

Climate change and vascular plant species interactions on sub-Antarctic Marion Island

by

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Declaration

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Azorella selago on Marion Island

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I thank and praise the Lord, through whom this work has been possible. “The LORD alone is God; God alone is our defense. He is the God who makes me strong, who makes my pathway safe. He makes me sure-footed as a deer; he keeps me safe on the mountains.” (Psalm 18: 31 - 33)

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Abstract

Shifts in species ranges are an important consequence of climate change, and can affect the composition, structure and functioning of ecosystems. Generally, in response to rising temperatures, species have increased their altitudinal and latitudinal distributions along their cooler boundaries, although there has been large variation between species. However, in addition to climatic factors, species range limits are also sensitive to biotic interactions. Therefore, interspecific interactions may be able to influence the impact of climate change on species distributions. In this thesis climate change, range shifts and spatial variation in plant-plant interactions are documented to examine the potential for biotic interactions to mediate climate-driven altitudinal range shifts on sub-Antarctic Marion Island.

The climate on Marion Island changed considerably between 1949 and 2003, with significant trends in biologically-relevant parameters encompassing average climatic conditions, variability in climate parameters and extreme weather events. Combining these trends showed that while environmental conditions have ameliorated for some species, they have become more abiotically stressful for others (e.g. hygrophilous species). Concurrent with changes in the island's climate, there have been rapid changes in the elevational distribution of Marion Island's native vascular flora. On average species ranges expanded upslope (as predicted in response to the warming experienced on the island), although individual range expansion rates varied greatly. As a result of the idiosyncratic expansion rates, altitudinal patterns of species richness and community composition changed considerably. Therefore, both species- and community-level changes occurred in the flora of Marion Island, demonstrating the community's sensitivity to climate change.

To determine the potential for interspecific interactions to have mediated these changes in species elevational ranges, spatial variation in the balance of positive and negative plant-plant interactions were examined. Increasing spatial association between four dominant species along an altitudinal severity gradient suggested that the intensity of facilitation, relative to the intensity of competition, is greater under more severe conditions. While, interaction strength varied between species pairs, the nature of relationship was consistent across the species. At a broader spatial scale, the performance of the grass *Agrostis magellanica* was compared in the presence and in

the absence of the cushion plant *Azorella selago* along the entire altitudinal range of both species. The influence of the cushion plant on *A. magellanica* switched from negative to positive with increasing environmental severity, reaching a positive asymptote under extreme environmental conditions. Therefore, on Marion Island the spatial variation in the nature of biotic interactions is related to environmental severity, and facilitative interactions can be strong under extreme environmental conditions.

These results show that positive biotic interactions are important at higher elevations on Marion Island, and could thus accelerate upslope range expansions in response to climate change. Nonetheless, competitive inhibition of upslope species movement, especially in areas of dense vegetation (i.e. mid or low altitudes), could have the opposite result, acting antagonistically with the effect of rising temperatures. This research highlights the importance of considering interspecific interactions when examining the biotic implications of climate change, both for affecting the rate at which species ranges change and the extent of species distributions.

Opsomming

Die verskuiwing van spesies se verspreidingspatrone is 'n belangrike gevolg van klimaatsverandering en kan die samestelling, struktuur en funksionering van ekosisteme affekteer. Oor die algemeen, in reaksie op verwarming, kom spesies op hoër hoogtes bo seespieël en hoër breedtegrade voor, alhoewel daar groot verskille tussen spesies in hierdie aspek is. Behalwe vir klimatologiese faktore, is spesies se verspreidingslimiete ook sensitief vir biotiese interaksies met ander spesies. Daarom kan interaksies tussen spesies die effek van klimaatsverandering op spesies-verspreiding verder beïnvloed. In hierdie verhandeling word klimaatsverandering, verandering in verspreiding van spesies en geografiese variasie in plant-plant interaksies ondersoek. Dit word gedoen ten einde die moontlikheid te toets dat biotiese interaksies die verandering in verspreidingspatrone van klimaat gedrewe spesies op sub-Antarktiese Marion Eiland beïnvloed.

Marion Eiland se klimaat het aansienlik tussen 1949 en 2003 verander, met betekenisvolle neigings in biologies-relevante parameters, insluitend gemiddelde klimaatstoestand, variasie in klimaat en uiterste weerstoestand. As die veranderinge saam beskou word, wys dit dat, terwyl omgewingstoestand vir sommige spesies verbeter het, toestand vir ander spesies abioties meer ongunstig geword het (bv. akwatiese plantsoorte). Tesame met die veranderinge in die eiland se klimaat, het die hoogte bo seespieël verspreiding van Marion Eiland se inheemse vaatplante vinnig verander. Gemiddeld het spesies-verspreiding se hoogte bo seespieël na hoër hoogtes verskuif (soos voorspel in reaksie op verwarming), alhoewel die tempo van verskuiwing na hoër hoogtes tussen spesies verskil het. As gevolg van hierdie idiosinkratiese reaksies, het die aantal en samestelling van plant spesies op verskillende hoogtes op die eiland aansienlik verander. Die sensitiwiteit van Marion Eiland se flora ten opsigte van klimaatsverandering word deur hierdie verandering gedemonstreer.

Om te bepaal of die interaksies tussen spesies verspreidingspatrone kan beïnvloed, is die geografiese variasie in die balans van positiewe en negatiewe interaksies ondersoek. Vier dominante vaatplante het meer geassosieerd geraak hoe hoër hulle bo seespieël voorgekom het. Dit is 'n aanduiding dat die sterkte van die

positiewe interaksies (fasilitering), relatief tot die sterkte van die negatiewe reaksie (kompetisie), groter onder uiterste omgewingstoestande is. Die sterkte van die interaksie het verskil tussen spesies pare, maar die verhouding tussen omgewingstoestande en die sterkte van die interaksie was dieselfde vir alle spesies. Op 'n breër geografiese vlak is die opbrengs van die gras *Agrostis magellanica* in die teenwoordigheid en afwesigheid van die polsterplant *Azorella selago* op alle hoogtes waar die plante saam voorkom vergelyk. Die invloed van *A. selago* op *A. magellanica* was negatief op lae hoogtes bo seespieël, maar het meer positief geraak met 'n toename in hoogte bo seespieël, tesame met omgewingshardheid. Die invloed van die polsterplant op die gras het 'n positiewe asimptoot onder uiterste omgewingstoestande bereik. Dus, op Marion Eiland is die geografiese variasie in biotiese interaksies verwant aan omgewingstoestande, en positiewe interaksies kan selfs onder die uiterste omgewingstoestande sterk wees.

Hierdie resultate wys dat positiewe biotiese interaksies tussen plante belangrik is by hoër hoogtes bo seespieël op Marion Eiland. Die interaksies kan dus die opwaartse verspreiding van spesies in reaksie op klimaatsverandering versnel. Nogtans kan negatiewe interaksies die teenoorgestelde effek hê aangesien kompetisie tussen plante, veral in plekke met digte plantegroei (d.w.s. lae of middel hoogtes bo seespieël) opwaartse verskuiwing van spesies kan verhinder. Hierdie navorsing dui aan hoe belangrik dit is om interaksies tussen spesies in ag te neem, aangesien die interaksies die tempo en omvang van veranderinge in verspreiding kan beïnvloed.

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Chapter 1 – General introduction

Ecological consequences of climate change

There is growing consensus that anthropogenic activities since the industrial revolution (c. 1800) have altered the earth's climate by driving changes in atmospheric composition and land surface cover (IPCC 2007; Karl and Trenberth 2005). Higher concentrations of greenhouse gasses and decreased planetary albedo have reduced the loss of long-wave radiation, leading to a positive planetary radiation balance (Bonan 2002; Mann et al. 1998). As a result, the mean global temperature has risen by 0.74 °C over the last 100 years (IPCC 2007). This change in the net planetary radiation budget has led to considerable changes in oceanic and atmospheric circulation (Karl and Trenberth 2005; Turner et al. 2007), which, in turn, has driven regionally heterogeneous changes in precipitation and wind patterns (IPCC 2007; Zhang et al. 2007). At a finer spatiotemporal scale, the frequency, intensity and duration of many types of extreme climatic events have also changed, with, for example, an increased intensity of tropical cyclones (Webster et al. 2005) and more widespread droughts (Easterling et al. 2000a; see also IPCC 2007). Thus, the nature of the global climate has changed considerably over the last century.

These large and rapid changes in climate have had considerable ecological consequences, affecting the abundance and distribution of many species, and altering the composition and functioning of communities and ecosystems globally (reviewed in Hughes 2000; McCarthy 2001; Parmesan 2006; Walther et al. 2002). The species-level impacts of changing climatic conditions have had three forms: 1) changes in species performance (e.g. direct effects on growth rate and reproductive output), 2) changes in species spatial distribution and/or phenology, and 3) *in situ* adaptation to the altered climatic conditions (i.e. changes in physiological tolerances driven by natural selection or phenotypic plasticity) (Hughes 2000). Some species have benefited strongly from climate change, expanding their spatial distributions, lengthening their growing season and increasing their growth and reproductive rates (e.g. Antarctic vascular plant species: Fowbert and Smith 1994; Smith 1994; some European Lepidoptera: Battisti et al. 2006; Davies et al. 2005; Thomas et al. 2001). By contrast, other species have been negatively affected. For example, the Golden

Toad, *Bufo periglenes*, was unable to adequately shift its spatial distribution, alter its phenology and adapt its physiological tolerances in response to climate change, leading to its extinction (Pounds et al. 1999). Thus, a wide range of ecological responses have been observed to recent changes in climate.

With the prospect of a further 220 - 1120 ppm increase in atmospheric CO₂ and the associated 1.8 - 4 °C warming and changes in atmospheric and oceanic circulation over the next century (IPCC 2007), understanding species and community response to continued changes in climate is a priority (McCarthy 2001). Because the biological impacts of climate change have serious implications for all facets of biodiversity (e.g. from genetic diversity to ecosystem functioning; Arft et al. 1999; Bradshaw and Holzapfel 2006; Chapin 2003) and every aspect of human existence (e.g. settlement and migration, agriculture, health, economics; Beniston 2003; Hinzman et al. 2005; Purse et al. 2005), improved forecasts of species responses to changing climatic conditions are invaluable for the management of natural ecosystems and the adaptation of anthropogenic activities.

Impacts of climate change on species distributions

Changes in species distributions in response to climatic change are particularly important for informing management and adaptation actions (Brooker et al. 2007). For example, climate change can affect the geographical ranges of disease vectors and agricultural pests (IPCC 2007; Purse et al. 2005), and the distribution of areas that are climatically suitable for different agricultural activities (Easterling and Apps 2005). Thus, understanding how species ranges may shift under further changes in climate is important for minimizing the negative impacts of climate change on human society. Conservation planning can also benefit from forecasts of changes in species ranges, because these predictions can guide the expansion of conservation networks to cover portions of the present and future distributions of target species (Hannah and Hansen 2005).

Fortunately, climate-driven changes in species distributions have been relatively widely documented in response to past climatic fluctuations and recent climate change (Huntley 1991; Parmesan 2006). From these studies it appears that species distributions have expanded along boundaries where climatic change ameliorated environmental conditions, and contracted more slowly along range

margins where climatic conditions became less favourable (Hickling et al. 2006; Parmesan 2006). Specifically, species have increased their altitudinal and latitudinal ranges along their cooler boundaries in response to rising temperatures (Aerts et al. 2006; Davis and Shaw 2001; Parmesan 2006).

However, despite a strong range shift trend, the size and direction of distribution changes in response to climate change have differed considerably between species. For example, over 30 years of warming in the French Alps, some forest breeding bird species expanded their upper altitudinal boundaries upslope (Archaux 2004). However, the ranges of a similar proportion of species contracted downslope, while the altitudinal ranges of the majority of species (> 66 % of the assemblage) did not change significantly (Archaux 2004). Indeed, species-specific responses to environmental changes have been widely observed in response to past climate fluctuations (Huntley 1991; Jablonski and Sepkoski 1996), recent climate change (Hill et al. 2002; Klanderud and Birks 2003) and climate manipulation experiments (Chapin and Shaver 1985; McGeoch et al. 2006). These individualistic responses appear to be due to species-specific physiological tolerances to a range of environmental factors (Chapin and Shaver 1985; Huntley 1991; Walther 2004). As a result, species distributions are sensitive to changes in multiple climate parameters (Bale et al. 2002; Gaston 2003; Norby and Luo 2004).

Role of biotic interactions in determining species ranges

In addition to climatic factors, biotic interactions can be important determinants of species ranges (Case et al. 2005; Stachowicz 2001), despite most methods for modeling species ranges only indirectly representing their effects (Davis et al. 1998; Pearson and Dawson 2003). For example, negative interspecific interactions (e.g. competition, predation, herbivory, parasitism and hybridization) can exclude species from abiotically-suitable areas that are within their dispersal range (Case and Taper 2000; Gaston 2003; Hochberg and Ives 1999). Of these interactions, competition is the most widely attributed to limiting species ranges, and is thought to determine the lower elevational or equatorial latitudinal boundaries of many species (Brown et al. 1996).

By contrast, positive interactions may extend some species distributions beyond their fundamental niches (Bruno et al. 2003; Crain and Bertness 2006;

Kikvidze and Nakhutsrishvili 1998). Facilitative interactions can be driven by various mechanisms which favourably alter biotic and abiotic conditions (e.g. amelioration of physical stresses, predation, resource limitation and competition: Stachowicz 2001), allowing species to occur in environments which would otherwise be too severe for their survival (Choler et al. 2001). For example, by ameliorating microhabitat conditions the nurse plant *Azorella monantha* enables the herbaceous *Cerastium arvense* to survive at higher altitudes than possible without facilitative interactions (Badano et al. 2007; see also Kikvidze and Nakhutsrishvili 1998). Therefore, a variety of mechanisms exist through which both negative and positive interactions can be important in determining species ranges (Brooker 2006).

Spatial variation in the balance of positive and negative interactions

While biotic interactions are known to be important determinants of species ranges, it is uncertain what factors determine the balance between positive and negative interactions (Callaway and Walker 1997; Stachowicz 2001), and therefore, under what conditions biotic interactions could extend or constrain species distributions (Brooker et al. 2008). The stress-gradient hypothesis (SGH) provides, to date, the best framework for understanding variation in the balance of positive and negative interspecific interactions (Brooker et al. 2008; Kawai and Tokeshi 2007). The hypothesis attributes variation in the relative strength of facilitative and competitive interactions to spatial variation in environmental severity (Bertness and Callaway 1994; Brooker and Callaghan 1998). Specifically, the SGH predicts that net plant interactions switch monotonically from competitive to facilitative with increasing environmental severity, due to changes in the strength of constituent positive and negative interactions (Brooker and Callaghan 1998). Because higher elevations are generally more stressful than lower altitudes (Dullinger et al. 2007; Körner 2007; although see also Cavieres et al. 2006), the SGH predicts increasingly positive net interactions at higher elevations, suggesting the potential for facilitative interactions to expand species upper altitudinal range boundaries further than in the absence of interspecific interactions.

However, recent studies have suggested that the SGH may not be a suitable model of how interactions are related to environmental severity, as plant interactions under extreme environmental severity (as would be experienced at species range

margins: Stachowicz 2001) may be neutral or negative (e.g. Maestre and Cortina 2004; Smit et al. 2007; Travis et al. 2006). Under such a scenario, biotic interactions would either have no effect or a negative influence the position of species upper elevational boundaries. Therefore, to understand the potential for biotic interactions to influence species ranges it is important to determine the generality of the SGH and, more broadly, to understand which factors determine the balance of positive and negative interactions between plants (Brooker et al. 2008; see also e.g. Rodriguez 2006).

Thesis outline: Climate change, range shifts and species interactions

Since species distributions can be affected by climate and interspecific interactions, it is possible that biotic interactions could affect range shifts caused by climate change. Indeed, this has been demonstrated, for example, by established vegetation impeding the upslope expansions of other species in response to warming (an antagonistic effect; Jablonski and Sepkoski 1996; see also Brooker et al. 2007; Dullinger et al. 2003). By contrast, facilitative interactions have been suggested to be able to accelerate upslope colonization in response to rising temperatures (a synergistic effect; Callaway et al. 2002; Dona and Galen 2007). Therefore, in this thesis I examine the potential for biotic interactions to mediate climate-driven altitudinal range shifts on Marion Island. While each research chapter (Chapters 2 – 5) has its own aims, results and discussion (and is formatted as a separate manuscript), their combined results allow an assessment of this broader question (Chapter 6).

- In Chapter 2, Marion Island's climatic record is analyzed to identify biologically-relevant changes in climate from 1949 to 2003. Particular attention is paid to climatic variation, extreme weather events and composite measures of climate since these parameters can be more closely linked to ecological processes than, for example, change in average annual temperature and rainfall (Easterling et al. 2000b).
- In Chapter 3, the past (1965/66) and current (2006/07) altitudinal limits of the island's native flora are compared to test if species altitudinal ranges have responded to the changes in climate. Because data were available for the island's entire native flora, both the species- and community-level consequences of climate change are assessed.

- Spatial variation in the balance of the positive (facilitative) and negative (competitive) components of interspecific interactions are then considered. In Chapter 4, altitude is shown to be a suitable proxy for environmental severity on Marion Island, because of colder temperatures, stronger winds and more mobile substrate at higher altitudes. The predictions of the stress-gradient hypothesis are then tested for four dominant vascular species by documenting changes in spatial association along altitudinal gradients. Because fine-scale spatial patterning of communities reflects the nature of the dominant ecological process at a site, these results are used to assess how the prevailing interspecific interaction varies with environmental severity (following e.g. Kikvidze et al. 2005; Tirado and Pugnaire 2005), and if this relationship is consistent between different pairs of species (Callaway 1998; see also e.g. Callaway et al. 2002).
- In Chapter 5, the shape of the stress-gradient hypothesis is tested to determine what type of interspecific interactions are dominant under extreme environmental stress. In this analysis, the performance of *Agrostis magellanica* in the presence and absence of *Azorella selago* are compared across the entire altitudinal range of both species, providing a robust test of recent suggestions that facilitative interactions are weak in areas of extreme abiotic and biotic stresses (Brooker et al. 2008). A range of performance measures are examined for *A. magellanica* to test if the interaction with *A. selago* affects morphological traits similarly (following e.g. Choler et al. 2001; Maestre et al. 2005).
- Finally, in Chapter 6 these results are synthesized, to assess if biotic interactions can potentially influence changes in species distributions in response to changes in climate on Marion Island.

Study site: Marion Island

Sub-Antarctic Marion Island, the larger of the two Prince Edward islands (46°54'S 37°45'E; 290 km²), was the site for this research. The island is of relatively recent volcanic origin (roughly 450'000 years; McDougall et al. 2001), and has an oceanic climate, with cold and stable temperatures, and high winds, humidity and rainfall (although currently experiencing rapid changes in climate; see below and

Chapter 2). The island supports a relatively depauperate biota, with 22 indigenous vascular plant species (twelve exotic species and four species of unknown origin also occur on the island; Table 1) and approximately 200 bryophyte and lichen species (Gremmen and Smith 2004). The vegetation of the island varies from high-productivity, closed-cover lowland vegetation to barren polar desert with sparse cryptophyte cover at higher elevations (Gremmen 1981; Huntley 1971).

Marion Island is particularly suited to testing questions relating to the biological consequences of climate change and variation in biotic interactions for several reasons, of which four are most pertinent. First, the island has experienced rapid changes in climate over the last half century. Mean air temperature has risen from 5.3 to 6.5 °C between 1969 and 1999, annual rainfall has dropped by 25 mm per year since the 1960's (decreasing from an average of 2697 mm to 1996 mm), and annual sunshine hours have increased by 3.3 hours annually over the same period (Smith 2002; Smith and Steenkamp 1990). Considering the hyper-oceanic nature of the island's climate, these changes are considerable (Smith 2002; Smith and French 1988). Second, because of Marion Island's extreme climate (low temperature, frequent freeze-thaw cycles, strong winds), species responses to changes in climate are expected to be pronounced (Callaghan et al. 1992; Tweedie and Bergstrom 2000). The island's harsh climate also means that positive interspecific interactions are likely to be common (Brooker and Callaghan 1998). Third, the island exhibits a strong and clear altitudinal stress gradient, with lower mean temperatures, stronger winds, more complete cloud cover and lower soil stability at higher altitudes (Boelhouwers et al. 2003; le Roux 2008). Because only a small proportion of the island's primary productivity is consumed by herbivores (Crafford et al. 1986; Smith and Steenkamp 1990), herbivory does not significantly influence environmental severity across the altitudinal gradient. Finally, Marion Island has been a site of biological research since the 1960's. As a result baseline ecological data and historical records exist and the physiology and ecology of many species have already been established (Hänel and Chown 1999).

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Table 1 Vascular plant species occurring on Marion Island (from Gremmen and Smith 2004).

| Species | Authority | Family | Indigenous |
|---------------------------------|------------------|------------------|--------------|
| <i>Azorella selago</i> | Hook. f. | Apiaceae | yes |
| <i>Polystichum marionense</i> | Alston & Schelpe | Aspidiaceae | yes |
| <i>Cotula plumosa</i> | Hook. f. | Asteraceae | yes |
| <i>Blechnum penna-marina</i> | (Poir.) Kuhn. | Blechnaceae | yes |
| <i>Pringlea antiscorbutica</i> | R.Br. | Brassicaceae | yes |
| <i>Callitriche antarctica</i> | Engelm. | Callitrichaceae | yes |
| <i>Cerastium fontanum</i> | Baumg. | Caryophyllaceae | no |
| <i>Colobanthus kerguelensis</i> | Hook. f. | Caryophyllaceae | yes |
| <i>Sagina procumbens</i> | L. | Caryophyllaceae | no |
| <i>Stellaria media</i> | (L.) Vill. | Caryophyllaceae | no |
| <i>Crassula moschata</i> | Forst.f. | Crassulaceae | yes |
| <i>Uncinia compacta</i> | R. Br. | Cyperaceae | yes |
| <i>Grammitis kerguelensis</i> | Tard. | Grammitidaceae | yes |
| <i>Hymenophyllum peltatum</i> | (Poir.) Desv. | Hymenophyllaceae | yes |
| <i>Juncus cf. effusus</i> | L. | Juncaceae | possibly not |
| <i>Juncus scheuchzerioides</i> | Gaud. | Juncaceae | yes |
| <i>Luzula cf. multiflora</i> | (Retz.) Lej. | Juncaceae | possibly not |
| <i>Lycopodium magellanicum</i> | Sw. | Lycopodiaceae | yes |
| <i>Lycopodium saururus</i> | Lam. | Lycopodiaceae | yes |
| <i>Agropyron repens</i> | (L.) P.Beauv | Poaceae | no, but rare |
| <i>Agrostis castellana</i> | Boiss. & Reut. | Poaceae | no, but rare |
| <i>Agrostis gigantea</i> | Roth | Poaceae | no, but rare |
| <i>Agrostis magellanica</i> | Lam. | Poaceae | yes |
| <i>Agrostis stolonifera</i> | L. | Poaceae | no |
| <i>Alopecurus australis</i> | Nees. | Poaceae | no, but rare |
| <i>Festuca rubra</i> | L. | Poaceae | no, but rare |
| <i>Poa annua</i> | L. | Poaceae | no |
| <i>Poa cookii</i> | Hook. f. | Poaceae | yes |
| <i>Poa pratensis</i> | L. | Poaceae | no |
| <i>Rumex acetosella</i> | L. | Polygonaceae | no, but rare |
| <i>Elaphoglossum randii</i> | Alston & Schelpe | Polypodiaceae | yes |
| <i>Montia fontana</i> | L. | Portulacaceae | yes |
| <i>Potamogeton spec.</i> | | Potamogetonaceae | possibly not |
| <i>Ranunculus biternatus</i> | Sm. | Ranunculaceae | yes |
| <i>Ranunculus moseleyi</i> | Hook. f. | Ranunculaceae | yes |
| <i>Acaena magellanica</i> | (Lam.) Vahl. | Rosaceae | yes |
| <i>Limosella australis</i> | R.Br. | Scrophulariaceae | yes |

Chapter 2 - Changes in climate extremes, variability and signature on sub-Antarctic Marion Island *

Introduction

The global climate has changed rapidly and considerably over the last century (IPCC 2001), with a variety of effects on species across the world (Hughes 2000; McCarthy 2001; Root et al. 2003; Walther et al. 2002; Walther 2004). However, while trends in mean temperature and rainfall are most readily and often investigated, the biotic impacts of climate change are also determined by other weather (i.e. atmospheric phenomena over small spatial and temporal scales; Bonan 2002) and climate (i.e. weather conditions averaged over longer spatial and/or temporal scales) parameters (Bonan 2002; Easterling et al. 2000b; Gutschick and BassiriRad 2003; Huth and Pokorná 2005; Parmesan et al. 2000; Stenseth et al. 2002; see also Gaines and Denny 1993). Partly as a consequence thereof, climate change studies (whether retrospective analyses of meteorological data or modeling of future climates) are expanding to document changes in parameters such as wind speed (Peltola et al. 1999), wind direction (Büßer et al. 2004), snow-pack duration (Inouye and McGuire 1991), number of frost events (Inouye 2000), number and timing of rainfall events (Cook and Heerdegen 2001; Cook et al. 2002; Ovadia and Schmitz 2004) and dry-season mist frequency (Pounds et al. 1999). Similarly, more recent analyses also consider changes in climatic variability, extreme weather events and integrative measures (e.g. indices or multivariate measures) of climate (Camarero and Gutiérrez 2004; Elagib and Mansell 2000; e.g. Karl et al. 1996; Klein Tank and Können 2003; Mysterud et al. 2001; Peltola et al. 1999; Pounds et al. 1999). This more comprehensive approach is important because some species respond to changes in climatic variability and the frequency and magnitude of extreme events (Drake 2005; Easterling et al. 2000a, b; Gaines and Denny 1993; Parmesan et al. 2000; Walther 2004). In addition, integrative measures of climate may, in some cases, be better

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descriptors of changes in climate and thus also better predictors of species responses than individual climate parameters (Forchhammer and Post 2004; Post and Stenseth 1999; but see also Hallett et al. 2004; Stenseth and Mysterud 2005).

Temporal variability in climate affects physiological and ecological processes (Benedetti-Cecchi 2003; Drake 2005; Kingsford et al. 2004; Ruel and Ayres 1999; Wichmann et al. 2003) and drives the evolution of life history characteristics (Ruel and Ayres 1999; Schmidt 2004; Sinclair et al. 2003). Thus, both short- and long-term consequences of changes in the temporal variability of climate parameters may be expected. For example, increased variability in rainfall has been shown to alter species' performance and to change community structure in several ecosystems (Cook and Heerdegen 2001; Cook et al. 2002; Fay et al. 2002; Hodkinson et al. 1999; Knapp et al. 2002; Taylor et al. 2004; Xiao and Moody 2004). Individual performance is also affected by changes in thermal variability, via changes in net metabolic activity (Ruel and Ayres 1999), phenology (Post and Stenseth 1999) and, possibly for insects, survival at low temperatures (Renault et al. 2004; Sinclair and Chown 2005). Thus, the predicted net increase in climatic variability under global warming scenarios (IPCC 2001) is likely to have significant ecological consequences.

Associated with greater climatic variability are higher probabilities of extreme weather events, such as higher maximum temperatures or longer and more widespread droughts (IPCC 2001; Katz and Brown 1992; Meehl et al. 2000; see also, e.g. Webster et al. 2005). Extreme events can also result from specific combinations of weather conditions which, when occurring simultaneously, present organisms with conditions very different from those usually experienced. For example, severe droughts can be experienced in years of average rainfall if temperatures (and therefore evapotranspiration) are high (Nicholls 2004), and inter-tidal zones can be unusually warm if low tides occur during the hottest time of the day (Helmuth et al. 2002; Helmuth and Hofmann 2001). Despite their inherently rare nature, extreme events have a disproportionately large effect on the abundance, distribution and evolution of species, and species are thus likely to be particularly sensitive to such events (Easterling et al. 2000b; Gaines and Denny 1993; Gutschick and BassiriRad 2003; Parmesan et al. 2000; Walther 2004).

Because species experience simultaneous changes in the mean, variation and extremes of several climate parameters, indices which synthesize aggregate changes in the climate system can provide meaningful summaries of climate change (Huth and

Pokorná 2005). For example, indices describing the North Atlantic Oscillation (NAO) or El Niño-Southern Oscillation (ENSO) characterize large-scale variation in climate systems (Bonan 2002; Mysterud et al. 2001; Stenseth and Mysterud 2002), while the Climate Extremes Index and Greenhouse Response Index quantify aggregate changes in the US climate associated with climate change (Karl et al. 1996). Due to their integrative nature, these indices may in some circumstances (particularly where a system has two alternate states; e.g. the positive and negative phases of NAO) provide a better measure of changes in a climate system (or at least provide additional insight) than a single climate parameter (Karl et al. 1996). As a result, these integrative indices can, in some cases, be superior predictors of the biological responses to climate change (Forchhammer and Post 2004; Post and Stenseth 1999; but see also Hallett et al. 2004; Stenseth and Mysterud 2005). This is likely where our understanding of the direct mechanistic links between climate change and its ecological consequences are still too limited to readily identify the specific variable(s) driving species performance and population dynamics (Hallett et al. 2004; Stenseth and Mysterud 2005). Alternatively, these integrative measure are also useful where the ecological consequences of climate change for a species are expressed through many indirect effects (e.g. via interacting species; Forchhammer and Post 2004). Thus, examining trends in a variety of weather and climate variables (i.e. ranging from single, short-duration events (e.g. absolute minimum temperature at a site during a winter) to broad spatiotemporal patterns (e.g. average heat sum over a landscape)) offers an improvement over simply describing changes in the mean value of the most common climate parameters, but is still a step away from explicit species-specific predictions based on mechanistic understandings (Forchhammer and Post 2004; Hallett et al. 2004; Helmuth et al. 2005; Stenseth and Mysterud 2005).

Therefore, in addition to changes in average conditions, a more inclusive climate analysis that aims to understand biotic consequences must examine trends in climatic variability and weather extremes, for individual climate parameters as well as the climate system as a whole. Such an in-depth analysis of subtle changes in climate, giving a detailed and synthetic understanding of the nature of climate change is particularly important for locations which are undergoing rapid climate change. One such location is the sub-Antarctic Prince Edward Islands, comprising the 290 km² Marion Island and the smaller, 19 km distant, Prince Edward Island (P.E.I.) (Hänel and Chown 1998). These islands were annexed by South Africa in 1948, and were

occupied primarily for the collection of meteorological data (Hänel and Chown 1998). This continuous meteorological record shows that the island's mean temperature has risen by 0.4 °C per decade, annual rainfall has dropped by 25 mm per year, and annual sunshine hours have increased by 3.3 hours annually since the 1960's (Chown and Smith 1993; Smith 2002; Smith and Steenkamp 1990). However, trends in other parameters and changes in climatic variability, extreme events or aggregate measures of climate have not been examined, despite evidence that the recent rapid changes in climate have already impacted both terrestrial and marine systems in the region (Chown and Smith 1993; Crawford et al. 2003; Pakhomov et al. 2004; Weimerskirch et al. 2003). Here, recent climate changes on Marion Island are documented in more detail than they have been previously, focusing on parameters likely to have particular significance for the island's biota. The potential ecological consequences of the changes identified are discussed in light of recent research on the biota of the sub-Antarctic.

Methods

Climate data for Marion Island (1949 – 2003) were obtained from the South African Weather Service for the meteorological station on the eastern side of Marion Island (46.8830° S, 37.8670° E, 24 m a.s.l.). Temperature data (°C; hourly recordings and daily maxima and minima) were available from 1951, and continuous precipitation data (mm; mostly falling as rain, and referred to as rainfall hereafter for convenience) from 1960 (rainfall data between 1950 and 1959 are incomplete). Cloud cover (oktas), and wind speed (m/sec) measurements were available for the entire period. Wind direction data were not analysed due to apparent instrument error (evident when data were examined at a daily scale). To standardize for differences in measurement frequency between months, annual climate statistics were calculated from the 8h00 reading on each day (the only consistent recording times throughout the study period were at 8h00, 14h00 and 20h00). The choice of 8h00 recordings is considered valid because daily variation in climate parameters has remained similar over the study period. Preliminary analyses showed that annual mean wind speed varied in a step-like manner. Although this is suggestive of changes in recording height, an investigation of the raw hourly data showed no discontinuities (which would be expected if recording height had been changed). This, therefore, suggests

that the data are an unbiased representation of wind strength. Additionally, wind speed measurements are likely to be affected by the location of the meteorological station (i.e. on the eastern, and thus probably more sheltered, side of the island; see Schulze 1971). However, these measurements are nonetheless representative for the eastern side of the island, and provide a valid indication of how wind speed has changed over the period.

Maxima and minima (e.g. annual maximum, average daily maximum) were used to define the magnitude of extreme weather events. The frequency of extreme events was calculated as the number of times an event occurred (e.g. days without rain) or a variable exceeded percentile thresholds (e.g. temperatures falling within the upper quartile). The coefficient of variation (CV) of a parameter was used as a measure of its variability (following, for example, Elagib and Mansell 2000). From these data the number of wind-still recordings (i.e. days when the wind was not blowing at 8h00), the total number of days without rain ('dry days'), the average number of consecutive days without rain ('mean duration without rain'), and the maximum number of consecutive days without rain ('maximum duration without rain') were calculated for each year. Years where more than three weeks' data were missing (i.e. > 6 % of observations) were excluded from calculations (nine years of cloud data, five years of wind and rainfall data, and four years of temperature data excluded). Where data were grouped into decades for analysis, data from 1949 were excluded and data from 2000 and 2003 grouped with data from the 1990's (since data from 1991, 1994 (in some analyses), 2001 and 2002 were excluded due to missing data). To test for long-term trends, annual climate statistics were regressed against year. The significance of each regression was tested by comparing the observed F-statistic against an F-distribution generated by bootstrapping (using Resampling Stats: Bruce et al. 1999; 10'000 repeats), because some variables violated the normality assumption of parametric statistics (Good 1999). Regressions were repeated including a multivariate El Niño index (data from the Climate Diagnostics Centre of the National Oceanic and Atmospheric Administration; <http://www.cdc.noaa.gov/ENSO>; Wolter and Timlin 1998) to test for the influence of El Niño – Southern Oscillation (ENSO) fluctuations on the climate parameters.

Trends in the co-occurrence of extremes in different climate parameters were examined, recording the number of times that sets of extreme conditions occurred simultaneously. The upper and lower quartiles of temperature and wind speed were

used to define the hottest, coldest and windiest 25 % of temperature and wind speed records. Analyses were repeated with more restrictive thresholds (80th, 90th and 95th percentiles), but gave similar results. The number of simultaneous occurrences of warm temperatures, high winds and lack of rainfall were calculated over each year as a measure of the number of days with potentially high evapotranspiration (Bonan 2002; see also Klok and Chown 1998). Similarly, the number of simultaneous occurrences of cold temperatures and high winds were summed as a measure of the number of days when extreme wind-chill (i.e. a very high cooling rate) would have occurred (Holness 2001). Minimum wind-chill was also calculated for each year as a measure of the most extreme combination of low temperature and high winds (Anonymous 2001).

Changes in the day-to-day temporal autocorrelation of climate parameters were also assessed. Strong positive temporal autocorrelation in a parameter indicates that consecutive values are more similar than expected by chance (Legendre and Legendre 1998), and thus strongly correlated with current conditions (and predictable to some measure). Temporal autocorrelation was calculated using 8h00 recordings for each day (daily records for rainfall), and assessed for up to a 15-day time lag. Analyses were conducted over five, nine-year periods (representing the 1950's, 60's, 70's, 80's and 90's), and compared. Years excluded due to missing data were removed from the time series, but the influence of these discontinuities was estimated to be small (less than 1 % of the pairs in the correlations affected for lags of up to 15 days). Small periods of missing data (≤ 3 days) were linearly interpolated; longer gaps (> 3 days) were filled by repeating data from the following period (the temperature record missed the most data, but still < 3.5 % of measurements). Both linear and seasonal trends were removed from the data because the calculation of autocorrelation coefficients assumes stationarity of the data series (Legendre and Legendre 1998). Linear trends were removed using regression residuals in analyses (Legendre and Legendre 1998). The extent of seasonal variation in the parameters was assessed using Fourier periodograms, and, where obvious, removed using the residuals of the regression of the parameter against a sinusoidal curve fitted to the annual cycle (following Gaines and Denny 1993).

Finally, ordination techniques were used to examine climatic similarity between years, and the relationship between individual climate parameters and particular years (Canoco 4.5: ter Braak and Šmilauer 2002; see also Huth and Pokorná

2005). Principle Component Analysis (PCA) and Redundancy Analysis (RDA) were used based on the gradient lengths from Detrended Correspondence Analysis; PCA to compare the similarity of climate in different years, and RDA to approximate the relationships between climate parameters and years (Lepš and Šmilauer 2003). Data were standardized, centred and log-transformed prior to analyses to give equal weight to each variable (Huth and Pokorná 2005; Lepš and Šmilauer 2003). Constrained RDA biplot ordinations were drawn only with climate parameters with at least 30 % of their variation explained by the 1st ordination axis included (i.e. well-fitting or discriminating climate parameters: Lepš and Šmilauer 2003). Analyses were repeated using a reduced data set where redundant parameters had been excluded (tolerance threshold for exclusion < 0.1 : Quinn and Keough 2002), but gave similar results and are thus not presented. Analyses were also repeated with the inclusion of climate data from the 1950's (which required the exclusion of rainfall data from the analyses), and the results of these were also similar.

Results

Over the last half-century the mean temperature on Marion Island, as well as daily and annual maxima and minima, has increased significantly (Table 1, Fig. 1a, c - f). Mean annual temperatures increased from 5.4 °C (1950's) to 6.4 °C (1990's), with the mean temperature of the five hottest years in the same periods increasing from 5.5 °C to 6.8 °C. Similarly, mean daily maxima and minima increased on average by 0.28 °C and 0.24 °C (respectively) per decade, rising from an average daily maximum of 7.6 °C (1950's) to 8.6 °C (1990's) and from an average daily minimum of 2.8 °C (1950's) to 3.7 °C (1990's; Table 1, Fig. 1c, d). In contrast, intra-annual variability in temperature has declined, with temperatures in 1996 and 1997 being the least variable on record (Table 1, Fig. 1b). Temperatures were positively autocorrelated over a lag of 1 - 3 days (maximum autocorrelation coefficient (AC) = 0.3), and also in some decades (more weakly) over a lag of seven to 13 days (Fig. 2). Daily mean, maximum and minimum temperatures exhibited the same temporal autocorrelation pattern, while CV of temperature was weakly positively autocorrelated (maximum AC < 0.07) over a lag of one to three days (correlograms only globally significant for the 1950's and 1970's). However, there was no trend for increasing or decreasing temporal autocorrelation of any of the temperature parameters over the recorded period.

Over a similar period, annual rainfall, mean rainfall event size and maximum daily rainfall (i.e. largest rainfall event) declined, and variability in daily rainfall increased (Table 1, Fig. 3a - c). Annual rainfall dropped from nearly 3000 mm per annum (1960's) to just over 2000 mm per annum (1990's), with average rainfall event size decreasing by 1.5 mm over the recorded period (Fig. 3a, b). The proportion of days without rain, and the mean and maximum duration of consecutive days without rainfall also increased (Table 1, Fig. 3d). The number of dry days (i.e. where rainfall was not recorded) increased from an average of 49.1 days (S.E. = 2.6) in the 1960's to more than 89.1 days (S.E. = 2.9) days in the 1990's. This was matched by an increase of nearly two days in the maximum duration between rainfall events (up from an average maximum of four days in the 1960's to six days in the 1990's). Two outliers were excluded from this analysis (long periods without rainfall in February 1992 and October 2001; possibly due to instrument failure) but these would have strengthened the trend. The 1990's was the driest decade on record, with the highest frequency of days without rain and the lowest frequency of all sizes of rainfall events (Fig. 3e). Larger rainfall events (> 5 mm) declined consistently over the four decades, while small (< 1 mm) and intermediate (1 – 5 mm) events did not show clear trends. Rainfall consistently lacked temporal autocorrelation in all decades (all correlograms $p > 0.05$).

Wind speed (both mean and mean daily maximum) increased significantly over the last five decades, although trends are less linear than other climate parameters (evident from Fig. 4a - d; a polynomial curve did not provide a significantly better fit to the average wind speed data, although it did explain more variation in the wind speed variability and number of wind-still recordings; see below). Since the 1950's, the number of wind-still recordings and the intra-annual variability in wind speed have declined (Table 1), although both parameters peaked in the mid 1960's (Fig. 4b, d; including the quadratic term Year^2 improved the fit to both; CV of wind speed: $R^2 = 0.35$, $F_{2,47} = 14.41$, $p < 0.001$; Wind-still recordings: $R^2 = 0.53$, $F_{2,47} = 28.47$, $p < 0.001$; compare to the values in Table 1). In the 1960's the maximum (mean \pm S.E.) number of wind-still recordings in a year was 80 (52.8 ± 6.9), but only 27 (5.3 ± 3.1) in the 1990's. In contrast to mean daily maximum wind speed, the speed of the each year's fastest wind has declined, from a maximum of 43 m/s in 1950 to a maximum of 25 m/s in 1998 (mean annual wind speed for the 1950's was 27.1 m/s and 22.1 m/s for the 1990's; Table 1, Fig. 4d). Wind speed (8h00

measurements, as well as daily mean and maximum wind speed) showed weak positive temporal autocorrelation (maximum AC < 0.15) over most time lags in all decades except the 1990's. Variation in wind speed was also weakly positively temporally autocorrelated (maximum AC = 0.20), particularly in the 1960's and 1980's.

Cloud cover varied non-linearly over the recorded period, peaking in the late 1970's (Fig. 4e; including the quadratic term Year² improved the fit; R² = 0.19, F_{2, 43} = 6.15, p < 0.005; compare to values in Table 1). Variability in cloud cover decreased over the recorded period (Table 1, Fig. 4f). Cloud cover was strongly temporally autocorrelated in the 1950's (correlograms globally significant; 8h00 recordings, daily mean, daily maximum), but only weakly (and rarely significantly) in other decades. Including the ENSO index did not significantly improve any of the models' fit (the increase in explained variation was not significant in any models; all models p > 0.10), although adjusted R² increased by up to 5 % for some variables (largest increases for mean wind speed, mean maximum wind speed and maximum duration without rainfall).

The number of days with potentially high evapotranspiration (i.e. simultaneously warm temperatures (upper quartile ≥ 7.8 °C), high winds (upper quartile ≥ 11.5 m/sec) and no rainfall) increased over the recorded period (R² = 0.34, F_{1, 36} = 18.59, p < 0.001; Fig. 5a). Similarly, the minimum wind-chill experienced on the island has increased (i.e. become more mild; R² = 0.11, F_{1, 46} = 5.72, p = 0.021; Fig. 5b). Surprisingly, despite the trend for increasing temperatures, the number of extreme wind-chill days (a co-occurrence of extreme cold (≤ 3.3 °C) and strong winds (≥ 11.5 m/sec); i.e. wind-chill < -3.1) has not changed, with cold temperatures and strong winds co-occurring in recent years as frequently as five decades ago (R² = 0.02, F_{1,46} = 0.76, p = 0.39).

Climatic conditions were often similar between consecutive years (Fig. 6). However, the extent of this similarity differed between decades, with interannual variability lowest in the 1970's and highest in the 1950's and 60's. Climatic differences between years were not always linked with the period between the years (i.e. temporal distance), as would be expected if the island's climate was changing linearly. For example, the relatively small distance between 1954 and 1989 on the ordination plot (Fig. 6) indicates that these years had similar climatic conditions despite a 35 year gap between them (see also 1977 and 1990, etc.). Years with

climatically extreme conditions were also identified by the ordination, due to their distance from other points. Therefore, for example, the combination of high temperatures, low thermal variability and low rainfall separates the climate of 1996 and 1997 from that of most other years (Fig. 6). Climate parameters were split into two groups by redundancy analysis ('trend complexes'; following Huth and Pokorná 2005) (Fig. 7). Those linked with the first axis (separating the 1980's and 90's from the 60's and 70's) explained 33.2 % of the variation in climate parameters. This axis represented a gradient of increasing temperatures, declining rainfall, fewer wind-still recordings and declining variation in annual wind speed and temperature. The second axis (separating the 1970's and 80's from the other decades; explaining 8.6 % of variation; test of significance of all canonical axes: $F = 9.07$, $p = 0.018$) represented a gradient of increasing wind speed.

Discussion

Over the last half century, the climate on Marion Island has not only become warmer and drier, but there have also been considerable changes in wind speed and cloud cover. The island's mean, minimum and maximum temperatures increased at a similar rate, maintaining a roughly constant daily temperature range. This was paired with a decline in thermal variability and an amelioration of minimum wind-chill. Over the same period, total rainfall, as well as the number and size of rainfall events declined, and the duration of dry spells increased. This was matched by increasing temporal variability in rainfall, and a greater likelihood of simultaneous warm temperatures and strong winds (enhancing potential evaporation). Cloud cover and wind speed fluctuated considerably, but day-to-day variability declined for both. Marion Island's climate has differed considerably across the past five decades. These differences have largely been driven by changes in the temperature and rainfall regimes, but also by variation in wind speed. Of the changes quantified here, three have particular significance to the island's biota; the increasing duration of dry spells, changes in wind speed, and changes in the extremes and variability in temperature.

Increasing duration between rainfall events

In some systems longer periods between rainfall events can have more serious consequences than declines in total rainfall for both plants and soil-dwelling

invertebrates (Weltzin et al. 2003). Changes in the temporal partitioning of rainfall are likely to have the strongest effects where soils have poor water-holding capacity and where strong winds increase evaporation (and thus which require regular rainfall to replenish soil water; Hodkinson et al. 1999; Körner 2003; Weltzin et al. 2003), such as the majority of higher elevation habitats of Marion Island. Thus, the 50 % increase in the maximum duration between rainfall events (from an average of four to six days), and the increase in the number of high potential evaporation events (as well as the declining total rainfall) are likely to have resulted in a dramatic change in the island's soil moisture regime. On the island, fellfield (due to its thin, mineral soils; Smith and Steenkamp 2001; see also e.g. Heilbronn and Walton 1984; Klok and Chown 1997) and scoria cone vegetation (due to good drainage; Holness 2004) are most likely to be sensitive to these changes. Specifically, fellfield plants such as the dominant, keystone species *Azorella selago* (Apiaceae) (Chapuis et al. 2004; le Roux et al. 2005), and species on well-drained soils (e.g. *Acaena magellanica* (Rosaceae) or *Pringlea antiscorbutica* (Brassicaceae): Chapuis et al. 2004; Hummel et al. 2004), or with shallow root systems (e.g. *Ranunculus* spp. (Ranunculaceae)), are likely to be most strongly affected by longer dry spells. Indeed, declines in these species have been recorded in response to similar declines in rainfall in the sub-Antarctic Kerguelen archipelago (Chapuis et al. 2004; Frenot et al. 1997). In addition, under experimental reduction in rainfall, *A. selago* on Marion Island suffered increased stem mortality and accelerated autumnal senescence (le Roux et al. 2005). The biomass and structure of the invertebrate community associated with this plant species were also significantly altered (McGeoch et al. 2006). Under the prevailing warming and drying trend, xeric fellfield is predicted to replace polar desert habitat in some areas (Smith et al. 2001). An alternative, however, is that the distribution of fellfield vegetation could contract to lower altitudes (being succeeded by polar desert), particularly due to the sensitivity of its dominant vascular plant species (*Azorella selago*) to changes in rainfall (Frenot et al. 1997; le Roux et al. 2005). Therefore, it can be predicted that higher altitude vegetation on Marion Island (where fellfield and scoria cone habitats are most common) will be severely affected by the increasing duration of dry spells.

At lower altitudes, where soils are moister and more organic, longer dry spells may also affect plant and invertebrate communities, particularly since lowland peat moisture content has already declined significantly between 1966 and 1991 (Chown and Smith 1993). Less frequent rainfall will result in higher soil salinity (wind-blown

salt-spray will accumulate for longer; Huntley 1971), which can be lethal even for salt-tolerant species like *Crassula moschata* (Crassulaceae) (Berjak 1979; see also Hummel et al. 2004). Furthermore, two of the most important decomposers, the kelp fly *Paractora dreuxi* (Diptera: Helcomyzidae) (littoral zone) and the flightless moth *Pringleophaga marioni* (Lepidoptera: Tineidae) (mire habitats), are predicted to be negatively affected due to their larvae's sensitivity to desiccation (Klok and Chown 1997; Klok and Chown 2001). Thus, both lowland and upland fauna and flora of Marion Island are likely to be significantly affected by longer periods without rainfall.

Changes in wind speed

The distribution of Marion Island's vegetation types is strongly linked to wind exposure (Smith and Steenkamp 1990). However, few studies (e.g. Cooper and Lutjeharms 1992; Smith et al. 2001) have considered the consequences of changes in wind patterns on the island. Changes in wind speed on Marion Island over the recorded period may already have altered the wind stress (e.g. damage from wind abrasion, altered evapotranspiration and evaporative cooling; Bate and Smith 1983; Ennos 1997; Grace 1977; Warren Wilson 1959) experienced by organisms in exposed habitats. One consequence of stronger winds (e.g. in the 1980's), and the resulting increase in wind stress, is that the upper altitudinal distribution limits of wind-sensitive species could shift downslope. As a result, while species' ranges are predicted to shift upslope in response to warming (Klanderud and Birks 2003; Parmesan 1996; Peñuelas and Boada 2003), stronger winds could override or negate this response in wind-sensitive species (Saetersdal and Birks 1997). For example, the altitudinal distribution of *Agrostis magellanica* (Poaceae), the second most widespread plant on the island (Huntley 1972), appears to be limited by wind exposure (le Roux 2004). Therefore the positive response to warmer temperatures expected from this species (similar to other grasses: Arft et al. 1999; Dormann and Woodin 2002; Norton et al. 1999) may be mediated by concurrent changes in wind speed.

At a finer scale, increased wind strength could also alter the spatial structure of some communities, since the growth, abundance and distribution of both plant and invertebrate species are affected by wind exposure (e.g. non-uniform distribution of invertebrates within, and of *Agrostis magellanica* on, *Azorella selago* cushion plants;

Hugo et al. 2004; le Roux 2004; see also Ashton and Gill 1965; Lynch and Kirkpatrick 1995). For example, increases in wind speed may restrict wind-sensitive species (e.g. species with large, unsclerified leaves, like *Acaena magellanica*, *Ranunculus biternatus* and *Agrostis stolonifera*; Huntley 1970; Pammenter et al. 1986; Taylor 1955) to more sheltered sites within their broader distribution. Even epiphytic *Agrostis magellanica*, despite its relatively sclerophyllous leaves, is chiefly confined to the leeward side of *Azorella selago* cushions in fellfield habitats (le Roux 2004). This evidence suggests that the changes in wind speed illustrated here may alter both the altitudinal and fine-scale distribution of wind-sensitive species.

Changes in the extremes and variability in temperature

On Marion Island maximum and minimum temperatures have increased at a similar rate, in contrast to many other areas where minima are increasing faster than maxima (Karl et al. 1993). As a result, the island's daily temperature range (DTR) has remained constant over the recorded period, while the global trend is for narrowing DTR (IPCC 2001; Karl et al. 1993). Interestingly, Macquarie Island, another sub-Antarctic site, has shown an increase in DTR between 1948 and 1998 (Tweedie 2000). The relatively constant DTR experienced on Marion Island is unexpected, as decreasing cloud cover, as observed for the island (Smith and Steenkamp 1990), is usually associated with the increased DTR (Karl et al. 1993). This could be due to an overriding influence of the surrounding sea surface temperatures on the island's thermal regime (Smith and Steenkamp 1990).

Warming of the island has been predicted to facilitate increases in the range and abundance of some species (Smith and Steenkamp 1990). An obvious exception, however, is where rising extreme temperatures (such as the 1.4 °C increase in average daily maxima over the recorded period) will exceed species upper thermal tolerances. This change is most likely to have negative consequences for the islands' invertebrate fauna as their upper thermal tolerances closely match current microhabitat temperatures and are relatively insensitive to acclimation (Chown 2001). While species sensitivity to heat stress depends on habitat selection and behavioural plasticity, it appears that the island's only Psocopteran species, *Antarctopsocus jeanneli* (Psocoptera: Elipsocidae), is particularly vulnerable to increasing maximum temperatures, due to its relatively low upper thermal limit (100 % mortality at 31.6 °C:

Slabber and Chown 2004; a temperature lower than microclimate maxima that have been recorded on the island by e.g. Avenant and Smith 2003 (36.4 °C) and Chown and Crafford 1992 (33.8 °C)) and its rockface habitat (see Crafford et al. 1986). Comparable magnitudes of warming have been experienced on Marion Island in the past 7000 years, and have caused large changes in the relative abundance of species (evident from pollen records; Scott 1985). However, these warming episodes were accompanied by increased rainfall. The current unique combination of warming and drying has no past analogue, making predictions based on these periods less reliable.

Despite rising temperatures and the accompanying decrease in frost days (Huysen et al. 2000), the number of very cold wind-chill events (based on the co-occurrence of extremes of wind speed and cold) has not changed over the last five decades. Therefore, when in exposed habitats, organisms still experience the same number of extreme wind-chill events as in earlier decades, and thus their response to ‘average’ warming may be constrained by rare cold events. For example, Goldberg (2004) suggested that continued warming could allow the invasive slug, *Derocerus caruanae* (Gastropoda: Limacidae), to extend its altitudinal distribution on Marion Island above its current limit of 200 m a.s.l.. This corresponds to the altitude above which temperature are regularly low enough to cause slug mortality (Goldberg 2004). However, given the species’ sensitivity to low temperatures and desiccation, the lack of change in the number of extreme wind-chill events, as well as the continued drying of the island, are as equally likely to restrict the species to low altitudes as warming is likely to increase its altitudinal distribution. These examples demonstrate that it is important to consider how multiple factors change concurrently. The amelioration of one environmental factor will not necessarily favour a species if its limiting factor does not change (Arft et al. 1999; see also Hayward et al. 2003).

As Marion Island has warmed, so its thermal regime has also become less variable (in agreement with global observations and predictions: IPCC 2001). Although the direct effects of this change are still uncertain, in other locations it has been shown to affect some temperature-dependent physiological process (Renault et al. 2004; Ruel and Ayres 1999; see also Sinclair and Chown 2005), population growth rates (Drake 2005; see also Stireman et al. 2005), as well as plant establishment (Camarero and Gutiérrez 2004) and the location of species’ range boundaries (see also McLaughlin et al. 2002; Perry et al. 2005). Less variable temperatures could also affect species indirectly, via changes in the frequency of freeze-thaw cycles

(Boelhouwers et al. 2003; see also Callaghan and Carlsson 1997). Based on a 1 °C increase in temperature, the frequency of freeze-thaw events is predicted to halve (Boelhouwers et al. 2003; although lower cloud and snow cover could have an opposite effect: Bannister et al. 2005; Sinclair 2001; Sinclair and Chown 2005), increasing soil stability and decreasing soil mixing and substrate weathering (Boelhouwers 2003; Jonasson 1986). This, in turn, will affect species' probabilities of establishment and, therefore, community composition (Inouye 2000; Jonasson 1986; Nyléhn and Totland 1999). Reduced thermal variability is likely to exacerbate the predicted decrease in the frequency of freeze-thaw events, since temperatures will cross the freezing threshold less often, enhancing the geomorphological and biological changes expected solely from warmer temperatures. Therefore, while Smith and Steenkamp's (1990) prediction that warmer temperatures will cause the spread of vascular plants on the island is probable, the response of each species will depend on the balance of the direct and indirect effects of the changes in average and extreme temperatures as well as variability in these parameters (Shaver et al. 2000).

Aggregate changes in climate

Ordination of years by their annual climate statistics revealed the wide range of inter-annual differences in climate, with some consecutive years being very similar (e.g. 1996 to 2000) and others differing greatly (e.g. 1995 and 1996). The climate of the years comprising the 1970's was particularly similar. Interestingly, this period coincides roughly with the modal age of *Azorella selago* plants on the island (le Roux and McGeoch 2004), suggesting that the establishment of this species could have been facilitated by the relatively mild and constant climate that prevailed during this decade. This suggests that the decade's mild conditions (relatively high temperatures and rainfall) prevailed for sufficiently long for this slow-growing species to establish (see e.g. Camarero and Gutiérrez 2004).

Multivariate analyses identified two major climate trends on the island; the first comprising increasing temperatures, decreasing rainfall and declining variability in wind speed and temperature. The second trend represented changes in average and maximum wind speed. Thus, the change in the climate system of Marion Island has not proceeded linearly. In other words, while the trends in warming, drying and decreased variability in temperature and wind speed were all roughly temporally

concurrent (evident from having nearly parallel vectors in the ordination), the changes in wind speed were not, leading to unique climate systems through time (i.e. distinctive combinations of climatic conditions). Therefore, since changes in wind speed have been unrelated to changes in temperature or rainfall, temporal trends in populations of wind-sensitive species (e.g. *Agrostis stolonifera*: Pammenter et al. 1986) are expected to have differed, and to possibly continue to be different, from those of wind-insensitive species (e.g. *Pringlea antiscorbutica*: Chapuis et al. 2000). This will bring about changes in plant community composition on the island (see e.g. Chapin and Shaver 1985; Huntley 1991).

Conclusion

This study demonstrates that a more comprehensive analysis of climate records can provide new insights into the nature of current climate change and its implications for local biota. As a result, more specific predictions of the biological consequences of current climate change may be made for Marion Island. This includes that the increasing duration of dry spells will have particularly severe effects on higher altitude vegetation. Additionally, changes in wind speed will mediate species' positive responses expected to warmer temperatures; stronger winds will cause wind-sensitive species distributions to contract, even under warmer conditions. It is also predicted that further reductions in thermal variability will strongly affect plant species establishment and distribution, particularly by altering soil stability and structure.

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Table 1 Trends in annual climate parameters on Marion Island, tested using linear regression, with bootstrapped p-values. The slope of each relationship represents the mean annual rate of change of each climate parameter (between 1960 and 2003 for rainfall parameters, between 1951 and 2003 for the others). Significance levels are unaffected by step-up False Discovery Rate adjustment (Garcia, 2004).

| Variables (abbreviations) | F | d.f. | p ≤ | Slope ± S.E. | R ² |
|------------------------------------|-------|-------|-------|-----------------|----------------|
| Temperature (Tmp) | | | | | |
| Mean | 91.44 | 1, 47 | 0.001 | 0.027 ± 0.003 | 0.66 |
| Coefficient of variation (CV) | 24.10 | 1, 47 | 0.001 | -0.183 ± 0.037 | 0.34 |
| Annual maximum | 1.13 | 1, 47 | 0.03 | 0.018 ± 0.017 | 0.02 |
| Annual minimum | 3.01 | 1, 47 | 0.01 | 0.021 ± 0.012 | 0.06 |
| Daily range | 0.02 | 1, 47 | 0.09 | -0.003 ± 0.023 | < 0.01 |
| Mean daily maximum (Mean max) | 90.96 | 1, 46 | 0.001 | 0.028 ± 0.003 | 0.66 |
| Mean daily minimum (Mean min) | 95.14 | 1, 46 | 0.001 | 0.024 ± 0.003 | 0.67 |
| Rainfall | | | | | |
| Annual total (Rainfall) | 65.57 | 1, 37 | 0.001 | -20.341 ± 2.512 | 0.64 |
| Mean rainfall event size | 15.32 | 1, 37 | 0.001 | -0.035 ± 0.009 | 0.29 |
| Coefficient of variation | 2.20 | 1, 37 | 0.02 | 0.208 ± 0.140 | 0.06 |
| Maximum rainfall event size | 1.60 | 1, 37 | 0.021 | -0.260 ± 0.206 | 0.04 |
| % days without rain (dry days) | 54.50 | 1, 37 | 0.001 | 0.342 ± 0.169 | 0.60 |
| Max. duration without rain | 6.67 | 1, 37 | 0.002 | 0.044 ± 0.017 | 0.15 |
| Mean duration without rain | 5.18 | 1, 37 | 0.003 | 0.005 ± 0.002 | 0.12 |
| Wind speed (WS) | | | | | |
| Mean | 2.35 | 1, 48 | 0.012 | 0.019 ± 0.012 | 0.05 |
| Coefficient of variation (CV) | 19.97 | 1, 48 | 0.001 | -0.307 ± 0.069 | 0.29 |
| Annual maximum (Max) | 0.65 | 1, 48 | 0.041 | -0.039 ± 0.048 | 0.01 |
| Mean daily maximum (Mean max) | 13.80 | 1, 48 | 0.001 | 0.067 ± 0.018 | 0.22 |
| Wind-still recordings (Wind-still) | 23.67 | 1, 48 | 0.001 | -0.809 ± 0.166 | 0.33 |
| Cloud cover | | | | | |
| Mean | 0.73 | 1, 44 | 0.039 | 0.002 ± 0.003 | 0.02 |
| Coefficient of variation | 13.75 | 1, 44 | 0.001 | -0.218 ± 0.059 | 0.24 |

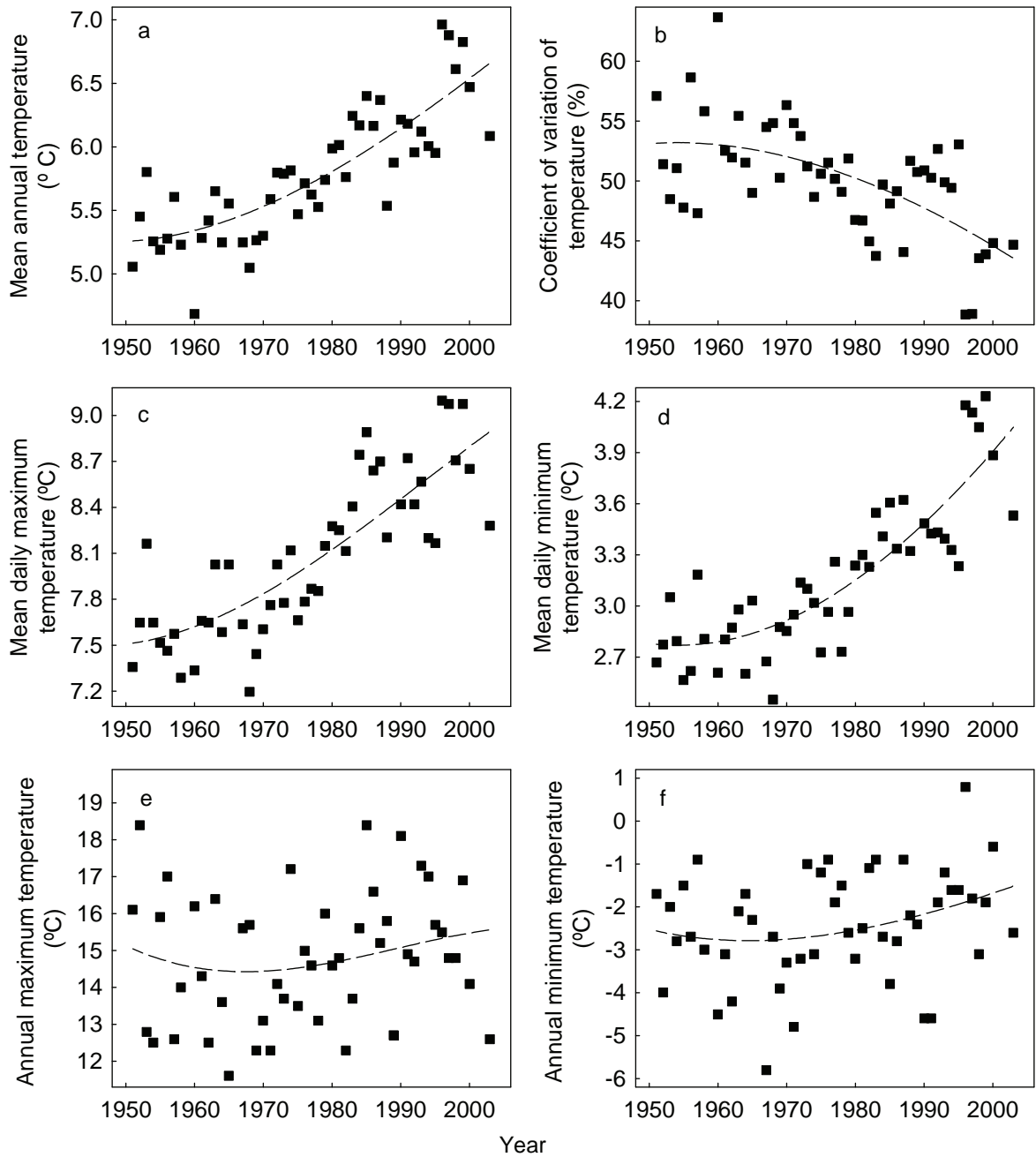


Fig. 1 Changes in temperature over the last five decades on Marion Island: mean annual temperature (a), daily temperature variability (b), mean daily maximum temperature (c), mean daily minimum temperature (d), annual maximum temperature (e), and annual minimum temperature (f). A negative exponentially-weighted curve has been fitted to the data in each graph. Results from linear regression of the data are presented in Table 1.

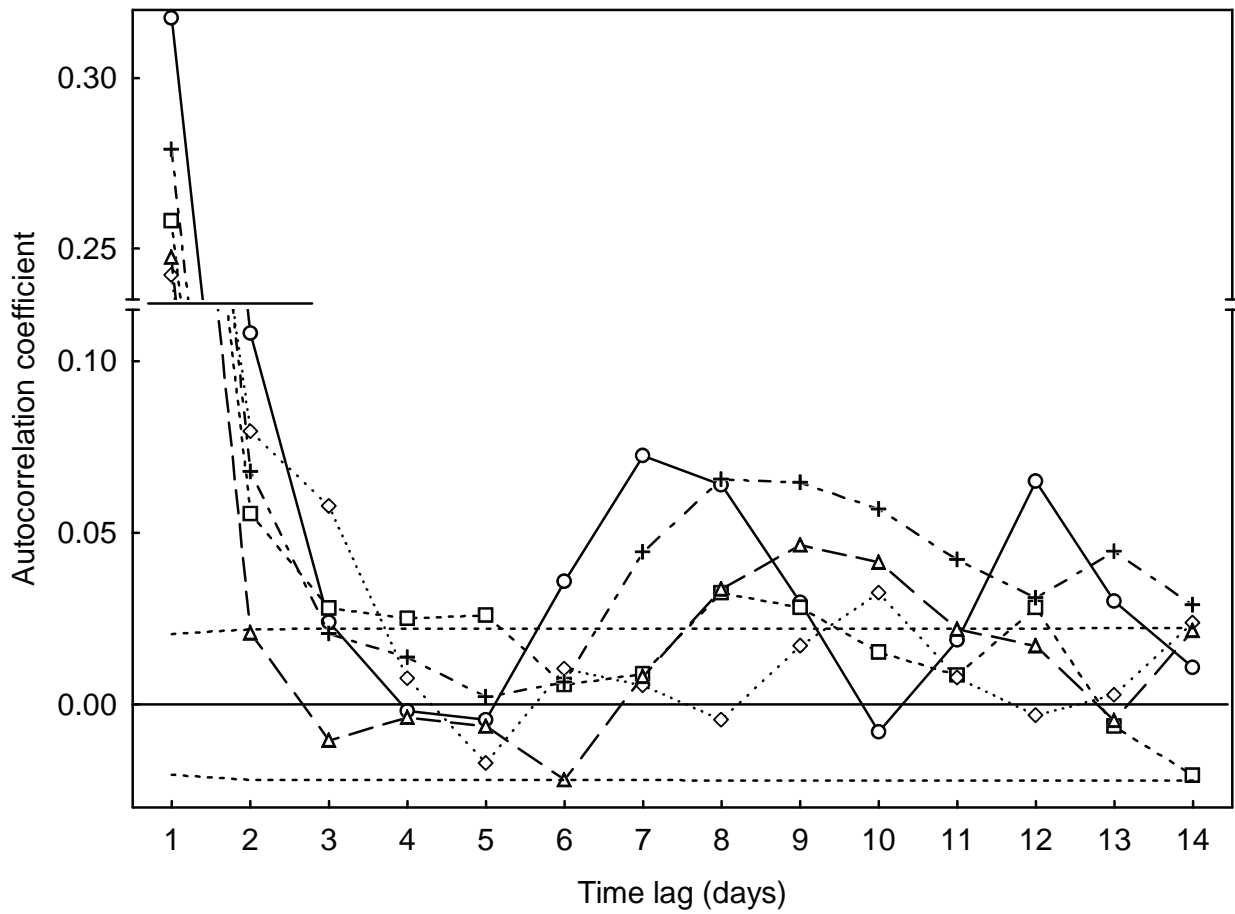


Fig. 2 Temporal autocorrelation of 8h00 air temperature recordings on Marion Island. Separate correlograms were calculated for each decade (all correlograms globally significant, with at least one point exceeding the Bonferroni adjusted p-level of $0.05 \div 14 = 0.0036$). Circles = 1950's, squares = 1960's, diamonds = 1970's, triangles = 1980's, crosses = 1990's and 2000. Autocorrelation coefficients exceeding the 95 % confidence intervals (represented by the dotted lines) are significant at the 0.05 significance level.

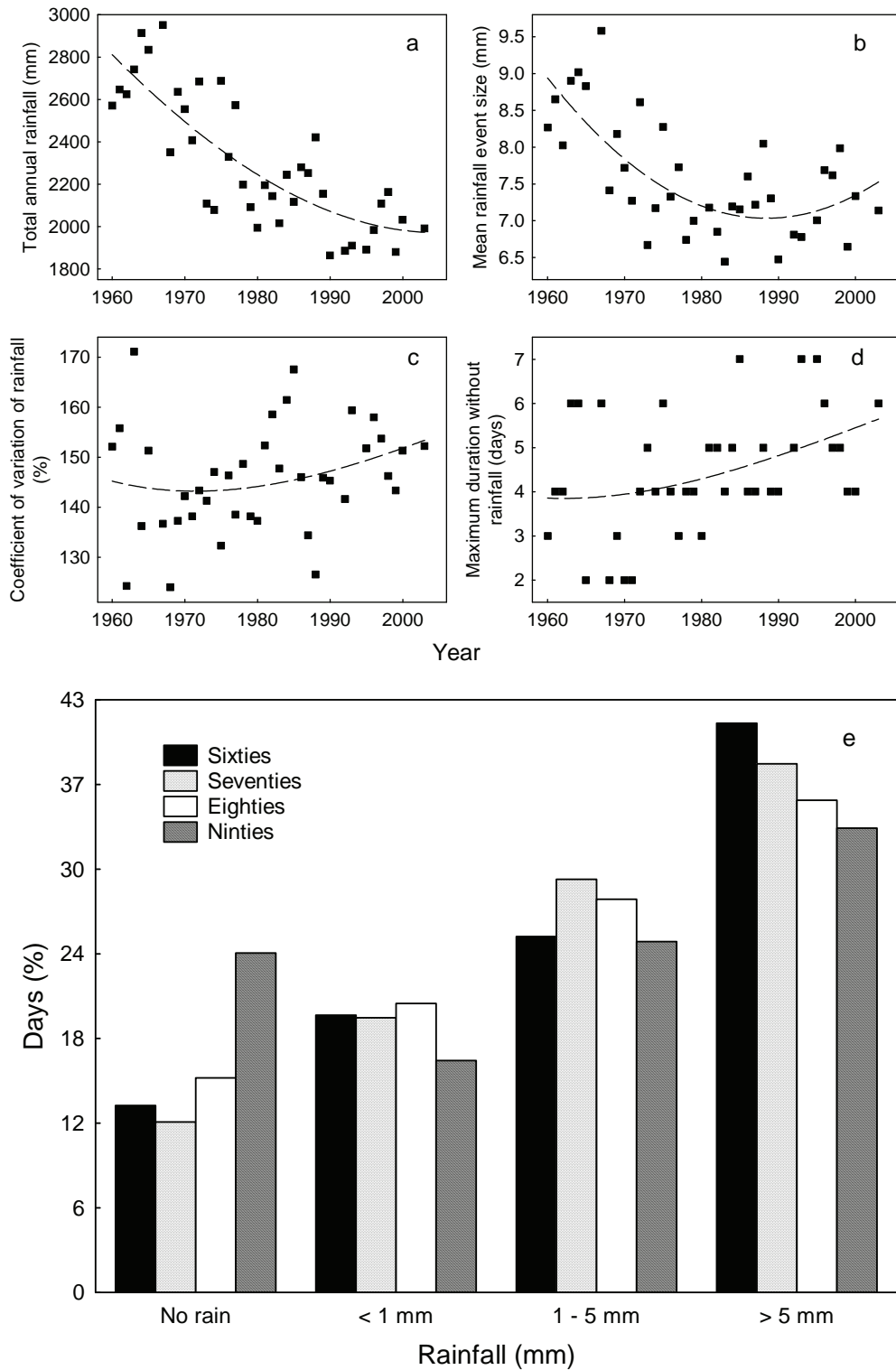


Fig. 3 Changes in rainfall over the last four decades on Marion Island: total annual rainfall (a), mean rainfall event size (b), daily rainfall variability (c), maximum dry spell duration (d), and the frequency of different sizes of rainfall events (e). A negative exponentially-weighted curve has been fitted to the data in the first four graphs. Results from linear regression of the data (a – d) are presented in Table 1. For (e), observations for each decade exceed 3275 recordings.

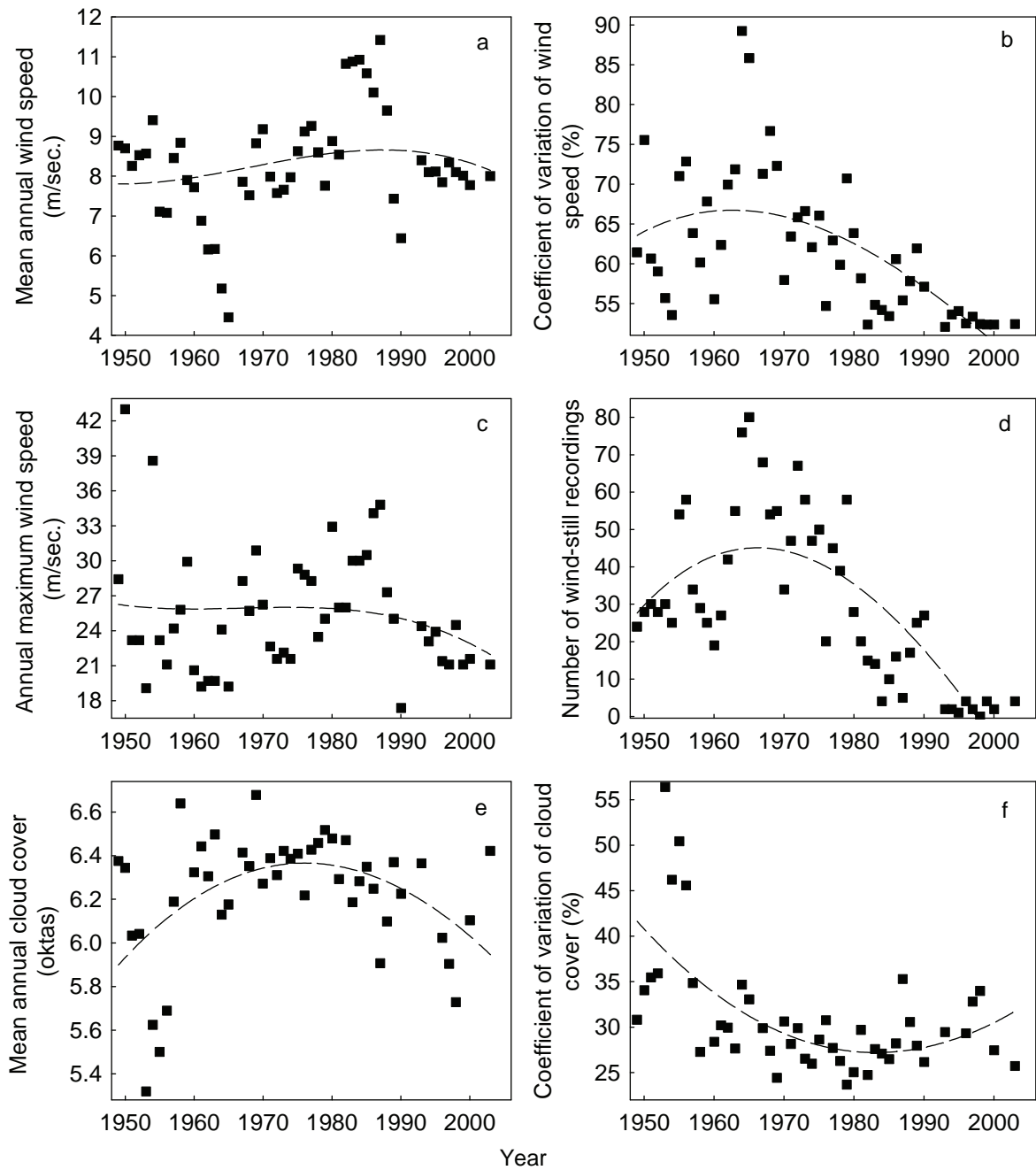


Fig. 4 Changes in wind speed and cloud cover over the last five decades on Marion Island: mean annual wind speed (a), daily wind speed variability (b), maximum annual wind speed (c), number of wind-still recordings (d), mean cloud cover (e), and daily cloud cover variability (f). A negative exponentially-weighted curve has been fitted to the data in each graph. Results from linear regression of the data are presented in Table 1.

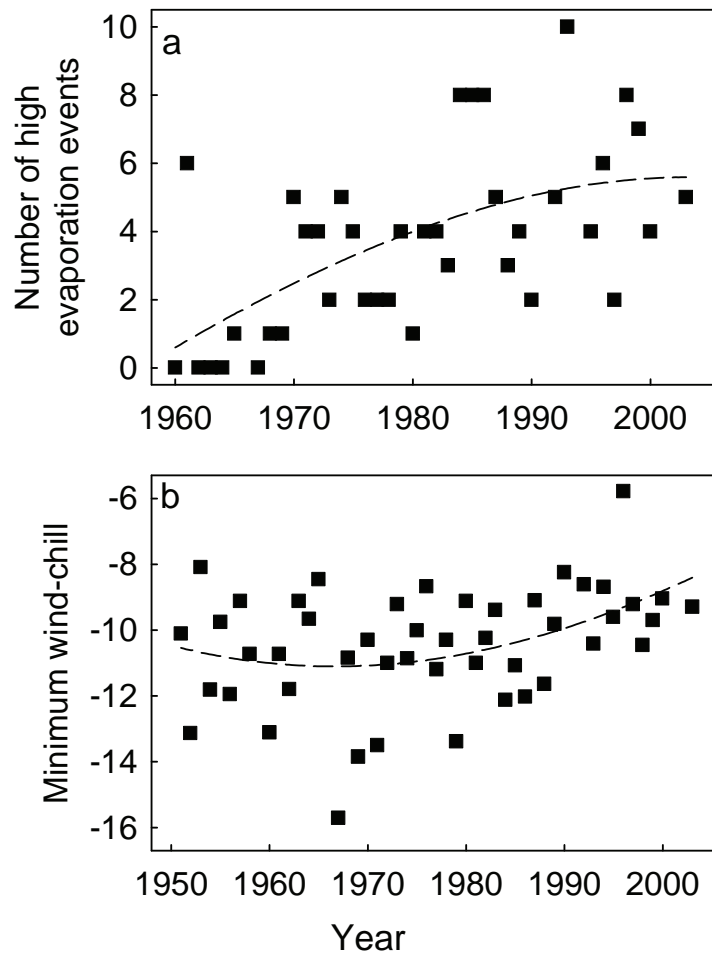


Fig. 5 Changes in extreme events; a) number of high evapotranspiration events (i.e. days when temperatures ≥ 7.8 °C, wind speed ≥ 11.5 m/sec and no rainfall was recorded), b) coldest wind-chill (formula from Anonymous, 2001). Statistics and details in the text.

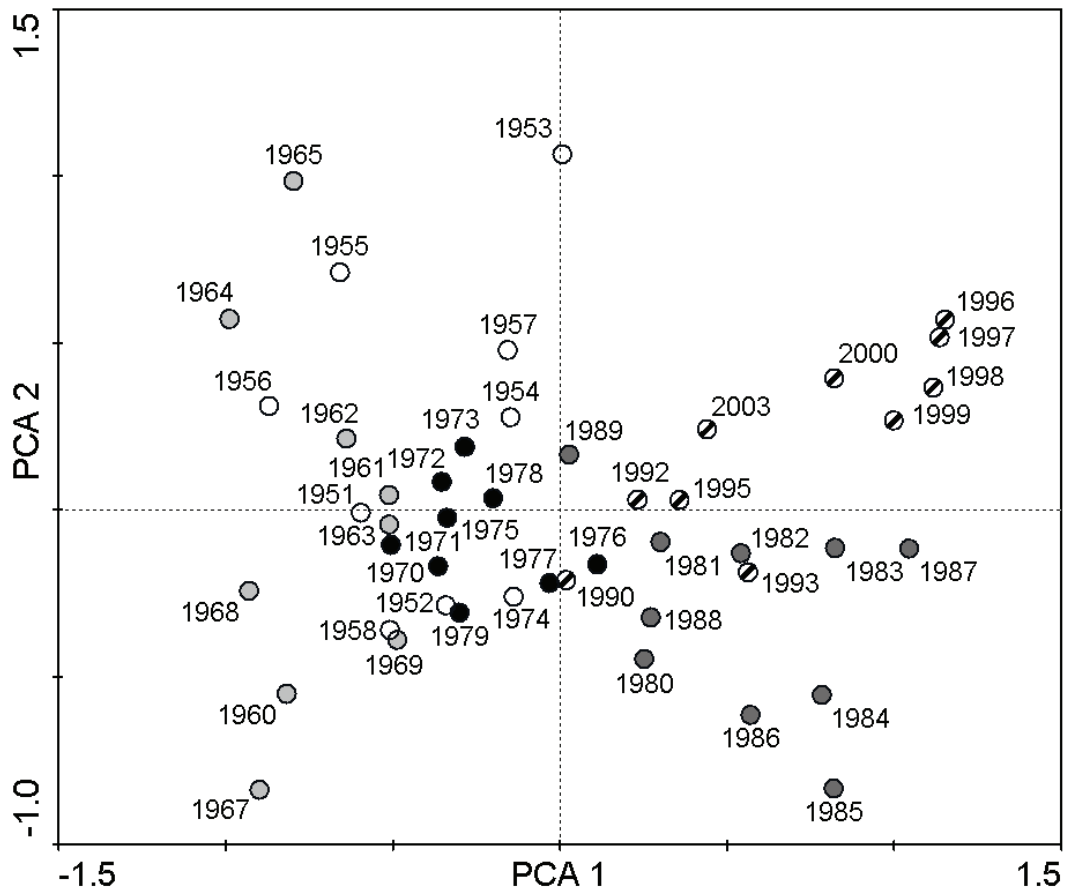


Fig. 6. Principle co-ordinate analysis ordination of years (1950 – 2003). Decades share the same shading of symbols. The first and second axes explain 38.5 and 17.0 % of the annual variation in climate respectively. Mean annual temperature (weighting: 0.90), average daily maximum temperature (0.88), daily minimum temperature (0.92), number of calm days (-0.80), coefficient of variation of temperature (-0.78), coefficient of wind speed (-0.78) and average daily maximum wind speed (0.70) were mostly heavily weighted on PC axis 1. PC axis 2 strongly represented changes in average cloud cover (weighting: -0.61), coefficient of variation of cloud cover (0.59) and temperature range (-0.59). Repeating the analysis including rainfall data (i.e. excluding climate data from the 1950's; see Methods) gave similar weightings, except with average annual rainfall (-0.79) and number of dry days (0.77) also contributing strongly to PC axis 1, and only wind speed metrics (annual average (0.80), daily maximum (0.73), annual maximum (0.87)) being heavily weighted on PC axis 2.

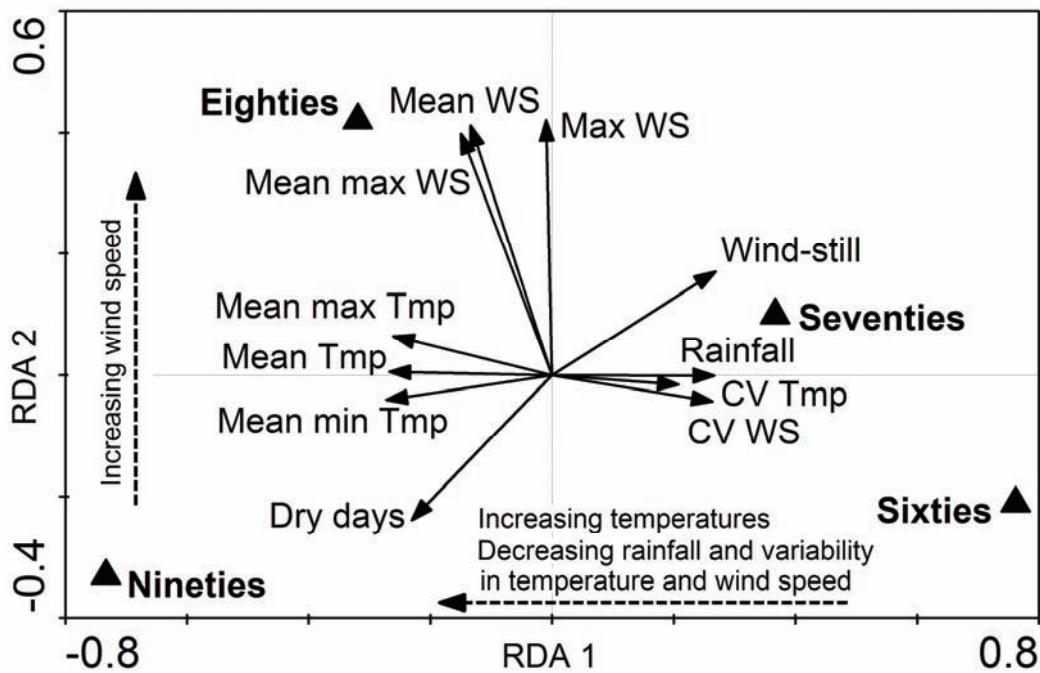


Fig. 7 Redundancy analysis distance (intra-distance samples) biplots of annual climate (excluding 1950's due to lack of rainfall data for that period; axes explain 33.2 + 8.6 % of annual variability) showing treatment centroids (triangles; represent the average climate of the decade) and fitted climate variables (arrows). The distance between decade centroids approximates the dissimilarity in their climate (as quantified by the parameters listed in Table 1). Climate arrows pointing in the direction of a particular decade centroid had the highest values in that decade, with arrow length equal to the relative contribution of that climate variable to the ordination subspace definition (Lepš and Šmilauer 2003). Only climate variables that had at least 30 % of their variation explained by the 1st ordination axis were included in the ordination, i.e. well-fitting variables (Lepš and Šmilauer 2003). Dashed arrows indicate hypothesized gradients across the ordination space. Abbreviations as in Table 1.

Chapter 3 - Rapid range expansion and community reorganization in response to warming *

Introduction

The expansion of species distributions along their cooler boundaries in response to rising temperatures appears to be a consistent biological consequence of recent climate warming (Parmesan 2006; Root et al. 2003). This “fingerprint” of global warming is evident in response to both past climatic fluctuations (Davis and Shaw 2001; Huntley 1991) and current climate change. Many species have expanded their latitudinal ranges poleward and their altitudinal distributions upslope in response to higher temperatures (e.g. 81% of 460 species with long-term range changes; Parmesan and Yohe 2003). This is well documented for the latitudinal ranges of a variety of taxa (Parmesan 2006). Comparatively few studies have considered altitudinal range expansion in response to current warming (Shoo et al. 2006), although these show a relatively consistent pattern of upslope range expansion by species to cooler elevations (e.g. Klanderud and Birks 2003; Konvicka et al. 2003; Kullman 2002; Wilson et al. 2005; although see also Archaux 2004). However, the response of a complete vascular flora to warming has yet to be documented for either latitudinal or altitudinal shifts.

One of the primary limitations to documenting changes in species distributions in response to climate change is the availability of accurate historic data to provide a baseline against which recent changes can be measured (Shoo and Williams 2004; Tryjanowski et al. 2005). Historical distribution data are often scarce and limited to common, conspicuous and/or economically-important species (e.g. butterflies, birds, trees and alpine herbs in terrestrial systems: Parmesan 2006). In consequence, current rates of range expansion and the proportion of species with shifting distributions are estimated from subsets of local flora and fauna. However, since the species for which data are available are generally non-random taxon subsets, their response to warming is unlikely to be representative of the full community. Specifically, the traits which

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cause a species to be common or conspicuous, and hence historically well-known, might also contribute to determining its responsiveness to changes in climate.

Indeed, individualistic species responses to warming have been widely observed, highlighting the variation within taxa to changes in climate (McGeoch et al. 2006; Parmesan 2006; Walther 2004; Warren et al. 2001). Individualistic responses are determined, at least in part, by species-specific physiological tolerances, biotic interactions and habitat requirements (Davis et al. 1998; Davis and Shaw 2001; Parmesan 2006; Walther 2004). As a result, biological responses to climate warming are mediated by concurrent changes in other environmental factors. For example, strengthening winds have inhibited upslope colonization by some tree species on exposed slopes in the Scandes, despite warming facilitating upslope range expansion by the same species along more sheltered slopes (Kullman 2006; see also Cannone et al. 2007; Saetersdal and Birks 1997). Similarly, warmer temperatures were expected to trigger butterfly range expansions across England, but habitat destruction led to range contraction in the majority of species investigated (Warren et al. 2001; see also Franco et al. 2006). Species-specific responses to a range of environmental factors may thus contribute to differential rates of range expansion and must be considered alongside warming as possible drivers of distribution change.

The community-level consequences of species-specific range changes are predicted to include the formation of no-analog communities, where extant species will co-occur in historically unknown combinations (Huntley 1991; Kullman 2006; Walther 2004). However, the degree to which community reorganization is occurring (and will occur) is unsure, in part due to uncertainties about species-level responses (Williams and Jackson 2007). For example, it has been suggested that in some communities rare species will increase in dominance, driving changes in community dominance patterns (Walther 2004). Thus, to avoid potential biases towards the responses of common or conspicuous (i.e. historically well-known) species, assessments of community-level responses to climate change require examination of either (1) random-subsets of species or (2) entire communities (see e.g. Wilson et al. 2007).

Here, I test if changes in the altitudinal range of a native vascular flora in the Antarctic (sub-Antarctic Marion Island) are consistent with the fingerprint of upslope range expansion in response to climate warming. Current and historic upper altitudinal limits were compared at three spatial scales, providing the first assessment

of an entire flora's response to recent changes in climate, considered over a 40 year period of rapid warming. Data for the entire indigenous vascular flora were also used to examine changes in community structure, by testing if the altitudinal patterns of species richness and community composition changed between 1966 and 2006. At the same time, I examined if altitudinal range changes are related to concurrent changes in the island's rainfall regime, wind patterns and manuring by seabirds, all of which are expected to cause downslope range contraction in some species. Our results show clear species- and community-level changes in the flora in response to climate warming, with a highly responsive subset of the community driving significant upslope range expansion and the formation of no-analog communities at intermediate and high altitudes.

Methods

Study site

Marion Island is the larger of the two islands comprising the Prince Edward Islands group, located in the southern Indian Ocean. The island is of relatively recent volcanic origin (roughly 450'000 years old; McDougall et al. 2001), and has an oceanic climate, with cold but stable temperatures, and high winds, humidity and rainfall. As for much of the sub-Antarctic region, the island has experienced rapid changes in climate over the last 50 years, with the island warming by 1.2 °C between 1965 and 2003 at a rate nearly double the global warming average (le Roux and McGeoch 2008a; Smith 2002). In addition, the island has experienced a 20 % decline in rainfall, increased intervals between rainfall events and a shift to more frequent northerly winds (le Roux and McGeoch 2008a; Rouault et al. 2005; Smith 2002). Warmer temperatures have been predicted to cause the upslope expansion of temperature-limited plants on the island (Smith and Steenkamp 1990), while species that are sensitive to rainfall and wind patterns have been predicted to retreat downslope to wetter, coastal sites or more sheltered areas (le Roux and McGeoch 2008a; see also Smith et al. 2001).

The island hosts 22 indigenous vascular plant species (twelve exotic species and four species of unknown origin also occur on the island) and approximately 200 bryophyte and lichen species (Gremmen and Smith 2004). Three subsets of vascular species can be identified based on habitat requirements: (1) species that are generally

restricted to nutrient-enriched environments (i.e. coprophilous species, requiring soils enriched by manuring; n = 3), (2) species that are generally restricted to high moisture levels (i.e. aquatic and mire species: hygrophilous species; n = 4), and (3) species that are restricted to saline salt-spray habitats (i.e. halophilous species, requiring wind-blown salt input; n = 2) (Huntley 1971). Due to their habitat requirements, these three subsets of species can be considered habitat specialists, with their distributions assumed to be disproportionately sensitive to changes in manuring intensity, rainfall and wind-transported salt-spray, respectively (the remaining 13 species are comparative habitat generalists). Five species dominate vascular plant standing crop and aerial cover: *Acaena magellanica*, *Agrostis magellanica*, *Azorella selago*, *Blechnum penna-marina*, *Poa cookii* (Smith 1976b).

In addition to changes in climate, other anthropogenic environmental changes on the island have been either minimal (e.g. habitat transformation) or well documented (e.g. introduction of alien species; Chown and Smith 1993; Gremmen and Smith 1999; see also Bergstrom and Chown 1999). The alien plant species introduced to the island are unlikely to have affected the upper altitudinal limit of native species, since non-native plants are uncommon at intermediate and high altitudes. For example, the highest altitude at which a non-native species was recorded was 508 m a.s.l., while the next highest species was observed only at 382 m (PCLR; pers. obs.). Even at lower altitudes, alien plant species dominate < 1 % of the island (Gremmen 1997) and are therefore unlikely to have altered the lower altitudinal limit of any native species.

By contrast, the introduction of feral cats (*Felis catus*; introduced in 1949, eradicated in 1991) to the island could have had an impact on the elevational range of native species. Marion Island is a breeding ground for 29 species of pelagic birds, which are an important source of allochthonous nutrients to the terrestrial ecosystem (Smith 1978). These ocean-derived nutrient inputs substantially alter soil nutrient levels due to the low inorganic nitrogen and phosphorus content of the island's soils, affecting both plant community composition and plant nutrient status (Smith 1976a; Smith 1978). However, predation by feral cats on burrowing seabirds lowered the allochthonous nutrient inputs to the island by 9.5 tonnes (dry mass) per year (Burger et al. 1978), thus reducing the suitable habitat for coprophilous plant communities (for similar examples see Croll et al. 2005; Norton et al. 1997). Indeed, the spatial extent of tussock grassland, a vegetation type dominated by the coprophilous grass *Poa*

cookii, has shrunk considerably on Marion Island over the last 30 years (Smith et al. 2001). In consequence, it is expected that the altitudinal distribution of coprophilous species will have contracted (or at least their range expansion in response to warming may have been constrained) in response to the decline in the availability of nutrient-enriched habitats. Therefore, changes in the island's rainfall and wind regimes and reduced habitat availability for coprophilous plant species represent three potential mechanisms that could have driven altitudinal range contractions, lowering the upper elevational limits of the vascular plants on Marion Island, in contrast to the changes predicted in response to warming temperatures.

Data collection

To determine changes in the upper altitudinal limits of indigenous vascular plants on Marion Island, the altitudinal boundaries of the species recorded in 1965 - 1966 (Huntley 1970) were compared with their current altitudinal boundaries. The 1965/66 surveys (abbreviated to 1966) comprised well-described protocols for sampling at three different spatial scales; (1) fine-scale altitudinal transects (seven transects on a single volcanic scoria cone, each spanning approximately 50 – 150 m elevation), (2) broad-scale altitudinal transects (four transects on different aspects of the island, each spanning > 900 m elevation), and (3) the entire island (maximum altitude of each species across Marion Island; i.e. island-scale) (Huntley 1970). Surveys at each of the three scales were repeated between 2005 – 2007 (abbreviated to 2006), following the methods of the original survey (Huntley 1970).

Fine-scale observations of species' upper altitudinal limits were made for five common species along seven 5 m-wide altitudinal transects. The transects were located on seven different aspects (corresponding to the cardinal and sub-cardinal directions) of Junior's Kop, a relatively large scoria cone on the island's north-eastern coastal plain (see le Roux and McGeoch 2008b for detailed description). More than five species occur in these transects, but in 1966 data were only collected for five species (Huntley 1970). Transects were intensively surveyed in April 2005 by PCLR, with the placement and width of the transects replicating the original study (Huntley 1970) to facilitate comparison of past and current altitudinal limits (see Shoo et al. 2006). In addition, the presence of seabird burrows in the scoria substrate was noted

for each transect, and compared to burrow density estimates from the same area in 1979/80 (Schramm 1986).

Broad-scale observations of species' altitudinal limits were made for 14 species along four 50 m-wide altitudinal transects (more species were present, but 1966 data were only available for 14 species; Huntley 1970). Surveys were conducted in April 2006 and April 2007, and transects ran from the island's interior plateau down to sea-level on different sides of the island (northern, eastern, southern and western aspects). The placement and width of the transects replicated the original surveys of Huntley (1970), with transect position following mapped routes (Fig. 1 in Huntley 1970). The transects began above 900 m a.s.l. (the most recent highest vascular plant record for the island was 840 m a.s.l.; Hedding 2006), and the highest altitude at which each species was observed was recorded. Two observers surveyed each transect, paying particular attention to microsites that were more likely to host vascular plant species (including bird burrows and nests, *Azorella selago* cushions and moss mats, streams and ponds, caves and overhangs), and recorded the habitat of the highest altitude individual for each species. Transects were completed in 6 – 8.5 hours, and therefore represent similar sampling effort to the original surveys.

The absolute (i.e. island-scale) upper altitudinal limits of all 22 indigenous vascular plant species were determined predominantly from the fine- and broad-scale transect data, but also from *ad hoc* observations. It was not possible to employ similar sampling effort at the island-scale survey as in the 1966 survey, since the original data were collected opportunistically over 16 months (Huntley 1970). Therefore, for three of the 22 species recent high elevation records taken by other researchers were used (*Limosella australis*: N.J.M. Gremmen 1998, *Azorella selago*: D.W. Hedding 2004, *Pringlea antiscorbutica*: J.E. Lee 2007).

Fine- and broad-scale transects were surveyed under snow-free conditions (or < 5 mm snow cover at the top of the transects), and without knowledge of the previous altitudinal limits of each species on each transect to avoid biases in search effort. Altitude was recorded using a barometric altimeter (Garmin Vista Mono; Garmin International, Kansas, USA; all measurements were taken within four hours of calibration at a point of known elevation) and confirmed by plotting each point's GPS co-ordinates on the most recent topographic map (Marion Island 2005, Department of Environmental Affairs and Tourism). The altitude measurements from

1966 were estimated to be accurate to within < 15 m (Huntley 1970), and current measurements of altitude are considered to be of similar accuracy.

This study's results were compared to the mean upslope migration rates of vascular plants in comparable assemblage studies (i.e. all studies explicitly considering changes in the upper altitudinal limits of multiple vascular plant species, either by revisiting previously surveyed plots or by comparison of past and present altitudinal limits; Table 2). All available comparable data were from northern and central Europe (this geographical bias was also noted by Parmesan 2006 and Shoo and Williams 2004).

Changes in species' lower altitudinal limits were assessed by comparing the current (*ad hoc* surveys in April of 2005, 2006 and 2007) and historic (1966; data extracted from Huntley 1971 and supplemented with records from Gremmen 1981) species composition between sea-level and 55 m a.s.l.. Lower altitudinal boundary records were not available for the four rarest species on the island (*Limosella australis*, *Ranunculus moseleyi*, *Elaphoglossum randii*, *Polystichum marionense*), as these species were not recorded in any past relevés (Gremmen 1981; Huntley 1971) or in our *ad hoc* sampling.

Analyses

The relationship between species richness and altitude was calculated from the 1966 and 2006 island-scale data. For these analyses it was assumed that all species are present within all altitudinal bands (100 m elevation intervals from 0 to 900 m a.s.l.) below their current upper altitudinal limit. This assumption is believed to be valid for all the vascular species on Marion Island, and has been observed for the 14 most conspicuous species (PCLR; pers. obs.). These data were further analyzed using multivariate ordination to describe changes in community composition. Presence/absence data for each species for each altitudinal band were analysed using non-metric multidimensional scaling in Primer 5 (following e.g. Jurasinski and Kreyling 2007). Without community reorganization (i.e. a uniform expansion in the altitudinal boundaries of all species), the species composition within each altitudinal band in 2006 would be expected to be similar to that of a lower altitudinal band in 1966 (i.e. 500 m a.s.l. community from 2006 would group with the 400 or 300 m community from 1966).

Results

Range expansion

The mean upper altitudinal limit of the indigenous vascular plant species on Marion Island increased between 1966 and 2006 at all three spatial scales examined (Table 1). Across the entire island, the mean (\pm S.E.) upper altitudinal limit of the vascular species expanded upslope by 69.62 (\pm 29.89) m over the 40 year period (Wilcoxon matched pairs test: $n = 21$, $T = 48.5$, $p = 0.035$; Fig. 1, Table 1). This equates to an altitudinal expansion of 1.8 m/year over the last four decades. Considering only the species with ranges that expanded upslope, the mean expansion rate was 3.4 ± 0.8 m/year. The maximum altitudinal limit of vascular plant growth (represented by *Azorella selago*) increased from 765 m to 840 m a.s.l.. The altitudinal ranges of five species expanded by more than 50 %, with four species expanding upslope by > 200 m over the period (Fig. 1, Table 1). All of the 18 species for which historic low altitude data were available were present between 5 and 55 m a.s.l. in 1966 and in 2006. Therefore, none of these species experienced altitudinal range contractions along their lower altitudinal boundaries of a magnitude similar to the mean altitudinal range expansion along their upper boundaries.

Individual species change

At the island-scale (i.e. maximum upper altitudinal limit across the entire island), 14 of the 21 species responded as predicted, with just under half of the native flora expanding upslope considerably (by > 10 % of their 1966 altitudinal range; Fig. 1). Although the trend was thus for upslope range expansion, the ranges of 24 % of the flora contracted and 33 % showed little change (i.e. changing by < 10 % of their 1966 altitudinal range; Fig. 1). Furthermore, considering both the size and the direction of range changes, species range expansion rates varied considerably (197 % coefficient of variation of changes in upper altitudinal boundary). The five species that dominate vascular plant biomass on the island on average expanded their upslope boundary by more than the mean for the entire flora (92.0 ± 25.9 m; Fig. 1; Table 1).

The range changes of three habitat specialist species subsets were not significantly different from each other or from the remaining species (Kruskal-Wallis

ANOVA, $H_{3, 21} = 2.70$, $p = 0.44$; Table 1). Species associated with high moisture conditions expanded upslope by as much as the entire flora (71.7 ± 31.8 m, $n = 3$), although one of the aquatic species, *Ranunculus moseleyi*, was not observed during 2006 (Table 1). Coprophilous species on average also extended their upper altitudinal boundary (32.0 ± 20.1 m, $n = 3$), although by less than the mean for the entire flora. By contrast, the species restricted to habitats receiving salt-spray exhibited a net range contraction (-20.5 ± 4.5 m, $n = 2$).

At the intermediate spatial scale surveyed (i.e. on the four broad-scale altitudinal transects) the upper altitudinal limit of indigenous vascular plants also expanded upslope, with significant expansions of 60.2 ± 23.0 m (paired t-test: $t = 2.62$, $n = 12$, $p < 0.03$) on the southern and 106.3 ± 23.5 m ($t = 4.01$, $n = 13$, $p < 0.01$) on the eastern transects. Mean upslope range expansions were also positive, but non-significant, for the northern (29.6 ± 47.3 m, $n = 11$) and western (40.58 ± 24.0 m, $n = 11$) transects. Of the 14 species for which data were available in both periods, seven species expanded their altitudinal ranges upslope in all the transects on which they were recorded (e.g. *Agrostis magellanica*; Fig. 2a). By contrast, four shifted downslope in one transect (but upslope in others) (e.g. *Montia fontana*; Fig. 2b), and the ranges of only three species contracted in two or more transects.

In the broad-scale altitudinal transects, some species were strongly associated with specific habitats at their upper altitudinal limits (Table 1; full data in Appendix A). Notably, two species were strongly associated with biotically-influenced habitats, while another five were more weakly associated with this habitat. Furthermore, at their upper altitudinal limits another two species were associated with moist habitats, one with moss mats and three with *Azorella selago* (growing as epiphytes on the plant) (Table 1). Therefore, many species (including habitat generalists) showed clear habitat associations at their upper altitudinal boundaries.

At the finest spatial scale surveyed, i.e. a single scoria cone, the upper altitudinal limit increased for three of the five recorded species (*Agrostis magellanica*, *Azorella selago*, *Blechnum penna-marina*) in all seven altitudinal transects over the period of comparison (Wilcoxon matched pairs test: all $n = 7$, $p < 0.02$; Table 1, see e.g. Fig. 2c). The potential size of the upslope expansions by these species at a fine scale may be underestimated since the species reached the top of the scoria cone on some transects, and were therefore physically limited in the extent to which they could move further upslope (Fig. 2c). By contrast, the two coprophilous species that

were surveyed in the fine-scale altitudinal transects did not spread upslope on all transects: *Montia fontana* increased its upper altitudinal limit on five of the seven transects ($n = 5$, $p < 0.05$; Table 1), but was absent on the other two transects despite being present there during the 1966 survey. The other coprophilous species, *Poa cookii*, expanded its altitudinal boundary on five transects (range: 1 – 32 m) but contracted on the other two transects (range: 10 - 72 m), resulting in a non-significant mean upslope expansion of 1.4 ± 13.4 m ($n = 7$, $p = \text{n.s.}$; Fig. 2d). No bird burrows were observed in the scoria slopes in these fine-scale altitudinal transects, demonstrating a current absence of manuring on these slopes.

Community change

Altitudinal variation in species richness changed considerably between 1966 and 2006 with species richness increasing at most altitudes (Fig. 3). The downslope range contraction of two species (*Elaphoglossum randii* and *Ranunculus moseleyi*, both of which are rare and cryptic) has driven a drop in species richness between sea level and 300 m a.s.l., while the range expansion of other species has increased species richness at higher altitudes. Most noticeable is the increase in the species richness above 600 m a.s.l., rising from one to seven species.

Community composition differed in all (except the highest) altitudinal bands between 1966 and 2006 (Fig. 4). Furthermore, the current species composition within most altitudinal bands is not similar to the past species composition at lower altitudes (2006 points did not cluster with 1966 points from lower altitudes and the direction of change in community composition was not towards the composition of lower altitudinal bands from the first survey period) (Fig. 4). The largest differences between past and present community composition were found at intermediate and high altitudes (between 400 - 700 m a.s.l.). At these altitudes the differences in community composition were larger between years (i.e. comparing the species present within the 400 m altitudinal band between 1966 and 2006) than between altitudinal bands (i.e. comparing the species composition within the 400 and 500 m bands in 1966 or 2006; Fig. 4).

Discussion

The native vascular flora of Marion Island has undergone a rapid expansion in altitudinal range over the last 40 years. Species have expanded their upper elevational boundaries by an average of 70 m in response to a temperature increase of 1.2 °C. The mean expansion rate of species with expanding distributions was particularly rapid at 3.4 ± 0.8 m/year, a rate matched by only a single comparable study (see reference in Table 2). This rate is also much greater than the only other estimate of upslope range expansion available for plants in the southern hemisphere (Wardle and Coleman 1992). Because the observed upslope expansion was not matched by a similar change in lower range boundaries, the flora of Marion Island has undergone range expansion rather than a range shift. This change is considered to represent long-term species range expansions because the highest altitude individuals of all the species were adult plants, many of which bore flowers or seeds (PCLR; pers obs). These changes in species distributions are thus apparently not a temporary response to short-term favourable weather, but rather represent an established presence at higher altitudes in several species.

While the flora's average response to warming was upslope expansion, individual species responses varied considerably. In particular, only a relatively small proportion of species actually expanded their distributions upslope. Indeed, the 43 % of species in the flora that clearly conformed with the prediction of upslope expansion is somewhat lower than the 54 – 69 % of species estimated from partial floras elsewhere (see references in Table 2). The upslope expansion of a portion of the island's flora was therefore strong enough to dominate the mean trend, overwhelming other, weaker responses. Thus, at least on Marion Island, the global fingerprint of warming has been driven by a highly responsive subset of the species pool.

In addition to species-specific responses, the flora's response to warming was slower than predicted on the basis of the rise in temperature alone. Since mean annual temperature has increased from 5.3 °C in the 1960s to 6.5 °C in the late 1990s (le Roux and McGeoch 2008a), isotherms on the island have shifted upslope by roughly 284 m (estimated from the mean of summer and winter lapse rates from the island; Schulze 1971). However, only six species increased their altitudinal ranges by even half this distance (although, surprisingly, the upper altitudinal limit of *Lycopodium magellanicum* increased by nearly 50% more than expected on the basis of

temperature alone; see Dubey et al. 2003 for a similar result). Thus, in agreement with previous studies (e.g. Danby and Hik 2007; Klanderud and Birks 2003), the size of the range shift was species-specific and lagged behind the maximum potential distribution change.

Strong species-habitat associations could be an important cause of the lagged and species-specific rates of range expansion. Indeed, related studies have shown that in some taxa the distributions of habitat generalists have expanded more rapidly in response to rising temperatures than those of habitat specialists (e.g. Warren et al. 2001). This is consistent with the distributional changes on Marion Island, because the six species with the largest upslope expansions were all habitat generalists. However, while halophilous species ranges contracted downslope and coprophilous species expanded upslope relatively slowly, not all habitat specialists had large temporal lags in upslope range expansion. Indeed, the altitudinal distribution of hygrophilous species expanded upslope at a rate similar to the habitat generalists. Nonetheless, even some of the habitat generalist species were clearly associated with specific habitats at their upper altitudinal limits (especially nutrient-enriched and moist microsites, *Azorella selago* cushion plants and moss mats). These habitats therefore appear to be disproportionately important for the recruitment of many species at their altitudinal limits. The habitats in question are comparatively scarce and patchily distributed at high altitudes on sub-Antarctic islands, suggesting that the presence of particular microsite conditions may be necessary for the upslope spread of some species (Hill et al. 2002). As a result, on Marion Island, differences in upslope range expansion rates between species could be related to the availability of suitable establishment sites for each species. Habitat specialists may thus experience a greater temporal lag as a consequence of lower probabilities of finding appropriate habitats relative to habitat generalists.

Species-specific rates of range expansion have probably also been influenced by concurrent changes in other environmental factors, that have altered the availability of some habitat types (e.g. Warren et al. 2001). Indeed, the biological consequence of concurrent environmental changes appears to be well illustrated by range contractions in the island's two halophilous plant species, *Cotula plumosa* and *Crassula moschata*. These two species, generally restricted to coastal habitats that regularly experience wind-blown salt-spray (Gremmen 1981; Huntley 1971), have both experienced altitudinal range retraction since 1966. This may be the result of a

decrease in mean wind speed on the island since the mid 1980's (le Roux and McGeoch 2008a) causing a reduction in the extent of the area receiving salt-spray (as predicted for the salt-spray vegetation under a scenario of weaker winds; Smith et al. 2001), driving a downslope contraction in their distribution. Thus, differential sensitivity to multiple environmental changes, expressed through species habitat requirements, may be partly responsible for species-specific range changes.

The coprophilous plant species on the island are also habitat specialists that suffered a decline in habitat availability, in this case as a result of predation of seabirds by introduced feral cats (Smith et al. 2001; Williams 1978). Indeed, the absence of bird burrows within the scoria slopes in the fine-scale altitudinal transects contrasts strongly with Schramm's (1986) estimates of densities of > 10 burrows/ha on the same scoria slopes in 1979/80, illustrating the severity of the feral cats' impact on Marion Island's seabird population (see also Williams 1978). There has thus been a significant reduction in the density of seabird burrows (and therefore associated localized manuring) on the scoria cone over 26 years. Although the negative consequences of reduced seabird manuring for coprophilous plant species were evident on some transects (partial or complete altitudinal range retraction), it was surprising that these species did not suffer larger and more uniform downslope range contraction. This suggests that seabird abundance (and therefore manuring) was less affected by cat predation at higher altitudes than at lower altitudes. Indeed, most studies concluded that cats were scarce above 500 m a.s.l. on Marion Island (Bloomer and Bester 1992). However, since the seabird species that nest at higher altitudes (van Zinderen Bakker 1971) were dominant prey of the cats on the island (Bloomer and Bester 1990), the likelihood of this explanation is uncertain. Nonetheless, the loss of *Montia fontana* from two transects and the downslope range contraction of *Poa cookii* on two of the seven fine-scale transects, suggests that the decrease in seabird abundance (as observed from lower burrow densities on the scoria cone) has negatively impacted their distributions. Sixteen years after their eradication, the biological consequences of the introduction of cats to Marion Island are still apparently evident in a component of the island's vegetation.

The effects of feral cats might also be manifest in the slower than expected rates of upslope range expansion by the plant community, since seabirds can be important propagule vectors in the sub-Antarctic (Hennion and Walton 1997; Scott 1990). For example, *Uncinia compacta* and *Acaena magellanica* seeds have

morphological features favouring animal dispersal (Hennion and Walton 1997), while various other species (including *Montia fontana*) are thought to be dispersed by gulls, skuas or giant petrels within and between sub-Antarctic islands (Bergstrom and Smith 1990; Ryan et al. 2003; Scott 1990). In particular, the decline in the abundance of sub-Antarctic skuas (*Catharacta antarctica*) on Marion Island, as well as a shift in their distribution away from inland areas (due to competition for prey with cats: Hunter 1990) could represent a reduction in vector-borne dispersal for plant species, particularly since skuas can transport plant material for nest building over large distances (see e.g. Scott 1990; Smith 1982). Therefore, both decreased habitat and dispersal vector availability may have constrained the upslope range expansion of some species, contributing to species-specific lags in upslope range expansion.

As a result of species-specific range changes, the altitudinal patterns of species richness and community composition also changed between 1966 and 2006. The present species composition of communities at higher altitudes is not an analogue of past community composition at lower altitudes, but rather constitutes a historically unique combination of species. For example, *Grammitis kerguelensis*, *Colobanthus kerguelensis* and *Pringlea antiscorbutica* have all extended their ranges upslope by >200 m elevation, contributing to novel combinations of species at higher altitudes. Indeed the greatest changes in community composition appear to be at mid and high altitudes (400 - 700 m a.s.l.), corresponding to the altitudes that have experienced the greatest increase in species richness.

Conclusion

Both species- and community-level changes were observed in the flora of Marion Island over a period of rapid warming. This demonstrates the strong sensitivity of sub-Antarctic vegetation to climate change (as shown by le Roux et al. 2005; and suggested by Chapuis et al. 2004; Chown and Smith 1993; Scott 1990; Smith et al. 2001). While on average the flora expanded upslope significantly, altitudinal range changes were highly species-specific. This idiosyncrasy in species responses lead to the formation of no-analog communities and altered the altitudinal pattern of species richness. Furthermore, since less than half of the species were responsible for the upslope expansion trend, the global fingerprint of warming may thus be driven by a highly responsive subset of the species pool.

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Table 1 Changes in the upper altitudinal limits of the indigenous vascular plant species on Marion Island at three spatial scales (positive values indicate range expansion, negative values range contraction). Species are split by habitat requirements. The five species that dominate vascular plant biomass and cover on the island are highlighted.

| Subset | Family | Species | Dominant habitat associations ¹ | Upper altitudinal boundary change (m) | | |
|--------------|------------------|--------------------------------|--|---------------------------------------|-----------------------------|----------------------|
| | | | | Island-scale | Broad-scale transects | Fine-scale transects |
| Coprophilous | | | | | | |
| | Callitrichaceae | <i>Callitriche antarctica</i> | Biotic | 0 | -203.6 ± 205.0 ² | |
| | Poaceae | <i>Poa cookii</i> | Moss | 69 | 67.5 ± 26.7 * | 1.4 ± 13.4 |
| | Portulacaceae | <i>Montia fontana</i> | Biotic | 27 | 52.0 ± 33.5 | 66.0 ± 13.5 * |
| Halophilous | | | | | | |
| | Asteraceae | <i>Cotula plumosa</i> | Salt-spray | -16 | -24.9 ± 6.2 ² | |
| | Crassulaceae | <i>Crassula moschata</i> | Salt-spray | -25 | -28.5 ± 11.8 ² | |
| Hygrophilous | | | | | | |
| | Cyperaceae | <i>Uncinia compacta</i> | Moist | 89 | 79.5 ± 17.3 * | |
| | Juncaceae | <i>Juncus scheuchzerioides</i> | Moist | 116 | 81.4 ± 19.3 * | |
| | Ranunculaceae | <i>Ranunculus moseleyi</i> | n/a ³ | | | |
| | Scrophulariaceae | <i>Limosella australis</i> | n/a | 10 | | |
| Generalists | | | | | | |

| | | | | | |
|------------------|---------------------------------|-----------------|------|---------------------------|---------------|
| Apiaceae | <i>Azorella selago</i> | 4 | 75 | 28.4 ± 16.8 | 40.6 ± 8.5 * |
| Aspidiaceae | <i>Polystichum marionense</i> | Rock | -5 | | |
| Blechnaceae | <i>Blechnum penna-marina</i> | | 146 | 157.0 ± 16.5 * | 76.4 ± 8.3 * |
| Brassicaceae | <i>Pringlea antiscorbutica</i> | | 234 | -44.3 ± 92.3 ² | |
| Caryophyllaceae | <i>Colobanthus kerguelensis</i> | <i>Azorella</i> | 275 | | |
| Grammitidaceae | <i>Grammitis kerguelensis</i> | Rock | 257 | 123.4 ± 109.7 | |
| Hymenophyllaceae | <i>Hymenophyllum peltatum</i> | Rock | -146 | | |
| Lycopodiaceae | <i>Lycopodium magellanicum</i> | | 388 | | |
| Lycopodiaceae | <i>Lycopodium saururus</i> | <i>Azorella</i> | -126 | | |
| Poaceae | <i>Agrostis magellanica</i> | | 158 | 151.5 ± 17.0 * | 60.3 ± 9.5 * |
| Polypodiaceae | <i>Elaphoglossum randii</i> | n/a | -110 | | |
| Ranunculaceae | <i>Ranunculus biternatus</i> | | 24 | 71.1 ± 30.7 * | |
| Rosaceae | <i>Acaena magellanica</i> | <i>Azorella</i> | 22 | 42.5 ± 71.0 | |
| | | Mean ± S.E. | | 69.9 ± 29.9 * | 55.0 ± 16.5 * |
| | | | | | 48.9 ± 13.2 * |

¹ a habitat association was considered dominant if the species was associated with that habitat in the broad-scale transects at its upper altitudinal limit in more than half of the transects where the species was observed (complete data in Appendix A), ² no statistical test could be performed because the species was only recorded in two transects in 1965, ³ n/a – species not recorded in the transects, ⁴ empty cells indicate that the species was observed growing in the substrate, away from any of the microsite types considered here. *Azorella* = growing epiphytically on an *Azorella selago* plant; Biotic = habitats enriched by seabird or seal manuring; Moist = habitats with high soil moisture, including mires and ponds; Moss = growing in a moss mat; Rock = growing directly onto rock faces or rock overhangs. * = a significant difference between species 1966 and 2006 upper elevational limits (Wilcoxon matched pairs test: alpha = 0.1 for analyses of species limits in the broad-scale transects to account for the small sample size (maximum n = 4); alpha = 0.05 for other tests).

Table 2 Upslope expansion rates from comparable studies examining changes in the upper altitudinal boundaries of multiple vascular plant species in response to climate warming, either by revisiting previously surveyed plots or by comparison of past and present altitudinal limits.

| Study | Number of species | Time period (years) | Species included in analyses | Upslope expansion rate (mean; m/year) |
|--------------|-------------------|---------------------|--|---------------------------------------|
| ¹ | 14 – 26 | 49 | Only species that shifted upslope (two mountains considered) | 3.4 – 4.5 |
| ² | 18 | 92 | Only species that shifted upslope | 2.8 |
| ³ | 60 | 68 | Only species that shifted upslope (53.5 % of 112 species examined) | 1.2 |
| ⁴ | 140 | 85 - 120 | All species, irrespective of size or direction of shift | 0.2 |
| ⁴ | 97 | | Only species that shifted upslope (69 % of species examined) | 0.5 ⁶ |
| ⁵ | 9 | 70 - 90 | Only species that shifted upslope | 0.1 |

¹ Kullman (2006), ² Walther *et al.* (2005), ³ Klanderud and Birks (2003), ⁴ Holzinger *et al.* (2007), ⁵ Grabherr *et al.* (1994), ⁶ calculated from appendix.

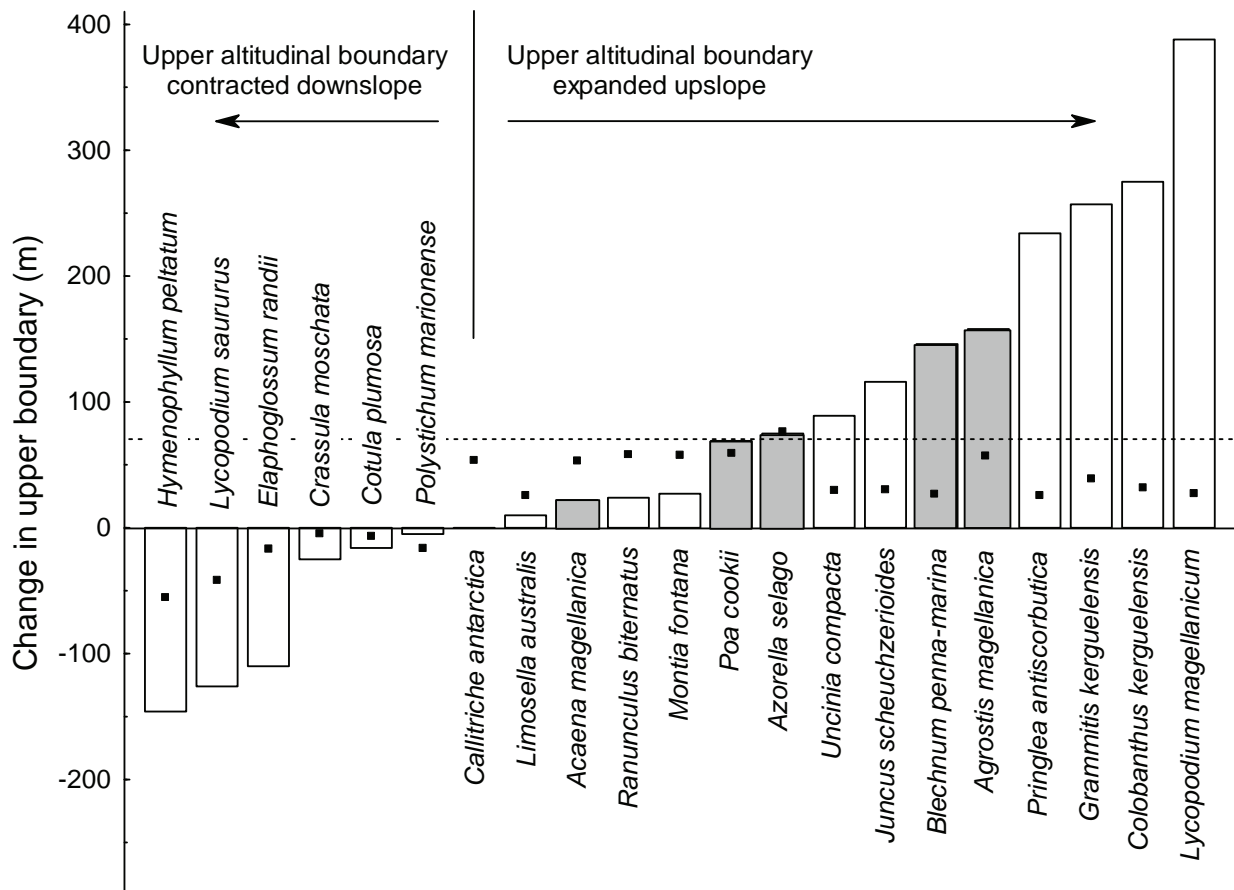


Fig. 1 Changes in the upper altitudinal boundaries of the indigenous vascular flora of Marion Island between 1966 and 2006. Points represent the size of a range boundary change equivalent to 10 % of the species altitudinal range in 1966. For example, *Uncinia compacta* has expanded upslope by 89 m, a change far exceeding 10 % (38 m) of its 1966 altitudinal range. The dashed line represents the mean change in the upper altitudinal boundary for the flora. Shaded bars are those species that dominate vascular plant biomass.

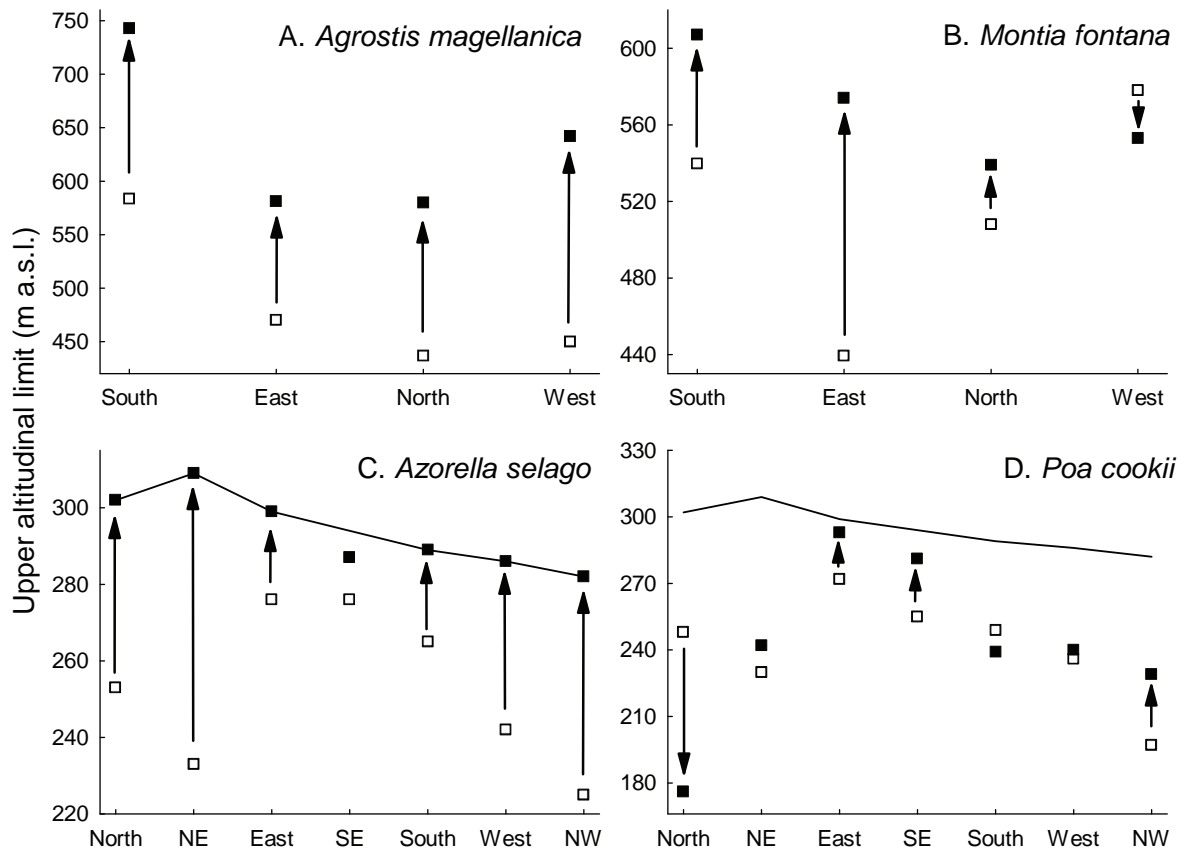


Fig. 2 Examples of variation in the upper altitudinal shifts of four species, using data from the broad-scale (a – b) and the fine-scale (c – d) altitudinal transects. Empty symbols: 1966; filled symbols: 2006. For clarity, arrows are drawn to indicate the direction of the shift. In c) and d) the solid line indicates the maximum altitude of the scoria cone on that transect. Symbols lying on the line indicate that the species is growing at the physical limit (peak) of the scoria cone on that transect.

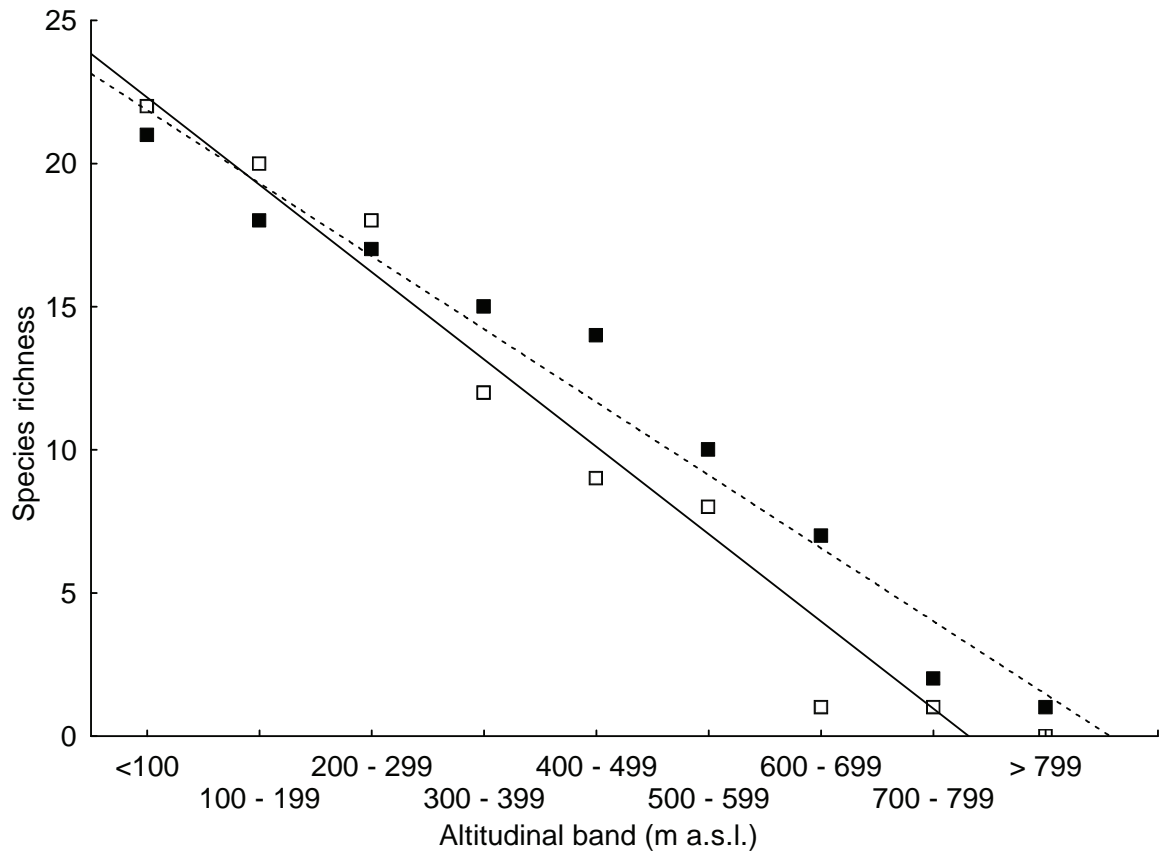


Fig. 3 Differences in indigenous vascular plant species richness across altitude between 1966 (empty symbols) and 2006 (filled symbols). The slope of the relationship between species richness and altitude was not significantly different between 1966 (slope \pm S.E. = -0.031 ± 0.002) and 2006 (-0.026 ± 0.002) ($t = 0.031$, d.f. = 14, $p = 0.17$).

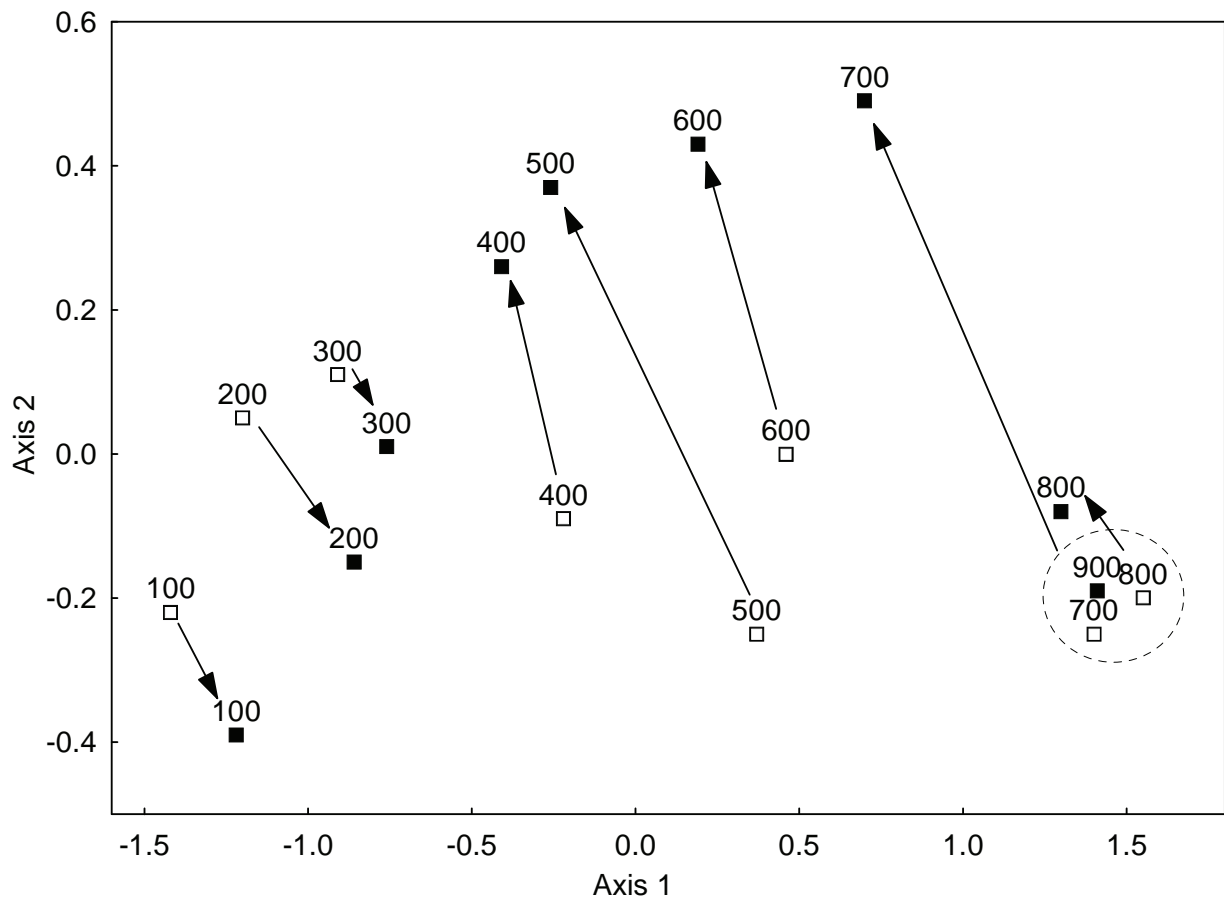


Fig. 4 Non-metric multidimensional scaling ordination of the indigenous vascular plant communities on Marion Island in 100 m altitudinal bands (the maximum altitude in each band labeled on the ordination) for the two survey periods (1966: empty symbols; 2006: filled symbols). The three points circled by the dashes ellipse overlapped (900 m from 2006 and 800 m from 1966 overlapped completely) and have been moved slightly for clarity. Arrows indicate the direction in which community composition has changed (ordination stress = 0.01).

Appendix A Habitat associations of the indigenous vascular plant species at their upper altitudinal limits in the four broad-scale altitudinal transects. Empty cells indicate that the species was observed growing in the substrate, away from any of the habitat types considered here.

| Subset | Species | Broad-scale transects | | | |
|--------------|---------------------------------|-------------------------|------------------------|-----------------|-----------------------|
| | | East | North | West | South |
| Coprophilous | | | | | |
| | <i>Callitriche antarctica</i> | Biotic | Biotic | Biotic | Biotic |
| | <i>Montia fontana</i> | Biotic | Biotic; Moss | Biotic | Biotic |
| | <i>Poa cookii</i> | <i>Azorella</i> | Moss | Biotic; Moss | Moss; <i>Azorella</i> |
| Hygrophilous | | | | | |
| | <i>Juncus scheuchzerioides</i> | Moist | Moist | Moist | Moist; Biotic |
| | <i>Limosella australis</i> | n/a | n/a | n/a | n/a |
| | <i>Ranunculus moseleyi</i> | n/a | n/a | n/a | n/a |
| | <i>Uncinia compacta</i> | Moist | Moist | Moist | |
| Halophilous | | | | | |
| | <i>Cotula plumosa</i> | | | Biotic | |
| | <i>Crassula moschata</i> | | | Biotic | |
| Other | | | | | |
| | <i>Acaena magellanica</i> | Biotic; <i>Azorella</i> | Moist; <i>Azorella</i> | Mire | <i>Azorella</i> |
| | <i>Agrostis magellanica</i> | Biotic | | Moss | <i>Azorella</i> |
| | <i>Azorella selago</i> | | | | |
| | <i>Blechnum penna-marina</i> | | | | |
| | <i>Colobanthus kerguelensis</i> | <i>Azorella</i> | <i>Azorella</i> | <i>Azorella</i> | <i>Azorella</i> |
| | <i>Grammitis kerguelensis</i> | Rock | Rock | Rock | Rock |
| | <i>Hymenophyllum peltatum</i> | Rock | n/a | n/a | n/a |
| | <i>Lycopodium magellanicum</i> | Biotic | <i>Azorella</i> | | |
| | <i>Lycopodium saururus</i> | <i>Azorella</i> | <i>Azorella</i> | | <i>Azorella</i> |
| | <i>Polystichum marionense</i> | Rock | n/a | n/a | Rock |
| | <i>Pringlea antiscorbutica</i> | | Stream bank | n/a | |
| | <i>Ranunculus biternatus</i> | Moist; <i>Azorella</i> | Moss; Biotic | <i>Azorella</i> | Moss; Moist |

n/a = the species was not observed on that transect; *Azorella* = growing epiphytically on an *Azorella selago* plant; Biotic = habitats enriched by seabird or seal manuring; Moist = habitats with high soil moisture, including mires and ponds; Moss = growing in a moss mat; Rock = growing directly onto rock faces or rock overhangs.

Chapter 4 - Spatial variation in plant interactions across a replicated severity gradient in the sub-Antarctic *

Introduction

The net interactions between plant individuals vary over space and time and between species, due to variation in the prevalence and intensity of interspecific competition and facilitation (Brooker and Callaghan 1998; Bruno et al. 2003). The balance of these positive and negative interactions between individuals can strongly influence the structure and composition of communities (Hacker and Gaines 1997; Michalet et al. 2006). However the factors that determine the importance and relative intensity of these types of interactions in different communities are still incompletely understood (Brooker 2006; Callaway and Walker 1997), although abiotic environmental conditions and certain species traits appear to be important (Callaway 1998). The stress-gradient hypothesis (SGH hereafter) suggests that some of the variation in the intensity of positive and negative interactions is related to abiotic environmental severity (comprising biotic and abiotic stresses and disturbances; Brooker and Callaghan 1998; see also Bertness and Callaway 1994). The hypothesis predicts that the beneficial impact of positive interactions on species performance will increase relative to the deleterious impact of negative interactions under increasingly severe conditions. This is based on the assumption that the positive effects of environmental modification by neighbouring individuals (predominantly amelioration of abiotic conditions, but also protection from herbivory, etc.) outweigh the negative effects of resource depletion in areas of high environmental severity (Bertness and Callaway 1994; Brooker and Callaghan 1998). Under more moderate conditions, the SGH predicts that negative interactions will dominate species interactions, with the effects of competition with nearby individuals overwhelming any positive effects of environmental amelioration.

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Studies have found support for the SGH across a variety of severity gradients. For example, the intensity of positive interactions (relative to negative interactions) has been shown to increase with increasing aridity (Pugnaire and Luque 2001) and disturbance (Franks and Peterson 2003) over space, as well as through time (Gómez-Aparicio et al. 2004; Tielbörger and Kadmon 2000). Similarly, using altitude as a surrogate for environmental conditions (representing more severe conditions at higher altitudes), positive interactions have been shown to be more dominant at higher elevations than at lower altitudes (Callaway et al. 2002; see also Badano et al. 2005 where aspect is used as a surrogate for environmental severity). Nonetheless, the generality of the SGH remains to be established. For example, a recent meta-analysis did not find general support for the hypothesis in arid environments (Maestre et al. 2005, 2006; although see also Lortie and Callaway 2006).

In contrast, the SGH has been supported by most investigations of variation in species interactions in the cold and windy alpine and Arctic environments (Callaway et al. 2002; Choler et al. 2001; Kikvidze et al. 2005). Positive interactions are often common in these environments (e.g. Carlsson and Callaghan 1991), and their intensity appears to increase with climatic severity (Callaway et al. 2002; Choler et al. 2001; Kikvidze et al. 2005; Klanderud and Totland 2004). Assuming the SGH is applicable to all cold and windy environments, it should then also explain some of the spatial variation in plant interactions in the sub-Antarctic (characterized by low temperatures, frequent freeze-thaw cycles and strong winds; le Roux 2008). In this region, where the SGH has yet to be tested, climate and microclimate are strongly related to altitude, aspect and topography (le Roux 2008), and therefore the nature of plant interactions may be predicted to vary with both elevation and aspect.

However, using altitude or aspect as a surrogate for abiotic severity recognizes that severity gradients are often not determined by a single abiotic factor, but rather comprise complex combinations of multiple abiotic stressors (Austin et al. 1984). This is well illustrated by Cavieres et al. (2006) in the central Chilean Andes where temperatures and soil moisture vary inversely along an altitudinal gradient. While plant species associations became more positive with increasing aridity (supporting the SGH), they simultaneously shifted to being more negative at more stressful temperatures (refuting the SGH) (Cavieres et al. 2006). Complex gradients, composed of multiple independently varying (or negatively correlated) stressors, may thus confound the detection of stress-driven patterns in plant communities.

Both experimental and observational methods can be used to assess spatial variation in species interactions. Using fine-scale patterns of species distributions to test the SGH implicitly assumes that the spatial distribution of individual plants reflects the dominant ecological process at a site (i.e. whether competitive or facilitative interactions have a greater intensity). This assumption is supported by recent research that used mensurate and experimental methods concurrently (Choler et al. 2001; Kikvidze et al. 2005; Tirado and Pugnaire 2003). Investigating the fine-scale spatial patterns of species associations, specifically testing for directionality, can also help to identify which facilitative mechanisms dominate at a site (following e.g. Alftine and Malanson 2004; Carlsson and Callaghan 1991; Haase 2001). This is useful considering that numerous facilitative mechanisms have been observed in alpine and Arctic areas, include warmer and less variable temperatures, sheltering from wind, enhanced soil development and stability, and decreased desiccation in the presence of neighbouring plants (Choler et al. 2001). While these mechanisms are not exclusive, investigating species fine-scale spatial patterns provides a means of eliminating some competing hypotheses.

The aim of this study was thus: first, to quantify abiotic severity gradients across altitude and aspects on a landform on sub-Antarctic Marion Island by documenting spatial variation in abiotic conditions and by considering results from a previous study of substrate mobility (Holness 2004). Once severity gradients were identified, predictions were formulated using the SGH concerning spatial variation in the balance of the intensity of positive and negative plant interactions along these gradients. Second, spatial variation in the balance between positive and negative interspecific interactions was inferred from species' association patterns, and compared to the predictions from the SGH. Third, fine-scale species association patterns were examined for directionality to identify probable facilitative mechanisms.

Methods

Study site

Marion Island is located in the southern Indian Ocean and has an oceanic climate, with cold but stable temperatures, and high winds (predominantly from the north-westerly sector), humidity and rainfall (le Roux 2008; le Roux and McGeoch 2008). The island supports 40 vascular plant species and approximately 200

bryophyte and lichen species (Smith 1987). Only a small proportion of the island's primary productivity is consumed by herbivores (principally insects; Smith and Steenkamp 1990).

The island has 130 pyroclastic scoria cones (also known as cinder cones), which are geomorphologically active landforms due to their relatively steep slopes and unconsolidated substrate (Holness 2004). Substrate mobility on scoria cones is a consequence of frost-heaving (due to regular diurnal freeze-thaw cycles) and small debris flows (Boelhouwers et al. 2000; Holness 2004). The vegetation of these cones varies from sparse cryptogam cover to near complete vascular plant cover, with the degree of vegetation cover generally negatively correlated with the cone's elevation (Holness 2004).

Junior's Kop (highest point: 46°54'02"S, 32°45'85"E) is a scoria cone on the north-eastern coastal plain of Marion Island, with an area of about 0.4 km². The cone consists mostly of loose scoria material underlain by a mixture of gravel and loam, with some stable scoria layers (referred to as tuff from hereon) surrounding the crater at the summit of the cone (Boelhouwers et al. 2000). Sediment movement rates on the cone vary with aspect and clast size, ranging from 0.7 m per year for fine substrates on a steep slope, to < 0.02 m per year for blocky clasts (see Table 1) (Boelhouwers et al. 2000; Holness 2004). Only on the south-western aspect, where the substrate is a basaltic lava flow in contrast to the unconsolidated scoria on the other aspects, is substrate movement lower. Substrate mobility was only measured at one altitude on Junior's Kop by Holness (2004), although also assessed on other scoria cones at different altitudes on Marion Island. Since sediment movement rates increased across altitude on these scoria cones, it is assumed that this altitudinal gradient in substrate mobility is also expressed across individual scoria cones, including Junior's Kop. The cone's vegetation is dominated by four species, and these were the focus of this study: the compact, prostrate cushion-forming *Azorella selago* (Apiaceae), the grass *Agrostis magellanica* (Poaceae), the creeping fern *Blechnum penna-marina* (Blechnaceae) and the low-growing woody shrub *Acaena magellanica* (Rosaceae) (hereafter *Azorella*, *Agrostis*, *Blechnum* and *Acaena*) (Huntley 1970; PCLR pers. obs.).

Abiotic conditions

During April 2005, altitudinal gradients in microclimate were quantified on eight different aspects of the cone (orientated radially from the crater rim, at approximately 45° intervals; i.e. corresponding to north, north-east, etc.). Thermochron iButton temperature loggers (Maxim Semiconductor Corporation, Dallas, USA) were placed 1 – 2 cm under unvegetated substrate at the top (on the crater rim; “Top”) and bottom of each transect (at the base of the cone; “Base”), as well as at two intermediate altitudes (“Low” and “High”). Temperatures were recorded at 15 minute intervals for 14 days (0.5 °C resolution). HoboPro RH/Temp dataloggers (Onset Computing, Bourne, USA) were used to measure air temperature and relative humidity (5 cm above ground) adjacent to the High iButton loggers on the northern (hereafter abbreviated to N), southern (S), eastern (E) and western (W) aspects (temperature resolution < 0.03 °C; relative humidity resolution = 0.5 %; hourly recordings). Paired wind speed, wind direction, air temperature and relative humidity measurements were taken at the bottom of the transects, using a hand-held sensor (AZ Instruments, Taichung, Taiwan; resolution = 0.1 m/s, 0.1 °C and 0.1 % respectively). Paired measurements of these variables were also taken at the top and bottom of the cone (i.e. at the highest point on the crater rim and at the bottom of the different transects). Rainfall was measured at ground-level at the bottom of the N, E, S and W transects (gauges emptied every 4 – 6 days).

Species cover data

The cover of all vascular plant species were determined in four altitudinal transects on the scoria cone during April 2005. Some species were occasionally also recorded epiphytically on *A. selago*. These individuals were excluded from analyses because different facilitative and competitive mechanisms are likely to determine the spatial patterning of epiphytic and non-epiphytic individuals. Transects were 5 m wide, and were surveyed from the cone’s crater rim to the base of the cone, orientated approximately in N, E, S and W directions (corresponding to the transects of Huntley 1970). Each transect was divided into grids of 5 x 2.5 m (shortest sides parallel to the slope), comprising two hundred 0.25 x 0.25 m grid cells. The cover of each vascular plant species was recorded in each cell, with contiguous grids sampled from the top of each transect downslope until cell occupancy exceeded ± 20 %. Thereafter, grids were

sampled at 15 m intervals downslope. The use of grid-based sampling in studies of spatial patterns gives comparable results to point-based sampling, and is appropriate when individual plants are difficult to distinguish (e.g. *Blechnum* and *Acaena*) or small and abundant (e.g. *Agrostis*) (Fehmi and Bartolome 2001). Species presence and total vegetation cover were also recorded in contiguous grids (also measuring 5 x 2.5 m) along altitudinal transects on the north-eastern (hereafter abbreviated to NE), north-western (NW), south-eastern (SE) and south-western (SW) aspects of the cone. The altitude of each grid was determined using a barometric altimeter (Garmin Vista Mono; Garmin International, Kansas, USA; all measurements were taken within an hour of calibration at a point of known elevation). Data from tuff, basaltic lava or flat areas (defined as shallower than $\pm 12^\circ$ slope) were excluded from analyses (< 10 % of observations) as these substrates are more stable than typical steep scoria slopes.

Spatial aggregation of individual species

Two methods, both offering distinct advantages, were used to quantify the spatial distribution of each species; Spatial Analysis by Distance Indices (SADIE) (based on species cover per grid cell) and the $L(t)$ function (the linearised form of the Ripley's K function; based on grid cell occupancy) (Haase 2001; Lancaster and Downes 2004; Perry 1998; Perry and Dixon 2002). Grids were only included in analyses for a species (or species pair; see below) where that species' (or both species in the pair) occupancy exceeded 15 % of grid cells.

SADIE provides a measure of aggregation that considers a sample's value relative to the values of surrounding samples, and is therefore different from methods which simply calculate local densities (Perry and Dixon 2002). SADIE calculates a standardized index of aggregation I_a for each grid, based on the minimum total distance that values in the observed arrangement need to be moved to achieve an even spatial distribution (Perry 1998). Large values of I_a indicate greater spatial aggregation. The significance of I_a can be tested by permutation methods. These analyses were implemented using SADIE software (available from <http://www.rothamsted.bbsrc.ac.uk/pie/sadie/>).

In contrast, the advantage of the $L(t)$ function is that it allows directional analyses of spatial associations (see next section). The $L(t)$ function is derived from the Ripley's $K(t)$ function compares the observed density of occupied grid cells (at a

set of different distances, measured by radius t) to the density expected if all occupied grid cells were randomly distributed, with larger values indicating greater spatial aggregation of occupied cells (Fehmi and Bartolome 2001; Haase 2001). The significance of the $L(t)$ function is determined by permutation methods (comparing the observed $L(t)$ value against a distribution of $L(t)$ values generated by multiple permutations of the data set, maintaining the number of occupied cells but randomly shuffling their spatial position) (Haase 2001; Lancaster and Downes 2004).

For all $L(t)$ function analyses (including the bivariate extension; described below), a toroidal edge correction was used (following e.g. Haase 2001). Since the distance between cell-centers sets the minimum limit for t in the analysis of grid-based data (Fehmi and Bartolome 2001), spatial association between species pairs was analyzed at 0.25 m intervals (three distance classes; 0.25, 0.50 and 0.75 m). This was judged a biologically realistic distance over which to measure association, since the roots of *Azorella selago* (and to a lesser extent *Agrostis magellanica*) can extend far beyond their aboveground cover ($> 3\text{m}$; Frenot et al. 1998). Results from the $L(t)$ function analyses were summarized by tallying the number of distance classes where spatial aggregation differed significantly from random for each species in each grid. The resulting $L(t)$ function index of aggregation could range from + 3 (i.e. occupied cells are significantly aggregated at all three distance classes) to -3 (i.e. occupied cells are significantly segregated in all distance classes), providing a summary of the $L(t)$ function which was used in further analyses. These analyses were conducted using Spatial Point Pattern Analysis (SPPA) software (Haase 2001; available from <http://haasep.homepage.t-online.de/>).

The cover of individual species was also analysed for directionality, to test if occupied cells were aligned relative to the slope or wind exposure. This was done in each transect for each species, by calculating the average cover of that species around every grid cell it occupied (termed a “focal grid cell”). The analysis was limited to ≤ 3 grid cells away from each focal grid cell, and tested if, after controlling for the effect of distance from the focal grid cell, average cover differed significantly in different directions. This was done by including two factors in these analyses, which were coded to represent two possible forms of directionality; the first, testing for “straight” patterns in species cover (i.e. where cover was greater parallel [0 and 180 °] or orthogonal [90 and 270 °] to the slope), the second testing for “diagonal” patterns (i.e. where cells at 45 ° and 225 °, or 135 ° and 315 ° from the focal grid cell had higher

cover values). Data were standardized so that 180 ° indicated the downslope direction and 90 ° represented the dominant local wind direction (see Table 1). Analyses where a direction term contributed significantly to explaining variation in the species cover were considered to indicate directionality in the species cover pattern.

Spatial association between species pairs

The first method used to quantify spatial association between species was the bivariate extension of SADIE (Perry and Dixon 2002). This method determines the strength of the association between two sets of values by comparing the degree of spatial overlap of groups of grid cells of higher (i.e. patches) or lower (gaps) than average values in each dataset, with a positive value of the SADIE index of association (X) indicating association of the species, and a negative value suggesting spatial segregation (Perry 1998; Perry and Dixon 2002).

The bivariate extension of $L(t)$ function was also used to measure the spatial association of species pairs (Haase 2001). The bivariate $L(t)$ function, $L_{12}(t)$, calculates the spatial association between two species by comparing the observed and expected (under a null model of one species being randomly spatial distributed relative to the other) density of cells occupied by a species within a radius t of all cells occupied by a second species. For these analyses, the more common species (over the entire survey) was used as the reference against which the spatial distribution of the less common species was tested (see Lancaster and Downes 2004). As for the univariate $L(t)$ function, the number of distances classes where the spatial pattern differed significantly from the null model were tallied for each species pair in each grid. However, the parallel slopes assumption of the proportional odds model (when conducting ordinal logistic regression; see below) were violated by this data. Thus the index was reduced to just three classes; -1 (including all cases which showed net spatial disassociation), 0 (random association), and 1 (net spatial association).

The $L_{12}(t)$ function also enabled tests for directionality in the spatial association between species (i.e. an unequal strength of spatial association in different directions; Haase 2001). Because the grids were sampled along exposed slopes, the spatial orientation of neighbouring plants were determined relative to the slope (upslope vs. downslope of an individual of a more common species) and wind exposure (on the windward side or in the lee of an individual of a more common

species, relative to the local dominant wind direction; see Table 1). Analyses were conducted using four 90° segments, corresponding to upslope-windward (UW), upslope-leeward (UL), downslope-windward (DW) and downslope-leeward (DL) directions. Directional association patterns are reported relative to the position of the more common species (i.e. species were associated in the downslope-leeward direction refers to the less common species occurring in the downslope-leeward position from the more common species).

Statistical analyses

Generalized Linear Models were used to analyse the environmental and vegetation data. The most appropriate error distribution and link function were chosen *a priori* based on the expected properties of the response variables (Quinn and Keough 2002). Species richness data were analysed using a Poisson error distribution and a log link function. Microclimate, species cover and aggregation directionality data were analysed using a normal distribution of errors and a log or identity link function (cover data arcsine-square root transformed prior to analysis).

SADIE indices were modeled using a normal distribution of errors and a log or identity link function (using Statistica v7). The relationship between SADIE indices and each explanatory variable was first tested individually using Log-likelihood (abbreviated to LL) χ^2 tests (Type III likelihood tests) to determine if the relationship was consistent across different species pairs. To deal with an unbalanced survey design in some situations (resulting from some species not being abundant enough in the southern transect to include in analyses; see Results below) Type I likelihood tests were used where required. Best subsets model building was then used to distinguish the minimum adequate model. All SADIE indices were included in analyses, even if they were not significantly different from zero since it is the change in the magnitude of the index which is relevant to testing the SGH.

$L(t)$ function indices were analysed using ordinal logistic regression (using a multinomial distribution of errors and a logit link function; using SAS v.9). Where there were no observations in a category (or just a singleton in one category, in which case the observation was excluded for that analysis), these analyses were equivalent to binary regression. As for the SADIE indices, the relationship between each explanatory variable and the $L(t)$ function indices was examined separately to test the

consistency of the relationship across different species pairs. Thereafter, best subsets analysis was used to determine which model best described the variation in spatial association. Analyses were corrected for over- or underdispersion where the deviance divided by the degrees of freedom differed significantly from unity. Due to the large number of variables that could be included in the directional analyses of the $L(t)$ function index of association, stepwise model building was used (instead of best subsets analysis) and interactions were limited to two-way interactions, except where graphical results suggested a three-way interaction could be important.

To control table-wide error rate in the resulting test-tables, the step-up False Discovery Rate adjustment was implemented (García 2004), but the adjustment did not alter any results.

Results

Severity gradients

The altitudinal extent of the transects ranged from 48 m (SW aspect) to nearly 150 m (N and E aspects), and all, with the exception of the SW, were scoria-covered (Table 1). The SW transect ran along a basaltic lava flow, while sections of the crater rim were broad and flat or comprised of tuff (see Fig. 1). These areas are thus distinct from the rest of the scoria cone as their substrate is more stable than the typical steep scoria slopes.

Substrate and air temperature generally declined with increasing altitude on all aspects of the cone (substrate temperature: Table 1; air temperature: Wilcoxon matched pairs test: $n = 12$, $Z = 2.43$, $p = 0.02$). However, substrate temperatures on the crater rim (Top) were not consistently cooler than substrates on the same aspect at lower elevations, probably due to longer exposure to solar insolation. Substrate and air temperatures were significantly warmer on the N and W than the S and E (comparing measurements taken at similar altitudes, i.e. 260 – 280 m a.s.l.) (substrate temperature: LL $\text{Chi}^2 = 246.30$, $p < 0.001$ and see Table 1; air temperature (mean \pm S.E.): North: $4.39\text{ }^\circ\text{C} \pm 0.20$, West: $4.47\text{ }^\circ\text{C} \pm 0.20$, South: $4.26\text{ }^\circ\text{C} \pm 0.19$, East: $4.25\text{ }^\circ\text{C} \pm 0.20$; LL $\text{Chi}^2 = 76.78$, $p < 0.001$).

Winds on the cone were predominantly from the NW quarter (63 % recordings showing winds blowing from the N, NW or W), except on the southern transect where SE winds dominated (56 % of wind recordings; Table 1). Wind speed was greater at

the top of the scoria cone than at its base (on average more than double the speed; Wilcoxon matched pairs test: $n = 8$, $Z = 2.37$, $p = 0.018$), and significantly faster on the NE and S aspects than on the E aspect (ANOVA on the difference from mean wind speed: $F_{7,144} = 3.83$, $p < 0.001$). Rainfall did not differ between aspects (Kruskal-Wallis test: $H_{3,16} = 1.38$, $p = 0.71$). Relative humidity also did not differ between aspects, whether using data from 260 – 280 m a.s.l ($n = 370$ measurements at three aspects (sensor malfunction on E aspect), LL $\text{Chi}^2 = 0.067$, $p = 0.80$) or data from base of the transects ($n = 76$ paired measurements, LL $\text{Chi}^2 = 7.45$, $p = 0.38$).

Therefore, a strong altitudinal severity gradient exists on the scoria cone. With rising elevation, temperatures generally decrease and wind speed and substrate mobility increase, providing increasingly severe environmental conditions at higher altitudes. In contrast, however, the transects could not be ranked to form a gradient of relative environmental severity since the environmental variables (e.g. temperature, wind speed, substrate mobility) did not change in a consistent manner between transects. For example, while the eastern aspect had the greatest substrate movement (i.e. high environmental severity), it had moderate substrate temperatures and the lowest mean wind speed (i.e. low severity). Thus, a clear aspect-related gradient of severity could not be defined from the environmental data. The data instead reveal a combination of abiotic factors varying independently of each other, combining in a complex severity gradient across aspects. Based on the SGH and the observed altitudinal severity gradient on the cone, the intensity of facilitative interactions was predicted to increase (relative to the intensity of competitive interactions) with elevation. Furthermore, due to the lack of an obvious aspect-related severity gradient, no predictions could be made based on the SGH about how the intensity of positive and negative interactions would vary between aspects.

Species richness and vegetation cover

Sixteen vascular plant species were recorded on the cone, with *Azorella*, *Agrostis*, *Blechnum* and *Acaena* comprising > 95 % of the vegetation cover. Six species pairs could be analysed in grids where all four species were common, although in the southern transect only *Azorella* and *Agrostis* had sufficient cover for analysis (Table 1).

Vegetation cover and species richness differed between transects, but were consistently negatively related to altitude in all, except the SW, transects (vegetation cover: see Fig. 1; species richness (excluding the SW transect): $p < 0.001$, deviance explained = 53.8 – 83.6 %). Including flat or tuff areas did not alter these results considerably. Nonetheless, after accounting for the effect of altitude, grids on tuff and shallow slopes had significantly higher cover (d.f. = 833, explained deviance = 50.0 %; Substrate: LL $\text{Chi}^2 = 39.84$, $p < 0.001$; Altitude: $\text{Chi}^2 = 526.07$, $p < 0.001$; Substrate*Altitude: $\text{Chi}^2 = 128.16$, $p < 0.001$) and species richness (d.f. = 833, explained deviance = 30.7 %; Substrate: $\text{Chi}^2 = 17.74$, $p < 0.001$; Altitude: $\text{Chi}^2 = 298.14$, $p < 0.001$; Substrate*Altitude: $\text{Chi}^2 = 17.15$, $p < 0.001$) than grids on steeper scoria slopes.

Individual species: Aggregation and directionality

The cover of each species was significantly aggregated within 89 % of grids (SADIE analyses). Intraspecific aggregation was significantly stronger in *Acaena* than in *Agrostis* (SADIE index of aggregation (mean \pm S.E.): *Azorella*: 2.0 ± 0.1 ; *Agrostis*: 1.8 ± 0.1 ; *Blechnum*: 2.4 ± 0.2 ; *Acaena*: 2.6 ± 0.4 ; explained deviance = 13.51 %, LL $\text{Chi}^2 = 14.52$, $p = 0.002$). Aspect, altitude and total vegetation cover did not explain a significant proportion of the variation in intraspecific aggregation within grids (all $p > 0.08$). There was insufficient variation in the spatial aggregation data for similar analyses when calculated by the $L(t)$ function index of aggregation, since significant aggregation was present in more than 97 % of grids and there were no grids with significant segregation.

All species showed significant cover directionality, but only in some transects. On the western transect, *Azorella* and *Blechnum* cover was higher on the downslope-leeward (and upslope-windward) sides of occupied grid cells. Also on the western transect, *Agrostis* cover was higher in cells at 90 and 270° from the occupied cells. In contrast, on the northern transect, *Acaena* cover was greater in the downslope-windward (and upslope-leeward) direction. Marginally significant directionality ($0.05 < p < 0.10$) was also observed for *Azorella* and *Acaena* in the eastern transect (higher cover in the downslope-leeward and upslope-windward directions) and for *Acaena* in the western transect (higher cover in the upslope and downslope directions). No

analysis of directionality of cover was performed for *Blechnum* and *Acaena* on the southern transect where these species were rare (4 and 1 occupied cells respectively).

Pair-wise patterns: Association values

Mean spatial association differed significantly between species pairs (using the SADIE index of association; Fig. 2), although not between transects (Type 1 likelihood test: deviance explained = 31.71 %; Aspect: d.f. = 3, LL $\text{Chi}^2 = 0.38$, $p = 0.94$; Species pair d.f. = 3, LL $\text{Chi}^2 = 29.39$, $p < 0.001$; Aspect*Species pair: d.f. = 6, LL $\text{Chi}^2 = 15.74$, $p = 0.41$). Thus, subsequent analyses were conducted individually for each species pair. Neither transect nor species pair explained a significant portion of the variation in spatial association when using the $L(t)$ function index of association (Species pair: d.f. = 3, Wald $\text{Chi}^2 = 1.80$, $p = 0.88$; Aspect: d.f. = 5, Wald $\text{Chi}^2 = 1.51$, $p = 0.68$; Aspect*Species pair: d.f. = 10, Wald $\text{Chi}^2 = 6.78$, $p = 0.74$).

The SADIE index of association values and the $L(t)$ function index of association values were similarly related to altitude and vegetation cover (Fig. 3), although models for SADIE index of association values had more significant terms and explained a higher proportion of the variance in spatial association (Table 2, see also Appendices A and B). For SADIE index of association values, spatial association between all species pairs was negatively related to total vegetation cover (e.g. Fig. 3a). The strength of spatial association was also negatively related to the cover of individual species and positively related to altitude in some cases (Fig. 3b, Appendix A). Similarly, for the $L(t)$ function index of association, the degree of spatial association between *Azorella* and *Agrostis* was significantly negatively related to total vegetation cover (Fig. 3c) and the cover of both species (Appendix B). Models for $L(t)$ function index of association for other species pairs were non-significant, but showed similar patterns. Thus, there was a consistent trend of spatial association increasing with altitude and decreasing with plant cover that did not differ between transects.

When considering directionality in the spatial association of species pairs, the strength of spatial association differed on different sides of plants, depending on wind exposure (i.e. sheltered by neighbouring plant versus exposed to the prevailing wind), slope position (i.e. upslope versus downslope of neighbouring plant) and, in this case, transect (Table 3). Three two-way interactions contributed significantly to the model,

suggesting that the effect of wind exposure varied with altitude and the plant's relative position on the slope, and that the effect of aspect differed between species pairs (Table 3, Fig. 4). The three-way interaction between wind exposure, slope position and aspect was also significant, suggesting that the interaction between wind exposure and slope position differed between transects (Table 3). Indeed, for all species pairs, strong spatial association was observed in the downslope-leeward direction on the N, E and S aspects, with weak association and moderate to strong disassociation in the other directions (Fig. 4). However, on the W aspect, the strongest spatial association was in the downslope-windward direction, with moderate to strong spatial disassociation in the other directions (Fig. 4). Therefore, while the altitudinal gradient in spatial association was consistent across transects, the directionality of spatial association around individual plants differed between transects.

Discussion

Spatial association between plant species on the scoria cone was found to be greater at higher than at lower elevations, demonstrating that interspecific spatial association increased along the abiotic severity gradient. Therefore, these results provide support for the stress-gradient hypothesis since the relative intensity of positive interactions increased with increasing abiotic severity. This study therefore extends the geographic range of high latitude and altitude regions within which the SGH has been useful for predicting variation in plant interactions. In addition, fine-scale directional intraspecific aggregation and interspecific association patterns were identified, nested within the broader-scale severity gradient.

The strong directionality of facilitative interactions that were found downslope from, and in the lee of, individuals of more common species suggests that sheltering from moving sediment and from dominant winds are the two most important facilitative mechanisms at this site. Plants that are sheltered from winds experience lower wind speeds and therefore less evapotranspiration, cooling and wind-scouring (Ennos 1997; Warren Wilson 1959). Similarly, individuals growing downslope of other plants are protected against burial by mobile substrate moving from upslope (Veblen et al. 1977). Therefore, a plant growing on the downslope-leeward side of an established plant will experience both milder microclimatic conditions (due to lower wind speeds) and less intense and frequent disturbances (due to reduced burial). These

results agree with studies from other Arctic, sub-Antarctic and alpine areas that have identified the importance of shelter from wind and substrate movement for the development of plant communities in cold and windy environments (e.g. Heilbronn and Walton 1984).

The importance of sheltering for plants was also supported by variation in slope and substrate conditions across the scoria cone. The greater plant cover and species richness that was found in areas with shallow slopes and immobile substrate, relative to adjacent steep loose scoria slopes, demonstrates that substrate instability is indeed an important determinant of vegetation characteristics on this landform. For example, in contrast to the other transects, vegetation cover varied independently of altitude on the stable lava flow of the SW aspect (see Fig. 1). Similarly, within the cone's crater, vegetation cover was more extensive (> 15 % cover) and species rich (13 vascular plant species) than the immediately adjacent vegetation on the exposed slopes, suggesting that vegetation develops more extensively when sheltered from the wind.

Mechanisms of facilitation other than sheltering from the wind and burial by mobile substrate would have produced different fine-scale patterns of spatial association and disassociation than those observed here (Haase 2001). For example, if the positive effect of neighbouring plants was predominantly due to buffered soil temperatures or enhanced soil moisture or nutrients, then species could be expected to be equally strongly associated in all directions (Haase 2001). An alternative explanation for the directional spatial association quantified could also be the uneven accumulation of seeds around established plants. However, seeds are expected to accumulate on the upslope, rather than the downslope, side of established plants (transported both by water and within the mobile substrate; e.g. Reichman 1984). Furthermore, while seeds are known to accumulate in the lee of topographical features that disrupt the flow of wind (e.g. depressions in the soil; Reichman 1984), seeds can also accumulate on the windward side of plants (due to direct interception; Bullock and Moy 2004). Therefore, while stronger spatial association of species on the leeward side of established plants could be due to seed deposition patterns, sheltering is more likely the dominant mechanism behind the downslope-leeward interspecific association patterns.

Interestingly, spatial association for all species pairs was better predicted by total vegetation cover than by altitude, suggesting that vegetation cover (at least for

sites of the same vegetation type) is a better surrogate of the multiple components of abiotic severity than altitude. Indeed, other studies have also shown a shift from positive to negative interactions between plants with increasing plant density or cover (Callaway and Walker 1997; Kikvidze et al. 2005; Klanderud and Totland 2004). While altitude is a surrogate for the overall abiotic conditions (Austin et al. 1984), total vegetation cover represents both the physical conditions at a site as well as the influence of the vegetation on those physical conditions. Indeed, the positive feedback of vegetation stabilizing the substrate and ameliorating the microclimate, and then leading to further expansion of plant cover, is probably an important mechanism in both the short-term vegetation dynamics and the long-term succession at this site and others with similar climates (see Choler et al. 2001; Veblen et al. 1977).

One of the consequences of enhanced facilitation in the downslope-leeward direction of established plants is the formation of stripes of vegetation on some mid-altitude areas of the scoria cone (PCLR pers. obs; Appendix C). Similar vegetation stripes have been observed in alpine areas with comparable climates, some of which are also believed to be a consequence of either wind (on flat areas) or wind and slope instability (on slopes) (Alftine and Malanson 2004; Veblen et al. 1977). Veblen et al. (1977) suggested that such patterns form on scoria slopes as a result of the chance establishment of single plants, which then stabilize scoria enough for other plants to establish. These plants then block the downslope movement of scoria locally (potentially affecting downslope areas far beyond their zone of frost-heave inhibition), creating safe sites for further plant establishment, and eventually leading to the creation of vegetation stripes. Furthermore, the orientation of these stripes can be influenced by wind patterns (Veblen et al. 1977), and on Junior's Kop scoria cone the stripes are deflected by the wind from being parallel with the slope (see Appendix C).

Current climate trends on Marion Island include warming temperatures, declining rainfall and changing wind patterns (le Roux and McGeoch 2008). These changes in climate are likely to alter the nature of the abiotic severity gradients on the island (and may to some extent already have done so), and potentially shift the balance of species interactions (Brooker 2006). Warmer temperatures are likely to reduce the frequency of frost-heave events at low altitudes (Boelhouwers et al. 2003), reducing substrate movement on the cone. This will decrease the relative benefit of growing downslope from established plants, since burial in upslope sites would be less common. Similarly, changes in wind strength could alter species interactions,

with the weakening of wind strength since the 1980s (le Roux and McGeoch 2008) potentially leading to less benefit for plants growing on the leeward side of an established plant (i.e. potentially leading to similar performance of seedlings on the windward and the leeward sides of established plants). However, the current rapid decline in rainfall experienced on the island could also lead to enhanced soil moisture and soil moisture storage becoming important facilitative mechanisms. On porous scoria increased spatial association of individuals could be particularly important, since clusters of plants can intercept surface flow more efficiently and retain the moisture for longer due to higher soil organic matter content (Scheffer et al. 2005). Therefore, with continuing drying and warming of the island, the vegetation on the scoria cone may become increasingly aggregated (improving interception and retention of soil moisture) and show less pronounced downslope directionality in plant cover patterns (in response to fewer freeze-thaw cycles). Indeed, the vegetation on the scoria cone is responsive to changes in climate as it has expanded upslope on the cone over the last 40 years (Chapter 3).

Despite abiotic differences between the aspects of the scoria cone, neither the aggregation of individual species nor the spatial association between species pairs differed between transects. This suggests that, despite differences in individual stressors, net environmental severity did not differ enough between transects to produce an observable difference in the balance of species interactions. If detailed physiological data were available for species the application of the SGH could be extended to such complex multi-factored severity gradients by using a measure of the change in net severity between sites, calculated for each species as the sum of the change in each abiotic stress weighted by the impact of that stress on the species' performance. Therefore, using such a metric, the relative intensity of positive interactions would be predicted to increase along a gradient of increasing net severity, rather than along a gradient of, for example, decreasing temperature (which could be confounded by changes in water availability, frost-frequency, etc.). However, given the limited information about the impact of different stresses on individual species, these results also identify a limitation to the application of the SGH in environments characterized by complex multivariate gradients.

Although there was no difference in the strength of aggregation or association between transects, some characteristics of the cone's vegetation did differ between transects. For example, *Blechnum* and *Acaena* were rare on the southern transect

despite being common on the other aspects of the cone, possibly due to the combination of cold and windy conditions on that transect (see Huntley 1971). Interestingly, the total vegetation cover on the southern aspect was similar to that on the eastern and western aspects, and greater than on the northern transect. Therefore, in the absence of *Blechnum* and *Acaena*, the cover of *Azorella* and *Agrostis* on the southern transect was high, suggesting the possibility of competition between *Azorella* and the mat-forming *Blechnum* and *Acaena* (as suggested for cushion plants and mat-forming species in the Mediterranean: Gavilán et al. 2002; and observed on sub-Antarctic Macquarie Island: Scott and Bergstrom 2005).

The strength of interspecific spatial association on the scoria cone also differed between species pairs. *Acaena* was most strongly associated with other species, and *Azorella* the least spatially associated with other species. Species identity is therefore clearly an important determinant of the nature of positive interactions (Callaway 1998). These results also, however, reveal the paradox that *Azorella* is a strong facilitator for species rooted within its canopy (Chapter 5; see also Huntley 1970), but appears to be relatively poor at facilitating species in the surrounding soil. Indeed, despite some *Azorella* plants on Junior's Kop supporting up to five vascular species epiphytically, *Azorella* was most weakly spatially associated with non-epiphytic individuals of the species studied. It is possible that *Azorella*'s streamlined and compact canopy causes only localized amelioration of microclimatic conditions, creating favourable conditions for epiphytes but not altering conditions for individuals adjacent to it.

Conclusion

The stress-gradient hypothesis correctly predicted spatial variation in the balance of positive and negative interspecific interactions along an altitudinal severity gradient on a sub-Antarctic scoria cone. However, the SGH was not useful for predicting aspect-related variation in the balance of species interaction because multiple abiotic factors varied independently between aspects of the cone. Strong and consistent differences in the directionality of positive associations at fine-scales were used to infer the mechanisms of facilitation. Positive interactions, between plants of the same or different species, appeared to be due to sheltering by neighbouring plants from the prevailing wind and from burial by sediment moving downslope. This study,

therefore, not only provides support for the stress-gradient hypothesis in the sub-Antarctic, but demonstrates fine-scale directional spatial patterns between plants nested within the severity gradient.

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Table 1 Physical and vegetation characteristics of the transects on Junior's Kop. Included are the number of quadrats where each species was present and occurred in more than 15 % of grid cells (i.e. adequate cover for analysis of spatial association), as well as the number of quadrats with adequate cover for each pair of species to be analysed. Abbreviations used for species names given in parentheses. f = fine (< 2 mm diameter), c = coarse (2 – 60 mm), b = blocky (> 60 mm). intermed. = intermediate

| | North | NE | East | SE | South | SW | West | NW |
|---|-------------|-------------|------------------|-------------|-------------|-------------|-------------|-------------|
| Physical characteristics | | | | | | | | |
| Altitude: bottom (m a.s.l.) | 162 | 162 | 163 | 181 | 233 | 237 | 232 | 170 |
| Altitude: top | 302 | 309 | 299 | 294 | 289 | 285 | 286 | 282 |
| Slope (degrees) ¹ | 27.8 | 21.3 | 21.9 | 20.7 | 15.5 | 22.0 | 29.4 | 29.1 |
| Length (m) | 335 | 390 | 370 | 415 | 200 | 170 | 145 | 260 |
| Scoria clast sizes ² | c - f | c - f | c - f | c - f | c - b | lava flow | c - b | c - f |
| Substrate movement ² | intermed. | | greatest | | intermed. | | lowest | |
| Substrate temperatures | | | | | | | | |
| Base (°C; mean ± SE) | 4.51 ± 0.06 | 4.73 ± 0.05 | 4.84 ± 0.04 | 3.90 ± 0.06 | 4.18 ± 0.06 | 3.78 ± 0.06 | 4.15 ± 0.09 | 4.10 ± 0.09 |
| Low | 4.24 ± 0.08 | 4.12 ± 0.07 | 3.82 ± 0.07 | 3.38 ± 0.06 | 3.50 ± 0.07 | 3.69 ± 0.07 | 3.23 ± 0.09 | 3.99 ± 0.13 |
| High | 3.98 ± 0.08 | 3.02 ± 0.09 | n/a ³ | 2.97 ± 0.07 | 2.56 ± 0.08 | 3.36 ± 0.07 | 3.48 ± 0.07 | 3.74 ± 0.06 |
| Top | 3.53 ± 0.09 | 2.97 ± 0.06 | 2.90 ± 0.07 | 2.93 ± 0.08 | 4.28 ± 0.06 | 3.39 ± 0.07 | 3.52 ± 0.05 | 2.95 ± 0.08 |
| Wind speed and direction | | | | | | | | |
| Direction (° from north; mean ± angular dispersion) | 312 ± 0.69 | 352 ± 0.68 | 312 ± 0.41 | 350 ± 0.63 | 131 ± 0.17 | 16 ± 0.47 | 237 ± 0.29 | 304 ± 0.44 |
| Speed (m/s; mean ± SE) | 0.73 ± 0.42 | 0.77 ± 0.58 | 0.52 ± 0.29 | 0.58 ± 0.42 | 0.51 ± 0.47 | 0.59 ± 0.51 | 0.45 ± 0.35 | 0.44 ± 0.31 |
| Vegetation characteristics | | | | | | | | |
| Species richness (non-epiphytic) | 10 | 11 | 12 | 13 | 9 | 11 | 11 | 11 |
| Total number of quadrats | 107 | 162 | 145 | 128 | 82 | 66 | 43 | 104 |
| % quadrats occupied by vascular plants | 21.5 | 60.5 | 68.3 | 86.7 | 65.9 | 100.0 | 55.8 | 93.3 |

| | | | | | | | | |
|-------------------------------------|--------|------|---------|------|---------|------|---------|----------|
| % quadrats with cover > 50 % | 2.8 | 27.8 | 15.2 | 27.3 | 8.5 | 22.7 | 2.3 | 26.0 |
| Presence (and cell occupancy > 15%) | North | | East | | South | | West | Total |
| <i>Azorella selago</i> (Az) | 15 (7) | | 46 (15) | | 30 (11) | | 24 (11) | 115 (44) |
| <i>Agrostis magellanica</i> (Ag) | 18 (7) | | 38 (9) | | 20 (9) | | 16 (5) | 92 (30) |
| <i>Blechnum penna-marina</i> (Bl) | 13 (7) | | 11 (4) | | 2 (0) | | 6 (2) | 32 (13) |
| <i>Acaena magellanica</i> (Ac) | 8 (5) | | 9 (5) | | 1 (0) | | 8 (5) | 25 (15) |
| Species pairs for analysis | | | | | | | | |
| Az-Ag | 7 | | 9 | | 9 | | 5 | 30 |
| Az-Bl | 7 | | 4 | | - | | 2 | 13 |
| Az-Ac | 5 | | 5 | | - | | 5 | 15 |
| Ag-Bl | 7 | | 4 | | - | | 1 | 12 |
| Ag-Ac | 5 | | 5 | | - | | 4 | 14 |
| Bl-Ac | 5 | | 3 | | - | | 2 | 10 |

¹ excluding flat areas at top or bottom of transect; ² from Holness (2004), ³ data lost from the High site on the East transect.

Table 2 The minimum adequate models (as determined by Analysis of Deviance) explaining a significant proportion of the variation in spatial association for each species pair (see Appendices A and B for details). In the absence of a significant model, the variable closest to explaining a significant proportion of the variation in the association index is shown in italics. % D.E. = percent deviance explained, Cover = total vegetation cover (%), Alt. = altitude, n.s. = the model explains a non-significant proportion of the deviance. Species abbreviations as in Table 1.

| Species pair | SADIE index of association | | <i>L(t)</i> function index of association | |
|--------------|---|--------|---|--------|
| | Model | % D.E. | Model | % D.E. |
| Az-Ag | Alt (+), Az cover (-) | 33.4 | Az cover (-) | 19.1 |
| Az-BI | Cover (-), Az cover (-) | 44.8 | <i>Cover (-)</i> | n.s. |
| Az-Ac | Cover (-), Az cover (-) | 43.9 | <i>Az cover (-)</i> | n.s. |
| Ag-BI | Cover (-) | 35.5 | <i>Alt (+)</i> | n.s. |
| Ag-Ac | Cover (-) | 55.1 | <i>Alt (+)</i> | n.s. |
| BI-Ac | Alt (+), Cover (-), <i>BI cover (-)</i> | 82.8 | <i>BI cover (-)</i> | n.s. |

Table 3 The best fit ordinal logistic regression model for $L(t)$ function index of association values. Data from the southern transect were excluded. Log likelihood $\text{Chi}^2 = 404.42$, $p < 0.001$, deviance explained = 39.2 %, residual deviance = 628.1, d.f. = 566, scaled deviance = 0.72. See text for details of analyses.

| Explanatory variables | d.f. | Wald Chi^2 | p |
|--|------|---------------------|---------|
| Species pair | 5 | 51.80 | < 0.001 |
| Transect (i.e. Aspect) | 2 | 10.22 | 0.006 |
| Altitude | 1 | 10.97 | < 0.001 |
| Slope (upslope or downslope of individual of more common species) | 1 | 101.72 | < 0.001 |
| Wind exposure (windward or leeward of individual of more common species) | 1 | 21.20 | < 0.001 |
| Species pair * Transect | 10 | 41.65 | < 0.001 |
| Wind exposure * Slope | 1 | 37.61 | < 0.001 |
| Wind exposure * Altitude | 1 | 18.45 | < 0.001 |
| Wind exposure * Slope * Transect | 2 | 127.55 | < 0.001 |

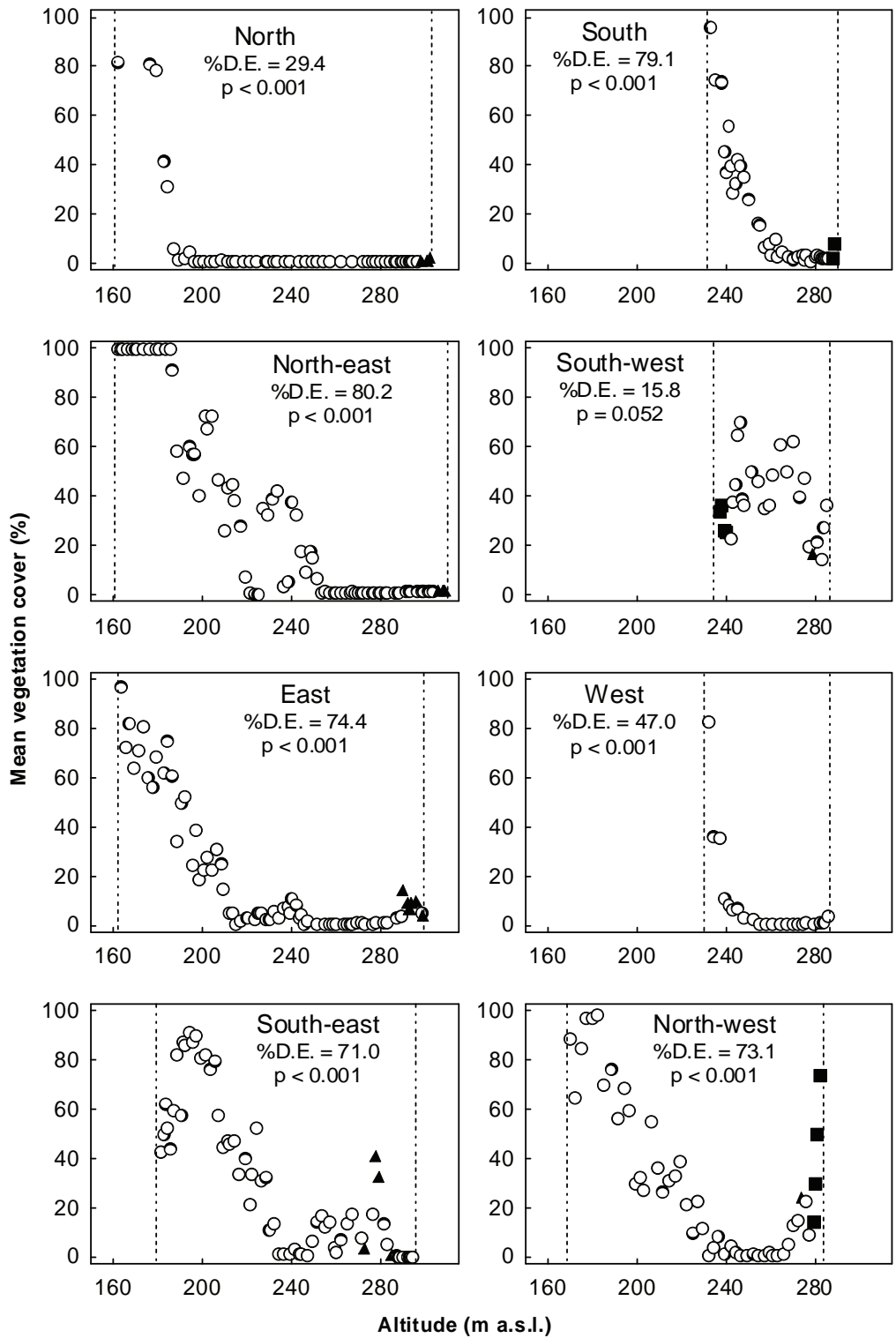


Fig. 1 Relationship between average vegetation cover and altitude for each transect. Axes were standardized across all eight plots, with the start and end altitude of each transect indicated by dashed vertical lines. Filled triangles (▲) indicate grids dominated by tuff; filled squares (■) indicate grids on relatively flat areas (slope $< 12^\circ$). % D.E. = percentage deviance explained. Portions of quadrats below 190 m a.s.l. on the south-eastern transect were on a black lava flow.

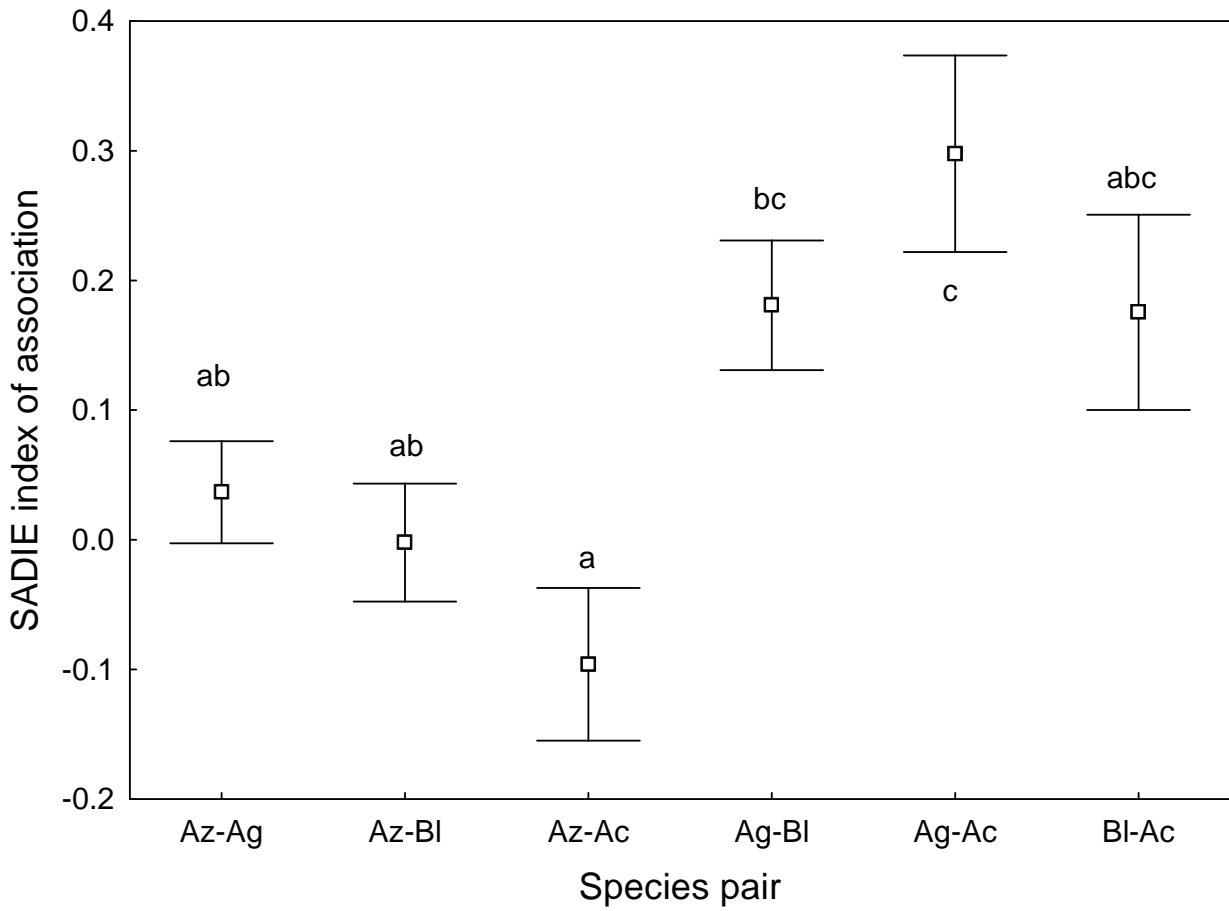


Fig. 2 Differences in the strength of spatial association (mean \pm S.E.) between species pairs (LL $\chi^2 = 25.01$, $p < 0.001$). Groups not sharing a common letter differ at the $\alpha = 0.05$ significance level (Post-hoc Tukey's Honest Significant Difference test). Az – *Azorella selago*; Ag – *Agrostis magellanica*; BI – *Blechnum penna-marina*; Ac – *Acaena magellanica*.

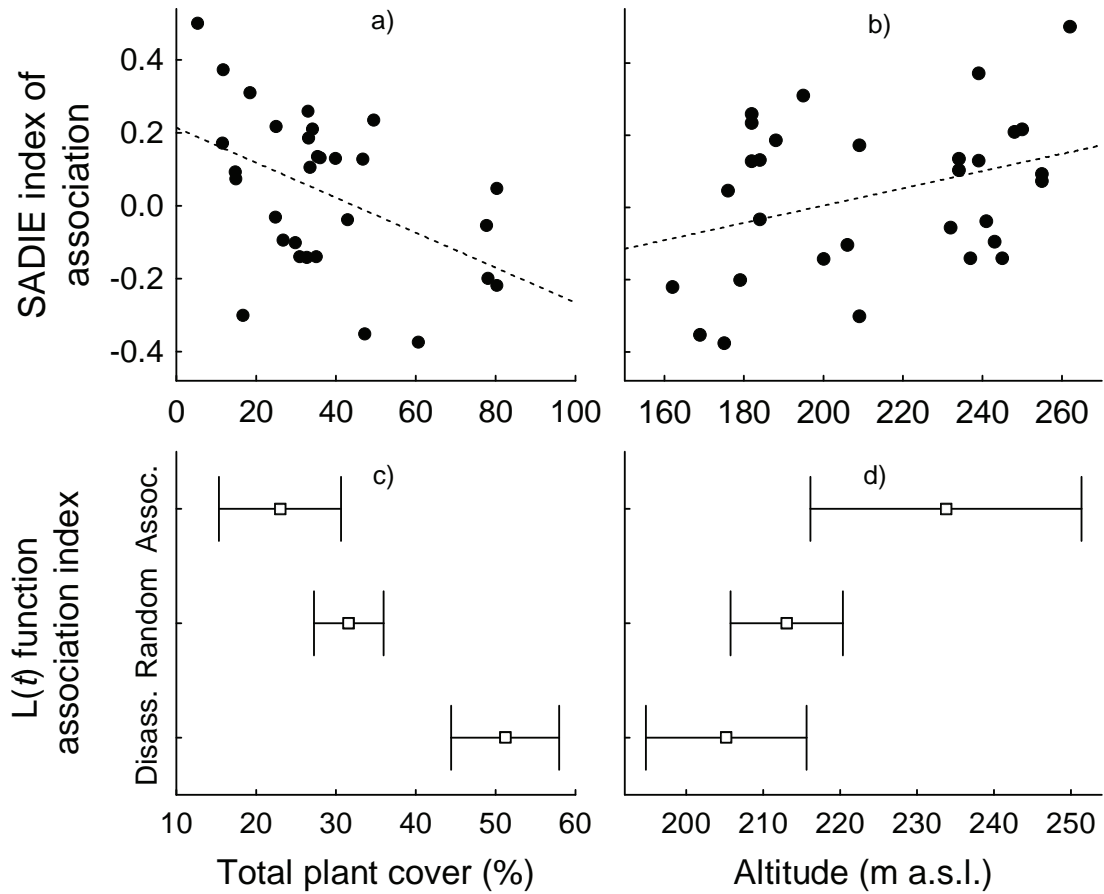


Fig. 3 The relationship between total vegetation cover (a & c) and altitude (b & d), and the strength of the spatial association between *Azorella selago* and *Agrostis magellanica*, calculated using the SADIE association index (top row) or the $L(t)$ function index of association (bottom row; mean \pm S.E.). Further details provided in the text; statistics provided in Appendices A and B (see also Table 2). Dotted line in a) and b) shows best linear fit to the data. Assoc. = significant spatial association, Disass. = significant spatial segregation.

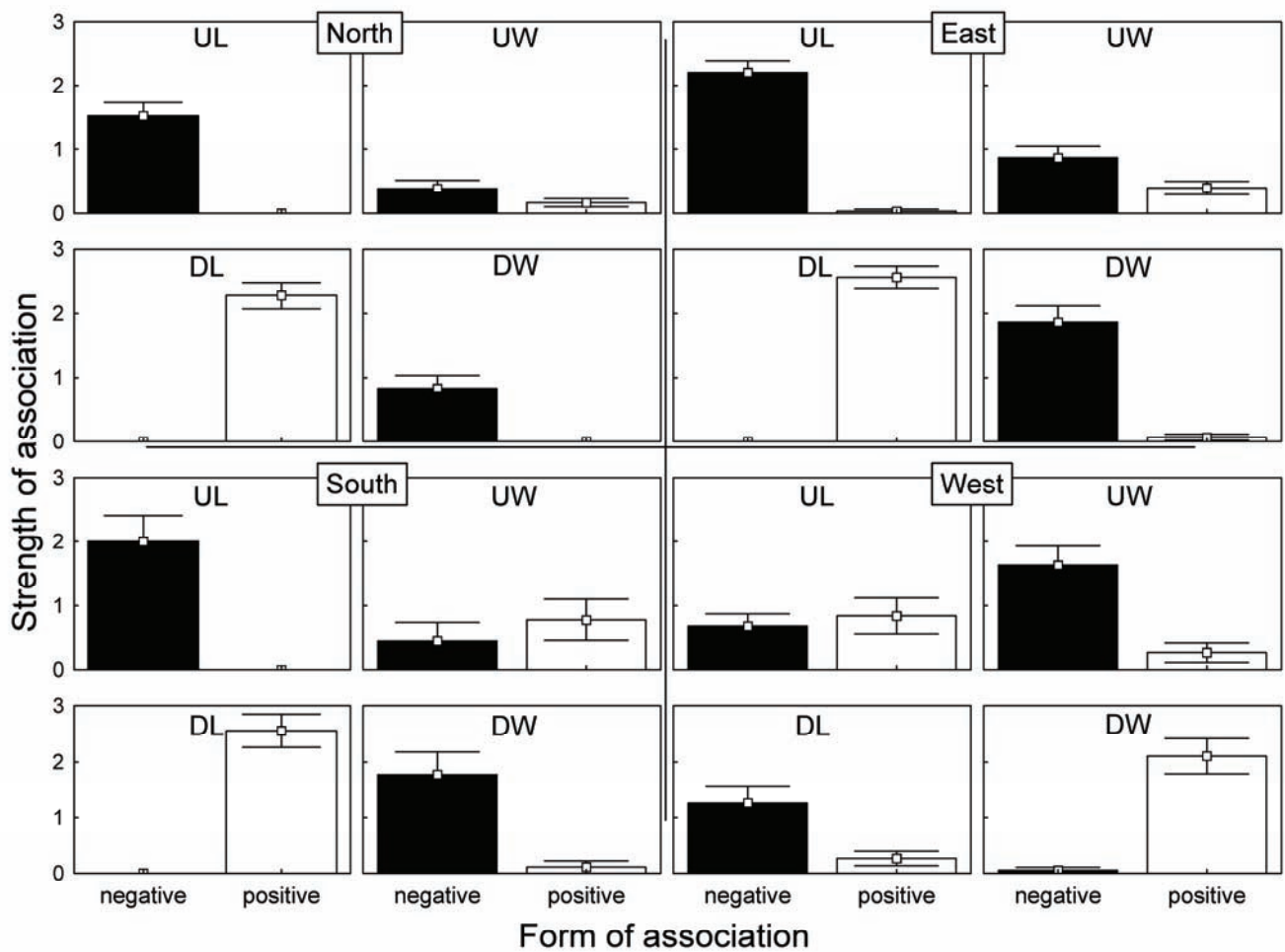


Fig. 4 Mean (\pm S.E.) number of distance classes in which negative (filled bar) and positive (empty bar) interspecific spatial associations were observed (maximum possible value = 3), averaged over all species pairs and altitudes. The figures are arranged by aspect (i.e. divided by the thick lines in the centre of the figure, e.g. top-left four graphics represent the northern transect), and by spatial orientation (where U = upslope from the individual of the more common species, D = downslope, L = on the leeward side of the individual of the more common species, and W = on the windward side).

Appendix A The relationship between the strength of spatial association (calculated as SADIE spatial association index) between different pairs of species and abiotic (altitude and aspect) and biotic (vegetation cover) factors. Tolerance values for all covariates included in models exceeded 0.50, and thus the variables were not collinear. Species names abbreviated as in Table 1. Sp. pair = species pair being analysed, Tot cover = % total plant cover, Sp1 = more common species of the species pair (listed first in pair name), Sp2 = less common species of the species pair, % D.E. = percentage of deviance explained, coeff. = coefficient for parameter. Significance of models indicated by asterisks (* = $p < 0.05$, ** = $p < 0.01$, *** = $p < 0.001$). The order of the levels of Aspect are indicated with “<”, with N = northern transect, E = eastern transect, S = southern transect and W = western transect.

| Sp. pair | | Univariate analyses | | | | | Best subsets model selection | | | | |
|----------|---------------|---------------------|-----------|-----------|-----------|---------|------------------------------|--------|--------|----------------|----|
| | | Altitude | Tot cover | Sp1 cover | Sp2 cover | Aspect | Variables | Coeff. | % D.E. | model χ^2 | n |
| Az - Ag | % D.E. | 12.19 | 21.67 | 15.94 | 13.34 | 8.24 | Altitude | 0.01 | 33.42 | 12.20** | 30 |
| | Wald χ^2 | 3.90* | 7.33** | 5.21* | 4.30* | 2.85 | Az cover | -0.01 | | | |
| | Coeff. | 0.01 | 0.01 | -0.01 | -0.03 | E<N<W<S | | | | | |
| Az - Bl | % D.E. | 9.64 | 25.62 | 23.78 | 0.99 | 29.89 | Tot cover | 0.01 | 44.83 | 7.73* | 13 |
| | Wald χ^2 | 1.32 | 3.85* | 3.53 | 0.13 | 4.62 | Az cover | -0.01 | | | |
| | Coeff. | 0.01 | 0.01 | -0.01 | 0.01 | W<N<E | | | | | |
| Az - Ac | % D.E. | 0.03 | 19.20 | 35.84 | 0.04 | 2.07 | Tot cover | 0.01 | 43.94 | 8.68* | 15 |
| | Wald χ^2 | 0.01 | 3.20 | 6.66* | 0.06 | 0.31 | Az cover | -0.01 | | | |
| | Coeff. | 0.01 | 0.01 | -0.02 | 0.01 | W<E<N | | | | | |
| Ag - Bl | % D.E. | 1.27 | 35.53 | 10.35 | 3.13 | 9.83 | Tot cover | -0.01 | 35.53 | 5.27* | 12 |

| | | | | | | | | | | | |
|---------|---------------|-------|----------|-------|-------|-------|-----------|-------|-------|----------|----|
| | Wald χ^2 | 0.15 | 5.27* | 1.31 | 0.38 | 1.24 | | | | | |
| | Coeff. | 0.01 | 0.01 | -0.02 | 0.01 | W<E<N | | | | | |
| Ag - Ac | % D.E. | 13.55 | 55.12 | 20.14 | 32.20 | 16.07 | Tot cover | -0.01 | 55.12 | 11.22*** | 14 |
| | Wald χ^2 | 2.04 | 11.21*** | 3.15 | 5.44* | 2.45 | | | | | |
| | Coeff. | 0.01 | -0.01 | -0.04 | 0.03 | N<W<E | | | | | |
| B1 - Ac | % D.E. | 37.67 | 32.07 | 8.27 | 7.25 | 32.68 | Altitude | 0.01 | 82.83 | 17.62*** | 10 |
| | Wald χ^2 | 4.73* | 3.87* | 0.86 | 0.75 | 3.96 | Tot cover | -0.01 | | | |
| | Coeff. | 0.01 | -0.01 | 0.01 | 0.22 | E<N<W | | | | | |

Appendix B The relationship between the strength of spatial association (calculated as the $L(t)$ function index of association) between different pairs of species and abiotic (altitude and aspect) and biotic (vegetation cover) factors. Tolerance values for all covariates included in models exceeded 0.50. Species names abbreviated as in Table 1. % D.E. = percentage of deviance explained, Tot cover = % total plant cover, coeff. = coefficient for parameter. Significance of relationships indicated by asterisks (* = $p < 0.05$, ** = $p < 0.01$, *** = $p < 0.001$). The order of the levels of Aspect are indicated with “<”, with N = northern transect, E = eastern transect, S = southern transect and W = western transect.

| Sp. pair | Univariate analyses | | | | | | Best subsets model election | | | | |
|----------|---------------------|----------|-----------|-----------|-----------|---------|-----------------------------|--------|--------|----------------|----|
| | | Altitude | Tot cover | Sp1 cover | Sp2 cover | Aspect | Variables | Coeff. | % D.E. | model χ^2 | n |
| Az - Ag | % D.E. | 3.68 | 14.48 | 19.10 | 18.38 | 3.02 | Az cover | -0.16 | 19.10 | 8.33** | 30 |
| | Wald χ^2 | 2.11 | 6.39* | 8.33** | 6.99** | 1.64 | | | | | |
| | Coeff. | 0.02 | -0.06 | -0.12 | -0.51 | E>N>S>W | | | | | |
| Az - Bl | % D.E. | 0.90 | 18.12 | 9.40 | 5.57 | QCS | Tot cover | --- | | | 13 |
| | Wald χ^2 | 0.13 | 2.05 | 1.22 | 0.77 | | | | | | |
| | Coeff. | -0.01 | -0.06 | -0.09 | -0.04 | | | | | | |
| Az - Ac | % D.E. | 1.27 | 0.36 | 6.92 | 1.54 | 3.71 | Az cover | --- | | | 15 |
| | Wald χ^2 | 0.36 | 0.11 | 1.69 | 0.42 | 1.01 | | | | | |
| | Coeff. | -0.01 | -0.01 | -0.11 | -0.08 | N>E>W | | | | | |
| Ag - Bl | % D.E. | 12.07 | 0.52 | 5.01 | 0.53 | QCS | Altitude | --- | | | 12 |
| | Wald χ^2 | 1.78 | 0.12 | 1.40 | 0.12 | | | | | | |
| | Coeff. | 0.10 | -0.01 | -0.21 | 0.01 | | | | | | |

| | | | | | | | | | |
|----------------------|---------------|-------|-------|-------|------|-----|----------|------------------|----|
| Ag - Ac ¹ | % D.E. | 50.36 | 15.49 | 1.43 | 4.20 | QCS | Altitude | --- ³ | 14 |
| | Wald χ^2 | 2.27 | 2.22 | 0.25 | 0.65 | | | | |
| | Coeff. | 0.26 | -0.05 | -0.09 | 0.12 | | | | |
| Bl - Ac | % D.E. | QCS | 11.01 | 21.14 | 0.85 | QCS | Bl cover | --- ³ | 10 |
| | Wald χ^2 | | 1.77 | 1.94 | 0.13 | | | | |
| | Coeff. | | -0.06 | -0.12 | 0.07 | | | | |

¹ data reduced to two response categories (one case of positive association was observed), ² QCS = quasi-complete separation of data (i.e. unable to compute maximum likelihood due to almost complete separation between values from different factor levels), ³ no significant model.

a)



b)



Appendix C Vegetation stripes on the a) north-western and b) western aspects of Junior's Kop.

Chapter 5 - Adding shape to the stress-gradient hypothesis: variation in interspecific interactions with altitude

Introduction

Positive and negative interspecific interactions occur throughout species ranges (Bertness and Callaway 1994; Bruno et al. 2003), with considerable broad- and fine-scale spatial variation in their relative intensity (Bertness and Ewanchuk 2002; Callaway et al. 2002; Dickie et al. 2005; Pugnaire and Luque 2001). The stress-gradient hypothesis (SGH) attributes this variation in the strength of positive and negative interactions to spatial variation in environmental severity. The original formulation of the SGH predicted that the strength of positive interactions, relative to negative ones, would increase monotonically with increasing abiotic and biotic stress (Bertness and Callaway 1994). This model was subsequently extended to gradients in disturbance, generalizing the model across all environmental severity gradients (Brooker and Callaghan 1998). 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 resource depletion (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, net plant interactions are hypothesized to gradually become more positive with increasing environmental severity, due to changes in the strength of constituent positive and negative interactions (Brooker and Callaghan 1998) (i.e. a linear “severity-interaction relationship” *sensu* Brooker et al. 2006).

Recent studies, however, show that the severity-interaction relationship (SIR) may be unimodal rather than monotonic (i.e. as predicted by the SGH). Indeed, some studies have observed net interspecific interactions to be most positive at intermediate levels of environmental severity (Brooker et al. 2008; Travis et al. 2006). However, even among studies reporting unimodal severity-interaction relationships, there has

been considerable variation in the exact form of the relationship. To date four distinct forms have been proposed for the shape of the SIR:

1) Linear. The relative strength of positive interactions is predicted to increase across the complete range of environmental severity, reaching a maximum before environmental conditions are severe enough to exclude species completely (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 2008b).

2) Symmetrical hump-shape. Net interactions are predicted to be most positive at moderate environmental severity, and (equally) negative under both low and extreme environmental severity (Fig. 1a). This model assumes that positive effects of neighbours cannot be sustained under high severity (e.g. due to species ameliorative abilities being overwhelmed under extreme severity), and that the negative impacts of neighbouring individuals increase with severity (or are approximately constant). Thus, under extreme severity individuals derive little benefit (and still incur a cost) from growing in close proximity to neighbouring individuals, resulting in a net negative impact of neighbours. There is support for this model along resource gradients (i.e. increasing stress due to decreasing resource availability), where under the most stressful conditions neighbours are no longer able to compensate for the low levels of resources (and therefore compete strongly; e.g. Anthelme et al. 2007; Maestre and Cortina 2004). Along consumer pressure gradients (i.e. increasing herbivory or predation) the same SIR shape may be generated where associational defenses (a positive impact of neighbours where palatable species are sheltered by unpalatable species) are overwhelmed by extreme consumer pressure (Brooker et al. 2006; Smit et al. 2007).

3) Asymmetrical hump-shape. As for the previous model, the net interaction is most positive at moderate environmental severity, but changes to neutral under more severe conditions (i.e. little effect of neighbours; Fig. 1a). This model assumes a weakening of both positive (since severe environmental conditions cannot be completely ameliorated) and negative interactions (due to plants being smaller and growing more slowly under extreme stress) beyond moderate environmental severity, with equally small costs and benefits from growing close to neighbours under the

most extreme environmental severity (see e.g. Kawai and Tokeshi 2007; Michalet et al. 2006). No studies have yet provided support for this model.

4) Plateau. This model predicts 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 environmental severity individuals have a more positive net interaction than at low environmental severity, although the strength of this net interaction is constrained. The two potential extremes in this model should, however, be distinguished as they represent very different ecological scenarios (although as they are the same shape, they are not differentiated in Fig. 1a). The first, when the level of the plateau corresponds to the maximum potential facilitative interaction, indicates that the most positive possible net interaction is reached beyond a threshold of environmental severity. Therefore, the benefits of growing close to a neighbouring individual greatly exceed the costs of competing with that neighbour beyond a threshold of environmental severity. By contrast, the second extreme occurs when the plateau's asymptote is much less than the maximum potential positive interaction. This suggests that the maximum strength of facilitation is limited, possibly due to the ameliorative effects of neighbours being overwhelmed by environmental conditions at higher severity levels (i.e. neighbours are unable to sufficiently ameliorate extreme conditions). Three studies provide some evidence for the plateau model (Callaway et al. 2002; Graff et al. 2007; Kawai and Tokeshi 2007).

The exact form of the SIR is important for understanding and predicting community properties along environmental gradients, and is therefore of central importance to ecology (Brooker et al. 2008; see also Agrawal et al. 2007). For example, when considering plant communities, models that incorporate the effect of positive interactions into the diversity-productivity relationship make qualitatively different predictions than models that ignore positive interactions. However, whether a linear or a hump-shape SIR is assumed also alters the diversity-productivity model's predictions (e.g. compare Hacker and Gaines 1997; and Michalet et al. 2006). Similarly, when considering the role of interspecific interactions in determining upper altitudinal distribution limits, different severity-interaction relationships lead to contrasting predictions. For example, a linear SIR predicts that a species will be able to establish at higher altitudes in the presence of species that ameliorate environmental conditions (e.g. nurse plants) than in areas where those species are

absent (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 theoretical work dealing with the ecological consequences of positive interactions, the exact form of the SIR has yet to be resolved.

Indeed, despite numerous studies testing the SGH, there is still uncertainty about which model best describes the shape of the SIR. This uncertainty stems in part from four methodological issues. First, the net effect interaction between species must be measured at multiple severity levels, since studies considering only one pair of sites (e.g. mesic and xeric, or 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 (i.e. there is the possibility that portions of the SIR are “veiled”). For example, a non-linear relationship will appear linear if viewed over a small portion of its range (Kawai and Tokeshi 2007). Third, shifts in the net interaction between species 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 (Callaway 1998; Gómez-Aparicio et al. 2004; Pennings et al. 2003; see also Elmendorf and Moore 2007). Therefore, the SIR should best be tested by considering the same set of species at different levels of environmental severity. Finally, investigations should simultaneously measure multiple species traits (e.g. abundance, growth rate, survival, reproductive output) as some traits may be favoured by an interaction and others not (e.g. improved survival but lowered reproductive output; Choler et al. 2001; see also Brooker et al. 2008; Maestre et al. 2005). Therefore, to effectively describe the shape of the SIR changes in the net interaction between the same set of species should be documented at multiple sites along a complete severity gradient, examining multiple plant traits.

The aim of this study was to test which of the proposed shapes of the severity-interaction relationship best fits the variation in the net interaction between two species along a complete severity gradient on the species-poor and abiotically-extreme sub-Antarctic Marion Island. This was done by comparing multiple performance measures of the grass *Agrostis magellanica* in the presence and in the absence of the cushion plant *Azorella selago*, along the entire altitudinal range of both species. Since a previous test of the SGH on the island observed an approximately linear increase in the interspecific spatial association of plants with rising elevation (le Roux and McGeoch 2008b), a linear severity-interaction relationship was expected. Altitudinal variation in both the importance and intensity of the *Azorella-Agrostis* interaction was assessed to determine how the absolute and relative (i.e. relative to all other environmental factors impacting *Agrostis* performance) effect of *Azorella* on *Agrostis* changes along an abiotic stress gradient. Finer-scale variation in the intensity and importance of the *Azorella-Agrostis* interaction was also investigated at three sites along an exposure gradient to test if the same form of the severity-interaction relationship would be observed along both types of stress gradients.

Methods

Study site

Marion Island is the larger of the two islands comprising the Prince Edward Islands group, located in the southern Indian Ocean (Chown and Froneman 2008). The island is of volcanic origin, and 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; Smith 2002). The island supports a relatively depauperate biota, with 40 vascular plant species (including 18 alien 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, stronger winds and more complete cloud cover (le Roux 2008; Meiklejohn and Smith 2008). Soil stability also decreases with altitude, with a greater frequency and depth of freeze-thaw at higher elevations (Boelhouwers et al. 2003; Holness 2004). Therefore, with the exception of the lowest coastal areas with high salinities due to salt-spray (Smith 1978), abiotic severity increases with altitude across Marion Island (le Roux and McGeoch 2008b).

Only a small proportion of the island's primary productivity is consumed by herbivores (principally insects) (Crafford et al. 1986; Smith and Steenkamp 1990), and herbivory probably does not influence environmental severity across the altitudinal gradient.

Study species

Azorella selago (Apiaceae) is a compact, low-growing, cushion-forming perennial plant (referred to as *Azorella* from hereon; Fig. 2a, b) (Frenot et al. 1993; Huntley 1972; Orchard 1989; Ternetz 1902). It is the most common and widespread plant on Marion Island, occurring from sea-level to the upper altitudinal limit of vascular plant growth at 840 m a.s.l. (Chapter 3). *Azorella selago* 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 (Barendse and Chown 2001; Hugo et al. 2004; le Roux et al. 2005). The latter effect appears to be primarily due to *Azorella* cushions' nurse plant ability (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 2008b; le Roux et al. 2005; McGeoch et al. 2008; Nyakatya and McGeoch 2007).

Agrostis magellanica (Poaceae) is a perennial grass and the second most common vascular plant species on the island (referred to as *Agrostis* from hereon; Fig. 2a, b) (Huntley 1971). This grass is dominant in mire habitats on Marion Island, but also occurs in most other habitats (Gremmen and Smith 2004; Huntley 1971), reaching altitudes of up to 600 m a.s.l. (max.: 740 m a.s.l; Chapter 3). *Agrostis* is the most common vascular epiphyte on *Azorella* (i.e. rooted within the cushion plant, rather than in the soil) (Huntley 1971; le Roux 2004). Indeed, *Azorella* appears to act as a nurse plant for *Agrostis* at some sites where the grass occurs at a higher abundance on *Azorella* than on the surrounding soil (Buwa 2007). A previous study along a short altitudinal gradient on Marion Island also provided evidence that *Azorella* facilitates non-epiphytic *Agrostis* (le Roux and McGeoch 2008b). Both the broad- (i.e. across sub-Antarctic islands) and fine-scale (i.e. growing on individual

Azorella plants) distribution of *Agrostis* suggest that the grass is sensitive to high winds and low soil moisture (le Roux 2004; le Roux et al. 2005; Taylor 1955). However, the distribution of *Agrostis* may be extended to higher altitudes as a consequence of being nursed by *Azorella* (i.e. occurring as an epiphyte) (as suggested by Huntley 1972).

Data collection

Agrostis individuals were collected off *Azorella* plants (i.e. epiphytic individuals) and from the adjacent soil (i.e. non-epiphytic individuals) along three altitudinal transects on the north-western (NW), north-eastern (NE) and south-eastern (SE) sides of the island. Pairs of *Azorella* cushions and adjacent soil (hereafter “paired samples”) were sampled along exposed ridges from sea-level to the upper altitudinal limit of vascular plant growth on Marion Island. 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) at approximately 20 m elevation intervals (altitude measured using a barometric altimeter; Garmin Vista Mono, Garmin, USA). 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 molded around the outer edge of each sampled *Azorella* cushion (i.e. to reproduce the size and shape of the cushion) and placed 0.1 m from the cushion in a randomly selected direction (Fig. 2c, d). If this area overlapped with another cushion (*Azorella* seedlings were ignored), 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 block 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:

$$X' = 100.X / (100 - R) \quad (\text{Eq. 1})$$

where X represents the performance measure, X' the scaled performance measure and R the percentage of the soil sample covered by rocks large enough to inhibit the growth of *Agrostis* seedlings.

In addition, fine-scale variation in the performance of *Agrostis* on *Azorella* and on soil along an 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 exposed, intermediate, sheltered). Therefore, the spatial extent of the exposure gradient (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 > 8 species and > 30 % cover to 3 species and \pm 10 % cover). Following the same methodology as the altitudinal transects, medium-sized *Azorella* cushions were selected using random distance and direction numbers. All *Agrostis* individuals were then collected from the cushion and from an adjacent soil area of the same size and shape (0.1 m from the edge of the *Azorella* cushion in a random direction).

All harvested *Agrostis* individuals were returned to the laboratory and dried at 60 °C. Each grass was weighed (both total mass and the mass of shoots and inflorescences; referred to as leaf mass hereafter), measured (basal diameter) and the number of inflorescences and inflorescence stalks counted. 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 represent more recent flowering events (i.e. within the last growing season), while the number of inflorescence stems provides an estimate of reproductive effort over a long span.

Data analysis

The impact of one species on another can be calculated simply as the arithmetic difference between the performance of the first species in the presence and in the absence of the second species. However, scaling this difference in performance relative to the actual performance of the species at that site (or across all other sites), allows the proportional impact of the interaction to be quantified. Thus, an increase of 1 g in *Agrostis* biomass in the presence of *Azorella* can represent either a small effect (if *Agrostis* biomass on the soil is high, e.g. 50 g) or a more substantial effect (if *Agrostis* biomass on the soil is low, e.g. 2 g). For this reason, the intensity of the effect of *Azorella* on *Agrostis* at each altitude was assessed by calculating the relative interaction index (RII; Armas et al. 2004). The relative interaction index is calculated as:

$$\text{RII} = (P_{T+N} - P_{T-N}) / (P_{T+N} + P_{T-N}) \quad (\text{Eq. 2})$$

where P_{T+N} and P_{T-N} represent the performance of *Agrostis* in the presence and absence of *Azorella* respectively. 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 (*sensu* Brooker et al. 2005). This index has performed well in other studies testing the severity-interaction relationship (e.g. Elmendorf and Moore 2007; Kikvidze et al. 2005; Schiffers and Tielbörger 2006; Tirado and Pugnaire 2005).

The importance (*sensu* Brooker et al. 2005; i.e. the impact of *Azorella* relative to all other environmental factors) of the *Azorella-Agrostis* interaction was calculated using the index of competitive importance (C_{imp} ; following Brooker et al. 2005). This index scales the intensity of the interactions at a sample (i.e. $P_{T+N} - P_{T-N}$) relative to the intensity of this same interaction across all sites being compared. Therefore,

$$C_{\text{imp}} = (P_{T+N} - P_{T-N}) / (\text{Max} [P_{T-N}; P_{T+N}] \text{ across all samples} - \text{Min}[P_{T-N}; P_{T+N}]) \quad (\text{Eq. 3})$$

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. The index was modified from Brooker *et al.* (2005), 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 indicate facilitative (competitive) interactions, and larger absolute values indicating greater importance of the interaction.

To distinguish which of the proposed shapes the *Agrostis-Azorella* severity-interaction most closely followed, the relationship between 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). First, a linear model was fitted to the data. Thereafter, four non-linear Huisman-Olff-Fresco models (HOF models hereafter) 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

$$\mu = M \frac{1}{1 + \exp(a + bx)} \frac{1}{1 + \exp(c - dx)} \quad (\text{Eq. 4})$$

where μ is the expected value (i.e. 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 modeled by setting b , c , and $d = 0$, and represents our null hypothesis (i.e. expected if there is no effect of altitude on the intensity or importance of the interaction).

Models were fitted to the data separately for each transect as initial analyses revealed clear differences between *Agrostis* performance along the three 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 modeling 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' degrees of freedom differed. However, models with the same degrees of freedom (e.g. HOF III and IV; linear model and HOF II) were distinguished using Pseudo R^2 values.

Therefore, I was able to test which of the five of 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 continues 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, RII and C_{imp} were again modeled 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 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 highest *Azorella* plants in each transect were found between 630 and 657 m a.s.l., and the lowest individuals just above the island's coastal cliffs (10 – 30 m

a.s.l.). The distribution of *Agrostis* was nested within that of *Azorella*, with approximately co-incident lower elevational limits but much lower upper limits than *Azorella* on all three transects (≤ 465 m a.s.l.; physical and biological details of sampling sites listed in Table 1).

Agrostis performance differed between transects, with the lowest combined (i.e. growing on soil and on *Azorella*) cover, abundance, biomass and reproductive effort in the NW transect (Table 1). By contrast, the cover of other vascular plants and mosses was greatest in the NW transect, particularly on the soil (Table 1).

Shape of the severity-interaction relationship

The intensity of *Agrostis*'s interaction with *Azorella* increased with altitude for most measures of performance in the NE and SE transects, generally shifting from strongly negative (i.e. a net competitive effect) at low altitudes, reaching a positive plateau at higher altitudes (i.e. a net facilitative effect; Fig. 3; see also Appendix A). In these transects *Agrostis* performed better in the presence of *Azorella* than in the absence of the cushion plant in most samples (Appendix B). HOF III models provided the best fit to the data for most relationships, with a plateau at $R_{II} = 0.48 - 0.92$ (Table 2; full results in Appendix C). In the three relationships where HOF V models performed significantly better than HOF III models, R_{II} values at high altitudes all equaled 1 (Table 2). In contrast, there was no relationship between the intensity of the interaction and altitude in the NW transects (e.g. Appendix D), where the performance of *Agrostis* was worse in the presence of *Azorella* than in the absence of the cushion plant in most samples (Appendix B).

Along the exposure gradient the intensity of the interaction increased from weakly positive to strongly positive with increasing exposure for all measures of *Agrostis* abundance, cover and biomass (Fig. 4, Table 3). The impact of *Azorella* on *Agrostis* performance was positive in 63 – 100 % of these sample pairs (Appendix B). However, when comparing the intensity of the interaction between sites along the exposure gradient for reproductive output, there was no difference between exposure levels (Table 3; full results in Appendix E). Thus, interaction intensity and environmental severity were significantly related in most analyses, with a plateau-shaped relationship across the altitudinal gradient, and a linear relationship over the shorter, exposure gradient.

By contrast, the importance of the *Azorella-Agrostis* interaction generally did not vary with altitude (Table 2; see e.g. Fig. 3). Only in the SE transect were four of the performance measures significantly related to altitude; three showed a positive plateau and one 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 and biomass. However, the importance of the *Azorella-Agrostis* interaction increased significantly with exposure for reproductive output (Table 3, Fig. 4). These results suggest that interaction importance and environmental severity are generally not significantly related, but tend to be non-linear when they are.

Discussion

Interaction intensity: Plateau-shaped severity-interaction relationship

Considerable variation was found in interspecific interaction strength and direction in this system. The impact of *Azorella* on *Agrostis* performance spanned the complete range of possibilities from the maximum achievable positive interaction (i.e. *Agrostis* only growing on *Azorella*) to the maximum negative interaction (i.e. *Agrostis* being limited to the soil). However, two patterns emerged: the intensity, but not the importance, of the *Azorella-Agrostis* interaction increased with environmental severity in most cases. Specifically, in two of the three transects a significant proportion of the spatial variation in the intensity of the *Azorella-Agrostis* interaction was explained by altitude, with the impact of *Azorella* on *Agrostis* performance becoming more positive with increasing environmental severity before reaching a positive asymptote at high altitudes. Thus, contrary to the SGH, our data strongly support the plateau model for the severity-interaction relationship (in agreement with Graff et al. 2007; Kawai and Tokeshi 2007; see also Callaway et al. 2002).

The significant plateau-shaped severity-interaction relationships encompassed a wide range of asymptote values. In the NE transect most asymptotes were close to 1, indicating that *Agrostis* was generally only able to recruit and reproduce successfully in the presence of *Azorella* (i.e. the most positive possible net *Agrostis-Azorella* interaction) at intermediate and high elevations. Smaller plateau values were observed in the SE transect, suggesting that the facilitative effect of *Azorella* was not as strong as in the NE transect. These lower plateau values possibly reflect better performance

of *Agrostis* on bare soil in the SE than in the NE transect (i.e. the proportional improvement of *Agrostis* performance by *Azorella* was lower in the SE transect; see Fig. S1). Nonetheless, since all plateau values were positive (0.5 – 1), *Agrostis* performed better when growing on *Azorella* than on soil at altitudes where the SIR reached an asymptote, providing evidence for a nurse effect at higher elevations. This is in agreement with other cushion plants in the same family (from the genera *Azorella*, *Laretia* and *Bolax*) that are well known to act as nurse plants to other vascular species (Badano et al. 2007; Cavieres et al. 2002, 2007; Cavieres et al. 2008; Molina-Montenegro et al. 2005). However, our results also 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. This suggests an abrupt limit to *Azorella*'s ability to facilitate *Agrostis*, but only at an altitude exceeding the elevational range of most soil-rooted grasses (e.g. in the NE and SE transects).

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 (i.e. sites where exposure was so severe that either *Agrostis* or *Azorella* was not present), the SIR increased monotonically over the range of exposure levels occurring on the landform that was sampled. This was particularly interesting because the SIR was thus consistently monotonic across both the altitudinal and exposure gradients, despite large differences in the spatial extent of the two gradients. Thus, the switch from net negative (or weakly positive) to strongly net positive *Azorella-Agrostis* interactions occurred along severity gradients at both fine and broad spatial scales.

Mechanisms of competition and facilitation

The change from competitive to facilitative interactions with increasing severity reflects a change in the balance of positive and negative effects of neighbours (Brooker and Callaghan 1998). The mechanisms by which *Azorella* could facilitate *Agrostis* include: 1) buffering the thermal regime, 2) buffering substrate moisture levels, 3) increasing nutrient availability, 4) decreasing wind exposure (although only on the leeward side of the cushion plant), and 5) decreasing substrate mobility (due to reduced frost heaving, as a result of buffered temperatures) (le Roux and McGeoch 2008b; McGeoch et al. 2008; Nyakatya and McGeoch 2007). Indeed, these

mechanisms are important for the facilitative effect of cushion plants on other species elsewhere (e.g. Badano et al. 2006; Cavieres et al. 2007; Perez 1987; Pyšek and Liška 1991). The strength of these positive interactions are likely to increase with altitude, since on Marion Island at higher elevations temperatures are colder, winds stronger and soils less developed. Therefore the relative impact of environmental amelioration by *Azorella* is probably greater under more severe environmental conditions (see e.g. Badano and Cavieres 2006). Similarly, along the exposure gradient the benefits of these mechanisms probably increase with wind exposure. Therefore, the switch from competition to facilitation with increasing altitude and exposure is likely a consequence of stronger ameliorative (i.e. positive) effects by *Azorella* under conditions of greater environmental severity (Badano and Cavieres 2006).

The alternative mechanism for the change in the net interaction with increasing severity, i.e. that competitive interactions are weaker at higher altitudes, is unlikely. *Azorella* and *Agrostis* compete for water and nutrients, since they both root into the cushion plant's organic humus-filled centre and the surrounding soil. The two species also compete for space when *Agrostis* grows on *Azorella*, with the cushion plant overgrowing small epiphytic grasses (and partly overgrowing larger *Agrostis* individuals; see Fig. 2b) and restricting their basal diameter growth (due to the cushion plant's compact canopy, as suggested for another *Azorella* species; Molina-Montenegro et al. 2000; see also Alliende and Hoffmann 1985). However, the strength of resource competition probably does not decrease with altitude, since slower decomposition in the colder higher elevations (Smith et al. 1993) can result in lower nutrient availability for plants. Similarly, cushion surface compactness tends to increase with altitude (Rautenbach 2007), progressively limiting the basal growth of the grass more strongly at higher elevations. *Azorella* growth rate, which determines the cushion plant's ability to overgrow *Agrostis*, is however inconsistently related to altitude (le Roux and McGeoch 2004). Thus the strength of negative interactions between *Azorella* and *Agrostis* may actually increase with elevation on Marion Island. This pattern is probably also consistent along the exposure gradient, with greater *Azorella* compactness and lower resource availability at more wind-swept sites. Therefore, in this system net interactions become more positive with increasing environmental severity as a likely consequence of a stronger positive component of the net interaction at high altitudes (see e.g. Pugnaire and Luque 2001).

Variation between transects

The plateau-shaped SIR was not consistent across transects in this study, and the frequency of significant severity-interaction relationships differed between the three transects. In particular the intensity of the impact of *Azorella* on *Agrostis* varied independently of altitude for all performance measures in the NW transect. Due to climatic differences between the western and eastern sides of the island, plants in the NW transect probably experience stronger winds, greater rainfall and more buffered temperatures than in the NE and SE transects (le Roux 2008; Nyakatya and McGeoch 2007). These physical differences appear to be important for *Agrostis* because the performance of the grass was poorest in the NW transect (in agreement with le Roux 2004). However, despite these east-west climatic differences, the NW transect covers a clear altitudinal severity gradient (as in the NE and SE transects) and therefore a significant trend in interaction intensity was expected along the transect.

The lack of a significant SIR in the NW transect is probably caused by biological differences between transects. On the NW transect there is conspicuously greater moss cover on the soil than in the other two transects, possibly due to moister conditions on the western side of the island. Because moss is able to provide nearly all the same facilitative mechanisms as *Azorella* (except sheltering from the wind) (e.g. Groeneveld et al. 2007), it is likely that the more abundant moss cover on the western transect could also have acted as a nurse plant for *Agrostis*. Indeed, other studies have also suggested that mosses can be important establishment sites for vascular plants (Carlsson and Callaghan 1991; Groeneveld et al. 2007; Ryser 1993; Sohlberg and Bliss 1984) and even for other *Azorella* species (Ashton and Gill 1965). Indeed, this is supported by the observation that on the NW transect the cover of moss and *Agrostis* on the soil are positively correlated (excluding sites without *Agrostis* cover on the soil: $r = 0.64$, $p = 0.02$), a relationship which is absent in the other transects where mosses attained lower cover. Thus, on the NW transect, an additional biotic interaction (i.e. a facilitative effect by mosses) altered the balance of the *Azorella*-*Agrostis* interaction, and therefore the shape of the severity-interaction relationship. More importantly, this result provides evidence that slight environmental differences between replicates of the same stress-gradient can affect the shape and significance of the severity-interaction relationship (in agreement with Crain 2008; see also Eskelinen 2008), highlighting the importance of replicated tests of the SIR.

Interaction importance: Non-significant severity-interaction relationship

The relationship between the importance of the *Azorella-Agrostis* interaction and environmental severity also varied in significance (and shape) between transects. In three of the analyses the importance of the *Azorella-Agrostis* interaction reached a positive (albeit low) plateau, indicating the relative impact of growing on *Azorella* for *Agrostis* performance was greater at higher altitudes than at low altitudes. Similarly along the exposure gradient, the importance of the *Azorella-Agrostis* interaction for reproductive output increased with environmental severity. This suggests that, at least for four performance measures, the impact of *Azorella* on *Agrostis* increases with environmental severity relative to the impact of other environmental factors on *Agrostis* performance. These results agree with previous studies that have generally found a significant positive relationship, where the proportion of the plant's performance determined by an interspecific interaction increases with environmental severity (Gaucherand et al. 2006; Sammul et al. 2000; see also Brooker et al. 2005). In such a case, the performance of a species under extreme environmental conditions depends primarily on whether a facilitator (e.g. nurse plant) is present or not. Under more moderate conditions the plant's performance is determined by other environmental factors (i.e. the presence or absence of the facilitator has less of an impact on performance).

However, in most analyses the importance of the *Azorella-Agrostis* interaction varied independently of altitude. This suggests that along the altitudinal gradient the increasing facilitative effect of *Azorella* was balanced by the increasingly negative effect of environmental severity, resulting in roughly constant proportional impact of the effect of the interaction on *Agrostis* performance. Therefore, for the majority of analyses, the presence or absence of *Azorella* had a relatively constant proportional impact on the performance of *Agrostis*.

While there were clear differences between transects in the importance and intensity of the *Azorella-Agrostis* interaction, there was little variation in the shape of the SIR for different plant performance measures. This was surprising as it had been suggested, for example, that growth and productivity should be responsive to increased environmental severity under moderate environmental conditions, but that survivorship would only be affected under more severe conditions (Kawai and

Tokeshi 2007). Similarly, studies have found the presence of neighbours to increase individual survival but to decrease reproductive output (Choler et al. 2001). Therefore, *a priori* different severity-interaction relationship shapes (or at least clear shifts in the SIR curves) were expected for different plant performance measures. However, in this system such differences were not marked, with *Agrostis* performance changing in a similar fashion with increasing severity across all measures of plant performance.

Ecological implications

The strong intensity of the *Azorella-Agrostis* interaction under severe environmental conditions suggests that the cushion plant effectively maintains *Agrostis* populations at higher elevations. Indeed, because *Agrostis* abundance and biomass are low on the soil at higher elevations, the grasses growing epiphytically on *Azorella* represent the majority of the population. This is particularly pronounced for the production of inflorescences with more than 90 % of the total inflorescence crop borne by epiphytic individuals. Thus, since epiphytic *Agrostis* comprise the bulk of the population and produce the majority of inflorescences under severe environmental conditions, source-sink dynamics may exist for *Agrostis* growing on *Azorella* (the source populations) and on the soil (the sink population) at higher elevations (see e.g. Nuñez et al. 1999; Tirado and Pugnaire 2003; although see also Kadmon and Tielbörger 1999).

Furthermore, it appears that the *Azorella-Agrostis* interaction extends the altitudinal limit of *Agrostis* beyond the range the grass would reach in the absence of *Azorella*, at least on the NE and SE transects. 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, while data is only available for three transects, 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 (i.e. the localized effects of facilitation are "scaled up" to have a wider effect; following e.g. Freestone 2006). Moreover, higher abundances of *Agrostis* may also facilitate increased abundances of micro-invertebrates at high elevations since mite and springtail species reach greater densities under epiphytic *Agrostis* than elsewhere on cushions or on the soil in sparse

vegetation (Hugo et al. 2004). Therefore, the fine-scale *Azorella-Agrostis* interaction could be affecting larger scale community composition patterns.

More broadly, the observation of a plateau-shaped SIR suggests that positive interactions are important even under extreme environmental conditions. This suggests that the predictions of community models that assume a linear SIR (e.g. Hacker and Gaines 1997) are more appropriate than those assuming a hump-shaped relationship (e.g. Michalet et al. 2006). Indeed, the two predictions of Hacker and Gaines (1997) are realized in our study. First, facilitation acts to increase the diversity of species at high altitudes, by increasing species richness through the facilitation of the occurrence of *Agrostis* at higher altitudes in the NE and SE transects (which is a substantial increase in the vascular plant species richness at high altitude sites; Chapter 3). Second, facilitation of *Agrostis* by *Azorella* at high altitudes also increases the diversity of interspecific interactions. Specifically, the presence of *Agrostis* provides an additional food source to many species of micro-arthropods, increasing the abundance of this group of animals within *Azorella* (Hugo et al. 2004). It is, however, important to note that if only a portion of the altitudinal gradient had been examined a qualitatively different shape could have been described for the severity-interaction relationship. 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. Therefore, changes in species interactions need to be considered along the full length of severity gradients to correctly identify the form of the SIR.

Conclusion

These results demonstrate the variation that may be expected in the shape (and significance) of the severity-interaction relationship, even in replicates of the same severity gradient. Nonetheless, net interspecific interactions generally became more positive with increasing environmental severity, leveling-off to a positive asymptote at intermediate and high altitudes. The results, therefore, provide clear support for the plateau-shaped severity-interaction relationship.

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

| | Altitudinal transects | | | Exposure gradient | | |
|---|-------------------------|-------------------------|-------------------------|------------------------|-------------------------|-------------------------|
| | NW | NE | SE | Exposed | Intermediate | Sheltered |
| All samples (irrespective of <i>Agrostis</i> presence) | | | | | | |
| Number of samples | 36 | 32 | 32 | 8 | 8 | 8 |
| Highest altitude (m a.s.l.) | 657 | 630 | 652 | 102 | 97 | 89 |
| Lowest altitude | 30 | 10 | 10 | -- ⁴ | -- ⁴ | -- ⁴ |
| Plant cover on all soil samples (mean ± S.E.) ¹ | | | | | | |
| <i>Agrostis</i> | 8.5 ± 2.6 | 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 | 31.6 ± 5.3 ^a | 14.3 ± 4.7 ^b | 16.5 ± 4.7 ^b | 2.8 ± 2.5 | 11.3 ± 10.2 | 6.5 ± 3.9 |
| Moss | 15.4 ± 2.7 ^a | 7.8 ± 1.9 ^b | 7.8 ± 1.9 ^b | 0.3 ± 0.3 | 1.9 ± 0.9 | 5.0 ± 1.6 |
| Epiphyte cover on all <i>Azorella</i> samples (mean ± S.E.) | | | | | | |
| <i>Agrostis</i> | 3.0 ± 0.8 ^a | 8.7 ± 1.6 ^b | 9.5 ± 1.7 ^b | 14.4 ± 1.5 | 21.9 ± 4.5 | 19.4 ± 2.9 |
| Other vascular species | 5.3 ± 1.1 ^a | 4.3 ± 1.5 ^{ab} | 1.9 ± 0.7 ^b | 1.5 ± 0.6 | 2.4 ± 1.8 | 2.1 ± 1.9 |
| Moss | 2.2 ± 0.4 ^a | 2.2 ± 0.7 ^{ab} | 0.7 ± 0.2 ^b | 0 ± 0 ^a | 0 ± 0 ^a | 3.8 ± 1.8 ^b |
| Samples with <i>Agrostis</i> present on soil | | | | | | |
| Number of samples | 20 | 14 | 22 | 8 | 8 | 8 |
| Highest altitude | 375 | 465 | 423 | 102 | 97 | 89 |
| Lowest altitude | 45 | 50 | 10 | -- ⁴ | -- ⁴ | -- ⁴ |
| Total abundance ² | 907 | 588 | 715 | 68 | 151 | 536 |
| Total biomass (g) ² | 128.0 | 29.8 | 61.8 | 1.2 | 38.6 | 47.5 |
| Total number of inflorescences ² | 182 | 47 | 125 | 4 | 12 | 8 |

| | | | | | | |
|--|------|-------|-------|-----------------|-----------------|-----------------|
| Maximum <i>Agrostis</i> abundance ³ | 139 | 197 | 123 | 14 | 41 | 172 |
| Heaviest <i>Agrostis</i> individual (g) ³ | 8.4 | 12.0 | 19.3 | 0.3 | 15.6 | 2.1 |
| Most inflorescences per <i>Agrostis</i> individual ³ | 23 | 30 | 56 | 2 | 5 | 5 |
| Samples with <i>Agrostis</i> present on <i>Azorella</i> | | | | | | |
| Number of samples | 20 | 18 | 23 | 8 | 8 | 8 |
| Highest altitude | 432 | 465 | 446 | 102 | 97 | 89 |
| Lowest altitude | 45 | 50 | 10 | -- ⁴ | -- ⁴ | -- ⁴ |
| Total abundance ² | 640 | 2677 | 3081 | 1169 | 1265 | 1806 |
| Total biomass (g) ² | 91.7 | 250.7 | 197.7 | 127.7 | 125.4 | 94.2 |
| Total number of inflorescences ² | 137 | 588 | 352 | 240 | 148 | 51 |
| Maximum <i>Agrostis</i> abundance ³ | 98 | 370 | 701 | 222 | 448 | 388 |
| Heaviest <i>Agrostis</i> individual (g) ³ | 5.9 | 8.1 | 5.6 | 7.0 | 5.5 | 1.2 |
| Most inflorescences per <i>Agrostis</i> individual ³ | 7 | 71 | 7 | 8 | 4 | 4 |
| Number of samples with <i>Agrostis</i> on soil and <i>Azorella</i> | 19 | 14 | 22 | 8 | 8 | 8 |

¹ sites not sharing a subscript letter differ significantly ($p < 0.05$), ² summed across all samples, ³ across all samples, ⁴ all sites within close proximity.

Table 2 The shape of the minimum adequate models describing the relationship between the intensity and importance of the *Azorella-Agrostis* interaction along an altitudinal gradient. Only significant models ($p \leq 0.05$) are listed. Where a plateau model provided the best fit to the data, the value of the asymptote is shown in parentheses. No models were significant for the NW transect. Except where indicated, the plateau-shape was best modeled by HOF III models. n.s. = no model explained a significant proportion of the variance. Complete statistics given in Appendix C, and selected relationships illustrated in Fig. 3 and Appendices A and D.

| Variable | NE transect | | SE transect | |
|---|--------------------------|-----------------------|----------------------------|-----------------------|
| | Shape (plateau value) | Pseudo R ² | Shape (plateau value) | Pseudo R ² |
| Interaction importance (C_{imp}) | | | | |
| Abundance | n.s. | | n.s. | |
| Total mass | n.s. | | n.s. | |
| Leaf mass | n.s. | | Plateau (0.14) | 0.26 |
| Canopy cover | n.s. | | Asymmetrical hump-shape | 0.46 |
| Basal area | n.s. | | n.s. | |
| Inflorescence stems | n.s. | | Plateau (0.14) | 0.33 |
| Inflorescences | n.s. | | Plateau (0.12) | 0.26 |
| Interaction intensity (RII) | | | | |
| Abundance | n.s. | | Plateau (0.66) | 0.74 |
| Total mass | Plateau ¹ (1) | 0.80 | Plateau (0.71) | 0.63 |
| Leaf mass | Plateau ¹ (1) | 0.81 | Plateau (0.72) | 0.64 |
| Canopy cover | Plateau (0.88) | 0.72 | Plateau (0.49) | 0.61 |
| Basal area | Plateau (0.85) | 0.74 | Plateau (0.75) | 0.65 |
| Inflorescence stems | Plateau ¹ (1) | 0.86 | Plateau (0.89) | 0.70 |
| Inflorescences | Plateau (0.92) | 0.91 | Plateau (0.90) | 0.70 |

¹ HOF V model gave best fit, but showed plateau shape.

Table 3 Differences in the net effect of *Azorella selago* on *Agrostis magellanica* at three sites along a wind exposure gradient. The proportion of the variance explained by significant models is estimated by the Pseudo R^2 , and the ranking of the effect of the different factor levels indicated by “>”. Complete statistics are given in Appendix E and selected relationships illustrated in Fig. 4. E = exposed site, I = intermediate exposure site, S = sheltered site.

| Variable | Model p-value | Pseudo R^2 | Factor level order |
|--------------------------------------|---------------|--------------|--------------------|
| Interaction importance (C_{imp}) | | | |
| Abundance | 0.294 | | |
| Total mass | 0.393 | | |
| Leaf mass | 0.501 | | |
| Canopy cover | 0.123 | | |
| Basal area | 0.311 | | |
| Inflorescence stalks | 0.039 | 29% | E>I>S |
| Inflorescences | 0.005 | 40% | E>I>S |
| Interaction intensity (RII) | | | |
| Abundance | 0.038 | 37% | E>I>S |
| Total mass | < 0.001 | 6% | E>I>S |
| Leaf mass | < 0.001 | 5% | E>I>S |
| Canopy cover | 0.021 | 37% | E>I>S |
| Basal area | 0.057 | 41% | E>I>S |
| Inflorescence stalks | 0.368 | | |
| Inflorescences | 0.431 | | |

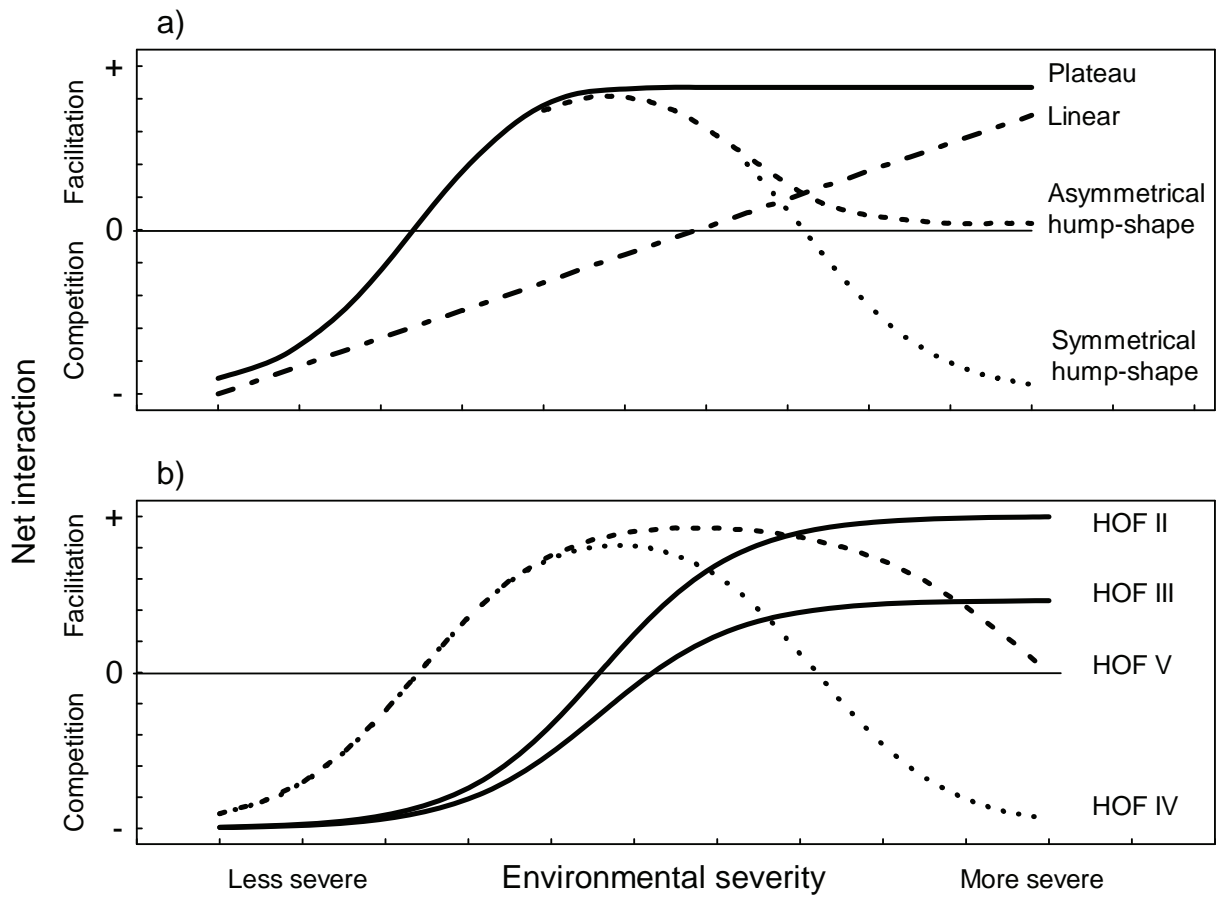


Fig. 1 The hypothesized shapes of the severity-interaction relationships (a) and the range of curves described by the Huisman-Olff-Fresco (HOF) models (b). Panel a) based on figure from Kawai and Tokeshi (2007). HOF curves (in b) used to model the hypothesized shapes of the severity-interaction relationship (in a) share the same line style (i.e. HOF II and III were used to model the plateau shape).

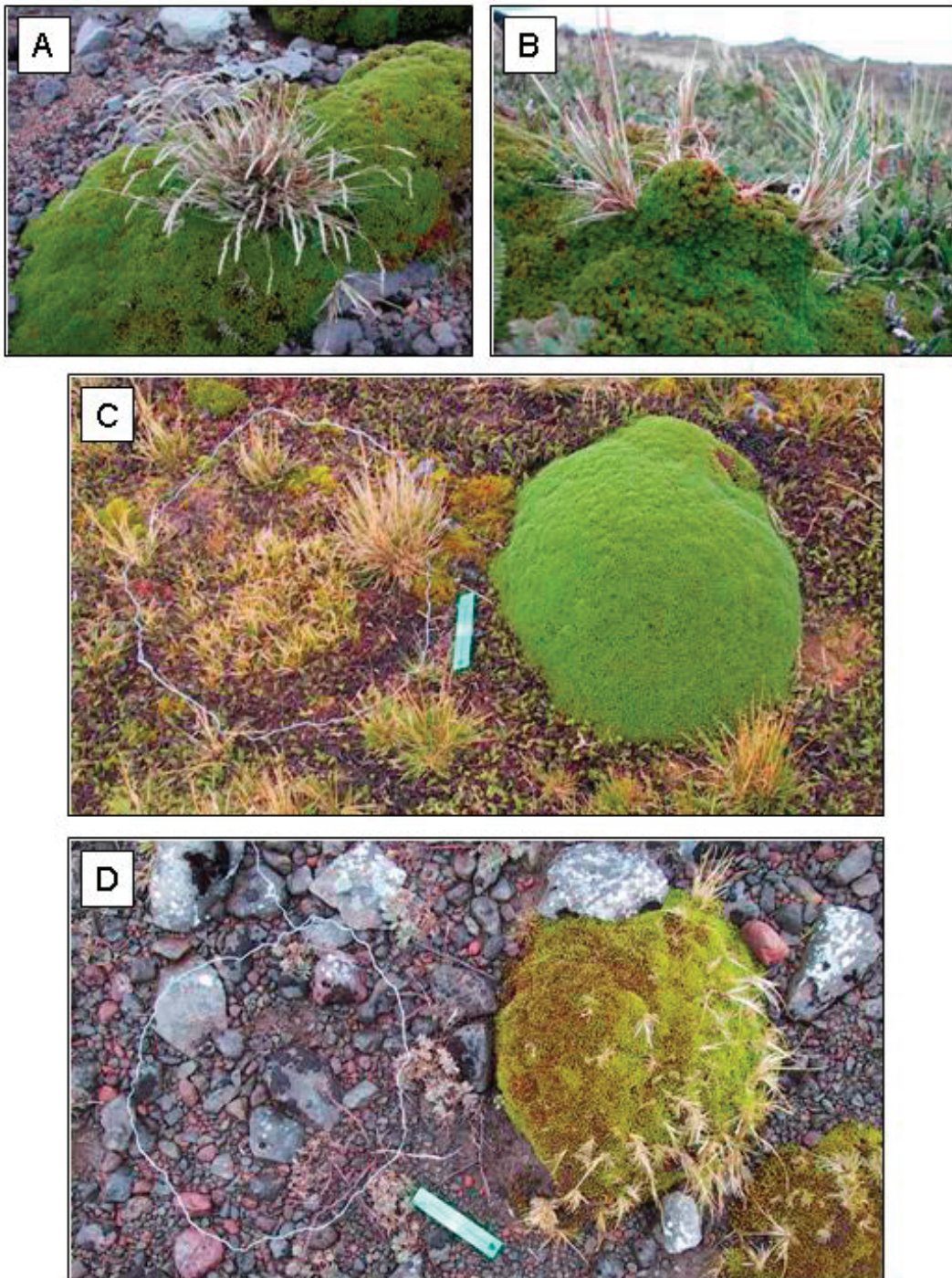


Fig. 2 The cushion plant *Azorella selago* and the grass *Agrostis magellanica*. a) Epiphytic *Agrostis* growing on *Azorella* (~ 450 m a.s.l.). b) Close-up of epiphytic *Agrostis* growing on *Azorella* (~ 50 m a.s.l.; the fern *Blechnum penna-marina* can also be seen growing epiphytically). c) and d) Paired soil and *Azorella* samples at very low (25 m a.s.l.) and moderate (166 m a.s.l.) altitudes on the SE transect. The green ruler in c) and d) is provided for scale (150 mm long).

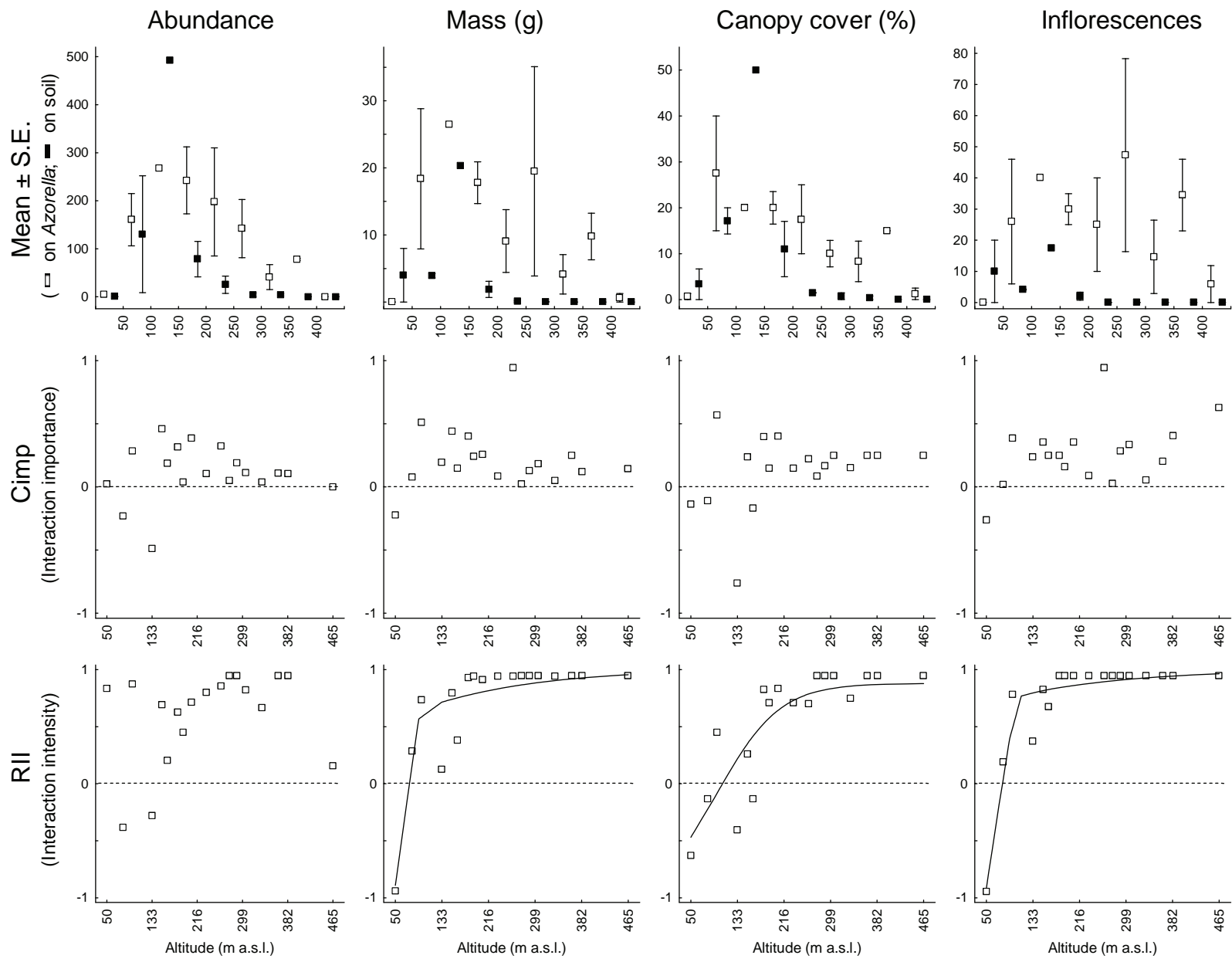


Fig. 3 Variation in the performance of *Agrostis magellanica* along the NE altitudinal gradient. Four performance measures are presented: abundance, mass, canopy cover and total number of inflorescences. The performance of *Agrostis* individuals in the presence (empty squares) and absence (filled squares) of *Azorella* is shown in the first row (binned into 50 m elevation bands), while altitudinal variation in the importance and intensity of the interaction between *Azorella* and *Agrostis* is shown in the second and third row respectively. The solid line shows the best fit model to the data. Complete statistics in Appendix C; see Appendices A and D for equivalent figures for the NW and SE transects.

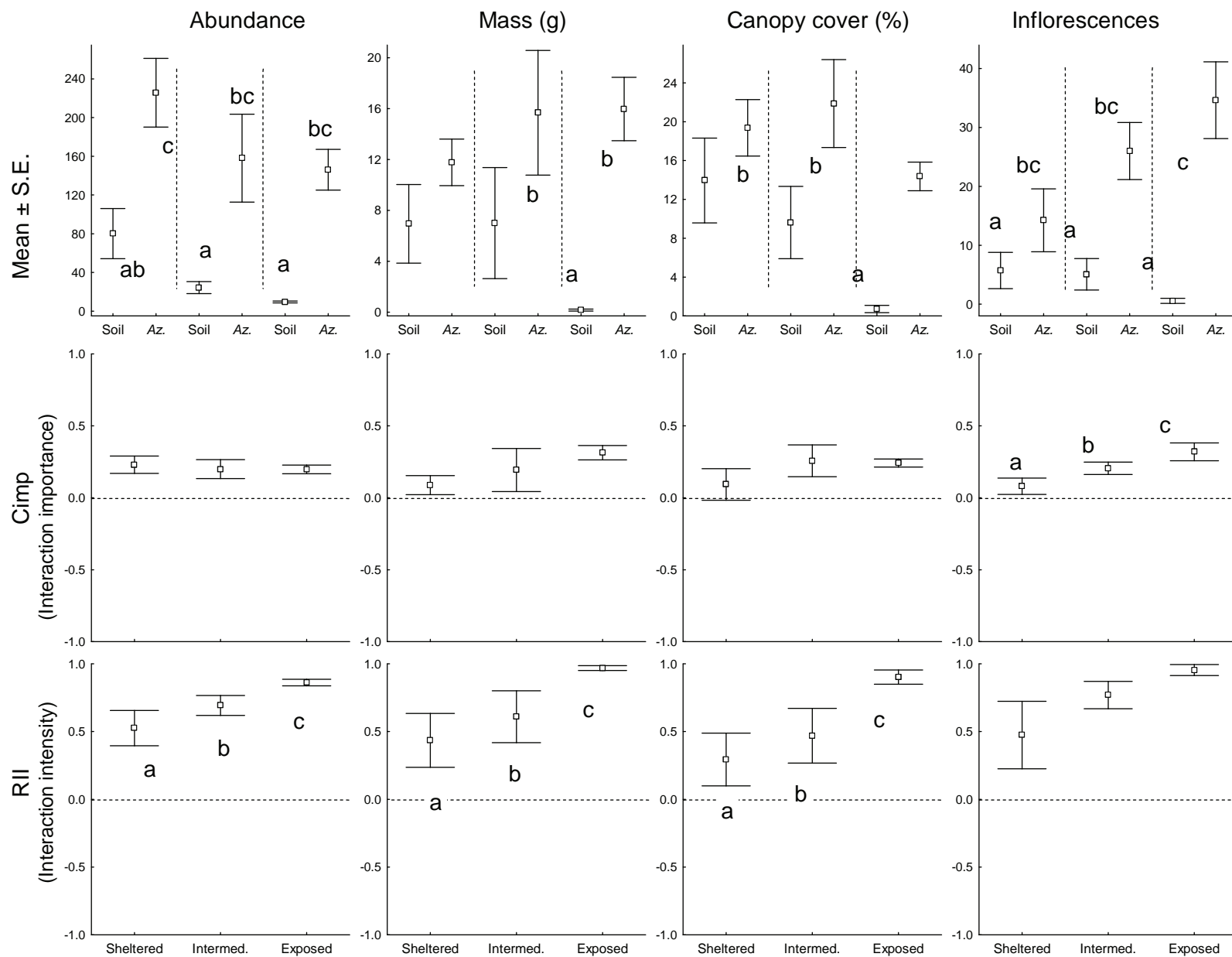
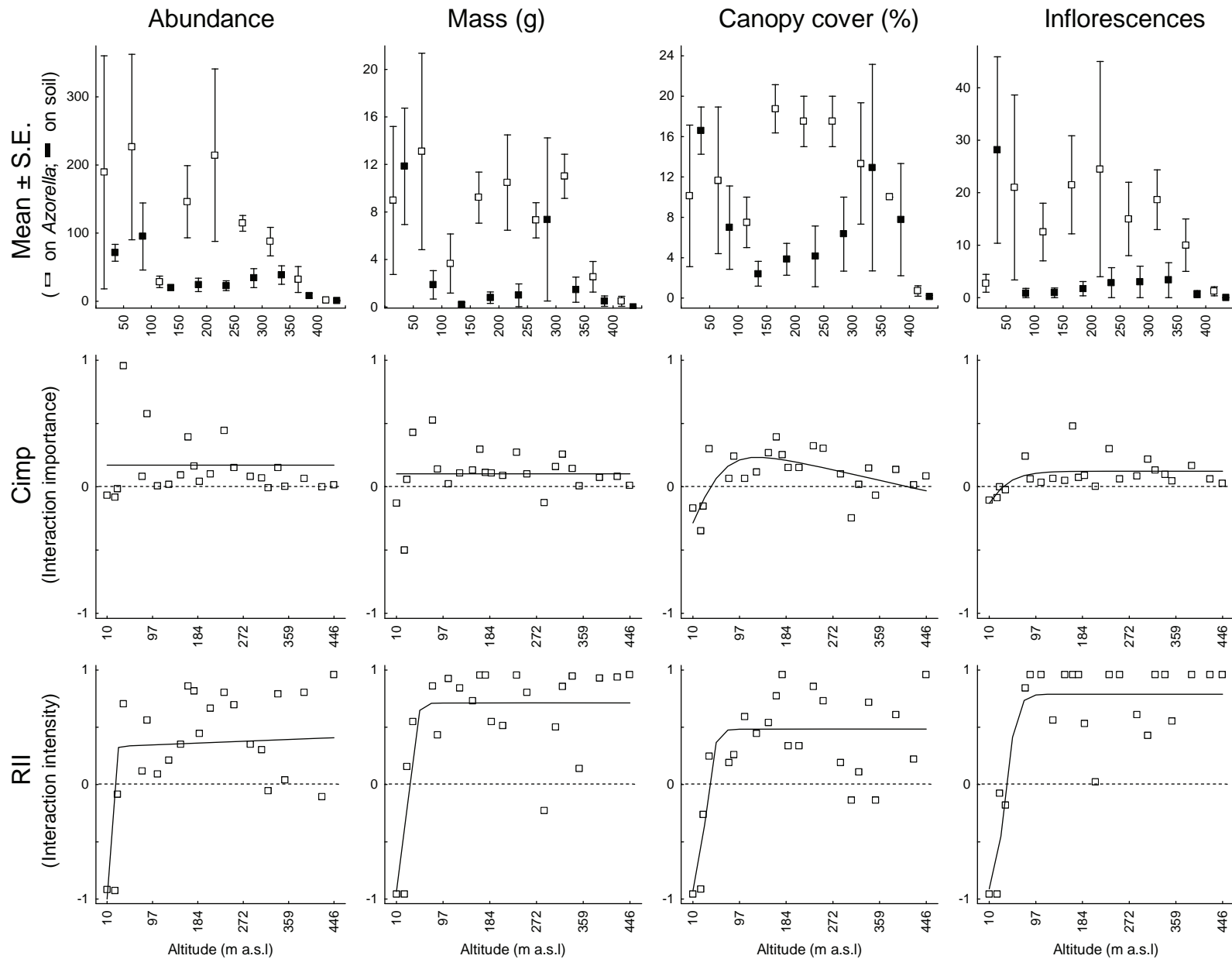


Fig. 4 Variation in the performance of *Agrostis magellanica* across a gradient of increasing exposure. Four performance measures are presented: abundance, mass, canopy cover and total number of inflorescences. The performance of *Agrostis* individuals in the presence (labeled “Az.”) and absence (labeled “soil”) of *Azorella* is shown in the first row, while variation in the importance and intensity of the interaction between *Azorella* and *Agrostis* with increasing exposure is shown in the second and third row respectively. Within each panel, groups not sharing common letters differ significantly ($p < 0.05$). Complete statistical results in Appendix E.



Appendix A The variation in the performance of *Agrostis magellanica* along the SE altitudinal gradient. Four performance measures are presented: abundance, mass, canopy cover and total number of inflorescences. The performance of *Agrostis* individuals in the presence (empty squares) and absence (filled squares) of *Azorella* is shown in the first row (binned into 50 m elevation bands), while altitudinal variation in the importance and intensity of the interaction between *Azorella* and *Agrostis* is shown in the second and third row respectively. The solid line shows the best fit model to the data. Complete statistical results in Appendix C

Appendix B The proportion of samples where the impact of *Azorella* on *Agrostis* performance was positive (% pos; i.e. improvement of *Agrostis* performance by *Azorella* exceeded ≥ 5 % of the range of impacts *Azorella* had on *Agrostis* at that site). Also indicated are the number of samples where the impact of *Azorella* was positive (“+”), neutral (“0”; i.e. the difference in *Agrostis* performance in the presence and absence of *Azorella* was < 5 % of the range of *Azorella* impacts at that site) or negative (“-“; i.e. *Agrostis* performance was lowered in the presence of *Azorella* by ≥ 5 % of the range of impacts *Azorella* had on *Agrostis* at that site). Samples along the altitudinal gradients were evenly split into three groups by altitude (low, intermediate and high altitudes) for this analysis.

| Site | Interaction effect | Agrostis cover | Abundance | Total mass | Total leaf mass | Basal area | Inflorescences | Inflorescence stems |
|--------------------|--------------------|----------------|-----------|------------|-----------------|------------|----------------|---------------------|
| NW transect | | | | | | | | |
| Low | % pos | 14% | 0% | 14% | 14% | 14% | 0% | 17% |
| | + / 0 / - | 1 / 3 / 3 | 0 / 3 / 4 | 1 / 2 / 4 | 1 / 2 / 4 | 1 / 3 / 3 | 0 / 3 / 3 | 1 / 2 / 3 |
| Intermed. | % pos | 0% | 29% | 57% | 57% | 43% | 57% | 43% |
| | + / 0 / - | 0 / 3 / 4 | 2 / 2 / 3 | 4 / 0 / 3 | 4 / 0 / 3 | 3 / 1 / 3 | 4 / 0 / 3 | 3 / 0 / 4 |
| High | % pos | 0% | 0% | 14% | 14% | 0% | 40% | 40% |
| | + / 0 / - | 0 / 6 / 1 | 0 / 2 / 5 | 1 / 2 / 4 | 1 / 2 / 4 | 0 / 3 / 4 | 2 / 0 / 3 | 2 / 0 / 3 |
| NE transect | | | | | | | | |
| Low | % pos | 33% | 50% | 83% | 83% | 50% | 83% | 67% |
| | + / 0 / - | 2 / 0 / 4 | 3 / 1 / 2 | 5 / 0 / 1 | 5 / 0 / 1 | 3 / 2 / 1 | 5 / 0 / 1 | 4 / 1 / 1 |
| Intermed. | % pos | 100% | 100% | 83% | 83% | 83% | 67% | 83% |
| | + / 0 / - | 6 / 0 / 0 | 6 / 0 / 0 | 5 / 1 / 0 | 5 / 1 / 0 | 5 / 1 / 0 | 4 / 2 / 0 | 5 / 1 / 0 |
| High | % pos | 100% | 83% | 100% | 100% | 100% | 100% | 100% |
| | + / 0 / - | 6 / 0 / 0 | 5 / 1 / 0 | 6 / 0 / 0 | 6 / 0 / 0 | 6 / 0 / 0 | 6 / 0 / 0 | 6 / 0 / 0 |
| SE transect | | | | | | | | |
| Low | % pos | 63% | 38% | 50% | 50% | 50% | 50% | 50% |
| | + / 0 / - | 5 / 0 / 3 | 3 / 3 / 2 | 4 / 2 / 2 | 4 / 2 / 2 | 4 / 2 / 2 | 4 / 1 / 3 | 4 / 2 / 2 |
| Intermed. | % pos | 100% | 100% | 88% | 88% | 88% | 88% | 88% |

| | | | | | | | | |
|--------------------------|-----------|-----------|-----------|-----------|-----------|-----------|-----------|-----------|
| | + / 0 / - | 8 / 0 / 0 | 8 / 0 / 0 | 7 / 0 / 1 | 7 / 0 / 1 | 7 / 0 / 1 | 7 / 1 / 0 | 7 / 1 / 0 |
| High | % pos | 57% | 57% | 71% | 86% | 71% | 100% | 100% |
| | + / 0 / - | 4 / 1 / 2 | 4 / 2 / 1 | 5 / 2 / 0 | 6 / 1 / 0 | 5 / 1 / 1 | 7 / 0 / 0 | 7 / 0 / 0 |
| Exposure gradient | | | | | | | | |
| Sheltered | % pos | 63% | 88% | 63% | 63% | 75% | 63% | 75% |
| | + / 0 / - | 5 / 1 / 2 | 7 / 1 / 0 | 5 / 0 / 3 | 5 / 0 / 3 | 6 / 0 / 2 | 5 / 2 / 1 | 6 / 0 / 2 |
| Intermed. | % pos | 88% | 100% | 88% | 88% | 88% | 100% | 100% |
| | + / 0 / - | 7 / 0 / 1 | 8 / 0 / 0 | 7 / 0 / 1 | 7 / 0 / 1 | 7 / 0 / 1 | 8 / 0 / 0 | 8 / 0 / 0 |
| Exposed | % pos | 100% | 100% | 100% | 100% | 100% | 100% | 100% |
| | + / 0 / - | 8 / 0 / 0 | 8 / 0 / 0 | 8 / 0 / 0 | 8 / 0 / 0 | 8 / 0 / 0 | 8 / 0 / 0 | 8 / 0 / 0 |

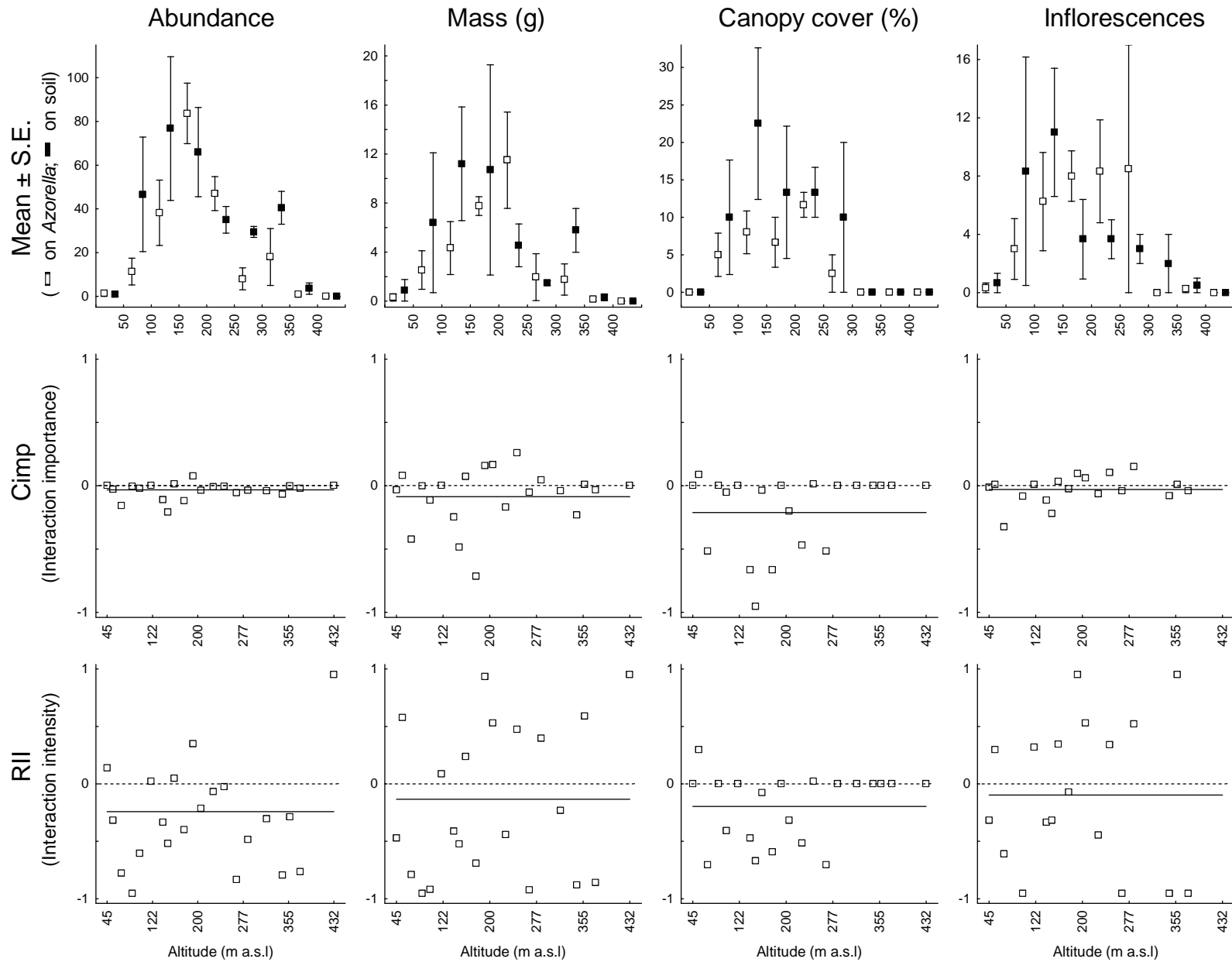
Appendix C Minimum adequate models of the intensity and importance of the effect of *Azorella* on the performance of *Agrostis* along three altitudinal transects. Results were calculated for seven *Agrostis* performance measures. HOF = Huisman-Olff-Fresco model (see Methods for details). * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$.

| Transect | | Model statistics | | | | | Parameter estimates | | | | |
|---|---------------------|------------------------|----------------------|---------|------|----------------|-----------------------|----------|----------|----------|----------|
| | | Minimum adequate model | Log-likelihood ratio | p-value | d.f. | Model deviance | Pseudo R ² | <i>a</i> | <i>b</i> | <i>c</i> | <i>d</i> |
| C_{imp} (Interaction importance) | | | | | | | | | | | |
| NW | Abundance | none | | | 19 | -82.41 | | 0.06* | | | |
| | Total mass | none | | | 19 | -27.86 | | 0.17 | | | |
| | Leaf mass | none | | | 19 | -32.50 | | 0.15 | | | |
| | Canopy cover | none | | | 19 | -15.77 | | 0.43* | | | |
| | Basal area | none | | | 19 | -32.62 | | 0.19 | | | |
| | Inflorescence stems | none | | | 16 | -37.81 | | 0.14 | | | |
| | Inflorescences | none | | | 16 | -53.34 | | 0.06 | | | |
| SE | Abundance | none | | | 21 | -21.48 | | -0.35* | | | |
| | Total mass | none | | | 21 | -43.73 | | -0.21* | | | |
| | Leaf mass | HOF III | 7.11 | 0.029 | 19 | -44.04 | 0.26 | -0.24 | -29.11* | -0.28** | |
| | Canopy cover | HOF V | 13.88 | 0.003 | 18 | -55.01 | 0.46 | -0.77* | 0.84 | -0.09 | 13.06 |
| | Basal area | none | | | 21 | -42.51 | | -0.13 | | | |
| | Inflorescence stems | HOF III | 9.82 | 0.007 | 19 | -40.99 | 0.33 | -0.01 | -19.06* | -0.30** | |
| | Inflorescences | HOF III | 7.19 | 0.027 | 19 | -68.73 | 0.26 | -1.23* | -14.87 | -0.25*** | |

| | | | | | | | | | | | |
|------------------------------------|---------------------|-----------------------------|---------|---------|--------|--------|---------|----------|------------|----------|-------|
| NE | Abundance | none | | | 16 | -30.21 | | -0.21 | | | |
| | Total mass | none | | | 16 | -18.53 | | -0.51*** | | | |
| | Leaf mass | none | | | 16 | -22.33 | | -0.44*** | | | |
| | Canopy cover | none | | | 16 | -18.12 | | -0.26 | | | |
| | Basal area | none | | | 16 | -16.41 | | -0.49** | | | |
| | Inflorescence stems | covar. ¹ | 5.26 | 0.022 | 15 | -22.96 | 0.20 | -0.59 | 2.19* | | |
| | Inflorescences | covar. ¹ | 5.90 | 0.015 | 15 | -20.48 | 0.22 | -0.53 | 2.01* | | |
| RII (Interaction intensity) | | | | | | | | | | | |
| NW | Abundance | none | | | 19 | -5.18 | | 0.49* | | | |
| | Total mass | none | | | 19 | -2.85 | | 0.27 | | | |
| | Leaf mass | none | | | 19 | -2.78 | | 0.21 | | | |
| | Canopy cover | none | | | 19 | -22.85 | | 0.40** | | | |
| | Basal area | none | | | 19 | -5.19 | | 0.44 | | | |
| | Inflorescence stems | none | | | 16 | -2.41 | | 0.26 | | | |
| | Inflorescences | none | | | 16 | -1.69 | | 0.20 | | | |
| | | | | | | | | - | | | |
| SE | Abundance | HOF III+covar. ² | 28.37 | < 0.001 | 18 | -32.24 | 0.74 | 47.47*** | 1046.78*** | -0.69*** | 0.18* |
| | Total mass | HOF III | 21.98 | < 0.001 | 19 | -42.90 | 0.63 | 3.21* | -64.59* | -1.78*** | |
| | Leaf mass | HOF III | 23.39 | < 0.001 | 19 | -43.93 | 0.64 | 3.20* | -61.22* | -1.81*** | |
| | Canopy cover | HOF III | 22.24 | < 0.001 | 19 | -25.94 | 0.61 | 3.00* | -54.72 | -1.06*** | |
| | | | | | | | | | - | | |
| | Basal area | HOF III+covar. ² | 22.52 | < 0.001 | 18 | -39.80 | 0.65 | 53.62*** | 1184.46*** | -1.09*** | 0.18* |
| | Inflorescence stems | HOF III | 27.60 | < 0.001 | 19 | -53.44 | 0.70 | 2.94*** | -41.50** | -2.08*** | |
| Inflorescences | HOF III | 28.39 | < 0.001 | 19 | -55.52 | 0.70 | 2.96*** | -42.84* | -2.14*** | | |

| | | | | | | | | | | | |
|----|---------------------|---------|-------|---------|----|--------|------|----------|----------|----------|----------|
| NE | Abundance | none | | | 16 | -21.49 | | | -1.34*** | | |
| | Total mass | HOF V | 28.14 | < 0.001 | 13 | -57.17 | 0.80 | -1.31* | -2.46* | 2.67** | 55.97*** |
| | Leaf mass | HOF V | 29.81 | < 0.001 | 13 | -59.07 | 0.81 | -1.35* | -2.48* | 2.73** | 56.33*** |
| | Canopy cover | HOF III | 21.84 | < 0.001 | 14 | -39.23 | 0.72 | 0.92* | -7.75*** | -2.74*** | |
| | Basal area | HOF III | 20.38 | < 0.001 | 14 | -48.45 | 0.74 | 1.38* | -15.42* | -2.53*** | |
| | Inflorescence stems | HOF V | 39.26 | < 0.001 | 13 | -70.35 | 0.86 | -1.76*** | -2.22* | 3.07*** | 53.87*** |
| | Inflorescences | HOF III | 51.82 | < 0.001 | 14 | -92.12 | 0.91 | 3.33*** | -289.06 | -3.22*** | |

¹ covar. = maximum diameter of the sample area alone contributed significantly to the minimum adequate model ²maximum diameter of the sample area contributed significantly to the minimum adequate model in addition to the terms of the HOF III model.



Appendix D The variation in the performance of *Agrostis magellanica* along the NW altitudinal gradient. Four performance measures are presented: abundance, mass, canopy cover and total number of inflorescences. The performance of *Agrostis* individuals in the presence (empty squares) and absence (filled squares) of *Azorella* is shown in the first row (binned into 50 m elevation bands), while altitudinal variation in the importance and intensity of the interaction between *Azorella* and *Agrostis* is shown in the second and third row respectively. The solid line shows the best fit model to the data. Complete statistical results in Appendix C.

Appendix E Minimum adequate models of the intensity and importance of the effect of *Azorella* on the performance of *Agrostis* at three sites along an exposure gradient. Results were calculated for seven *Agrostis* performance measures. HOF = Huisman-Olff-Fresco model (see Methods for details).

| Variable | Model statistics | | | Coefficients | | | Post-hoc comparisons of levels | | | |
|---|-----------------------------------|---------|-----------------------|-----------------|-----------------|-----------|--------------------------------|----------------|------------------------------|-------|
| | Log-likelihood ratio ¹ | p-value | Pseudo R ² | | Estimate ± S.E. | Wald stat | p-value | t ² | Order of levels ³ | |
| C_{imp} (Interaction importance) | | | | | | | | | | |
| Abundance | 4.0 | 0.294 | 14% | Intercept | -0.20 ± 0.37 | -0.56 | 0.578 | E vs I | 0.03 | S>I>E |
| | | | | High exposure | -0.12 ± 0.14 | -0.81 | 0.417 | E vs S | 0.81 | |
| | | | | Medium exposure | -0.11 ± 0.14 | -0.79 | 0.433 | I vs S | 0.78 | |
| | | | | Low exposure | 0 | | | | | |
| | | | | Sample area | 0.02 ± 0.01 | 1.89 | 0.058 | | | |
| Total mass | 3.2 | 0.393 | 11% | Intercept | 0.49 ± 0.69 | 0.71 | 0.476 | E vs I | 0.67 | E>I>S |
| | | | | High exposure | 0.48 ± 0.27 | 1.79 | 0.074 | E vs S | 1.79 | |
| | | | | Medium exposure | 0.23 ± 0.26 | 0.89 | 0.375 | I vs S | 0.89 | |
| | | | | Low exposure | 0 | | | | | |
| | | | | Sample area | -0.01 ± 0.02 | -0.50 | 0.619 | | | |
| Leaf mass | 2.5 | 0.501 | 8% | Intercept | 0.28 ± 0.86 | 0.32 | 0.746 | E vs I | 0.04 | E>I>S |
| | | | | High exposure | 0.46 ± 0.34 | 1.38 | 0.169 | E vs S | 1.38 | |
| | | | | Medium exposure | 0.45 ± 0.33 | 1.35 | 0.177 | I vs S | 1.35 | |
| | | | | Low exposure | 0 | | | | | |
| | | | | Sample area | 0.00 ± 0.02 | -0.15 | 0.879 | | | |
| Canopy cover | 6.6 | 0.123 | 22% | Intercept | 1.36 ± 0.6 | 2.28 | 0.023 | E vs I | 0.09 | E>I>S |
| | | | | High exposure | 0.38 ± 0.23 | 1.65 | 0.099 | E vs S | 1.65 | |

| | | | | | | | | | | |
|------------------------------------|---------|---------|-----|-----------------|----------------------------|---------|---------|--------|------------|-------|
| | | | | Medium exposure | 0.35 ± 0.23 | 1.55 | 0.121 | I vs S | 1.55 | |
| | | | | Low exposure | 0 | | | | | |
| Basal area | 3.9 | 0.311 | 14% | Sample area | -0.03 ± 0.01 | -2.04 | 0.042 | | | |
| | | | | Intercept | 0.69 ± 0.62 | 1.12 | 0.264 | E vs I | 1.14 | E>I>S |
| | | | | High exposure | 0.44 ± 0.25 | 1.77 | 0.076 | E vs S | 1.77 | |
| | | | | Medium exposure | 0.05 ± 0.24 | 0.21 | 0.837 | I vs S | 0.21 | |
| | | | | Low exposure | 0 | | | | | |
| Inflorescence stems | 10.0 | 0.039 | 29% | Sample area | -0.01 ± 0.02 | -0.73 | 0.463 | | | |
| | | | | Intercept | 0.03 ± 0.36 | 0.09 | 0.931 | E vs I | 0.91 | E>I>S |
| | | | | High exposure | 0.42 ± 0.14 | 2.94 | 0.003 | E vs S | 2.94 | |
| | | | | Medium exposure | 0.24 ± 0.14 | 1.73 | 0.084 | I vs S | 1.73 | |
| | | | | Low exposure | 0 | | | | | |
| Inflorescences | 17.1 | 0.005 | 40% | Sample area | 0.00 ± 0.01 | 0.47 | 0.641 | | | |
| | | | | Intercept | -0.42 ± 0.43 | -0.97 | 0.332 | E vs I | 1.36 | E>I>S |
| | | | | High exposure | 0.59 ± 0.17 | 3.49 | < 0.001 | E vs S | 3.49 | |
| | | | | Medium exposure | 0.27 ± 0.16 | 1.68 | 0.093 | I vs S | 1.68 | |
| | | | | Low exposure | 0 | | | | | |
| | | | | Sample area | 0.01 ± 0.01 | 1.31 | 0.191 | | | |
| RII (Interaction intensity) | | | | | | | | | | |
| Abundance | 9.2 | 0.038 | 37% | Intercept | 1.61 ± 0.82 | 1.97 | 0.049 | E vs I | 1.36 | E>I>S |
| | | | | High exposure | 1.06 ± 0.34 | 3.11 | 0.002 | E vs S | 3.11** | |
| | | | | Medium exposure | 0.44 ± 0.3 | 1.45 | 0.148 | I vs S | 1.45 | |
| | | | | Low exposure | 0 | | | | | |
| | | | | Sample area | -0.01 ± 0.02 | -0.58 | 0.562 | | | |
| Total mass | 7.2E+09 | < 0.001 | 6% | Intercept | 9.4x10 ⁷ ± 1.31 | 7.2E+07 | < 0.001 | E vs I | 4.1E+06*** | E>I>S |
| | | | | High exposure | 3.5x10 ⁷ ± 0.51 | 6.9E+07 | < 0.001 | E vs S | 6.9E+07*** | |

| | | | | | | | | | | |
|---------------------|---------|---------|-----|-----------------|----------------------------|----------------------|---------|--------|-----------------------|-------|
| | | | | Medium exposure | $3.2 \times 10^7 \pm 0.5$ | 6.4×10^7 | < 0.001 | I vs S | 6.4×10^7 *** | |
| | | | | Low exposure | 0 | | | | | |
| Leaf mass | 1.2E+09 | < 0.001 | 5% | Sample area | $3.8 \times 10^9 \pm 0.03$ | 1.2×10^{11} | < 0.001 | | | |
| | | | | Intercept | $3.7 \times 10^7 \pm 1.31$ | 2.8×10^7 | < 0.001 | E vs I | 11.165*** | E>I>S |
| | | | | High exposure | $1.2 \times 10^7 \pm 0.51$ | 2.4×10^7 | < 0.001 | E vs S | 2.4×10^7 *** | |
| | | | | Medium exposure | $1.2 \times 10^7 \pm 0.5$ | 2.5×10^7 | < 0.001 | I vs S | 2.5×10^7 *** | |
| | | | | Low exposure | 0 | | | | | |
| Canopy cover | 9.2 | 0.021 | 37% | Sample area | $1.5 \times 10^9 \pm 0.03$ | 4.8×10^{10} | < 0.001 | | | |
| | | | | Intercept | 3.69 ± 1.28 | 2.89 | 0.004 | E vs I | 1.699 | E>I>S |
| | | | | High exposure | 1.62 ± 0.51 | 3.20 | 0.001 | E vs S | 3.200** | |
| | | | | Medium exposure | 0.45 ± 0.46 | 0.97 | 0.330 | I vs S | 0.974 | |
| | | | | Low exposure | 0 | | | | | |
| Basal area | 8.8 | 0.057 | 41% | Sample area | -0.08 ± 0.03 | -2.47 | 0.014 | | | |
| | | | | Intercept | 3.45 ± 1.3 | 2.65 | 0.008 | E vs I | 1.524 | E>I>S |
| | | | | High exposure | 1.30 ± 0.51 | 2.56 | 0.011 | E vs S | 2.555* | |
| | | | | Medium exposure | 0.24 ± 0.47 | 0.51 | 0.612 | I vs S | 0.507 | |
| | | | | Low exposure | 0 | | | | | |
| Inflorescence stems | 4.2 | 0.368 | 24% | Sample area | -0.06 ± 0.03 | -1.93 | 0.054 | | | |
| | | | | Intercept | 2.42 ± 1.33 | 1.82 | 0.069 | E vs I | 0.855 | E>I>S |
| | | | | High exposure | 0.87 ± 0.52 | 1.67 | 0.095 | E vs S | 1.672 | |
| | | | | Medium exposure | 0.25 ± 0.5 | 0.51 | 0.611 | I vs S | 0.509 | |
| | | | | Low exposure | 0 | | | | | |
| Inflorescences | 4.3 | 0.431 | 22% | Sample area | -0.03 ± 0.03 | -0.89 | 0.372 | | | |
| | | | | Intercept | 2.79 ± 1.4 | 1.99 | 0.047 | E vs I | 0.571 | E>I>S |
| | | | | High exposure | 0.79 ± 0.54 | 1.46 | 0.144 | E vs S | 1.461 | |
| | | | | Medium exposure | 0.36 ± 0.53 | 0.68 | 0.494 | I vs S | 0.683 | |

| | | | |
|--------------|--------------|-------|-------|
| Low exposure | 0 | | |
| Sample area | -0.04 ± 0.03 | -1.21 | 0.225 |

¹ degrees of freedom for all models = 20, ² degrees of freedom for all post-hoc comparisons = 14, ³ order of factors shown irrespective of significance, E = exposed site, I = intermediate site, S = sheltered site. * p < 0.05, ** p < 0.01, *** p < 0.001

Chapter 6 - Conclusion

The global climate has changed considerably over the last 100 years (IPCC 2007), with widespread and diverse ecological impacts (Hughes 2000; Parmesan 2006). However, larger and more rapid changes in climate are forecast for the next century (Meehl et al. 2005), which are likely to have far greater impacts on biodiversity (Aerts et al. 2006; Thomas et al. 2004). Shifts in species ranges are an important consequence of climate change, and can lead to the alteration of the composition, structure and functioning of communities and ecosystems (see e.g. Hinzman et al. 2005; Tape et al. 2006). In addition to climate, interspecific interactions can also affect species distributions (Case et al. 2005), with negative interactions limiting portions of some species ranges (Brönmark and Edenhamn 1994; Crain et al. 2004), and positive interactions extending the distribution of others (Cavieres et al. 2007; Choler et al. 2001; Kikvidze and Nakhutsrishvili 1998). While the stress-gradient hypothesis provides some predictions about whether positive and negative interactions will dominate (Brooker and Callaghan 1998), the factors that determine when biotic interactions will limit or expand species ranges are still to be fully understood (Agrawal et al. 2007). Nonetheless, interspecific interactions can have large impacts on species distributions (Case et al. 2005; Davis et al. 1998). Therefore, since climate and biotic interactions are both important determinants of species ranges (Gaston 2003), there is the potential for plant-plant interactions to mediate climate-driven changes in species distributions (Brooker 2006; Hulme 2005; see e.g. Brooker et al. 2007; Dona and Galen 2007). In this thesis, changes in climate, the altitudinal distribution of species and spatial variation in species interactions were examined on Marion Island, with the aim of determining whether interspecific competition or facilitation could influence climate-driven range shifts in the island's native vascular plants.

Climate change, range shifts and species interactions on Marion Island

Conforming to global trends, Marion Island's climate has changed rapidly over the last 50 years (Chapter 2). Not only have the average climatic conditions changed (e.g. warmer mean temperatures and lower annual rainfall), but the

variability in these parameters has also shown clear trends (e.g. declining day-to-day variation in temperature, wind speed and cloud cover, but more variation in daily rainfall). The characteristics of extreme weather events on the island have also changed, with, for example, rising maximum temperatures, longer durations between rainfall events and fewer wind-still recordings. Combining these trends showed that while environmental conditions have ameliorated for some species, they have become more abiotically stressful for others (e.g. hygrophilous species).

Concurrent with changes in the island's climate, there have been rapid changes in the elevational distribution of Marion Island's native vascular flora (Chapter 3). Species on average expanded their upper altitudinal limits upslope, although the distributional changes by the island's flora encompassed a broad range of responses. This idiosyncrasy in species responses caused considerable changes in the altitudinal patterns of species richness on the island and resulted in the formation of no-analog communities. Some of the variation in species responses was related to species-specific habitat requirements (e.g. range contraction in halophilous species), although most of the variation between species was unexplained. Nonetheless, the elevational distribution of Marion Island's vascular flora was responsive to changes in climate, with most species responding as predicted in responses to warmer temperatures.

Spatial variation in the balance of positive and negative interactions was then considered. On Junior's Kop scoria cone higher altitudes were colder and windier, and had greater substrate mobility than at lower altitudes, demonstrating an elevational gradient in abiotic severity (Chapter 4). This altitudinal severity gradient was matched by stronger fine-scale interspecific spatial association between the four dominant species at higher altitudes and in areas of lower vegetation cover. This suggests that the intensity of facilitation, relative to the intensity of competition, is greater under more severe conditions, supporting the stress-gradient hypothesis at the community-level. The strength of these interactions varied between species pairs (e.g. *Agrostis magellanica* and *Acaena magellanica* were most strongly spatially associated, and *Azorella selago* and *Acaena magellanica* most weakly associated), but the nature of the relationship between environmental severity and the occurrence of facilitative interactions was consistently positive.

At a broader spatial scale, a comparison of the performance of *Agrostis magellanica* in the presence and absence of the cushion plant *Azorella selago* showed that the influence of the cushion plant on *A. magellanica* shifted from negative to

positive with increasing environmental severity along island-scale altitudinal transects (Chapter 5). The relationship was, however, not linear, but on average plateau-shaped, demonstrating that facilitative interactions can be strong even under extreme environmental conditions. These results were consistent for seven measures of *A. magellanica* performance, suggesting that the interaction has a positive effect on the survival, growth and reproduction of the grass at higher altitudes. Therefore, on Marion Island spatial variation in the nature and strength of biotic interactions are closely related to environmental severity.

Can biotic interactions mediate climate-driven changes in species ranges?

Because strong interspecific interactions occur between some species at high and low altitudes on Marion Island (Chapters 4 and 5), it is possible that plant-plant interactions could mediate the ecological consequences of climate change (as suggested by e.g. Dona and Galen 2007; Lortie et al. 2004). There is, for example, the potential for climate-driven range expansions to be accelerated by facilitative interactions at species upper elevational limits. However, positive (and negative) interactions are not equally likely between all species pairs (Callaway 1998; see also e.g. Gómez-Aparicio et al. 2004). Furthermore, the presence of positive or negative interactions is only the first requirement for biotic interactions to be able to influence the rate (or size) of range shifts. In the following sections the requirements for the occurrence of positive interspecific interactions and for facilitative interactions to accelerate upslope range expansions are considered. Finally, the possibility for negative interactions to also affect changes at the upper edge of species distributions is briefly discussed. Only changes in species upper altitudinal limits are explicitly considered here because species lower range boundaries have been static on Marion Island (Chapter 3). Changes in species lower elevational range margins can also be affected by biotic interactions (Hampe and Petite 2005), although different mechanisms may be important at species upslope and downslope distributional limits (e.g. Merrill et al. 2008).

Benefactor species at higher altitudes

A facilitative interaction requires at least one benefactor (i.e. a species that is able to facilitate another species) and one beneficiary (i.e. a species that is able to

benefit from the presence of a benefactor; *sensu* Tewksbury and Lloyd 2001). Benefactor species favourably modify environmental conditions that constrain the performance of other species (Callaway 1998; Tewksbury and Lloyd 2001), by decreasing abiotic stresses, increasing the availability of a limited resource, creating new habitats, or reducing predation or competition (Rodriguez 2006; Stachowicz 2001). Larger plants generally have a greater ameliorative effect on microclimatic conditions and can effect greater increases in resource availability than smaller individuals (e.g. Nuñez et al. 1999; Tewksbury and Lloyd 2001). Similarly, plants with greater canopy compactness, architectural complexity and longevity are usually more effective at ameliorating environmental conditions (Stachowicz 2001). Indeed, among cushion plant species, compactness is a good indicator of a species ability to alter its surrounding microhabitat (Brooker and Callaghan 1998; Molina-Montenegro et al. 2006; Pyšek and Liška 1991).

For facilitation to accelerate upslope colonization, suitable benefactor species must be established at higher altitudes before beneficiaries colonize those areas. The greater the number of benefactor species (and the higher the abundance of each benefactor species) present at higher altitudes, the higher the probability that facilitative interactions can be realized. On Marion Island, *Azorella selago*, *Acaena magellanica* and *Agrostis magellanica* all grow to large sizes, have relatively compact canopies (i.e. causing them to alter microclimatic conditions) and occur at high altitudes. As a result, these species are probably suitable benefactors for beneficiaries from lower altitudes. Indeed, most of vascular plants on Marion Island have been recorded growing epiphytically on *Azorella* (17 native species: McGeoch et al. 2008) and many vascular plants occur in *Acaena*- and *Agrostis*-dominated habitats (stream-banks and mires, respectively: Gremmen et al. 1998; Huntley 1971). This suggests that these species do not outcompete other vascular plants and have the potential to act as benefactors.

Responsive beneficiary species

The morphological, physiological and life history traits important for beneficiary species can be summarized to three general characteristics that, at least in abiotically extreme environments, increase the probability that the species will benefit from interacting with a benefactor species (Brooker and Callaghan 1998; Callaway

and Walker 1997; Padilla and Pugnaire 2006; Tewksbury and Lloyd 2001). First, a beneficiary species must be able to exploit environmental conditions that have been modified by other plants ("beneficiary ability": Tewksbury and Lloyd 2001). This partly depends on the degree of the match between the environmental factors being ameliorated by the benefactor and the factors that are stressful to the beneficiary (see Crain and Bertness 2006). A species' phenotypic plasticity is also important, as it determines how strongly the plant can respond to changes in environmental conditions affected by another species (Callaway et al. 2003). Species from abiotically harsh environments often have constrained growth forms, life histories and phenotypic plasticity (Callaghan and Carlsson 1997), and can therefore be poor beneficiaries.

The second trait which increases a species probability of benefiting from interactions with benefactor species is its ability to tolerate the negative effects of growing in close association with other plants (competitive-response ability; Liancourt et al. 2005). Again, the match of the benefactor and the beneficiary is important since species which overlap more in resource requirements will compete more strongly, and therefore have a lower probability of interacting positively (Klanderud and Totland 2004). This may explain why facilitation is most common between species with different growth forms (Dullinger et al. 2007; see also e.g. Gavilán et al. 2002), since species with similar growth forms are likely to have stronger overlap in the acquisition of resources than those of different growth forms. Competitive-response ability differs from beneficiary ability, because the former deals with the species' ability to tolerate the negative effects of a neighbour, while the latter deals with the species' ability to benefit from the positive effects of a neighbour.

Finally, a species is only likely to exhibit positive interactions with other species when it is stressed (i.e. environmental conditions are sub-optimal for the species' productivity) (Liancourt et al. 2005; see also Choler et al. 2001; Michalet et al. 2006). Since species are generally stressed at climatically-determined range edges, this criterion is probably met by many species when growing near their altitudinal limit (Choler et al. 2001; Liancourt et al. 2005). However, not many species on Marion Island meet the first two criteria for being beneficiary species. Habitat specialists, for example are restricted to conditions that other plants have a limited ability to provide (Chapter 3). Nonetheless, some of the habitat generalist species have high phenotypic plasticity (e.g. *Acaena magellanica*, *Agrostis magellanica*, *Montia fontana*, *Ranunculus biternatus*) (Chastain 1958; Huntley 1971; Walton 1976)

and appear to tolerate competition (since they persist in some closed canopy low altitude vegetation types). Therefore, these species might benefit from interacting with benefactor species at higher altitudes. By contrast, other species, for example *Grammitis kerguelensis*, are unlikely to experience positive interactions as they appear to have little morphological plasticity and rarely occur in association with other vascular plant species. Interestingly, some beneficiary species can also become benefactors when they grow large enough to affect microclimatic conditions (e.g. *Acaena magellanica* and *Agrostis magellanica*; see e.g. Miriti 2006; Valiente-Banuet and Verdu 2008).

Therefore, facilitative interactions are most probable between species which are long-lived and densely-growing (i.e. benefactors) and species which are stressed, have high phenotypic plasticity, are able to tolerate competition and are limited by environmental factors that are ameliorated by the benefactor (i.e. beneficiaries). As a result, the possibility of facilitative interactions (and the possibility of accelerated upslope expansions) is dependent on species identity (Callaway 1998). Indeed, species pairs on Junior's Kop differed in their mean spatial association, suggesting that the strength of interactions differ between species (Chapter 4). Therefore, on Marion Island biotic interactions could have contributed to the idiosyncratic species range expansions, with the strength and nature of species interactions affecting the magnitude of species responses.

Ecologically-significant facilitation

However, even for beneficiary species with suitable benefactors present at higher altitudes, positive interactions will not necessarily effect faster (or further) range expansion in beneficiary species. Some positive interactions only have fine-scale impacts which do not affect broader community patterns (e.g. Ramírez et al. 2006), while others can have effects at larger spatial scales (e.g. Choler et al. 2001; see also Freestone 2006). For a facilitative interaction to impact on a species spatial distribution (or rate of spread) it would need to benefit the species in all its life stages, enhancing survival and reproductive output (i.e. "important facilitation"; *sensu* Brooker et al. 2008). Considering the *Azorella selago* – *Agrostis magellanica* interaction, there is some evidence for such an effect because all measures of *Agrostis* performance were enhanced by *A. selago* at high altitudes (in at least two transects;

Chapter 5). Furthermore, the impact of the interaction appears to have enabled *A. magellanica* to colonize higher altitudes in association with *A. selago* that when growing separately. Thus, for at least one species pair on Marion Island, it appears that facilitation can have a large-scale, ecologically-significant effect. However, further research is necessary to determine if fine-scale facilitation can have broader-scale consequences consistently across species. Therefore on Marion Island, the requirements for facilitation to accelerate range expansion are met, at least for one species pair, highlighting the potential for positive interaction to act synergistically with climate change to expand the upper altitudinal boundaries of some species.

Competitive interactions and upslope range expansions

In contrast with facilitation, competitive interactions are important at lower altitudes and areas of high vegetation cover on Marion Island (Chapters 4 and 5; see also Dullinger et al. 2007; Kikvidze et al. 2005). Indeed, positive plant-plant interactions are possibly uncommon (and therefore competition particularly dominant) at low elevations on Marion Island since protection from herbivores is an unimportant facilitative mechanism on the island. Previous studies have found that competitive interactions can retard the upslope range expansion of species from low altitudes in response to past climate fluctuations (Jablonski and Sepkoski 1996). There is also evidence for upslope range expansions in response to recent changes in climate being inhibited by competitive interactions (Dullinger et al. 2003; see also e.g. experiments of Davis et al. 1998 and simulation models of Brooker et al. 2007). Thus, similar to the way in which established native vegetation can resist invasion by non-native species (Brooker 2006), so higher altitude vegetation could competitively resist the spread of species from lower elevations ("prior-residence advantage": Jablonski and Sepkoski 1996). On Marion Island this is only likely, however, where vegetation cover is extensive and disturbances are uncommon, because competitive interactions are unlikely in areas with sparse vegetation and/or frequent disturbance (Klanderud and Totland 2007). For this reason, *Blechnum penna-marina* slopes (i.e. closed fernbrake slope habitat) are probably effective at retarding the range expansion of other species, as this habitat has nearly complete vegetation cover, offering few opportunities for other species to establish. Furthermore, because this vegetation type is the second most common at altitudes between 0 – 100 m a.s.l. (and third most

common from 100 – 300 m a.s.l.: Smith et al. 2001), it possibly represents an important barrier to the upslope movement of some species.

Signals of biotic interactions affecting plant range expansions on Marion Island

Considering the potential for biotic interactions to affect climate-driven range shifts may explain some of the variation in species range shifts observed on Marion Island (Fig. 1). Most of the species with high altitudinal limits in 1965 (> 450 m a.s.l.) expanded their distribution upslope (only *Hymenophyllum peltatum* contracted downslope, while the distribution of *Callitriche antarctica* was unaltered). These species spread upslope to elevations with low vascular plant cover (Smith et al. 2001) and, therefore, low potential for competition or facilitation (Brooker et al. 2007). Thus, these range changes were probably relatively unaffected by biotic interactions. *Azorella selago* had the highest elevation limit both in 1965 and 2005, suggesting that nearly all other species had a suitable benefactor for positive interactions present at higher altitudes. However, the relative scarcity of *A. selago* (and other vascular plant species) above 600 m a.s.l. (Phiri et al. submitted), may be the reason why the range shifts were not as pronounced for some of the species from mid altitudes.

Indeed, on average, the species with their 1965 upper altitudinal limits at mid altitudes (200 – 450 m a.s.l.) extended their elevational range by more than species at higher or lower altitudes (Fig. 1). It is possible that “mid altitude” beneficiary species were able to take advantage of the ameliorating climatic conditions and the presence of benefactors at higher altitudes. Indeed, the two species that expanded upslope the furthest are associated with *Azorella* at their elevational limits, suggesting that they form positive interactions with at least one species from higher altitudes (Chapter 3). Furthermore, other species reaching their elevational limit at these altitudes, including *Blechnum penna-marina* (see e.g. Chapter 4), *Pringlea antiscorbutica*, *Juncus scheuchzerioides* and *Uncinia compacta*, also are thought to benefit from the presence of *A. selago* (McGeoch et al. 2008).

By contrast, the altitudinal ranges of species with low upper elevational limits (<200 m a.s.l.) did not expand (Fig. 1). In fact, the elevational range of the two salt-spray habitat specialists (*Cotula plumosa* and *Crassula moschata*) contracted downslope (see Chapter 3). Similarly, the upper elevational limit of *Elaphoglossum randii* was reduced, while *Polystichum marionense* did not show a considerable

change. The lack of range expansion by both fern species could have been due to the changes in the island's rainfall regime (Chapter 2). However, their altitudinal ranges could also have been constrained by competitive interactions at their upper range limits. Interestingly, excluding habitat specialist species did not change this pattern, suggesting that species interactions may even be important for species with specific habitat requirement.

Conclusion

Positive biotic interactions can be important at species upper elevational range margins, and could thus accelerate range expansions to higher altitudes in response to climate change (Dona and Galen 2007). Nonetheless, competitive inhibition of upslope species range expansions, especially in areas of dense vegetation, could have the opposite result, acting antagonistically with the effect of climate change (Brooker et al. 2007). This research highlights the importance of considering interspecific interactions, both for their potential to affect the rate at which species ranges change (Brooker et al. 2007; Dona and Galen 2007) and the extent of species distributions (Badano et al. 2007; Choler et al. 2001; Sthultz et al. 2007). Thus, more attention should be given to the role of biotic interactions in mediating the ecological consequences of climate change.

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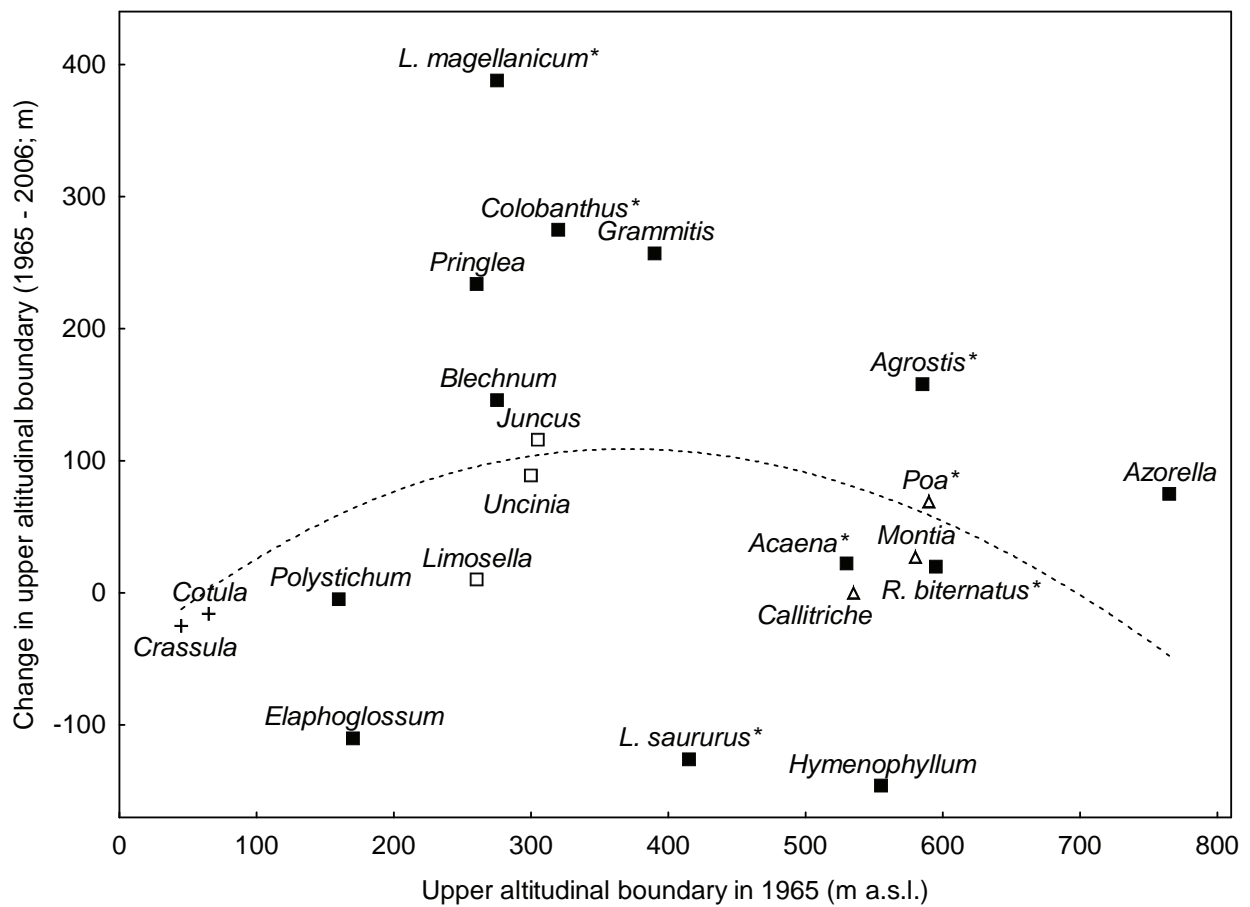


Fig. 1 The relationship between the change in species upper altitudinal boundaries and their past (1965/66) upper limit. Habitat specialists are identified by symbols on the plot (+ halophilous species, Δ coprophilous species, □ hygrophilous species), and species that were associated with *Azorella* or moss-mats at their upper altitudinal limits are indicated by asterisks (Chapter 3). A negative exponentially-weighted curve has been fitted to the data to estimate the shape of the relationship.