similar patterns, results are only detailed here for *A. magellanica* abundance and the number of inflorescence stalks (see Supporting Information Figs S1 and S2 for results of analyses of *A. magellanica* mass and number of inflorescences).

Data analysis

The mass of *A. magellanica* individuals collected in this study ranged from 0.5 mg to 19.3 g. Because most individuals were small (43% weighed < 10 mg), plant mass was log_{10}-transformed before analysis. *Agrostis magellanica* individuals were then categorized into 13 size classes (0.25-mg-interval log_{10}-transformed mass bins), with all individuals with a mass exceeding 10^3 mg grouped into the heaviest size class. Analyses were repeated using eight and 16 size classes, but as all analyses gave similar results, only results using 13 size classes are presented. Data from the two altitudinal transects showed similar patterns and were therefore pooled for analysis. These data were split into three altitude categories (< 150 m asl, low altitude; 150–300 m asl, mid altitude; > 300 m asl, high altitude) to represent three levels of increasing abiotic stress, with the first category comprising the elevations over which the majority of competitive impacts of *A. selago* on *A. magellanica* had been observed by le Roux & McGeoch (2010).

The impact of *A. selago* on *A. magellanica* was quantified using the relative interaction index (RII):

$$RII = (P_{T+N} - P_{T-N})/(P_{T+N} + P_{T-N}), \qquad \text{Eqn 1}$$

where P_{T+N} and P_{T-N} represent the performance of *A. magellanica* in the presence and absence of *A. selago* respectively (Armas *et al.*, 2004). RII is bounded between −1 and 1, with positive values indicating net facilitative interactions, negative values indicating competition, and larger absolute values indicating stronger intensity of the interaction. This index has performed well in other studies investigating the severity–interaction relationship (e.g. Schiffers & Tielbörger, 2006). RII was calculated for each size class of *A. magellanica* for each stress level, quantifying the impact of *A. selago* on the performance of the different size classes of the grass (i.e. abundance or number of inflorescence stalks; RII_{abund} and RII_{inflor}, respectively). The relationship between RII and *A. magellanica* size class was modelled using linear and second-order polynomial functions. Models were fitted using maximum likelihood estimation and assuming a beta distribution of the response variables. The beta distribution is suitable for modelling the dependent variables, as RII values are bounded continuous data (Ferrari & Cribari-Neto, 2004). The proportion of variance explained by each model was calculated as a pseudo R^2 value (Ferrari & Cribari-Neto, 2004), and analysis of deviance was used to distinguish between competing models. Models were fitted using the gnlm package (Lindsey,

2007) in the R statistical programming language (R Development Core Team, 2011).

Quantile regression (Cade & Noon, 2003) was subsequently used to examine the lower boundary of the RII–*A. magellanica* size relationship ($\tau = 0.25$; i.e. using the first quartile of the data), investigating whether the impact of *A. selago* on *A. magellanica* was constrained by the size of *A. magellanica* individuals (following e.g. Miriti, 2006). Linear and second-order polynomial models were fitted using the quantreg package (Koenker, 2009) in R, implementing an ANOVA (through the anova.qr function) to determine whether more complex models explained a significantly greater amount of the variation in the data than simpler nested models. Where quadratic models provided the best fit to the data, the fitted curve's turning point was determined and the 95% confidence intervals around the turning point were calculated (Zhou *et al.*, 1993).

Kolmogorov–Smirnov (KS) tests were used to compare the distribution of *A. magellanica* size classes between different substrates and stress levels, employing Bonferroni-adjusted *P* values to account for multiple tests on the same data. These tests use the relative abundance of *A. magellanica* in each size class as a measure of the grass's population structure.

The mass of the smallest flowering *A. magellanica* individual was determined for each substrate (*A. selago* or soil) and stress level (low, mid or high altitude or wind exposure) to estimate the size threshold for reproduction in the grass under different conditions. In view of the greater abundance of *A. magellanica* on *A. selago* than on the soil, we also calculated the rarefied minimum mass of flowering *A. magellanica* growing on *A. selago* using a resampling approach. By randomly selecting (with replacement)

the same number of flowering *A. magellanica* individuals growing on *A. selago* as were sampled from the soil, bias towards lower minimum flowering masses of *A. magellanica* growing on *A. selago* (as a consequence of sampling effects resulting simply from the greater abundance of grasses growing on the cushion plant) was avoided. This procedure was repeated 100 times, and the mean minimum mass of flowering *A. magellanica* calculated across all repeats.

Agrostis magellanica root:shoot ratios were calculated for each sample, with the Mann–Whitney *U* statistic used to test for significant differences between substrates and stress levels after trimming the 10% most extreme outliers (extreme values were predominantly associated with the smallest grasses, as the calculation of the ratio was imprecise for individuals with weights that were low relative to the sensitivity of the balance used to weigh them).

Results

The impact of *A. selago* on *A. magellanica* was generally positive, increasing the grass's abundance and inflorescence production relative to individuals growing on the adjacent soil in most size classes (i.e. 85% of all RII_{abund} values > 0 and 90% of RII_{inflor} values > 0; Table 1). Furthermore, *A. selago*'s effect on *A. magellanica* abundance was significantly related to the size class of grasses considered (Table 1). Along the wind exposure gradient, the relationship between RII_{abund} and *A. magellanica* size was best described at all stress levels by quadratic functions (all with negative quadratic coefficients; Fig. 1a, Table 1). Therefore, *A. selago* increased the abundance of intermediate-sized *A. magellanica* most, relative to the abundance of the same

Table 1 Results from regression of interaction intensity (relative interaction index (RII)) against *Agrostis magellanica* size class, for both types of stress gradient (wind exposure and altitude) and all stress levels (low, mid and high; relationships illustrated in Fig. 1)

				Beta regression			Quantile regression				
		n	Proportion RII values positive	Minimum adequate model	χ^2	*P*	Turning point ± SE	Minimum adequate model	*F*	*P*	Turning point ± SE
Exposure gradient											
Abundance	Low	99	0.81	Quadratic	6.94	0.031	0.48 ± 0.04a*	Quadratic	29.83	<0.001	1.10 ± 0.06a
	Mid	99	0.92	Quadratic	10.35	0.006	0.67 ± 0.05b	Quadratic	5.10	0.008	1.99 ± 0.16b
	High	102	0.97	Quadratic	27.33	<0.001	0.74 ± 0.04b	Quadratic	9.84	<0.001	2.60 ± 0.15c
Inflorescences	Low	36	0.78	None				Null			
	Mid	47	0.96	None				Quadratic	3.18	0.051	2.13 ± 0.40
	High	54	0.98	None				Null			
Altitudinal gradient											
Abundance	Low	136	0.57	None				Quadratic	2.57	0.080	1.54 ± 0.13a
	Mid	206	0.93	Quadratic	24.70	<0.001	0.65 ± 0.02	Quadratic	12.08	<0.001	2.29 ± 0.16b
	High	126	0.88	Linear	4.74	0.029		Linear	10.99	0.001	2.88 ± 0.23†c
Inflorescences	Low	49	0.69	None				Linear	8.43	0.006	
	Mid	96	0.95	None				Null			
	High	54	0.96	None				Null			

n, number of data points (sum of size classes represented in each sample); χ^2 and *P*, model test statistic and *P* value when compared with the null model of no relationship.
*Quadratic models not sharing letters differ significantly ($P < 0.05$) in their turning points.
†Turning point presented for comparison, although the quadratic fit was not significantly better than the linear fit.
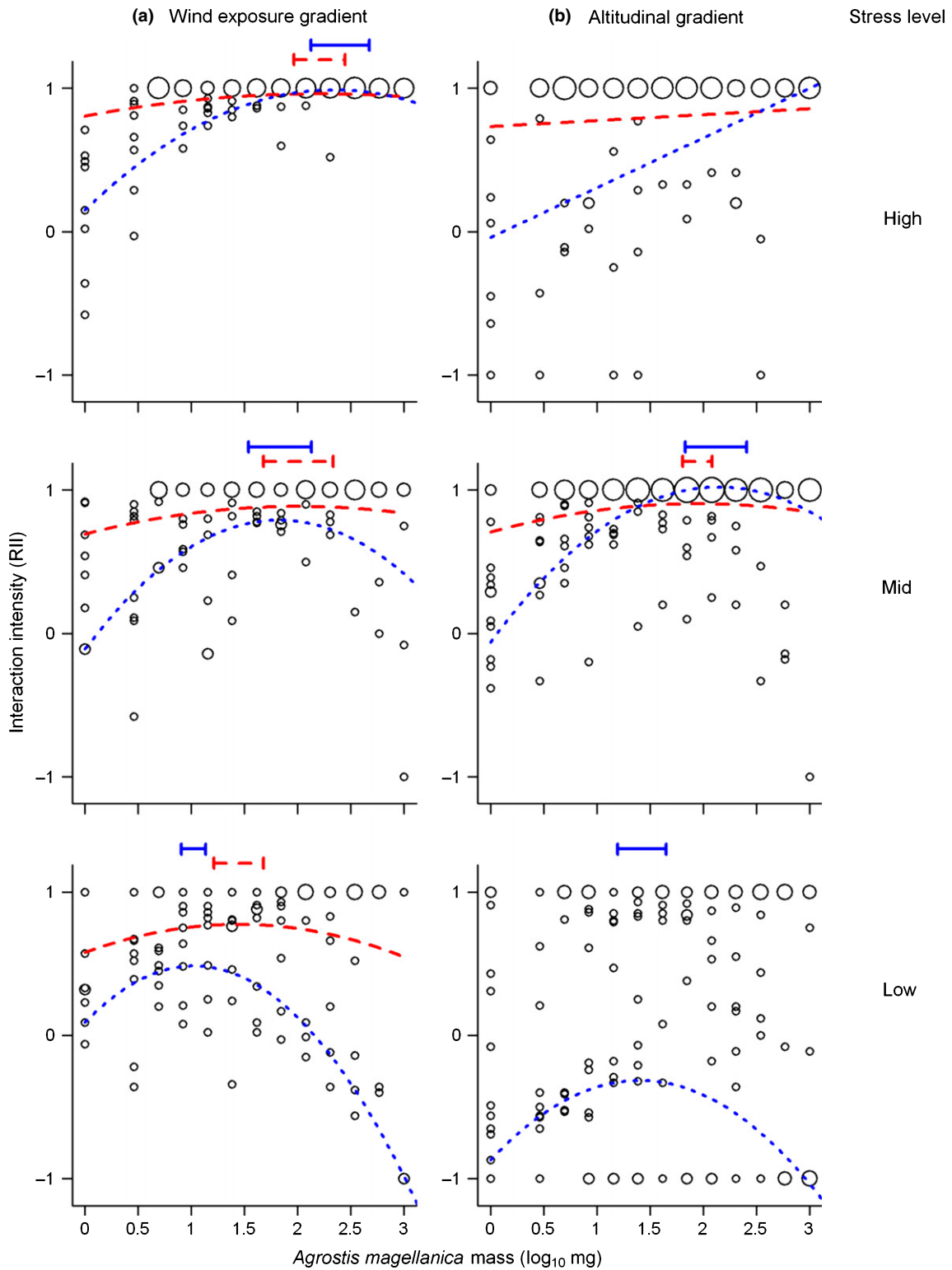
Fig. 1 Relationship between interaction intensity (relative interaction index for the *Agrostis megellanica* abundance (RII$_{abund}$); i.e. the impact of *Azorella selago* on *A. magellanica* abundance) and *A. magellanica* mass. (a) Wind exposure gradient; (b) altitudinal gradient. The size of symbols reflects the number of overlapping data points. Dashed lines show the best beta regression fit to the data, and dotted lines the best quantile regression fit (details in text and statistics in Table 1). Where a quadratic function gave the best fit, error bars above the panel indicate 1 SE on either side of the turning point. [Correction added after online publication 6 June 2013: in the preceding sentence the definition of RII$_{abund}$ has been corrected.]

A. magellanica size classes on the adjacent soil. By contrast, along the altitudinal gradient the form of the relationship differed according to stress level (Fig. 1b; Table 1); at low elevations the

RII$_{abund}$ was not related to *A. magellanica* size, while at intermediate altitudes the relationship was quadratic, with *A. selago* increasing the abundance of medium-sized grasses most. At high

altitudes (i.e. under more stressful conditions) *A. selago* had the most positive effect on the abundance of the largest grasses (i.e. a positive linear relationship; Fig. 1b, Table 1).

Quantile regression revealed that the impact of *A. selago* on *A. magellanica* abundance was constrained by the size of *A. magellanica* individuals (Table 1). In five of the six stress gradient–stress level combinations, quadratic models provided a better fit than linear models to the lower bound of the RII_{abund}–*A. magellanica* size relationship. Along the exposure gradient, the location of the turning points of the RII_{abund}–size relationship occurred at significantly greater size under higher environmental stress (Table 1, Fig. 1a). Similarly, along the altitudinal gradient the turning point in the quadratic curves was at increasingly larger *A. magellanica* sizes under progressively greater environmental severity (with no turning point at the highest elevation; Table 1, Fig. 1b). By contrast, the impact of *A. selago* on the number of *A. magellanica* inflorescences did not consistently vary with the size of grasses along the exposure or altitudinal gradient when using either beta or quantile regression (Table 1, Fig. S3).

Comparison of the population structures of *A. magellanica* growing on *A. selago* and on the soil revealed a positive effect of *A. selago* on the abundance of *A. magellanica* (Table 2), and particularly on the relative abundance of intermediate and large individuals (Figs 2, S4). The largest impact of *A. selago* on *A. magellanica* abundance was in the intermediate size classes (e.g. $10^{0.75}$–$10^{2.75}$ mg; Figs 2, S1), with *A. magellanica* abundance on *A. selago* three to 17 times higher than on the soil (Table 2). Along the altitudinal gradient, *A. magellanica* population structure differed significantly between substrates (i.e. comparing grasses on *A. selago* and on soil at the same stress level; Table 3). By contrast, population structure did not differ between altitudinal bands when comparing grasses growing on the same substrate (i.e. size-class distribution was not different between low, mid and high altitudes for grasses growing on the same substrate; Table 3, see e.g. Fig. 2). The same trend was evident for *A. magellanica* population structure on the exposure gradient (i.e. higher KS statistics when comparing population structure

Table 3 Results of Kolmogorov–Smirnov tests comparing *Agrostis magellanica* size-class distributions across stress levels (high, mid and low altitude) and substrate types (growing on *Azorella selago* versus growing on the adjacent soil) along the altitudinal gradient

Stress level	Substrate comparison	D statistic	P value
Low	Soil versus *A. selago*	0.320	< 0.001*
Mid	Soil versus *A. selago*	0.353	< 0.001*
High	Soil versus *A. selago*	0.474	< 0.001*
Substrate	Stress level comparison		
Soil	Low versus mid	0.078	0.093
Soil	High versus mid	0.091	0.650
Soil	Low versus high	0.170	0.033
A. selago	Low versus mid	0.017	0.862
A. selago	High versus mid	0.078	0.005
A. selago	Low versus high	0.076	0.010

*Significant after Bonferroni correction.

between substrates than when comparing between wind exposure levels; Fig. S4, Table S1).

The minimum flowering size (i.e. reproductive threshold) of *A. magellanica* differed between individuals growing on the soil and on *A. selago*, with the grass flowering at a smaller minimum size on *A. selago* (Table 2; see also Figs 2, S4). Rarefied estimates of *A. magellanica*'s minimum flowering size on *A. selago* were considerably higher than the observed values, but were still significantly smaller than for grasses growing on the soil in three comparisons (Table 2). Moreover, more inflorescences were produced by grasses growing on *A. selago* than by those growing on the adjacent soil at all stress levels, with > 99% of inflorescence stalks at high altitudes and wind exposure being carried by *A. magellanica* individuals growing on *A. selago* (Table 2). Root : shoot ratios were consistently higher in soil-rooted *A. magellanica* than in individuals growing on *A. selago*, with the differences being significant in four of the six comparisons, indicating a greater proportion of biomass allocated to below-ground growth in soil-rooted individuals (Table 2).

Table 2 The abundance and reproductive effort of *Agrostis magellanica* growing on the soil and on *Azorella selago* cushion plants at three stress levels (low, mid and high) along two types of stress gradient (altitude and wind exposure)

	Number of *A. magellanica* per sample (mean ± SE)		Number of *A. magellanica* inflorescence stalks per sample		Minimum mass of flowering *A. magellanica* (mg)			*Agrostis magellanica* root : shoot ratio (mean ± SE)	
	Soil	*A. selago*	Soil	*A. selago*	Soil	*A. selago*	*A. selago* (rarefied; mean ± SE)	Soil	*A. selago*
Altitudinal gradient									
Low	68.4 ± 17.1	174.8 ± 63.0	11.5 ± 6.2	14.4 ± 5.1	114	19	53.2 ± 2.5*	0.32 ± 0.03	0.19 ± 0.04*
Mid	23.6 ± 7.8	178.5 ± 27.6*	0.7 ± 0.3	24.3 ± 5.5*	428	8	54.6 ± 3.7*	0.38 ± 0.05	0.25 ± 0.02*
High	6.8 ± 2.3	52.2 ± 11.4*	0.3 ± 0.3	21.8 ± 5.9*	30	7	66.0 ± 4.9*	0.37 ± 0.07	0.29 ± 0.03
Exposure gradient									
Low	67.0 ± 21.9	225.8 ± 35.5*	4.3 ± 2.2	13.3 ± 5.2	43	29	43.1 ± 1.3	0.40 ± 0.08	0.25 ± 0.01*
Mid	18.9 ± 5.2	158.1 ± 45.5*	3.3 ± 1.4	24.8 ± 4.7*	116	17	60.0 ± 3.1*	0.37 ± 0.08	0.22 ± 0.02
High	8.5 ± 1.0	146.1 ± 21.1*	0.5 ± 0.4	33.9 ± 6.4*	121	12	134.8 ± 15.8	0.42 ± 0.07	0.19 ± 0.01*

The mass of the smallest flowering *A. magellanica* and the mean root : shoot ratio at each stress level on each gradient are also indicated.
*Significant difference between *A. magellanica* samples growing on *A. selago* and on the adjacent soil (*P* < 0.05; Mann–Whitney *U*-test).
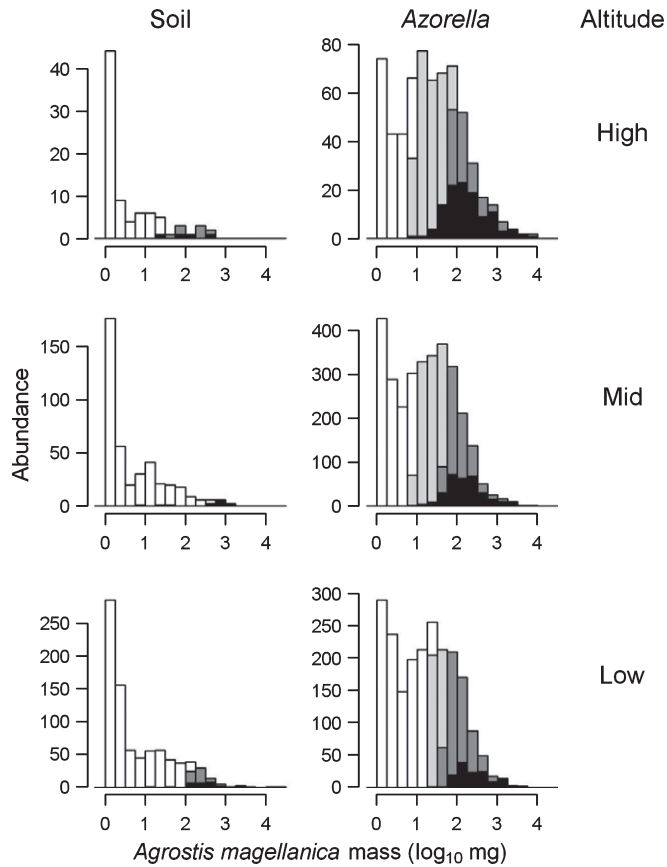
Fig. 2 Size-class distribution of *Agrostis magellanica* rooted in *Azorella selago* or in the adjacent soil, in three altitudinal bands (low, < 150 m above sea level (asl); mid, 150–300 m asl; high, > 300 m asl). Black bars indicate the size-class distribution of flowering individuals, while light and dark grey bars indicate all individuals greater than the observed or rarefied size threshold for flowering, respectively. Note the differences in the scaling of the *y*-axis between panels.

Discussion

The impact of *A. selago* on *A. magellanica* was related to *A. magellanica* size, but not consistently so, with the form of the relationship varying with *A. magellanica* performance measure and stress gradient type. Moreover, none of the significant ontogenetic shifts documented were of the expected form (i.e. monotonically negative), with the most positive impact of *A. selago* on the abundance of intermediate-sized grasses. However, despite the variability in the ontogenetic shifts, there was a clear trend for the shift towards more negative interactions to be delayed under greater environmental severity. As a result, the hypothesis that ontogenetic shifts in plant interactions are delayed under more stressful conditions could not be rejected.

Effects of ontogenetic stage

The nonmonotonic relationship between RII_{abund} and *A. magellanica* size was unexpected, as seedlings are generally the most strongly facilitated life stage, while the largest individuals usually have neutral or negative interactions with other plants

(although more complicated ontogenetic shifts have been described; e.g. Rousset & Lepart, 2000). The *A. selago–A. magellanica* interaction contrasts with this expected pattern, as the abundance of the smallest *A. magellanica* individuals was not most strongly increased by *A. selago* (Fig. 1). This pattern was more pronounced in the quantile regression, suggesting that, while other factors also influence the impact of *A. selago* on *A. magellanica* abundance, the occurrence of strong negative interactions are least likely for grasses of intermediate size. The ontogenetic shift observed suggests that there may be multiple facilitative and competitive components to the *A. selago–A. magellanica* interactions. Indeed, it is likely that with increasing size *A. magellanica* individuals probably compete more strongly with *A. selago* for space, nutrients and water, while the benefit of environmental amelioration by the cushion plant probably remains similar (or declines slightly) for larger grasses. However, an additional mechanism that exerts a strong negative effect on the smallest grasses growing on *A. selago* must also be important to produce a unimodal RII_{abund}–*A. magellanica* size relationship. One potential mechanism is the overgrowing of small *A. magellanica* grasses by *A. selago*, thereby reducing their survival. Indeed, this is quite possible as *A. selago* shows rapid shoot elongation under shading (le Roux *et al.*, 2005; although other mechanisms may also contribute, including inhibited germination; Olofsson *et al.*, 1999). Therefore, intermediate-sized grasses may benefit most from the interaction with *A. selago* by being large enough that *A. selago* cannot overgrow them, but still small enough to avoid strong competition with *A. selago* and to benefit from environmental amelioration by the cushion plant. By contrast, *A. magellanica* individuals growing in the open soil probably have a consistently lower probability of mortality with increasing size, as the more extensive root systems of larger individuals would reduce their vulnerability to soil moisture deficits and the chance of frost-heaving (Kleier & Rundel, 2004; Haussmann *et al.*, 2010).

The difference between the shape and significance of the RII–*A. magellanica* size relationship for the abundance of individuals and of inflorescences fit with the current understanding that the impact of plant interactions differs between performance measures (Brooker *et al.*, 2008). Previous studies have shown that plant survival generally responds strongly to environmental amelioration by neighbouring plants, but that reproduction is less affected by changes in environmental severity caused by the presence or absence of facilitators (Goldberg *et al.*, 1999; Maestre *et al.*, 2005). Thus, a similar pattern may exist in the size dependence of an interaction, with ontogenetic shifts in the benefactor's impact being more pronounced on the beneficiary's abundance than on its reproductive output.

Impacts on population structure

The *A. selago–A. magellanica* interaction altered the population structure of *A. magellanica*, with a disproportionately strong increase in medium-size grasses. The shape of the *A. magellanica* size-class distribution was more strongly affected by the occurrence of *A. selago* than by differences in altitude, suggesting that the plant–plant interaction has a stronger impact than variation

in environmental severity, at least along one of the stress gradients. Differences in the population structure of *A. magellanica* growing on the soil and on *A. selago* are probably a result of improved growth and/or survival of individuals on *A. selago*, with the lower root:shoot ratio observed for the grasses growing on the cushion plant suggesting one possible mechanism. The lower root:shoot ratio probably reflects a reduced requirement for resource allocation to the production of roots when growing on *A. selago* as a result of the more stable substrate (especially in contrast to the frequent freeze–thaw cycles in the soil; Boelhouwers *et al.*, 2003) and increased availability of water and nutrients that the cushion plant offers (McGeoch *et al.*, 2008; Anthelme *et al.*, 2012). Therefore, through altering the fine-scale environmental conditions experienced by *A. magellanica*, *A. selago* also affects the expression of a functional trait in *A. magellanica* (Cavieres *et al.*, 2005), which may contribute to the interaction's impact on *A. magellanica* population structure.

Reproductive effort

The presence of *A. selago* also strongly impacted *A. magellanica*'s reproductive output, increasing the grasses' inflorescence production greatly. Our results identified three *A. selago*-driven changes in the biology and population structure of *A. magellanica* which contribute to the 1.3- to 73-fold difference in reproductive output between soil-rooted and *A. selago*-associated *A. magellanica* populations. First, *A. magellanica* individuals growing on *A. selago* tended to flower at smaller sizes than individuals growing on the soil, possibly as a result of the altered resource allocation associated with changes in the root:shoot ratio. The observation that grasses growing on the soil initiate reproduction at a larger size is in agreement with previous studies that demonstrated that flowering is increasingly delayed under progressively more negative interactions (Weiner, 1988). Secondly, the *A. selago*–*A. magellanica* interaction disproportionately increased the relative abundance of medium-sized, and thus potentially reproductive, grasses. Finally, the total abundance of *A. magellanica* individuals of all sizes was increased by *A. selago*. As a result, a larger number (in absolute and relative terms) of *A. magellanica* grasses exceed the grasses' minimum flowering size when growing on *A. selago*, thereby increasing the abundance of potentially reproductive individuals. Thus, the population's reproductive effort is positively affected by *A. selago* via changes in the grass's abundance, population structure and size threshold for reproduction, highlighting the diverse mechanisms through which this facilitative interaction operates.

Conclusions

Three important conclusions are evident from this study. First, there is a strong ontogenetic shift in the effect of *A. selago* on *A. magellanica*, with this size-dependent interaction showing a previously undocumented form (i.e. strongest facilitation for intermediate-size individuals). Secondly, our results provide support for Schiffers & Tielbörger's (2006) hypothesis that

ontogenetic shifts may be delayed under greater environmental severity, illustrating that the nature of ontogenetic shifts can be dependent on environmental conditions. Finally, we show for the first time that the relative abundance structure of a beneficiary species is more strongly affected by its interaction with the benefactor species than by variation in abiotic conditions, demonstrating that biotic interactions can be more important than environmental severity in some situations.

As a consequence of the potential for ontogenetic shifts in plant–plant interactions, studies examining interactions need to consider facilitative (or competitive) effects on both the abundance and population structure of beneficiary species, as focusing on the former alone may fail to capture important aspects of the latter. Thus, following the recent calls for the refinement of the stress-gradient hypothesis to reflect improved understanding of competition and facilitation (Maestre *et al.*, 2009; Malkinson & Tielbörger, 2010), we argue that ontogenetic shifts in plant–plant interactions also need to be included in this framework. More generally, by examining the changes in the *A. selago*–*A. magellanica* interaction along two environmental gradients, these results highlight the potential for climate change to affect ontogenetic shifts in species interactions. Because shifts in temperature and/or precipitation patterns may affect both the phenology and ontogeny of species (Parmesan, 2006; Barton, 2010), this is a mechanism through which changing climatic conditions could alter species interactions (Klanderud, 2005; Cavieres & Sierra-Almeida, 2012), a key challenge for climate change impact forecasting (Wisz *et al.*, 2013). Therefore, models aiming to accurately predict species- and community-level responses to changing environmental conditions need to consider how shifts in species' ontogenies (via changes in development rates and/or phenology) may affect their interactions with co-occurring species (Barton, 2010; Yang & Rudolf, 2010).

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Supporting Information

Additional supporting information may be found in the online version of this article.

Fig. S1 Relationship between interaction intensity and *Agrostis magellanica* mass.

Fig. S2 Relationship between interaction intensity and the abundance of *Agrostis magellanica* inflorescences.

Fig. S3 Relationship between interaction intensity and the abundance of *Agrostis magellanica* inflorescence stalks.

Fig. S4 Size-class distribution of *Agrostis magellanica* growing in the presence and absence of *Azorella selago*, at three wind exposure levels.

Table S1 Results of Kolmogorov–Smirnov tests comparing *Agrostis magellanica* size class distributions across stress levels and substrate types along the wind exposure gradient

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