Inter- and intra-specific interactions affect the performance and distribution of plants in the sub-Antarctic

By

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Declaration:

I, the undersigned, hereby declare that the work contained in this thesis is my own original work and that I have not previously in its entirety or in part submitted it at any university for a degree.

Signature: Krüger Date: 29/08/2019

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Authors’ contributions

Chapter 2: Morgan Raath-Krüger (MRK) and Peter le Roux (PR) designed the study with input from Melodie McGeoch (MM) and Christian Schöb (CS). MRK collected the data. MRK ran the analyses (with input from PR and CS) and wrote the chapter, with input from PR, MM and CS.

Chapter 3: MRK and PR designed the study with input from MM and CS. MRK collected the data. MRK ran the analyses (with input from PR and CS), and MRK and PR wrote the chapter with input from CS.

Chapter 4: MRK and PR designed the study with input from MM and CS. MRK collected the data, with additional data provided by PR and Michelle Greve (MG). MRK ran the analyses and wrote the chapter, with input from PR, MM, CS, and MG.

A view of the south-western sector of Marion Island

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Abstract

Although the unidirectional impacts of benefactor species on associated beneficiary species have been well-established, beneficiary feedback effects (i.e. the impact of beneficiaries on their benefactors) and benefactor-mediated interactions among beneficiaries (i.e. interactions among beneficiaries that are the result of facilitation by benefactors) are relatively poorly understood. Additionally, fine-scale biotic interactions could influence broad-scale species distributions by either constraining (through negative interactions) or expanding (through positive interactions) the range of conditions under which a species can occur; however, while several studies have found evidence for this from species distribution modelling, none have explicitly tested this idea using field-quantified data. The aim of this project was, therefore, to examine the consequences of inter- and intra-specific interactions on species' distributions and performance. I use a dominant species pair, *Azorella selago* (a widespread cushion plant) and *Agrostis magellanica* (a dominant perennial grass species that most frequently occurs with *A. selago*), on sub-Antarctic Marion Island as a model system.

First, I examined the benefactor-beneficiary feedback effect of *A. magellanica* on *A. selago*, using a long-term dataset of repeated measures. I expected *A. magellanica* cover to have a negative effect on *A. selago* due to shading. However, *A. magellanica* had no long-term effect on the growth and vitality of *A. selago*. Therefore, for the first time using a long-term dataset, I show that the cost of facilitation to the benefactor may be negligible, in contrast to the majority of short-term studies. The effect of *A. magellanica* cover on *A. selago* performance did, however, vary between *A. selago* performance measures, when analysing data from a single time period. This, therefore, highlights that studies examining beneficiary feedback effects need to move beyond just using snapshot approaches and/or short-term experiments.

Second, I tested whether (inter-specific) facilitation by benefactors has consequences for (intra-specific) interactions among beneficiaries. Specifically, I hypothesized that where *A. selago* favours the establishment of high densities of *A. magellanica*, intra-specific competition may subsequently impede *A. magellanica* performance. However, observational data from six altitudinal transects showed that *A. magellanica* performance was significantly positively related to conspecific density (potentially reflecting facilitation among *A. magellanica* conspecifics), and this effect was significantly greater on *A. selago* cushion plants than on the adjacent substrate. In contrast, experimentally thinning of *A. magellanica* had no impact on *A. magellanica* performance, suggesting that *A. magellanica* may respond slowly to changes in

biotic interactions. Therefore, in this study system, facilitation, both within and between plant species, may be more important than competition.

Finally, I tested the potential for fine-scale positive plant-plant interactions to expand species' upper distributional limits, examining the influence of *A. selago* on the upper distributional limit of an entire vascular plant assemblage. *Azorella selago* had a positive impact on the upper altitudinal limits of three out of nineteen vascular plant species, suggesting that *A. selago* can allow species to occur in areas that would otherwise be abiotically unfavourable. Therefore, fine-scale positive plant-plant interactions do have the potential to expand species' upper distributional limits, although their impact may be strongly species-specific.

Chapter 1:

General Introduction

“Positive interactions play a critical, but underappreciated, role in ecological communities by reducing physical or biotic stresses in existing habitats and by creating new habitats on which many species depend.”

- Stachowicz (2001)

Stachowicz, J.J. Mutualism, facilitation, and the structure of ecological communities: positive interactions play a critical, but underappreciated, role in ecological communities by reducing physical or biotic stresses in existing habitats and by creating new habitats on which many species depend (2001) *BioScience*, 51, 235–246.

Inter- and intra-specific biotic interactions

In ecosystems, biotic interactions, which range from positive (e.g. mutualism and facilitation) to negative (e.g. parasitism and competition), may strongly shape ecological communities, with evidence accumulating about how these interactions scale up from the individual- and species-level to the population- and community-levels (Arroyo *et al*., 2003; Bruno *et al*., 2003; He & Cui, 2015; Bulleri *et al*., 2016; Lamb *et al*., 2009; Chen *et al*., 2015; Ettinger & HilleRisLambers, 2017; Hupp *et al*., 2017; Llambí *et al*., 2018; Eurich *et al*., 2018; Kunstler *et al*., 2019). The effects of inter-specific interactions can be direct (i.e. where one species affects the performance or reproduction of another species), or secondary (i.e. if one species modifies the environment to the benefit or detriment of another species). An understanding of the consequences of these interactions, in addition to the impact of abiotic and environmental variables, is especially valuable for explaining spatio-temporal variation in species' performances and distributions (Armas *et al*., 2011; He & Bertness, 2014; Jones & Gilbert, 2016; Ettinger & HilleRisLambers, 2017; Filazzola *et al*., 2018) and for predicting species' responses to future climate change (Araújo & Luoto, 2007; HilleRisLambers *et al*., 2013).

Inter-specific interactions are typically assumed to be negative (Eurich *et al*., 2018), with much evidence for improved species' performance if, for example, one species from an interacting pair is experimentally removed (see Toumey & Kienholz, 1931; Eurich *et al*., 2018). It is also generally expected that intra-specific interactions will have negative outcomes, with self-thinning typically reducing conspecific abundance due to greater niche overlap within species than between species (e.g. Goldenheim *et al*., 2008; Fajardo & McIntire, 2011; García-Cervigón *et al*., 2013; Zhang & Wang, 2016; Andivia *et al*., 2018). For example, individuals of the same species that are grown in low-density stands typically perform better than individuals grown in high-density stands (e.g. Tilman & Cowan, 1989; Kufel *et al*., 2018; but see in contrast, Leicht-Young *et al*., 2011). Therefore, both negative inter- and intra-specific interactions can strongly influence individuals and species in ecological communities.

Negative biotic interactions, both within- and between-species have been relatively well studied as drivers of species- and community-level patterns, with competitive interactions dominating most of the research on biotic interactions up until the mid-nineties (Toumey & Kienholz, 1931; Tilman, 1994; Yokozawa *et al*., 1998; Sóberon & Arroyo-Peña, 2017; Eurich *et al*., 2018). However, the importance of positive interactions (i.e. facilitation) in structuring ecological communities, has gained recognition in the past three decades (Bertness & Callaway, 1994; Bruno *et al*., 2003; Filazzola *et al*., 2018). Positive interactions, which are important especially in abiotically stressful or disturbed environments (e.g. in deserts, salt marshes, coastal systems, alpine systems, and arctic tundra; Armas & Pugnaire, 2005; Fajardo *et al*., 2008; Goldenheim *et al*., 2008; le Roux & McGeoch, 2008a; García-Cervigón *et al*., 2013; He & Cui, 2015; Zhang & Wang, 2016; Hupp *et al*., 2017; Filazzola *et al*., 2018), can increase species' fecundity and survival, provide a mechanism for species coexistence, and maintain species diversity and community stability (Stachowicz, 2001; Cavieres *et al.* 2007; Butterfield, 2009; Dangles *et al*., 2018; Filazzola *et al*., 2018). Intra-specific interactions can also be positive (Eränen & Kozlov, 2008; Goldheim *et al*., 2008; Fajardo & McIntire, 2011; García-Cervigón *et al*., 2013; Zhang & Wang, 2016; Svanfeldt *et al*., 2017). For example, individuals of the same species growing at high densities can mitigate the impact of abiotic stress on one another, thereby benefitting each other (e.g. Goldenheim *et al*., 2008). Therefore, both inter- and intra-specific facilitation may be important when examining plant species' survival and performance.

Irrespective of whether inter- and intra-specific interactions are positive or negative, their outcome can vary considerably across different spatial scales and is strongly linked to abiotic and/or environmental conditions (Bertness & Callaway, 1994; Olsen *et al*., 2016; O'Brien *et al*., 2017). The stress-gradient hypothesis (SGH) describes the environment-dependent outcome of biotic interactions and is a useful model for assessing how the effects of biotic interactions vary through space and time (Bertness & Callaway, 1994). A higher prevalence of positive interactions (i.e. facilitation) is expected under greater environmental severity (Bertness & Callaway, 1994; He *et al*., 2013). However, under moderate environmental conditions, negative interactions (i.e. competition) are predicted to generally dominate. Although the SGH is formulated for inter-specific interactions, it may apply to intra-specific interactions too (Fajardo & McIntire, 2011; Zhang & Wang, 2016; Svanfeldt *et al*., 2017).

While evidence exists to support the SGH (Choler *et al*., 2001; Arroyo *et al*., 2003; García-Cervigón *et al*., 2013; He *et al.*, 2013; Chen *et al*., 2015; Zhang & Wang, 2016; Anthelme *et al*., 2017), the SGH is still under discussion (see e.g. Maestre & Cortina, 2004; Maestre *et al*., 2005; Maestre *et al*., 2009; Holmgren & Scheffer, 2010). For example, four forms have been observed for the relationship between species interactions along stress gradients (Fig. 1 A-D) (Kawai & Tokeshi, 2007; Maestre *et al*., 2009; le Roux & McGeoch, 2010). All models predict the outcome of biotic interactions to be negative under low environmental severity (i.e. reflecting the dominance of competitive interactions). The linear model describes an increase in the relative strength of positive interactions between species with increasing environmental severity (Fig. 1A); whereas, all other models predict the outcome of biotic interactions to be most positive under intermediate levels of environmental severity. Beyond this intermediate level of environmental severity (i.e. under high environmental severity), the net outcome of interactions can plateau (Fig. 1B), weaken and become negative again (e.g. described by a symmetrical hump-shaped relationship; and representing a collapse of facilitation under extreme abiotic, water or nutrient stress: Fig. 1C; see also Maestre & Cortina, 2004; Maestre *et al.*, 2005; Maestre *et al.*, 2009; Michalet *et al.*, 2014; Svanfeldt *et al.*, 2017) or weaken and become neutral (e.g. described by an asymmetrical hump-shaped relationship; Fig. 1D). Therefore, further refinements to the model are required because discrepancies exist between observed patterns and predictions of the SGH (He *et al.*, 2013). For example, the outcome of biotic interactions varies depending on the types of severity gradients that are used (e.g. resource vs. non-resource gradients: Michalet, 2006; Michalet, 2007; Maestre *et al*. 2009; but see Lortie & Callaway, 2006; Armas *et al.*, 2011), and the spatial scales at which the interactions are examined (Raath-Krüger *et al.*, 2019). Studies also generally only consider the response of biotic interactions to a single environmental factor, whereas, multiple co-occurring environmental variables can operate independently and simultaneously on interacting species within systems (Kawai & Tokeshi, 2007; Mod *et al.*, 2014).

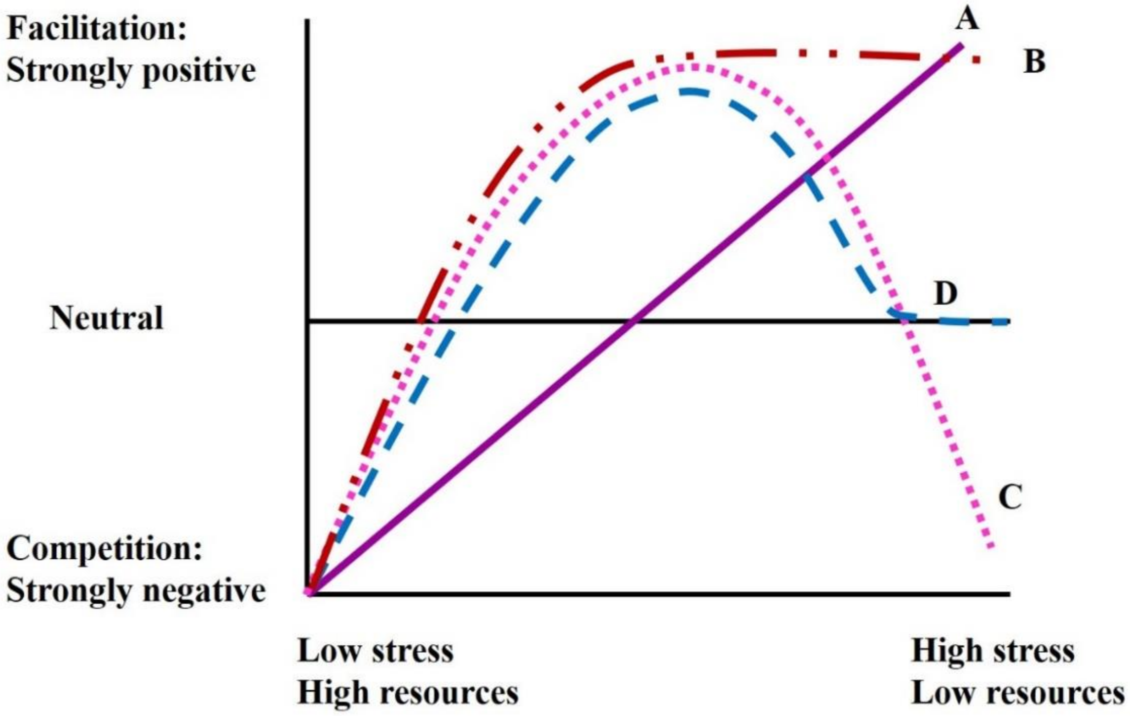

Figure 1. Different stress-interaction relationships reproduced from le Roux & McGeoch (2010): a) linear relationship, b) plateau-shaped relationship, c) symmetrical hump-shaped relationship and d) asymmetrical hump-shaped relationship.

High-altitude and high-latitude systems (e.g. alpine, arctic and sub-Antarctic systems) have a pronounced variability in environmental conditions over small spatial scales and are therefore useful systems for examining the SGH (Brooker & Callaghan, 1998; Mod *et al.*, 2014). These systems are also amongst the most climatically severe systems on Earth (Körner, 2003). Substrate and air temperature generally decrease with altitude and latitude within these systems, whereas wind speed increases (Körner, 2003; le Roux & McGeoch, 2010; le Roux *et al.*, 2013). Consequently, plant biomass, cover, abundance and the richness of species decreases with increasing altitude and latitude (Choler *et al.*, 2001; Bruun *et al.*, 2006). Thus, positive interactions (e.g. facilitation and mutualism) within and between species in these regions may be important for vegetation dynamics and the maintenance of plant communities and plant diversity (Cavieres *et al.*, 2014; Cavieres *et al.*, 2016), although the impacts of negative interactions cannot be ignored (Gross, 2008; Soliveres *et al.*, 2015).

In high-altitude and high-latitude systems, the climate experienced by an organism (i.e. the microclimate) is one of the most important factors affecting species (Cavieres *et al.*, 2007; Nyakatya & McGeoch, 2008; He & Cui, 2015; Hupp *et al.*, 2017). Indeed, microclimates are influenced by aspect, landforms, substrate and topography (Bennie *et al.*, 2008; Nyakatya &

McGeoch, 2008); however, certain species (i.e. benefactor species) can also alter the microclimate to which they and other species (i.e. beneficiary species) are exposed (Cavieres *et. al.*, 2007; Nyakatya & McGeoch, 2008; He & Cui, 2015; Molina-Montenegro *et al*., 2015; Hupp *et al*., 2017). Moreover, benefactor species may increase resource availability and improve substrate stability for beneficiary species. They are, therefore, important facilitators in high altitude and high latitude systems (Molenda *et al*., 2012; Schöb *et al*., 2013; Bonanomi *et al*., 2016; Hupp *et al*., 2017). While the positive impact of benefactors on species' performance, richness and diversity in these systems has been well-established (Badano & Cavieres, 2006a; Badano & Cavieres, 2006b; Badano & Marquet, 2008; Molenda *et al*., 2012; Chen *et al*., 2015; Hupp *et al*., 2017), there are at least three avenues of research related to facilitation that remain poorly understood, and which I specifically addressed in this thesis. I considered a known facilitative interaction between a dominant species pair on sub-Antarctic Marion Island.

Study site

sub-Antarctic Marion Island

Marion Island and the smaller Prince Edward Island form the sub-Antarctic Prince Edward Islands and are located in the southern Indian Ocean (Chown & Froneman, 2008). Marion Island has a hyper-oceanic climate, with high precipitation and humidity, low but very stable temperatures, cloud cover on most days and strong winds (Smith, 2002; le Roux, 2008). The island exhibits a clear altitudinal gradient of increasing abiotic severity, with greater wind speeds and soil instability, and lower mean temperatures at higher elevations (Boelhouwers *et al*., 2003; le Roux, 2008). Consequently, plant species richness (le Roux & McGeoch, 2008b; Chown *et al*., 2013), cover (Smith *et al*., 2001) and productivity (Smith, 2008) generally decline with elevation on the island (Fig. 2).

The island's climate has changed significantly over the past 50 years (le Roux & McGeoch, 2008b), with a c. 1.2 ˚C rise in temperature, a c. 1000 mm decline in rainfall and an increase in the interval between rainfall events (Smith, 2002; le Roux & McGeoch, 2008c). The biological consequences of climate change are already evident on the island. For example, increases in the population densities of the introduced house mouse (*Mus musculus* L. Muridae) are attributed to warming (Smith, 2002), thereby indirectly affecting indigenous species that the mice feed on (e.g. Chown & Smith, 1993). Warming has additionally caused the upper distributional ranges of vascular plant species on the island to expand by a mean rate of 3.4 ± 0.8 m/year (see le Roux & McGeoch, 2008c). Plant species on the island are therefore vulnerable to the effects of climate change.

Figure 2. A typical landscape on Marion Island. The foreground is at c. 50 m a.s.l., with the highest peak in the image reaching c. 900 m a.s.l. Image taken by Christien Steyn.

Study species

On Marion Island, and in similar stressful environments, plant species exhibiting cushion growth forms are often prominent benefactor species (Cavieres *et al*., 2002; Chen *et al*., 2017; Hupp *et al*., 2017). A total of 1309 cushion plant species from 272 genera and 63 families occur in nearly all alpine systems worldwide, with temperate Asia containing the greatest number of species with this growth form (Aubert *et al*., 2014; Chen *et al*., 2017). These species typically grow slowly and are long-lived, and can persist in alpine habitats (Chen *et al*., 2017). Cushion plants can affect local microhabitat conditions, both by ameliorating abiotic extremes and increasing resource availability (Nyakatya & McGeoch, 2008; Hupp *et al*. 2017). Cushion plants can moderate microhabitat conditions by ameliorating soil temperatures, increasing soil moisture, improving soil nutrient status and enhancing substrate stability. Cushion plants can also provide other species with protection from wind (see e.g. le Roux & McGeoch, 2010).

Marion Island supports 21 indigenous and 18 alien vascular plant species, and over 200 bryophyte and lichen species (Gremmen & Smith, 2008; Greve *et al*., 2019). *Azorella selago* Hook. (Apiaceae) is a widespread plant species in the sub-Antarctic, and on Marion Island (Fig. 3), and occurs in all vegetation types, from the interior of Marion Island (up to 840 m a.s.l.) down to sea-level (le Roux & McGeoch, 2008b). It is also the dominant vascular plant species in the largest vegetation type on the island: the fellfield habitat complex (Fig. 4). Fellfield consists of mineral soils, lava rocks and scoria (Huntley, 1972; Frenot *et al*., 1993; Gremmen & Smith, 2008). *Azorella selago* is a long-lived pioneer species, with a compact, hemispherical growth form (Huntley, 1972; McGeoch *et al*., 2008). The leaves of *A. selago*, which are small, lobed and tough, are packed tightly together (Orchard, 1989). Stems, which arise from a central taproot, are also compact. These plants stop growing in autumn and go through autumnal senescence which is completed in winter (Orchard, 1989). The senesced leaves are retained, and as a result, a moist, organic-matter rich environment is formed within the plant (Huntley, 1971). Large morphological variability is also evident in *A. selago*, with, for example, cushions growing in sheltered environments having larger leaves, greater stem growth, and a more hemispherical shape than individuals in exposed habitats (Huntley, 1971; Huntly, 1972).

Figure 3. *Azorella selago* growing on Marion Island. Cushion plants are all medium-sized (> 0.15 m in diameter) and the white blocks on the cushion plants are tags.

Because of its cushion growth form, *A. selago* can modify the local microclimate and microenvironment (e.g. ameliorate temperature conditions: Nyakatya & McGeoch, 2008; McGeoch *et al*., 2008) and therefore has the potential to positively impact species associated with it, particularly in cold, wind-exposed areas where the cushion plant is commonly found. At least 20 vascular and 17 nonvascular plants have been recorded growing epiphytically on *A. selago* (le Roux *et al*., 2004). In addition, *A. selago* hosts an array of invertebrates (Hugo *et al*., 2004) and facilitates the growth of vascular plants at higher altitudes, where some species are restricted to growing on the cushion plants (Huntley, 1972; but see also e.g. Cavieres *et al*., 2002; Badano & Cavieres, 2006a for other cushion plant species). This, along with the important role that *A. selago* plays in succession (i.e. by colonizing recent lava flows, glacial forelands and scoria slopes; Huntley, 1972; also see Frenot *et al*., 1998), makes the plant an ecosystem engineer and keystone species on Marion Island (Hugo *et al*. 2004).

Figure 4. *Azorella selago* and *Agrostis magellanica* growing in the fellfield habitat complex on Marion Island.

Agrostis magellanica is a dominant perennial grass species on Marion Island and is the most common vascular plant species found to grow on *A. selago* (Huntley, 1971). *Agrostis magellanica* occurs in most of the island's habitats and has the second largest altitudinal range (c. 0 - 600 m a.s.l.) after *A. selago* (Huntley, 1971; le Roux & McGeoch, 2008b). *Azorella selago* is known to facilitate *A. magellanica* on Marion Island, where *Azorella* presence has been shown to alter *A. magellanica* population structure and increase *A. magellanica* reproductive output and abundance compared to surrounding areas where *A. selago* is absent (le Roux & McGeoch, 2008a; le Roux & McGeoch, 2010; le Roux *et al.*, 2013). However, support for the positive effect of *A. selago* on other vascular plant species is lacking. *Azorella selago* and *A. magellanica*, together, form the model system of my study.

Thesis objectives and outline

The objective of this thesis was to provide insights into the impacts of inter- and intra-specific plant-plant interactions on plant species' performance and distributions on sub-Antarctic Marion Island. To achieve this, my thesis comprised of three research chapters (detailed briefly below), each with a distinct study aim:

1) to examine the long-term consequences / impacts of the interaction between *A. selago* and *A. magellanica*.
2) to assess the impact of an inter-specific interactions (between *A. selago* and *A. magellanica*) on the outcome of intra-specific interactions (between *A. magellanica* individuals) across a severity gradient.
3) to examine whether the local-scale interactions between *A. selago* and associated species scale up to shape broad-scale species distributions.

Each research chapter was written as a stand-alone manuscript, prepared for submission to specific journals. As a result, there may be some repetition in the description of the study area and the study species.

Chapter 2: Does **Agrostis magellanica** *cover have a negative impact on* **Azorella selago***?*

The outcome of inter-specific interactions may vary considerably spatially, i.e. across gradients of environmental severity (with a switch from competition to facilitation typically observed with increasing abiotic severity: e.g. Bertness & Callaway, 1994; He *et al*., 2013; Zhang & Wang, 2016; Kunstler *et al*., 2019). However, studies describing the temporal variation in the outcome of biotic interactions in systems where facilitation is prominent are lacking (but see Armas & Pugnaire, 2005; Miriti, 2006; García *et al*., 2016; Metz & Tielbörger, 2016). Understanding the reciprocity of biotic interactions is also important because it can provide insights into habitat dynamics and/or the evolutionary consequences for the species involved (Bronstein, 2009b; Barraclough; 2015; Revilla & Encinas-Viso, 2015; Michalet *et al*., 2016). For example, if two interacting species (Fig. 5) have a positive impact on one another, a stable mutualism may evolve and the species may co-exist (Bronstein, 2009b; Michalet *et al*., 2016). In contrast, if beneficiaries have a negative impacts on their benefactors, benefactors may either 1) evolve to tolerate the beneficiaries by selecting for traits that reduce the negative impact of beneficiaries, or 2) avoid beneficiaries by selecting for traits that reduce densification by other plants (Bronstein, 2009b). Alternatively, the benefactor may select for traits that reduce competition between the benefactor and the beneficiary (e.g. via niche partitioning; Lawrence *et al*., 2012) or both species may co-evolve in an arms race to reduce the costs and maximize the benefits from the interaction (e.g. Bell, 2007). In these ways, the interaction between a benefactor and beneficiaries can shift from a parasitism to a commensalism.

Moreover, while the positive impact of benefactor species on associated beneficiary has been well established, particularly in abiotically stressful environments (Badano & Cavieres, 2006a; Badano & Cavieres, 2006b; Badano & Marquet, 2008; le Roux & McGeoch, 2010; Molenda *et al*., 2012; Schöb *et al*., 2013; Chen *et al*., 2015; Bonanomi *et al*., 2016; Hupp *et al*., 2017), biotic interactions are bidirectional in nature (e.g. Holzapfel & Mahall, 1999; Callaway *et al*., 2002; Lortie & Turkington, 2008; García *et al.*, 2016; Douda *et al*., 2018; but see Metz & Tielbörger, 2016; Pearson *et al*., 2017). Few studies (none of which have been conducted in the sub-Antarctic) have examined the feedback effects of beneficiary species on their cushion plant benefactors (but see Schöb *et al*., 2014a; Schöb *et al*., 2014b; Llambí *et al*., 2018), and even fewer studies have examined reciprocal interactions using long-term data (see e.g. Metz & Tielbörger, 2016; Pearson *et al*., 2017). Therefore, while facilitation has been defined as an interaction in which at least one of the species involved benefits (i.e. the beneficiary; Stachowicz, 2001), the beneficiary species may impact the benefactor either positively (Pugnaire *et al*., 1996), neutrally (Lortie & Turkington, 2008) or negatively (Michalet *et al*., 2011; Cranston *et al*., 2012; Schöb *et al*., 2014b; García *et al*., 2016; Michalet *et al*., 2016; Llambí *et al*., 2018), with the latter being the most frequently observed.

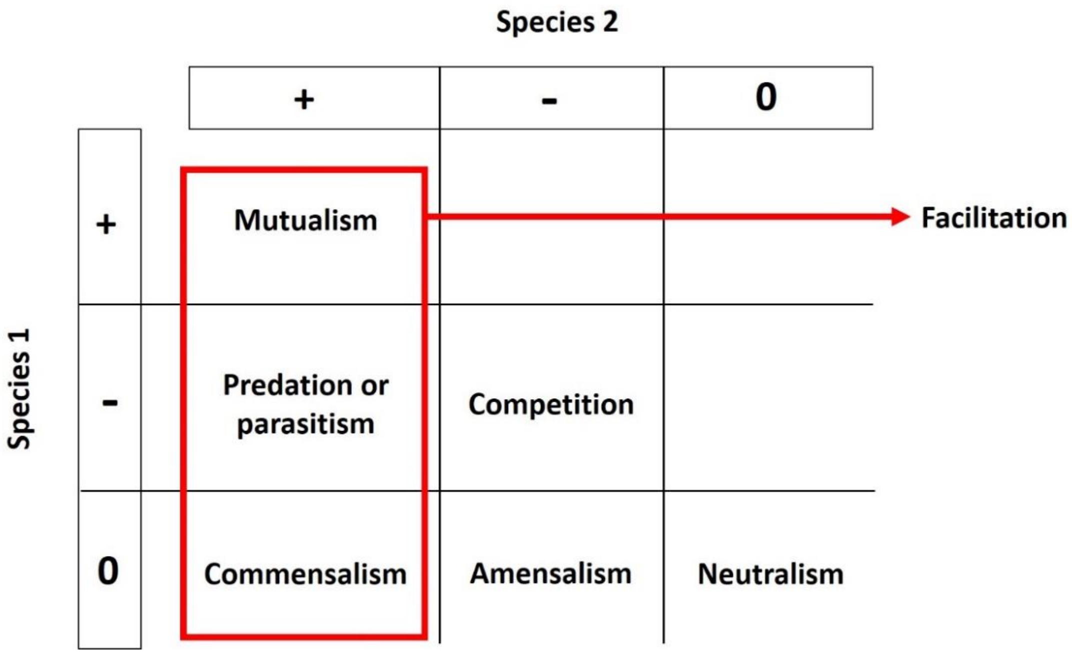

Figure 5. Illustration of the potential outcomes of an interaction between two species (Modified from Bronstein 2009b). Each species may either benefit (+), lose (-) or be unaffected (0) by the interaction. In a facilitative interaction, species 1 has a positive effect on species 2 but species 2 can have a positive, neutral or negative impact on species 1 (suggesting either a mutualism, commensalism or parasitism).

Therefore, in this chapter, I first examined the long-term impact and bidirectional nature of the interaction between *A. selago* and *A. magellanica* using a long-term (± 13-year) dataset of repeated measurements. I documented changes in *A. selago* size and stem mortality in relation to *A. magellanica* cover to test if the changes in *A. magellanica* cover are correlated with changes in of *A. selago* size and vitality. This enabled me to test the reciprocity of interactions (sensu Schöb *et al*., 2014a; Schöb *et al*., 2014b) between *A. selago* and *A. magellanica* over a relatively long period of time. Moreover, variation in the outcome of the interaction between *A. selago* and *A. magellanica* has been documented along transects spanning the grass species' entire altitudinal range (in line with predictions by the SGH; le Roux & McGeoch, 2010). While *Azorella* has a negative impact on *Agrostis* performance at low altitudes, *Agrostis* increasingly benefits from *Azorella* under greater environmental stress (i.e. with increasing altitude). However, no data are available to describe the reciprocal impact of *A. magellanica* on *A. selago* with increasing abiotic severity. Therefore, I also examined the reciprocity of the *Azorella-Agrostis* interaction across a gradient of environmental severity (i.e. with increasing altitude).

I expected to find that *A. magellanica* has a long-term negative impact on *A. selago* (following Michalet *et al*., 2011; Schöb *et al*., 2013; Schöb *et al*., 2014a), possibly due to shading (see le Roux *et al*., 2005). I also expected that *A. magellanica* to have a negative impact on *A. selago* at the highest altitudes due to competition for resources.

Chapter 3: Does inter-specific facilitation alter the outcome intra-specific interactions?

Where facilitation by benefactor species alters beneficiary species' composition and abundance, this could have consequences for interactions among beneficiary species and/or individuals (e.g. Aguiar & Sala, 1994; Tielbörger & Kadmon, 2000; Saccone *et al*., 2010; García-Cervigón *et al*., 2013; Schöb *et al*., 2013; Zhang & Wang, 2016; Llambí *et al*. 2018). For example, if benefactors increase the density of beneficiaries, beneficiaries may experience stronger competition (Tielbörger & Kadmon, 2000; García-Cervigón *et al*., 2013). The positive impact of benefactors on beneficiaries may therefore be negated by the negative effect of high beneficiary densities on reproduction (Fig. 6). Alternatively, the positive impact of benefactors on the beneficiaries could outweigh the negative effect of beneficiaries on one another, allowing beneficiaries a greater degree of co-existence and/or improved performance than in the absence of the benefactor (Fig. 6; Armas *et al*., 2008; see also e.g. Feldman & Morris, 2011). Inter-specific facilitation could, therefore, drive the outcome of interactions among beneficiaries see e.g. Armas *et al*., 2008; García-Cervigón *et al*., 2013; Schöb *et al*., 2013; Llambí *et al*. 2018).

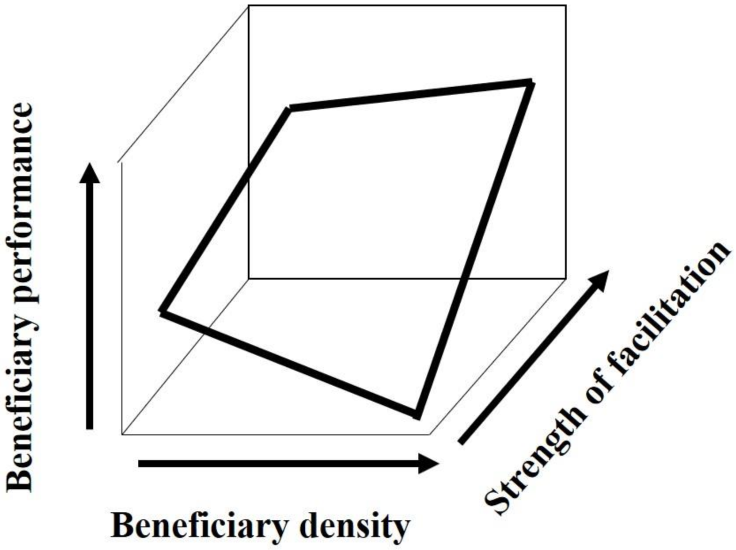

Figure 6. Conceptual model illustrating increasing beneficiary performance (i.e. reproduction) against increasing beneficiary density and increasing strength of facilitation by a benefactor. Under harsh abiotic conditions, when facilitation is very strong, increasing beneficiary density increases beneficiary performance (i.e. facilitation by the benefactor outweighs competition among beneficiaries). Under benign abiotic conditions, where competition is strong, increasing beneficiary density reduces beneficiary performance. Image modified from Callaway & Walker (1997).

In this chapter, I combined an experimental and observational approach to examine the impact of intra-specific interactions within a facilitative system (see e.g. Fajardo & McIntire, 2011; Garcia-Cervigon *et al*., 2013; Zhang & Wang, 2016; Svanfeldt *et al*., 2017). Since the impact of *A. selago* on *A. magellanica* (i.e. the inter-specific interaction) is positive (le Roux & McGeoch, 2008a; le Roux & McGeoch, 2010; le Roux *et al*., 2013) and may therefore influence intra-specific interactions (among *A. magellanica* conspecifics) (see e.g. Llambí *et al*. 2018), I examined impact of *A. magellanica* density (i.e. the role of intra-specific interactions) on *A. magellanica* performance (e.g. reproductive effort) within the context of facilitation by *A. selago* (i.e. as a result of facilitation by *A. selago*). I hypothesised that the negative influence of intra-specific competition between *Agrostis* individuals could potentially outweigh the positive influence of the positive impact of *A. selago* on *A. magellanica*, when, for example, higher densities of *A. magellanica* are negated by the negative effect of crowding on *A. magellanica* reproduction (Fig. 7). I expected to see a negative relationship between *A. magellanica* performance and *A. magellanica* density both in the presence and absence of *A. selago*, but I expected to see a stronger negative relationship in the presence of *A. selago* where *A. magellanica* density is highest (see e.g. Zhang & Wang, 2016).

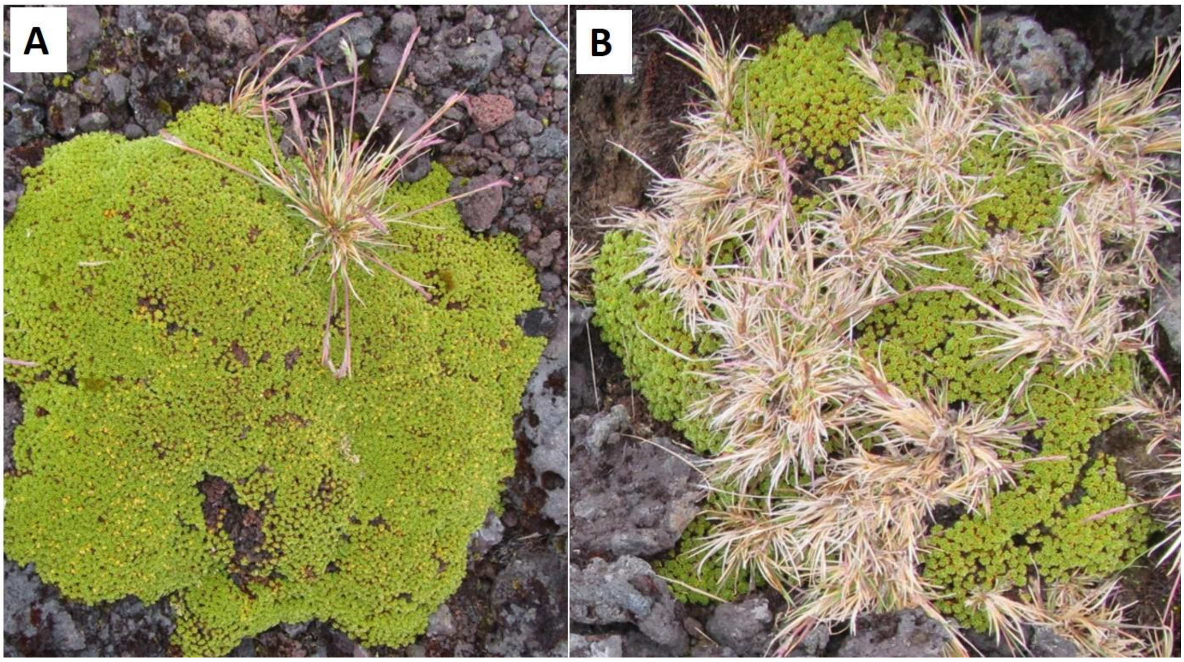

Figure 7. *Azorella selago* individuals with A) low and B) high densities of *Agrostis magellanica*. The positive effect that *A. selago* has on the abundance of *A. magellanica* (in B) may be negated by the negative effect of high *A. magellanica* density on *A. magellanica* reproduction.

Chapter 4: Can fine-scale biotic interactions scale-up to influence species' distributions?

While climate is proposed to be the main factor governing species' distributions at broad spatial scales, biotic interactions are expected to be more important at fine scales (Pearson & Dawson, 2003). It is, however, still unclear whether these fine scale interactions could scale up to shape communities at broader extents (although see evidence from species distribution modelling: Araújo & Luoto, 2007; Filazzola *et al*., 2018). Biotic interactions among species may influence species-environment relationships (López *et al*., 2018). As a result, biotic interactions may affect species' realized niches (He & Bertness, 2014; Jones & Gilbert, 2016; Sóberon & Arroyo-Peña, 2017; Filazzola *et al*., 2018), and potentially limit (via negative interactions) or expand (via positive interactions) the conditions under which species can occur (Fig. 8; Jones & Gilbert 2016; Filazzola *et al*., 2018). Therefore, positive interactions (especially when driven by amelioration of stressful environmental conditions) could allow species to establish and survive at higher altitudes by increasing the niche space that the species can occupy (Bruno *et al*., 2003; He & Bertness, 2014; He & Cui, 2015; Filazzola *et al*., 2018).

I hypothesised that fine-scale positive plant-plant interactions could scale up to affect plant communities at broader extents. In my final research chapter, I therefore examined whether *A.*

selago could facilitate the colonisation of associated species at higher altitudes and therefore expand species' realized niches (Fig. 8). While many studies have examined the performance of plant species on or away from cushion plants at different altitudes (Arroyo *et al*., 2003; Badano & Cavieres, 2006a; Badano & Marquet, 2008; Schöb *et al*., 2013; Chen *et al*., 2015), none have explicitly determined the upper distributional limits of species in the presence and absence of cushion plants. Past studies have also been limited to subsets of communities, while in this study, species' upper distributional limits (in the presence and absence of *A. selago*) are examined using an entire vascular plant assemblage.

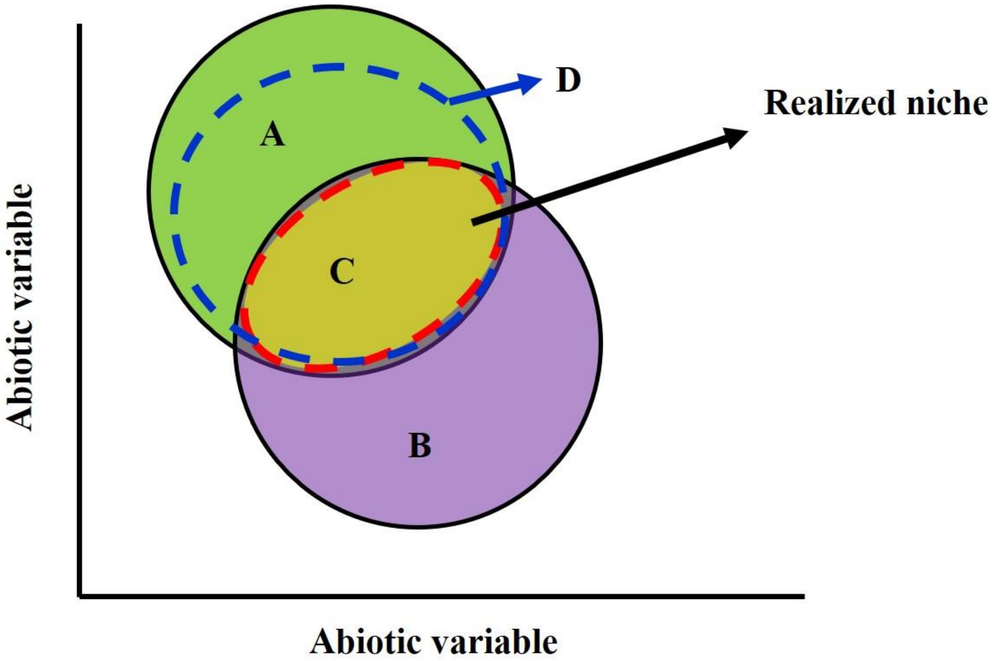

Figure 8. The occurrence of species is affected by: A) Abiotic variables, B) Dispersal ability (i.e. accessibility) and species interactions which either: C) limit the total area where a species occurs (i.e. inter-specific competition constrains species' realized niches) or D) scale up to expand the total area in which a species occurs, if dispersal does not limit the species (i.e. inter-specific facilitation expands species' realized niches). Image modified from the BAM model of Soberòn (2007).

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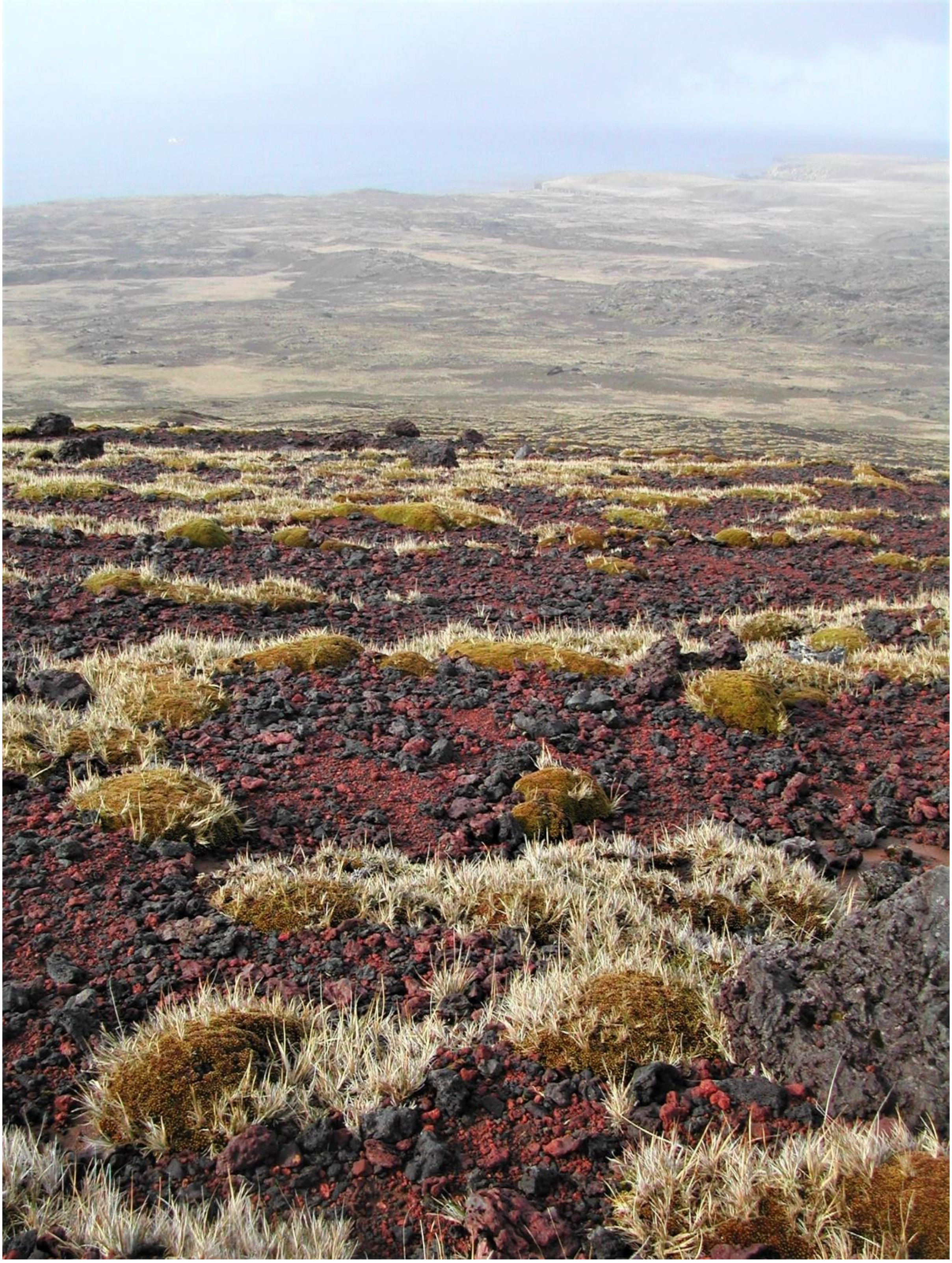

***Agrostis magellanica* growing on *Azorella selago* on Marion Island**

Chapter 2:

Long-term spatially-replicated data show no cost to a benefactor species in a facilitative plant-plant interaction

*In prep for submission to *Functional Ecology*: Raath-Krüger, M.J., Schöb, C., McGeoch, M.A. & le Roux, P.C. *In prep*. Long-term spatially-replicated data show no cost to a benefactor species in a facilitative plant-plant interaction.

Abstract

Facilitation is defined as an interaction where one species (the benefactor) positively impacts another species (the beneficiary). However, the feedback effects of beneficiaries on benefactor species, and therefore the reciprocity of these biotic interactions, are infrequently considered and are typically only documented using short-term datasets and/or correlations within a single time period. However, a long-term repeated measures approach documenting changes in benefactor performance in relation to beneficiary cover and composition could potentially be used to more robustly examine the impact of bidirectional plant-plant interactions. Here, I use two dominant species: *Azorella selago*, a cushion plant species and facilitator, and a perennial grass species, *Agrostis magellanica*, on sub-Antarctic Marion Island as a model system, comparing individual plants over a 13-year period. I hypothesized that final *A. selago* size and vitality would be negatively affected by initial *A. magellanica* cover (due to, e.g., shading), and that final *A. magellanica* cover would be positively related to initial *A. selago* dead stem cover (since dead stems do not inhibit grass colonization or growth). I observed three main findings: 1) *A. magellanica* had no long-term effect on *A. selago* size and vitality; however, 2) the feedback effect of *A. magellanica* varied depending on the type of approach used (i.e. a snapshot vs. a repeated measures approach) and the performance measure examined, and 3) *A. selago* dead stem cover was not related to *A. magellanica* cover. Therefore, I found no evidence for a long-term negative impact of *A. magellanica* on *A. selago*. For the first time using a long-term dataset, I show that the cost of facilitation to a benefactor species may be negligible, in contrast to the majority of short-term studies. Long-term datasets may, therefore, be more practical, and possibly more robust, for assessing beneficiary feedback effects than snapshot approaches in systems where benefactors are slow-growing.

INTRODUCTION

Biotic interactions strongly shape ecological communities, with clear evidence existing for these interactions affecting plant fitness, abundance, cover and survival, and scaling up to influence species' richness, distributions and community composition (Bruno *et al*., 2003; Armas & Pugnaire, 2005; Bulleri *et al*., 2016; Zhang & Wang, 2016; Pearson *et al*., 2017; Douda *et al*., 2018; Eurich *et al*., 2018; Kufel *et al*., 2018; Kunstler *et al*., 2019; Raath-Krüger *et al*., 2019). The impact of biotic interactions, however, can vary considerably both spatially

(Bertness & Callaway, 1994; Zhang & Wang, 2016; Kunstler *et al.*, 2019) and temporally (Holzapfel & Mahall, 1999; Armas & Pugnaire, 2009; Butterfield, 2009; Zhu *et al.*, 2015; Zhang & Wang, 2016; Ribeiro *et al.*, 2018). Indeed, the outcomes of biotic interactions are strongly linked to environmental conditions in many systems (Kawai & Tokeshi, 2006; O'Brien *et al.*, 2017; Michalet *et al.*, 2015; Olsen *et al.*, 2016; Zhang & Wang, 2016; Svanfeldt *et al.*, 2017), with a higher prevalence of net positive interactions (e.g. facilitation) typically observed under greater environmental severity (as posited by the Stress Gradient Hypothesis SGH; Bertness & Callaway, 1994).

Facilitation is defined as an interaction where at least one of the interacting species benefits (Schöb *et al.*, 2014a). However, while most research only documents the positive impact of one species (i.e. the benefactor species) on associated beneficiaries (see Hupp *et al.*, 2017; Filazzola *et al.*, 2018), the impacts of beneficiaries on their benefactors (i.e. beneficiary feedback effects) are often ignored (but see Pugnaire *et al.*, 1996; Reid *et al.*, 2014; Schöb *et al.*, 2014b; García *et al.*, 2016; Michalet *et al.*, 2016; Bai *et al.*, 2018; Dangles *et al.*, 2018; Llambí *et al.*, 2018). Studies that have documented the bidirectional (i.e. reciprocal) nature of interactions between benefactor and beneficiary species have found that beneficiary species can have positive (e.g. Pugnaire *et al.*, 1996), neutral (Lortie & Turkington, 2008) or negative (e.g. Michalet *et al.*, 2011; Cranston *et al.*, 2012; Schöb *et al.*, 2014b; García *et al.*, 2016; Michalet *et al.*, 2016; Llambí *et al.*, 2018) effects on their benefactors, with the latter being the most frequently observed (see e.g. Holzapfel & Mahall, 1999; Armas & Pugnaire, 2009; Michalet *et al.*, 2016). For example, Schöb *et al.* (2014b) documented lower seed set and flower density of the cushion plant *Arenaria tetraquetra* under greater beneficiary species cover. In contrast, Pugnaire, *et al.* (1996) showed a mutualistic interaction between a benefactor shrub (*Retama sphaerocarpa*) and an associated beneficiary species, where both species displayed improved performance when co-occurring. Finally, Llambí *et al.* (2018) examined the complexity of reciprocal effects between the cushion plant *Arenaria musciformis*, a native plant species and a non-native plant: cushion plant flower density decreased with increasing native plant density, but the non-native plant species had an indirect positive effect on the cushion plants due to its negative impact on the density of the native species. Reciprocal interactions within a plant-plant facilitative system may therefore have both diverse and significant impacts, and thus an understanding of the bidirectional nature of biotic interactions is essential for accurately assessing the consequences of plant-plant interactions (Schöb *et al.*, 2014a; Schöb *et al.*, 2014b).

To date, studies examining reciprocal plant-plant interactions that include facilitation have typically used data from short-term experiments (e.g. Holzapfel & Mahall, 1999; Lortie & Turkington, 2008; Douda *et al*., 2018; but see Metz & Tielbörger, 2016; Pearson *et al*., 2017) and/or observations from a single time period (e.g. Pugnaire *et al*., 1996; Llambí *et al*., 2018). Therefore, studies describing the long-term impact of biotic interactions in systems where facilitation is prominent are lacking (but see Armas & Pugnaire, 2005; Miriti, 2006; García *et al*., 2016). The approach of monitoring the same species and/or individuals using long-term datasets (i.e. through repeated measurements or repeat photography of the same interacting individuals) is an effective methodology for examining changes in community structure and composition (e.g. Crimmins & Crimmins, 2008; Magurran *et al*., 2010; Elmendorf *et al*., 2015; Yang *et al*., 2018). Monitoring approaches can, however, also provide valuable insights into the long-term consequences of biotic interactions (see e.g. Báez & Collins, 2008; Ribeiro *et al*., 2018). For example, extended monitoring of interacting individuals can disentangle short- and long-term responses to a disturbance (e.g. experimental removal of individuals to examine the influence of competition; see Barnes & Archer, 1999; Maestre *et al*., 2003; Kikvidze *et al*., 2006). Moreover, monitoring approaches may be especially valuable for examining interactions between slow-growing and/or long-lived perennial species (e.g. as is typical for many species in abiotically-stressful environments; Armas & Pugnaire, 2005) because these species may respond slowly to changes in some biotic interactions (see e.g. Raath-Krüger *et al*. in prep). Monitoring approaches could therefore be used to accurately examine both the outcome and the reciprocity of biotic interactions.

Understanding the complexity and bidirectional nature of biotic interactions is important because it can provide insights into habitat dynamics and/or the evolutionary consequences for the species involved (Bronstein, 2009; Schöb *et al*., 2014; Barraclough, 2015; Michalet *et al*., 2016). For example, if two interacting species positively affect each other, a stable mutualism may evolve (Bronstein, 2009; Michalet *et al*., 2016), with both species potentially selecting for traits that reduce the costs and increase the benefits of coexistence (Login *et al*., 2011). In contrast, if a beneficiary species has a negative reciprocal effect on a benefactor species, the benefactor could either tolerate the beneficiary species by selecting for traits that reduce the negative impact of the beneficiary species, or the benefactor could limit the cover of beneficiary species by selecting for traits that reduce the spread of the beneficiary species (Bronstein, 2009). In addition, if a beneficiary feedback effect is negative, the strength of the negative interaction may be reduced if both species evolve to a new equilibrium state via, e.g., niche partitioning (Lawrence *et al*., 2012). The impact of biotic interactions on species coexistence may therefore be detrimental, beneficial or dynamic within populations and communities. Thus, it is important to understand the reciprocity of interactions between species because they may strongly affect populations and, where the interacting species are dominant species in the system, community dynamics (Báez & Collins, 2008; Lortie & Turkington, 2008; Bai *et al.*, 2018).

The aim of this study is therefore to examine the impact and bidirectional nature of an interaction between two dominant species. I use a widespread cushion plant species and facilitator, *Azorella selago* (*Azorella* hereafter), and a dominant perennial grass species, *Agrostis magellanica* (*Agrostis* hereafter), on the sub-Antarctic Marion Island as a model system. I document changes in *Azorella* size and vitality in relation to *Agrostis* cover over a 13-year time period, and test if the changes in the cover of *Agrostis* are correlated with changes in the characteristics of *Azorella* (i.e. size and stem mortality). This enables us to test bidirectional interactions between *Azorella* and *Agrostis* over a relatively long time period. I also examine the *Azorella*-*Agrostis* interaction across a gradient of environmental severity because the outcome of biotic interactions may shift in response to changing abiotic conditions (e.g. Kawai & Tokeshi, 2006; Zhang *et al.*, 2018).

Variation in the impact of *Azorella* on *Agrostis* has been documented along environmental gradients (le Roux & McGeoch, 2010; le Roux *et al.*, 2013). For example, along transects spanning the grass species' entire altitudinal range, le Roux & McGeoch (2010) demonstrated that *Azorella* has a negative impact on *Agrostis* performance at low altitudes, but that the grass benefits from the interaction as environmental stress increases (i.e. with increasing altitude). Moreover, across a smaller spatial extent (i.e. along a wind exposure gradient), they also found that the intensity of the *Azorella*-*Agrostis* interaction is increasingly positive under more wind exposed conditions. These results suggested that the impact of *Azorella* on *Agrostis* can switch from negative to positive with increasing environmental severity across both fine and broad spatial extents. However, in contrast to the impact of *Azorella* on *Agrostis*, I hypothesise that there may be negative beneficiary feedback effects, with *Azorella* growth decreasing and *Azorella* stem mortality increasing under greater *Agrostis* cover at all altitudes (following Arrendondo-Núñez *et al.*, 2009; Michalet *et al.*, 2011; Schöb *et al.*, 2014a).

METHODS

Study site and species

Marion Island (46°55’S, 37°45’E), the larger of the two Prince Edward Islands, is located in the southern Indian Ocean, and has a hyper-oceanic climate (Smith & Steenkamp, 1990), with low but very stable temperatures, along with high precipitation and humidity, cloud cover on most days and frequent strong winds (le Roux, 2008). There is also a clear elevational gradient of increasing abiotic severity, with greater wind speeds and lower mean temperatures and soil stability at higher elevations on the island (Boelhouwers *et al*., 2003; le Roux, 2008). Consequently, plant species richness (le Roux & McGeoch, 2008b; Chown *et al*., 2013), cover (Smith *et al*., 2001) and productivity (Smith, 2008) decline with elevation on the island.

Marion Island supports 22 indigenous and 17 alien vascular plant species and over 200 bryophyte and lichen species (Smith, 1987; Greve *et al*., 2019; Kalwij *et al*., 2019). *Azorella selago* Hook. (Apiaceae) is a widespread cushion plant species (i.e. a compact, hemispherical species that can create favourable microhabitats for other species) occurring on multiple sub-Antarctic islands and in many habitat types on those islands. Due to its cushion growth form, *Azorella* is thought to ameliorate stressful environmental conditions (see Nyakatya & McGeoch, 2008; McGeoch *et al*., 2008), particularly in cold, wind-exposed areas where the cushion plant is commonly found. Consequently, *Azorella* hosts an array of species, including invertebrates and other plant species (Huntley, 1971; Huntley, 1972; Barendse & Chown, 2001; Barendse *et al*., 2002; Hugo *et al*., 2004), which makes the plant an important ecosystem engineer and keystone species (Hugo *et al*. 2004).

Agrostis magellanica (Lam.) is a dominant perennial grass species on Marion Island and is the most common vascular plant species growing on *Azorella* (Huntley, 1972). *Agrostis* occurs in most habitats on Marion Island and has the second largest altitudinal range of all the vascular plant species after *Azorella* (Huntley, 1971; le Roux & McGeoch, 2008b). *Azorella* and *Agrostis* are characteristic species of the dominant vegetation type on Marion Island – the fellfield vegetation complex (Gremmen & Smith, 2008). The fellfield occupies 61 % of the terrestrial surface on Marion Island between 0 and 500 m a.s.l. and 15 % of the total area above 500 m a.s.l. (Smith *et al*., 2001).

Data collection

The outcome of the interaction between *Azorella* and *Agrostis* was inferred from changes in *Azorella* size and dead stem area and *Agrostis* cover through time. Six long-term monitoring plots, which were established in 2002 at three altitudes (c. 200, 400 and 600 m a.s.l) on the island's eastern and western aspects (Nyakatya & McGeoch, 2008), were resurveyed in 2016. Plots were established using complete sampling, i.e. a central starting point was selected, and the area encompassing a minimum of 50 *Azorella* cushion plants (excluding *Azorella* individuals < 15 cm in diameter) from that starting point was considered as a plot (see Nyakatya, 2006). The plots were clearly marked with corner markers. The exact locations of each plot were randomly selected within certain constraints: 1) plots had to be located in an *Azorella*-dominated area; 2) plots had to be located within the correct altitudinal band (i.e. at 150 - 250 m a.s.l., 350 - 450 m a.s.l. or > 550 m a.s.l.); and, 3) plots needed to be in the correct general location to form an altitudinal transect (see Nyakatya, 2006). Each of 50 *Azorella* individuals within each plot were photographed in the summer of 2002/2003 (Nyakatya & McGeoch, 2008; Nyakatya, le Roux & McGeoch, unpublished data) from directly above at a height of 1.5 m, with a scale bar included within each photograph. Each *Azorella* individual was photographed again in 2016 using the same sampling methods (Fig. 1). Digital cameras were used in both 2003 (Nikon E885, 300) and in 2016 (Canon PowerShot D30). There was a difference in the resolution of the images taken between the two years (300 dpi in 2003; and 180 dpi in 2016); however, this did not affect the measurements as outlining each cushion plant and measuring the several components on each cushion plant was not ever performed at the highest resolution. Both cameras had standard lenses which created minimal distortion. Because cushion plants were always photographed in the centre of the images, any distortions around the edges of cushion plants were negligible. To assess how *Azorella* size and stem mortality have changed in relation to *Agrostis* cover, the photographs for each year were analysed in Fiji ImageJ (Schindelin *et al.*, 2012) and Adobe Photoshop (Adobe Photoshop CS, 2004). *Azorella* size and dead stem area were measured using the polygon area selection tool and the wand tracing tool in Image J (Fig. S1: Appendix S1). *Azorella* size was defined as the total horizontal surface area of the cushion plants (including live stems, dead stems enclosed by live stems, dead stems contiguous with live stems, and parts of the cushion plants that were covered by other vascular plant species and mosses) as observed from directly above in the photographs. The extent of dead stems was used here as a measure of plant vitality, where higher cover of dead stems on an individual plant is assumed to represent lower vitality (following Huntley, 1972). The area of *Agrostis*, other vascular plants, non-vascular plants and rock were also measured using the same methods (Fig. S1: Appendix S1). Where other vascular and nonvascular plant species were growing on the edge of cushion plants and the edges of the cushion plants were not directly visible, I interpolated the plant edge based on the shape of the cushion plants. Similarly, I interpolated the cover of other vascular plant species and mosses when their cover was obscured by *Agrostis* cover; although, this was a very rare occurrence. Dead stems were defined as any portions of *Azorella* individuals that were black or grey in colour (and/or had very low stem densities) and/or if *Azorella* stem tips consisted entirely of brown leaves (following Bergstrom *et al.*, 2015; this did not include autumnal senescence due to photographs in this study being taken in mid- or late-summer).

Due to windiness and the unevenness of the substrate/topography there was some random variation in the quality of the photographs, and, if the variation between images was large, those images were excluded from the dataset: of the 600 images that were analysed, 172 images were excluded from the dataset because 1) the images were of poor quality (e.g. snow or mist in the photographs limited the accuracy of the measurements); 2) the images were taken at slightly different angles in the two years; 3) the incorrect individuals were re-photographed in 2016; or 4) the *Azorella* individuals died or only fragments of the individuals remained. One additional image was removed from the dataset as an outlier because the *Azorella* individual had a very high cover of non-vascular species (i.e. 31 % cover of two different non-vascular plant species). Only cushion plant individuals with suitable photographs from both 2003 and 2016 were included in the final analyses.

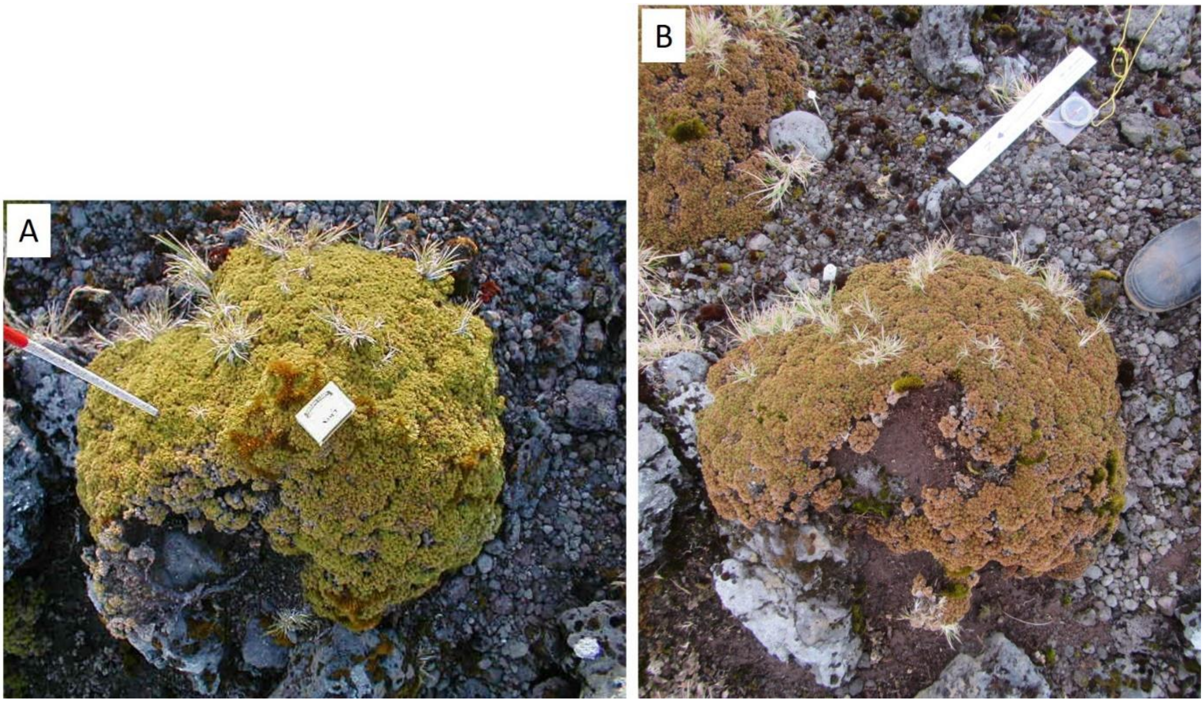

Figure 1. Pictures of the same *Azorella selago* individual photographed in 2003 (A) and 2016 (B) respectively, at the low altitude site on the western side of Marion Island. Photographs were taken directly from above with a scale bar (5.2 cm matchbox and 30 cm ruler) included. Possible causes of *A. selago* damage on Marion Island include wind, mouse burrowing and pathogens.

Data analysis

To test if *Agrostis* has a long-term negative effect on *Azorella* growth, a general linear mixed model (LMM) was used to model final *Azorella* size (i.e. *Azorella* area in 2016) in response to initial *Agrostis* cover on *Azorella* (i.e. % cover in 2003), initial *Azorella* dead stem cover on *Azorella*, initial total cover of other vascular plants and mosses on *Azorella*, aspect and altitude (eqn. 1). To examine whether *Agrostis* has a negative impact on *Azorella* vitality the same models were run using final *Azorella* dead stem cover as a response variable (eqn. 2). Finally, because dead *Azorella* stems are less densely packed than live *Azorella* stems, and dense cushion plants can have a lower epiphyte cover than lax cushions (Bonanomi *et al*., 2016; Jiang *et al*., 2018), we test if dead *Azorella* stems facilitated an increase in the final *Agrostis* cover by modelling final cover of *Agrostis* on *Azorella* in response to initial *Azorella* size, initial *Azorella* dead stem cover, initial cover of other vascular plants and mosses on *Azorella*, aspect and altitude (eqn. 3). The initial size variables of each of the corresponding response variables were included into each model as an offset variable. The images were re-analysed, and the analyses were repeated to include only the plant cover within the perimeter of each cushion plant. Additional models were run using the absolute change in:1) *Azorella* size, 2) *Azorella* dead stem area, and 3) *Agrostis* area as response variables. However, results from these models did not differ considerably and are therefore reported in Table S1-S3 in Appendix S1.

The initial cover of other vascular plants and mosses were included into all models to account for the effect of these other, sub-ordinate species. To account for the spatial structure of the data, a random effect of "Plot" was included in all models. Current *Azorella* dead stem cover was approximately normally distributed; however, current *Azorella* size and current *Agrostis* cover were log- and square root-transformed respectively as the data were not normally distributed. When initial *Azorella* size was used as a predictor variable (eqns. 2 & 3), it was rescaled using a log-transformation. Therefore, the coefficients for *Azorella* size presented from these analyses are for the transformed data. All *Azorella* individuals from the high-altitude plots were excluded from the analysis of eqn. 3 as *Agrostis* was absent from most of these individuals (93%) in both the current and initial year of survey.

$$\begin{aligned}
&\log(current\ Azorella\ size\ (cm2)) \sim initial\ Agrostis\ cover\ (\%) \\
&+ initial\ Azorella\ dead\ stem\ area\ (\%) + Altitude + Aspect \\
&+ initial\ combined\ cover\ of\ other\ vascular\ plants\ and\ mosses\ (\%) \\
&+ (initial\ Agrostis\ cover\ (\%)\ x\ Altitude) + (initial\ Agrostis\ cover\ (\%)\ x\ Aspect) \\
&+ offset\ (\log(initial\ Azorella\ size\ (\%))) \\
&+\ (1|Plot) \qquad (eqn. 1)
\end{aligned}$$

$$\begin{aligned}
&Current\ \ Azorella\ dead\ stem\ cover\ (\%){\sim}\ initial\ Azorella\ size\ (cm2) \\
&+ initial\ Agrostis\ area\ (\%) + Altitude + Aspect \\
&+ initial\ combined\ cover\ of\ other\ vascular\ plants\ and\ mosses\ (\%) \\
&+ (initial\ Agrostis\ cover\ (\%)\ x\ Altitude) + (initial\ Agrostis\ cover\ (\%)\ x\ Aspect) \\
&+ offset(initial\ Azorella\ dead\ stem\ cover\ (\%)) \\
&+\ (1|Plot) \qquad (eqn. 2)
\end{aligned}$$

$$\begin{aligned}
&\mathit{sqrt}\big(\mathit{current\ Agrostis\ cover}\ (\%)\big) \sim \mathit{initial\ Azorella\ size}\ (\mathit{cm}2)\\
&+ \mathit{initial\ Azorella\ dead\ stem\ cover}\ (\%) + \mathit{Altitude} + \mathit{Aspect}\\
&+ \mathit{Combined\ cover\ of\ other\ vascular\ plants\ and\ mosses}(\%)\\
&+ (\mathit{initial\ dead\ stem\ cover}\ (\%)\ x\ \mathit{Altitude}) + (\mathit{initial\ dead\ stem\ cover}\ (\%)\ x\ \mathit{Aspect})\\
&+ \mathit{offset}(\mathit{initial\ Agrostis\ cover}\ (\%))\\
&+\ (1|\mathit{Plot}) \qquad\qquad (\mathit{eqn}.3)
\end{aligned}$$

To reproduce the analyses that are typically used to examine beneficiary feedback effects, I additionally ran complementary linear mixed models to examine the response of *Azorella* size, *Azorella* dead stem cover and *Agrostis* cover against the above-mentioned predictor variables based only on data from a single time period (i.e. from 2003 and from 2016, using a snapshot approach separately for each time period; e.g. Pugnaire *et al*., 1996; Llambí *et al*., 2018). For these analyses, I only included the same cushion plants that were used in the first analyses to allow a clear comparison of the two approaches.

Finally, analyses of *Azorella* growth were complemented with analyses, using only a snapshot approach, of two other measures of *Azorella* performance: number of flower buds and number of fruits. Data were only available from a single time period (i.e. 2003). A generalized linear mixed effects model (assuming a negative binomial distribution to account for overdispersion and using plot as a random effect) was used to test if *Agrostis* density was negatively related to 1) the number of flower buds and 2) the number of fruits on *Azorella* (data from Nyakatya, 2006).

All analyses were conducted in R v.3.3.3 (R Core Team 2017) using the packages “car” (Fox & Weisberg, 2011), “lme4” (Bates *et al*., 2011) and glmmADMB (Fournier *et al*., 2012).

RESULTS

Five out of the 300 monitored *Azorella* individuals died over the 13 years (i.e. an annual mortality rate of c. 0.1% p.a. for plants > 15 cm diameter). The mean *Agrostis* cover on these 5 individuals (mean ± SE initial *Agrostis* cover: 5.3 ± 3.1 % in 2003) was less than the mean *Agrostis* cover on the surviving *Azorella* individuals (mean ± SE initial *Agrostis* cover: 9.6 ± 1.0 % in 2003). *Agrostis* cover increased on c. 55 % of the 214 *Azorella* individuals across the timer period (only considering plants with suitable photographs from both 2003 and 2016; see Table 1). Across all cushion plants, *Agrostis* cover on *Azorella* increased on average from 12.0 ± 1.1 % in 2003 to 19.1 ± 1.6 % in 2016 at the low altitude sites, and from 13.0 ± 1.4 % to 18.8 ± 1.9 % at the mid altitude sites (*Agrostis* was absent from the majority of *Azorella* individuals at the high-altitude sites in both years). The majority of *Azorella* cushion plants (c. 93 %; Table 1) increased in size. Dead stem cover also increased on most (c. 85 %) of the *Azorella* cushion plants (dead stem cover increased from 18.4 ± 0.8 % in 2003 to 25.7 ± 0.9 % in 2016), while *Azorella* live stem area increased on average by 1378.7 cm^2 in 2003 to 1779.2 cm^2 in 2016 despite stem deaths.

In contrast to the very slow vertical growth rate of 0.43 ± 0.01 $cm.yr^{-1}$ (mean ± SE) reported for *Azorella* (le Roux & McGeoch, 2004), average cushion plant diameter increased by 1.99 ± 0.1 $cm.yr^{-1}$. The sizes of *Azorella* individuals recorded and measurements recorded for *Agrostis* cover from the images correlated strongly and significantly with size measurements of the same individuals taken in the field, i.e. for circumference (R^2 = 0.89 in 2003 and 0.79 in 2016), maximum diameter (R^2 = 0.81 in 2003 and 0.85 in 2016) and *Agrostis* cover (R^2 = 0.82 in 2016).

Table 1. The number and percentage of *Azorella selago* individuals with increasing or decreasing: A) size, B) *Agrostis magellanica* cover and C) dead stem cover, based on measurements in 2003 (i.e. initial data; indicated with subscript *i*) and in 2016 (i.e. final data; indicated with subscript *f*). For individual *Azorella* plants, *Agrostis* cover and *Azorella* dead stem cover increased from zero initial cover ($0_i + x_f$) or increased from some initial cover ($x_i + x_f$), decreased from some initial cover ($x_i – x_f$) or lost all *Agrostis* cover despite having some cover initially (x_i to 0_f).

	Category	Number of *Azorella* individuals	% *Azorella* individuals
A	*Azorella* increased in size ($x_i + x_f$)	198	92.5 %
	Azorella decreased in size ($x_i – x_f$)	16	7.5 %
B	*Agrostis* cover gained ($0_i + x_f$)	15	7.0 %
	Agrostis cover gained ($x_i + x_f$)	117	54.7 %
	Agrostis cover lost ($x_i - x_f$)	13	6.1 %
	Agrostis cover lost ($x_i - 0_f$)	1	0.5 %
	Agrostis absent in both years	68	31.8 %
C	Dead stem cover increased ($x_i + x_f$)	182	85.0 %
	Dead stem cover increased ($0_i + x_f$)	2	0.9 %
	Dead stem cover decreased ($x_i – x_f$)	30	14.0 %

Azorella size and stem mortality were not significantly related to *Agrostis* cover in my multivariate models (Table 2). Current *Azorella* size was significantly positively related to cover of other vascular plants and mosses, and significantly negatively related to initial *Azorella* dead stem cover. Current *Azorella* dead stem cover was not significantly related to any of the predictor variables. More generally, neither *Azorella* size nor *Azorella* vitality were significantly related to altitude or aspect (Table 2; Appendix S1: Fig. S2 & S3). Current *Agrostis* cover was not related to initial *Azorella* dead stem cover (Table 2).

Analysis based only on data from the single time period suggested that the relationship between *Agrostis* cover and *Azorella* size may be negative (Table S4: Appendix S1). For example, the relationship between *Agrostis* cover and *Azorella* size was stronger on the eastern side of Marion Island than the western side (Table S4, Fig. S4: Appendix S1). Cushion plant vitality was not significantly related to any predictor variables in 2003 (Table S4), but in 2016 smaller cushion plants had significantly greater dead stem cover than larger cushion plants. In 2016, *Agrostis* cover was also negatively related to dead stem cover and positively related to *Azorella* size and the cover of other vascular plants and mosses.

Lastly, data from a single time period revealed that *Agrostis* cover was not related to the number of flower buds on *Azorella* (Table S5: Appendix S1). However, the number of *Azorella* fruits was significantly negatively related to *Agrostis* cover, with a stronger negative relationship on the western side of the island than on the eastern side (Fig. S5). The number of flower buds and fruits on *Azorella* were also significantly related to both aspect and altitude, with more flower buds on the western side of Marion Island than the east, and less flower buds and fruits on *Azorella* at low and mid altitudes compared to high altitudes.

Table 2. Modelling *Azorella selago* size (n = 214, p = 0.01), *A. selago* dead stem cover (n = 214, p = 0.529) and *Agrostis magellanica* cover (n = 154, p = < 0.01) using linear mixed effects models. Standard deviation of random effect (1|Plot) for *A. selago* size: intercept = 0.02 and residual = 0.60; current *A. selago* dead stem cover: intercept = 98.86 and residual =168.90; and current *A. magellanica* cover: intercept = 0.003 and residual = 1.77. The initial measurement of each response variable was included into each of the corresponding models as an offset variable. Marginal (m) and conditional (c) R^2 values are given in the last column. Cover of other = combined cover of other vascular plant species and mosses. For both categorical variables (Altitude and Aspect) the order of factor levels is indicated.

					Predictor variables: measurements in 2003					
Response variables		**Intercept**	***Agrostis* cover (%)**	**Dead stem cover (%)**	**Cover of other (%)**	**Altitude**	**Aspect**	**% *Agrostis* x Altitude**	**% *Agrostis* x Aspect**	**R^2**
	Value	0.342	-0.146	-0.005	0.037	H < L < M	E > W	0.146	0.004	m = 0.10
Final *Azorella* size (cm^2)	SE	0.137	0.289	0.002	0.012	-	-	0.289	0.006	c = 0.30
	t	2.499	-0.503	-3.061	3.113	0.505	-0.205	0.505	0.616	
	p	0.149	0.616	**0.003**	**0.003**	0.615	0.86	0.614	0.539	
		Intercept	***Agrostis* cover (%)**	***Azorella* size (cm^2)**	**Cover of other (%)**	**Altitude**	**Aspect**	**% *Agrostis* x Altitude**	**% *Agrostis* x Aspect**	**R^2**
	Value	3.83	-13.768	-0.555	-0.012	M > H > L	W > E	13.612	-0.133	m = 0.05
Final dead stem cover (%)	SE	13.365	13.468	1.361	0.569	-	-	13.468	0.278	c = 0.40
	t	0.287	-1.022	-0.408	-0.021	0.954	0.541	1.011	-0.477	
	p	0.78	0.308	0.684	0.984	0.444	0.647	0.313	0.634	
		Intercept	***Azorella* size (cm^2)**	**Dead stem cover (%)**	**Cover of other (%)**	**Altitude**	**Aspect**	**% Dead stem x Altitude**	**% Dead stem x Aspect**	**R^2**
	Value	1.014	0.063	-0.019	0.027	L > M	E > W	-0.021	0.027	m = 0.1023
Final *Agrostis* cover (%)	SE	1.473	0.179	0.015	0.023	-	-	0.018	0.018	c = 0.1038
	t	0.688	0.350	-1.254	1.205	-1.987	0.633	-1.194	1.509	
	p	0.492	0.727	0.212	0.230	0.879	0.602	0.235	0.134	

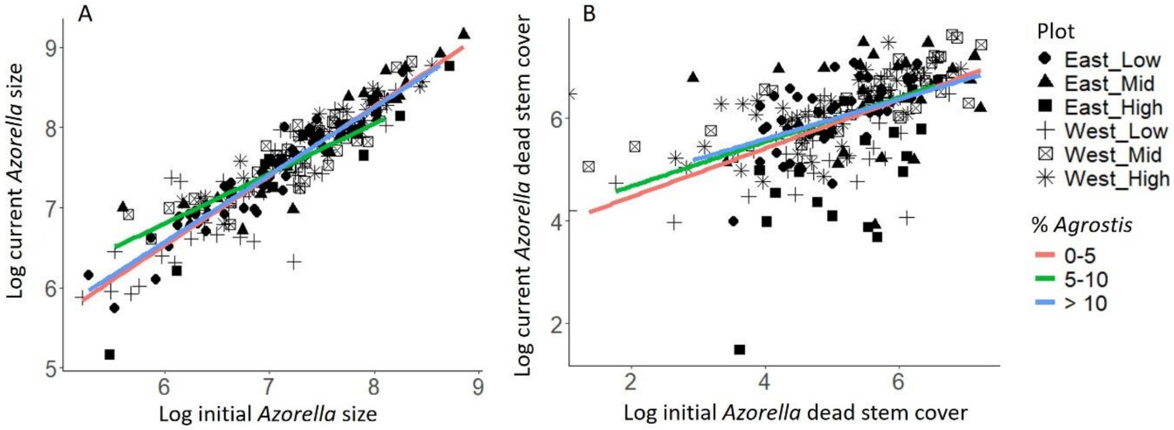

Figure 2. The relationship between A) current and initial *Azorella selago* size and B) current and initial *Azorella selago* dead stem cover with individual regression lines drawn for three categories of *Agrostis magellanica* cover (i.e. 0-5%, 5-10 % or > 10 %; as measured in 2003). *Agrostis* cover was calculated as: [(*Agrostis* area in 2003/*Azorella* size in 2003) x 100]. Symbols represent the sectors of the island (East or West) on which *Azorella* individuals were located and the altitude (low: c. 200 m a.s.l., mid: c. 400 m a.s.l. and high: c. 600 m a.s.l.) at which each individual occurred. Linear regression showed that A) the relationship between current and initial *Azorella* size did not differ with *Agrostis* cover (F = 0.31, p = 0. 735), B) the relationship between current and initial *Azorella* dead stem cover did not differ with *Agrostis* cover (F = 0.24, p = 0.786).

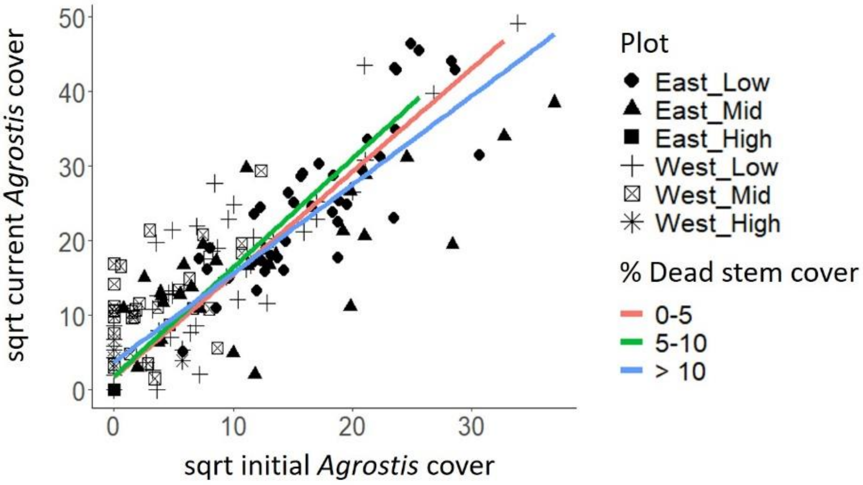

Figure 3. The relationship current and initial *Agrostis magellanica* cover with individual regression lines drawn for three categories of *Azorella selago* dead stem cover (i.e. 0-5%, 5-10 % or > 10 %; as measured in 2003). Dead stem cover was calculated as: [(dead stem area in 2003/*Azorella* size in 2003) x 100]. Linear regression showed that the relationship between current and initial *Agrostis* cover did not differ with *Agrostis* cover (F = 0.09, p = 0.909).

DISCUSSION

The impact of benefactors on associated beneficiaries has been documented from a range of plant communities (Kawai & Tokeshi, 2006; Armas *et al*., 2011; Chen *et al*., 2015; He & Cui, 2015; Hupp *et al*., 2016; Filazzola *et al*., 2018). However, the feedback effects of beneficiaries on their benefactors is infrequently considered and is typically only examined using short-term datasets and/or correlations over a single time period (see Pugnaire *et al*., 1996; Schöb *et al*., 2014b; Michalet *et al*., 2016; Bai *et al*., 2018; Dangles *et al*., 2018; Llambí *et al*., 2018). Here I used a dataset of repeated measurements to examine the consequences of an interaction between a pair of species that characterizes a dominant sub-Antarctic habitat type. I observed three main findings: 1) there was no relationship between beneficiary species' cover and the size and vitality of the benefactor plant species; however, 2) the impact of the beneficiary species varied between benefactor performance measures and depended on the type of approach used (i.e. snapshot vs. repeated measures approaches), and 3) benefactor dead stem cover was not related to an increase in beneficiary cover.

In this study, I confirm that *A. selago* is a slow-growing species and show that *Agrostis* cover increased on the majority of *Azorella* individuals. However, my results reveal no evidence for a long-term negative interaction between *Agrostis* and *Azorella* and, instead, suggest that the relationship between *Agrostis* and *Azorella* is neutral (in agreement with findings from some other benefactor-beneficiary systems; Armas & Pugnaire, 2005; Lortie & Turkington, 2008). Therefore, despite evidence for *Azorella* altering *Agrostis* population structure, and increasing *Agrostis* biomass, reproductive output and abundance compared to surrounding areas where *Azorella* is absent (le Roux & McGeoch, 2008a; le Roux & McGeoch, 2010; le Roux *et al.*, 2013; Raath-Krüger *et al.* in prep), I conclude that *Agrostis* has a neutral impact on cushion plant growth, vitality and survival. Our results, therefore, suggest that the *Azorella*-*Agrostis* interaction could be considered a commensalism (see e.g. Bronstein, 2009; and in contrast to Buwa, 2007: Text S1, Appendix S1).

By using data from a single time period (i.e. a snapshot approach) a broader range of benefactor performance metrics could be examined. However, these results contrasted slightly with those from the repeated measures approach (i.e. from a long-term dataset), suggesting beneficiary feedback effects were either neutral or negative for different measures of benefactor performance. This finding highlights that measurements from a single time period can give different results depending on the timing of the measurement (see e.g. Trinder *et al*., 2013). For example, in this study, the snapshot approach suggests that the relationship between *Agrostis* and *Azorella* is neutral at one time, but negative in another time. However, this interpretation is based on the relative difference in cover of the two species at a single time. If, for example, the relative difference in the cover of *Agrostis* and *Azorella* decreases through time (e.g. due to a faster growth rate in *Agrostis*), a negative correlation between *Agrostis* cover and *Azorella* performance may be observed. Therefore, measurements of beneficiary feedback effects may vary at different points in time.

I used a long-term repeated measures approach in this study and suggest that it may be superior to methods using data from a single time period. However, my correlative approach also has methodological limitations, including its inability to reveal causal relationships (Metz & Tielbörger, 2016). In this study, specifically, microhabitat differences may have caused covariation between *A. selago* and *A. magellanica* growth. Experimental approaches may, therefore, be especially valuable because they provide a mechanistic understanding of the relationship between interacting species and the abiotic environment (Metz & Tielbörger, 2016). However, on Marion Island, a repeated measures approach is more practical, and possibly more robust, for assessing beneficiary feedback effects than an experimental approach because *A. selago* is so slow-growing (le Roux & McGeoch, 2004) and may, therefore, respond gradually over longer periods to changes in biotic interactions and/or disturbances. Our results therefore also highlight the value of long-term datasets (Metz & Tielbörger, 2016) and suggest that perhaps, to accurately assess the reciprocity of biotic interactions, observations from snapshot approaches examining the bidirectional nature of biotic interactions should be explicitly compared to and/or combined with long-term observational and/or long-term experimental approaches across a range of ecological systems where facilitation is prominent.

Our findings also suggest that, based on data from a snapshot approach, beneficiary feedback impacts may vary for different measures of benefactor performance, suggesting that the interaction between *Agrostis* and *Azorella* may be antagonistic for some, but not all, measures of *Azorella* performance and during some moments in time, but not constantly (see e.g. Trinder *et al*., 2013). Therefore, despite *Agrostis* perhaps negatively affecting *Azorella* reproduction, the grass does not impact *Azorella* growth and vitality. Differences in measures of benefactor performance in response to beneficiary cover have been documented from other studies, with, for example, beneficiary cover negatively affecting flower production but not infructescence and fruit densities (García *et al*., 2016), and beneficiary cover and abundance reducing seed set, and flower densities of benefactors but having no effect on benefactor fruit set and seed quality (Schöb *et al*., 2014a). Therefore, different beneficiary feedback effects may be operating simultaneously on different benefactor performance traits. Additionally, the effects of beneficiaries on benefactors are not universal and may depend on other factors such as the life history stage of the interacting individuals (Armas & Pugnaire, 2005; Yang *et al.*, 2017), beneficiary and/or benefactor identity or gender (Lortie & Turkington, 2008; Cranston *et al.*, 2012), beneficiary species richness, phylogenetic diversity or the intensity of the facilitative effect of the benefactor (Schöb *et al.*, 2014a; Schöb *et al.*, 2014b) and abiotic conditions (Michalet *et al.*, 2011). Therefore, to accurately assess the impacts of beneficiary feedback effects, multiple benefactor performance measures need to be considered across a range of systems.

The second key finding from this study was that initial *Azorella* dead stem cover was not related to current *Agrostis* cover, suggesting that *Azorella* cushion plants with many dead stems may not favour an increase in *Agrostis* cover. Therefore, changes in *Agrostis* cover are not affected by *Azorella* compactness, despite compact cushion plants typically being associated with greater species cover, biomass and richness, possibly due to higher soil nutrient contents, more effective heat trapping and greater stability than loose cushion plants (Schöb *et al.*, 2013; Jiang *et al.*, 2017; Yang *et al.*, 2017, but see Al Hayek *et al.*, 2015; Bonanomi *et al.*, 2016). However, the opposite effect of compactness has also been observed in some cushion species (Michalet *et al.*, 2011). For example, *Agrostis* grows easily on the dead parts of a congeneric cushion plant species on Macquarie Island, *Azorella macquariensis* (Whinam *et al.*, 2014). However, the response of *Agrostis* varies depending on the type of damage present on *A. macquariensis*. The response of *Agrostis* to dead stem cover may therefore potentially depend on the cushion plant species examined and/or the type of damage responsible for stem mortality (e.g. damage by mice vs wind vs pathogens). However, in this study, because *Azorella* dead stem cover is not related to *Agrostis* cover, one could speculate that this may be the reason why high *Agrostis* cover does not slow *Azorella* growth (i.e. there is no evidence of a positive feedback loop between *Agrostis* expansion, *Azorella* damage and decreased stem density).

To further understand reciprocal interactions, there are at least two challenges that remain. First, it has been speculated that the effect of benefactors on beneficiaries could shift under changing environmental conditions (in line with the SGH; see Armas *et al.*, 2011; le Roux *et al.*, 2013). However, it is equally important to consider how the feedback effects of beneficiaries on their benefactors could change with shifting environmental conditions (e.g. le Roux *et al.*, 2005; Lin *et al.*, 2012; Schöb *et al.*, 2014b; García *et al.*, 2016; Michalet *et al.*, 2016). For example, Lin *et al.* (2012) demonstrated that symmetric facilitation (i.e. mutualisms) increased the survival of interacting species at the extreme ends of stress gradients; however, asymmetric facilitation (i.e. commensalisms) only increases species' survival under intermediate stress. Therefore, in commensalisms, under more benign conditions (e.g. through climate warming), it may be expected that the growth rate of beneficiary species may increase disproportionately quickly (relative to benefactor species, which are typically stress-tolerators), and this may limit the performance of associated benefactors (le Roux *et al*., 2005; Schöb *et al*., 2014a) and, under extreme circumstances, potentially even lead to the local extinction of the benefactor (Anthelme *et al*., 2014). Second, the outcome of beneficiary feedback effects may be dependent on the life history strategies of the beneficiaries (Liancourt *et al*., 2005). For example, all else being equal, stress-tolerant species may benefit less from facilitation than stress-sensitive species (e.g. competitive species; see Liancourt *et al*., 2005; Maestre *et al*., 2009; Liancourt *et al*. 2017). Therefore, it may be expected that if conditions become more benign, facilitation of stress-sensitive species by benefactor species will collapse (Michalet *et al.*, 2014). Thus, it may be more important to consider the response of beneficiary species to changing abiotic conditions than the response of benefactor species when trying to predict the outcome of biotic interactions in response to warming.

In conclusion, while previous studies have reported negative impacts of beneficiary cover and/or abundance on benefactor performance and vitality (Holzapfel & Mahall, 1999; Michalet *et al*., 2011, Cranston *et al*., 2012; Schöb *et al*., 2014a), I show that beneficiary feedback effects can also be neutral (in line with Lortie & Turkington, 2008). However, the methodology used to examine the feedback effect is also important, as it may affect the observed outcome of biotic interactions (see e.g. Metz & Tielbörger, 2016). A better understanding of the accuracy of long-term monitoring vs. the snapshot approach needs, therefore, to be determined and compared to experimental approaches. The apparent contradiction between results also highlights the potential importance of long-term datasets in assessing the reciprocity of biotic interactions and suggests that studies examining beneficiary feedback effects need to move beyond just using contemporary snapshot approaches and/or short-term experiments because reciprocal interactions are dynamic, and considering temporal dynamism between interacting species may be key in understanding species co-existence in communities (see e.g. Trinder *et al*., 2013; Schofield *et al*., 2018).

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Appendix S1.

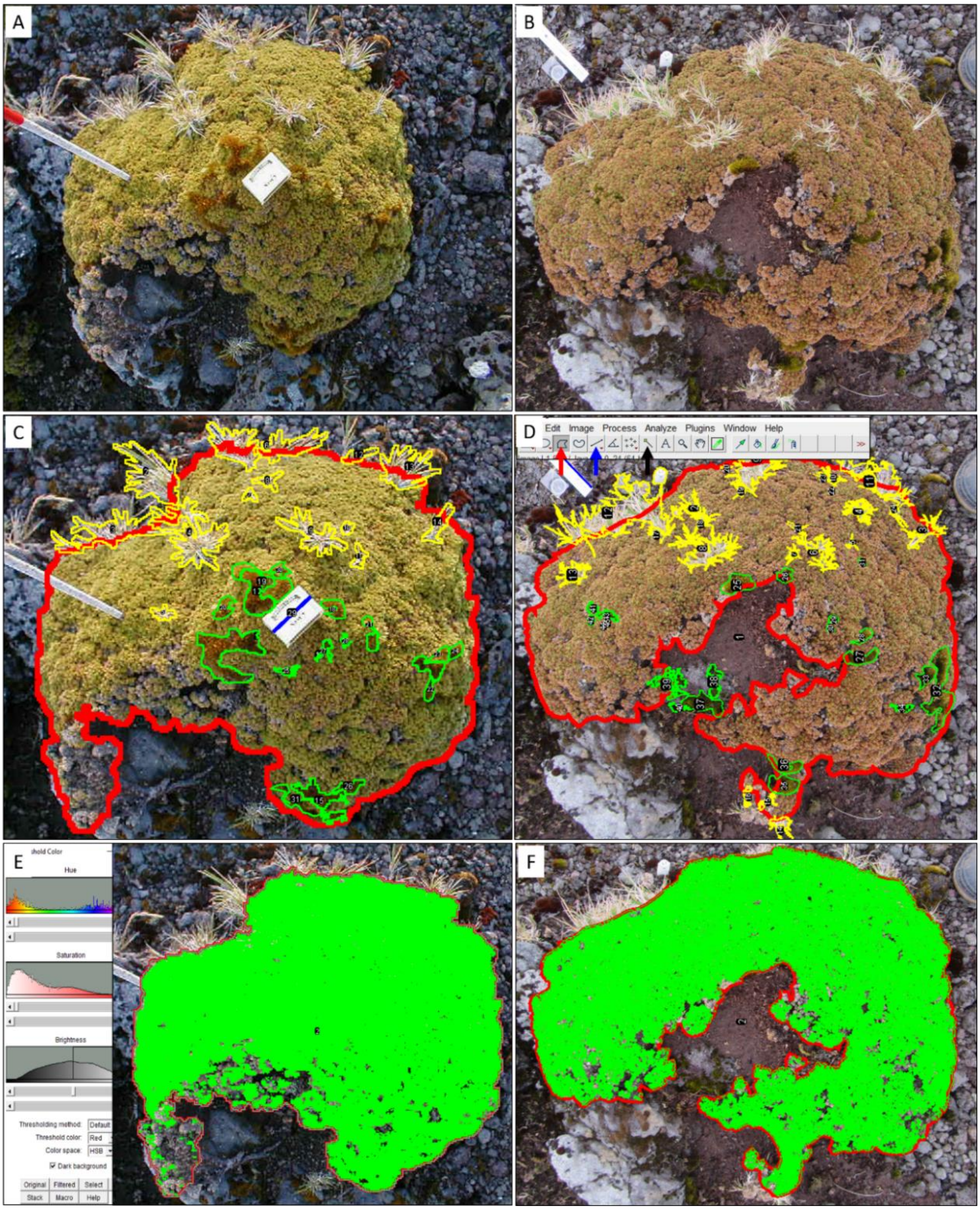

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Figure S1. Pictures of the same *Azorella selago* individual photographed in 2003 (A) and 2016 (B) respectively at a low altitude site on the western side of Marion Island. Each photograph was analysed in Image J. C & D) The scale of the image was set by using the length of a matchbox and ruler (blue lines and blue arrow); cushion plant circumference and area (red lines) were measured using the area selection tool (red arrow); and *Agrostis magellanica* area (yellow outlines) and the area of other vascular and non-vascular plants (green outlines) were measured by selecting *A. magellanica* individuals and other vascular and non-vascular plant individuals using the wand tracing tool (black arrow). E & F) Dead stem cover on each cushion plant was measured by adjusting the colour threshold on each image (see left inset in panel E): green shading represents the live stem area on each cushion plant and the remaining transparent regions are where cushion plant stems were dead after excluding the other cover types.

Table S1. *Azorella selago* size (n = 214, p = 0.02), *A. selago* dead stem cover (n = 214, p = 0.282) and *Agrostis magellanica* cover (n = 154, p = 0.07) in relation to the listed fixed and random effects, where the cover of *A. magellanica* shoots extending beyond the cushion plant perimeter were excluded from analyses during image analysis (i.e. by cropping images to the outline of each *A. selago* plant). Standard deviation of random effect (1|Plot) for *A. selago* size: intercept = 0.01 and residual = 0.07; current *A. selago* dead stem cover: intercept = 63.98 and residual = 170.76; and current *A. magellanica* cover: intercept = < 0.001 and residual = 0.994. The initial measurement of each response variable was included into each of the corresponding models as an offset variable. Marginal (m) and conditional (c) R^2 values are given in the last column. Cover of other = combined cover of other vascular plant species and mosses. For both categorical variables (Altitude and Aspect) the order of factor levels is indicated.

				Predictor variables: measurements in 2003						
Response variables in 2016		**Intercept**	***Agrostis* cover (%)**	**Dead stem cover (%)**	**Cover of other (%)**	**Altitude**	**Aspect**	**% *Agrostis* x Altitude**	**% *Agrostis* x Aspect**	**R^2**
Final *Azorella* size (cm^2)	Value	0.347	-0.004	-0.005	0.026	H < L < M	E > W	0.004	-0.002	m = 0.08
	SE	0.114	0.004	0.002	0.011	-	-	0.006	0.009	c = 0.23
	t	3.048	-1.004	-2.936	2.371	0.974	-0.126	0.769	-0.205	
	p	0.110	0.317	0.003	0.019	0.448	0.914	0.444	0.838	
		Intercept	***Agrostis* cover (%)**	***Azorella* size (cm^2)**	**Cover of other (%)**	**Altitude**	**Aspect**	**% *Agrostis* x Altitude**	**% *Agrostis* x Aspect**	**R^2**
Final dead stem cover (%)	Value	6.716	0.023	-0.920	-0.181	M > H > L	W > E	-0.056	-0.359	m = 0.04
	SE	12.405	0.195	1.377	0.511	-	-	0.265	0.436	c = 0.30
	t	0.541	0.118	-0.668	-0.355	0.790	0.693	-0.212	-0.824	
	p	0.595	0.907	0.505	0.723	0.513	0.565	0.832	0.411	
		Intercept	***Azorella* size (cm^2)**	**Dead stem cover (%)**	**Cover of other (%)**	**Altitude**	**Aspect**	**% Dead stem x Altitude**	**% Dead stem x Aspect**	**R^2**
Final *Agrostis* cover (%)	Value	0.937	-0.011	-0.016	0.005	L > M	E > W	0.008	0.026	m = 0.08
	SE	0.927	0.126	0.011	0.003	-	-	0.014	0.014	c = 0.08
	t	1.011	-0.087	-1.359	1.496	-0.917	-0.697	0.582	1.854	
	p	0.314	0.931	0.176	0.137	0.361	0.487	0.561	0.070	

Table S2. Analyses based only on data from a single time period (i.e. either in 2003 or in 2016) where the cover of *Agrostis magellanica* shoots extending beyond the cushion plant perimeter were excluded from analyses. *Azorella selago* size, *A. selago* dead stem cover and *A. magellanica* are modelled in response to cover in 2003 (initial measurements) and 2016 (final measurements) using linear mixed effects models. Standard deviation of random effect (1|Plot) for A. selago size in 2003 and 2016 respectively: intercept = < 0.001 and residual = 0.441 and; current A. selago dead stem cover: intercept = 11.03 residual =132.11 and; and current *A. magellanica* cover: intercept = 0.210 and residual = 1.431 and. Marginal (m) and conditional (c) R^2 values are given in the last column. For both categorical variables (Altitude and Aspect) the order of factor levels is indicated (> = greater than, < = less than).

		Predictor variables: measurements in 2003								
Response variables in 2003		**Intercept**	***Agrostis* cover (%)**	**Dead stem cover (%)**	**Cover of other (%)**	**Altitude**	**Aspect**	**% *Agrostis* x Altitude**	**% *Agrostis* x Aspect**	**R^2**
Azorella size (cm^2)	Value	7.482	0.017	-0.002	-0.037	H > M > L	E > W	-0.008	0.055	m = 0.214
	SE	0.131	0.009	0.004	0.024	-	-	0.011	0.019	c = 0.214
	T	56.942	1.839	-0.545	-1.539	-5.251	0.196	-0.782	2.876	
	P	< 0.01	**0.009**	0.586	0.125	0.180	0.845	0.435	**0.020**	
		Intercept	***Agrostis* cover (%)**	***Azorella* size (cm^2)**	**Cover of other (%)**	**Altitude**	**Aspect**	**% *Agrostis* x Altitude**	**% *Agrostis* x Aspect**	**R^2**
Dead stem cover (%)	Value	16.789	-0.025	-0.636	0.530	M > H > L	W > E	-0.499	0.142	m = 0.104
	SE	9.658	0.169	1.210	0.439	-	-	0.366	0.218	c = 0.173
	T	1.738	-0.147	-0.526	1.207	1.335	0.147	-1.362	0.649	
	P	0.086	0.884	0.600	0.229	0.299	0.897	0.177	0.520	
		Intercept	***Azorella* size (cm^2)**	**Dead stem cover (%)**	**Cover of other (%)**	**Altitude**	**Aspect**	**% Dead stem x Altitude**	**% Dead stem x Aspect**	**R^2**
Agrostis cover (%)	Value	0.686	0.509	0.011	0.022	L > M	E > W	0.005	-0.032	m = 0.616
	SE	1.165	0.146	0.014	0.052	-	-	0.016	0.017	c = 0.665
	T	0.588	3.485	0.799	0.421	-3.442	-2.920	0.283	-1.917	
	P	0.560	**< 0.001**	0.426	0.675	0.067	0.084	0.778	0.060	

Table S2. continued

		Predictor variables: measurements in 2016								
Response variables in 2016		**Intercept**	***Agrostis* cover (%)**	**Dead stem cover (%)**	**Cover of other (%)**	**Altitude**	**Aspect**	**% *Agrostis* x Altitude**	**% *Agrostis* x Aspect**	**R^2**
Azorella size (cm^2)	Value	7.853	0.057	-0.006	-0.029	H < L < M	E > W	-0.040	0.019	m = 0.241
	SE	0.121	0.506	0.003	0.012	-	-	0.506	0.010	c = 0.241
	T	64.689	0.113	-1.831	-2.441	-5.269	0.870	-0.079	1.848	
	P	**< 0.001**	**< 0.001**	**0.070**	**0.040**	0.000	0.385	0.937	0.154	
		Intercept	***Agrostis* cover (%)**	***Azorella* size (cm^2)**	**Cover of other (%)**	**Altitude**	**Aspect**	**% *Agrostis* x Altitude**	**% *Agrostis* x Aspect**	**R^2**
Dead stem cover (%)	Value	34.40	-4.57	-2.68	0.11	M > H > L	W > E	4.45	-0.29	m = 0.198
	SE	12.25	10.10	1.38	0.25	-	-	10.10	0.24	c = 0.392
	T	2.81	-0.45	-1.94	0.44	1.96	2.15	0.44	-1.20	
	P	**0.04**	0.65	**0.05**	0.66	0.19	0.19	0.66	0.23	
		Intercept	***Azorella* size (cm^2)**	**Cover of other (%)**	**Dead stem cover (%)**	**Altitude**	**Aspect**	**% Dead stem x Altitude**	**% Dead stem x Aspect**	**R^2**
Agrostis cover (%)	Value	1.640	0.532	0.082	-0.026	L > M	E > W	0.002	0.003	m = 0.616
	SE	1.383	0.161	0.025	0.014	-	-	0.016	0.016	c = 0.649
	T	1.185	3.303	3.252	-1.772	-3.402	-3.703	0.116	0.161	
	P	0.239	**0.001**	**0.002**	**0.005**	0.021	0.015	0.907	0.872	

Table S3. Analyses based only on the absolute change in *Azorella selago* size, dead stem area and *Agrostis magellanica* area (between 2003 and 2016) in response to the listed predictor variables (Abs. = Absolute change) where the cover of *A. magellanica* shoots extending beyond the cushion plant perimeter were excluded from analyses. Standard deviation of random effect (1|Plot) for absolute change in *A. selago* size: intercept = 6463 and residual = 203073 and; absolute change in *A. selago* dead stem area: intercept = 13532 and residual = 66047 and; absolute change in *A. magellanica* area: intercept = 0 and residual = 32948 and. Marginal (m) and conditional (c) R^2 values are given in the last column. For both categorical variables (Altitude and Aspect) the order of factor levels is indicated (> = greater than, < = less than).

		Predictor variables in 2003								
Response variables (cm^2)		**Intercept**	***Agrostis* cover (%)**	**Dead stem cover (%)**	**Cover of other (%)**	**Altitude**	**Aspect**	***Agrostis* cover x Altitude**	***Agrostis* cover x Aspect**	**R^2**
Absolute change *Azorella* size	Value	758.264	2.050	-11.407	16.630	L < H < M	E < W	7.410	9.712	m = 0.01
	SE	159.169	7.997	3.332	20.799	-	-	10.262	17.150	c = 0.15
	t	4.764	0.256	-3.423	0.800	-0.970	0.164	0.722	0.566	
	p	**0.036**	0.798	**< 0.001**	0.425	0.435	0.886	0.476	0.573	
		Intercept	***Agrostis* cover (%)**	***Azorella* area (cm^2)**	**Cover of other (%)**	**Altitude**	**Aspect**	***Agrostis* cover x Altitude**	***Agrostis* cover x Aspect**	**R^2**
Absolute change dead stem area	Value	-888.129	-5.783	134.430	3.715	M < H > L	W > E	7.692	-14.523	m = 0.110
	SE	274.058	4.353	30.704	11.377	-	-	5.908	9.706	c = 0.340
	t	-3.241	-1.328	4.378	0.326	0.678	0.584	1.302	-1.496	
	p	0.004	0.186	**< 0.001**	0.744	0.567	0.621	0.195	0.136	
		Intercept	***Azorella* area (cm^2)**	**Dead stem cover (%)**	**Cover of other (%)**	**Altitude**	**Aspect**	**Dead stem x Altitude**	**Dead stem x Aspect**	**R^2**
Absolute change *Agrostis* area	Value	-658.871	131.259	-1.863	8.083	L > M	E > W	1.702	-0.575	m = 0.242
	SE	174.335	23.222	2.189	8.044	-	-	2.594	2.676	c = 0.248
	t	-3.779	5.652	-0.851	1.005	-2.354	-1.209	0.656	-0.215	
	p	**< 0.001**	**< 0.001**	0.396	0.318	0.166	0.251	0.513	0.830	

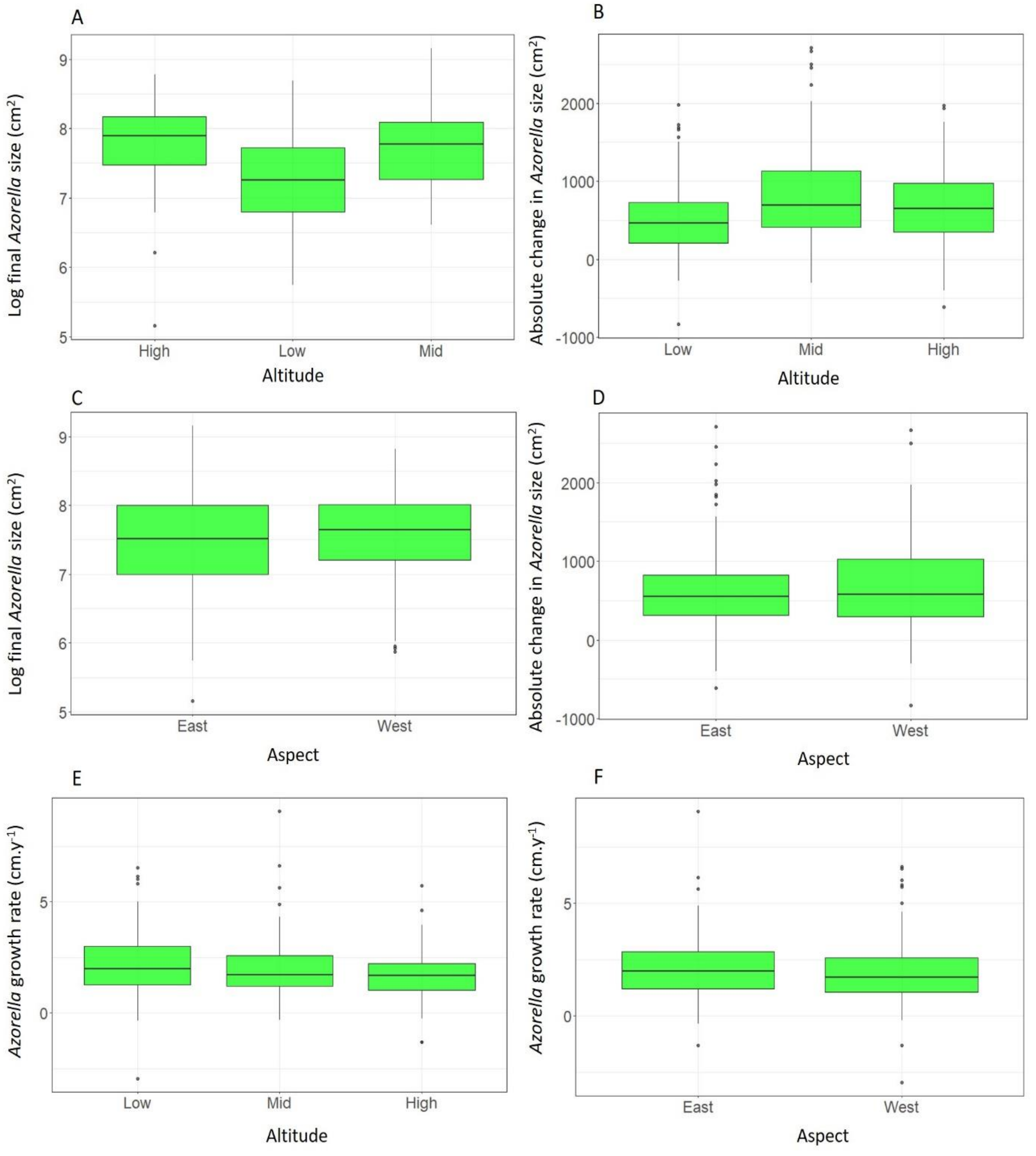

Figure S2. Current *Azorella selago* size (A & C), absolute change in *Azorella* size (B & D) and *Azorella* horizontal growth rate calculated from the maximum diameter (E & F) at different altitudes and on different aspects. None of the differences illustrated here are significant. See Table 2 in the main text for more details.

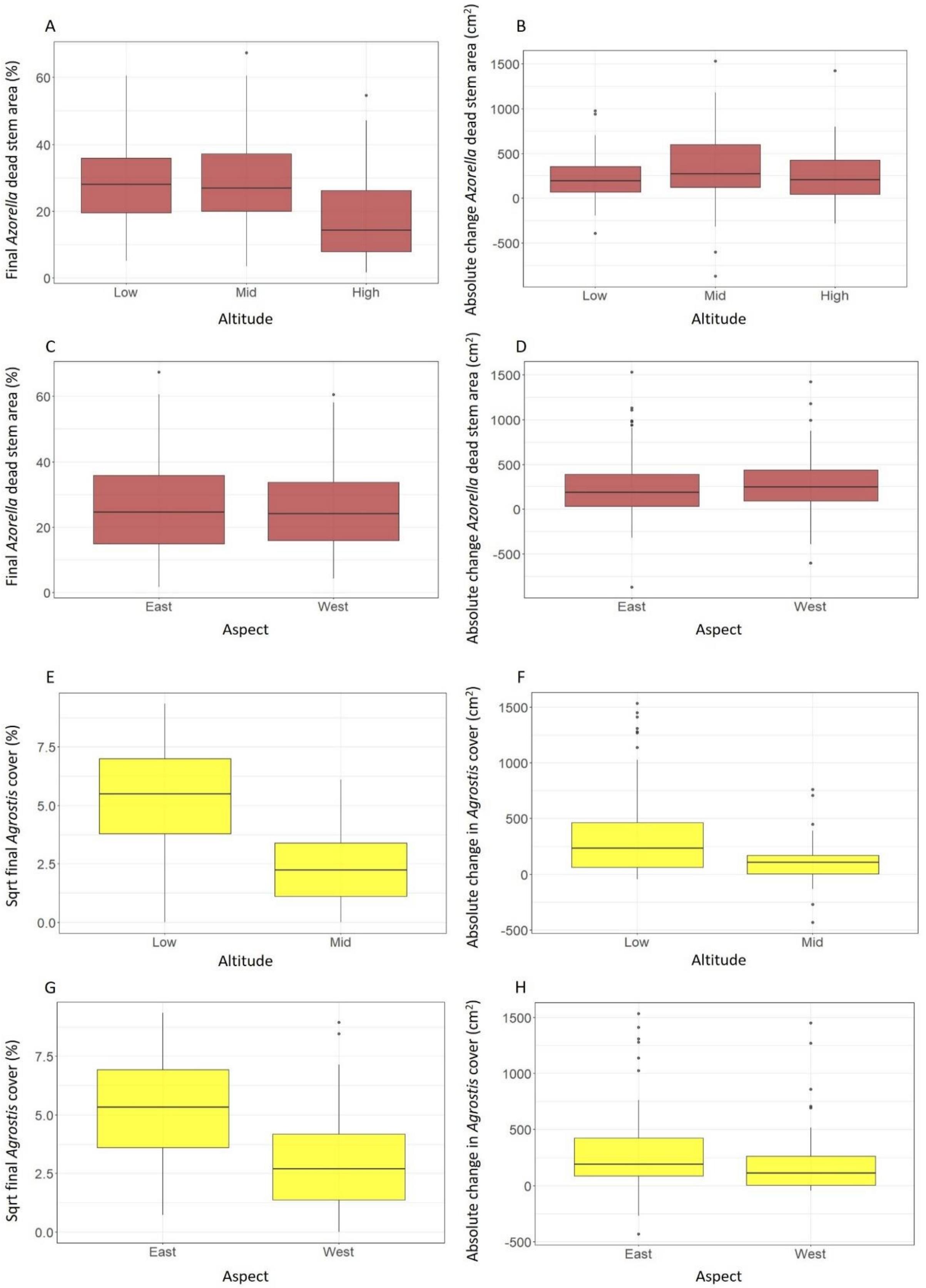

Figure S3. Current *Azorella selago* dead stem cover (A & C), absolute change in *Azorella* dead stem cover (B & D), current *Agrostis magellanica* cover (E & G) and absolute change in *Agrostis* cover at different altitudes and on different aspects. None of the differences illustrated here are significant. See Table 2 in the main text for more details.

Table S4. Analyses based only on data from a single time period (i.e. either in 2003 or in 2016). *Azorella selago* size, *A. selago* dead stem cover and *Agrostis magellanica* are modelled in response to cover in 2003 (initial measurements) and 2016 (final measurements) using linear mixed effects models. Standard deviation of random effect (1|Plot) for *A. selago* size in 2003 and 2016 respectively: intercept = < 0.001 and 0.0163 and residual = 0.447 and 0.375; current *A. selago* dead stem cover: intercept = 6.15 and 41.03 and residual =127.23 and 140.60; and current *A. magellanica* cover: intercept = 0.246 and 0.328 and residual = 1.77 and 2.54. Marginal (m) and conditional (c) R^2 values are given in the last column. For both categorical variables (Altitude and Aspect) the order of factor levels is indicated (> = greater than, < = less than).

		Predictor variables: measurements in 2003								
Response variables in 2003		**Intercept**	***Agrostis* cover (%)**	**Dead stem cover (%)**	**Cover of other (%)**	**Altitude**	**Aspect**	**% *Agrostis* x Altitude**	**% *Agrostis* x Aspect**	**R^2**
	Value	7.619	0.808	-0.003	-0.078	H > M > L	E > W	-0.811	0.034	m = 0.209
Azorella size (cm^2)	SE	0.138	0.693	0.004	0.027	-	-	0.693	0.011	c = 0.209
	T	55.377	1.165	-0.757	-2.835	-1.17	-0.942	-1.17	3.025	
	P	**< 0.001**	0.245	0.45	**0.01**	0.251	0.613	0.243	**0.003**	
		Intercept	***Agrostis* cover (%)**	***Azorella* size (cm^2)**	**Cover of other (%)**	**Altitude**	**Aspect**	**% *Agrostis* x Altitude**	**% *Agrostis* x Aspect**	**R^2**
	Value	18.293	20.358	-0.861	0.834	M > H > L	W > E	-20.28	-0.181	m = 0.13
Dead stem cover (%)	SE	9.433	11.672	1.181	0.479	-	-	11.674	0.214	c = 0.17
	T	1.939	1.744	-0.729	1.743	0.267	0.866	-1.737	-0.843	
	P	0.055	0.083	0.467	0.083	0.294	0.866	0.084	0.406	
		Intercept	***Azorella* size (cm^2)**	**Dead stem cover (%)**	**Cover of other (%)**	**Altitude**	**Aspect**	**% Dead stem x Altitude**	**% Dead stem x Aspect**	**R^2**
	Value	3.391	0.252	0.008	0.008	L > M	E > W	-0.004	-0.017	m = 0.62
Agrostis cover (%)	SE	1.334	0.169	0.016	0.006	-	-	0.018	0.019	c = 0.67
	T	2.542	1.496	0.472	1.356	-3.619	-3.17	-0.219	-0.883	
	P	**0.014**	0.137	0.638	0.177	0.132	0.122	0.827	0.379	

Table S4 continued.

		Predictor variables: measurements in 2016								
Response variables in 2016		**Intercept**	***Agrostis* cover (%)**	**Dead stem cover (%)**	**Cover of other (%)**	**Altitude**	**Aspect**	**% *Agrostis* x Altitude**	**% *Agrostis* x Aspect**	**R^2**
Azorella size (cm^2)	Value	7.872	0.025	-0.007	-0.014	H < L < M	E > W	-0.02	0.004	m = 0.17
	SE	0.165	0.249	0.004	0.01	-	-	0.249	0.006	c= 0.21
	T	47.828	0.099	-2.021	-1.407	-2.845	0.131	-0.081	0.775	
	P	**< 0.01**	0.096	**0.045**	0.01	0.202	0.908	0.936	0.451	
		Intercept	***Agrostis* cover (%)**	***Azorella* size (cm^2)**	**Cover of other (%)**	**Altitude**	**Aspect**	**% *Agrostis* x Altitude**	**% *Agrostis* x Aspect**	**R^2**
Dead stem cover (%)	Value	35.68	-2.652	-2.869	0.039	M > H > L	W > E	2.634	-0.123	m = 0.19
	SE	11.913	4.83	1.345	0.202	-	-	4.829	0.127	c =0.44
	T	2.995	-0.549	-2.133	0.191	0.191	0.629	0.546	-0.975	
	P	**0.005**	0.584	**0.034**	0.849	0.06	0.598	0.586	0.332	
		Intercept	***Azorella* size (cm^2)**	**Cover of other (%)**	**Dead stem cover (%)**	**Altitude**	**Aspect**	**% Dead stem x Altitude**	**% Dead stem x Aspect**	**R^2**
Agrostis cover (%)	Value	3.651	0.426	0.074	-0.023	L > M	E > W	-0.002	0.001	m = 0.55
	SE	1.831	0.214	0.027	0.018	-	-	0.021	0.021	c = 0.60
	T	1.994	1.992	2.707	-1.228	-3.232	-2.497	-0.076	0.043	
	P	**0.05**	**0.048**	**0.008**	**0.04**	0.128	0.177	0.939	0.966	

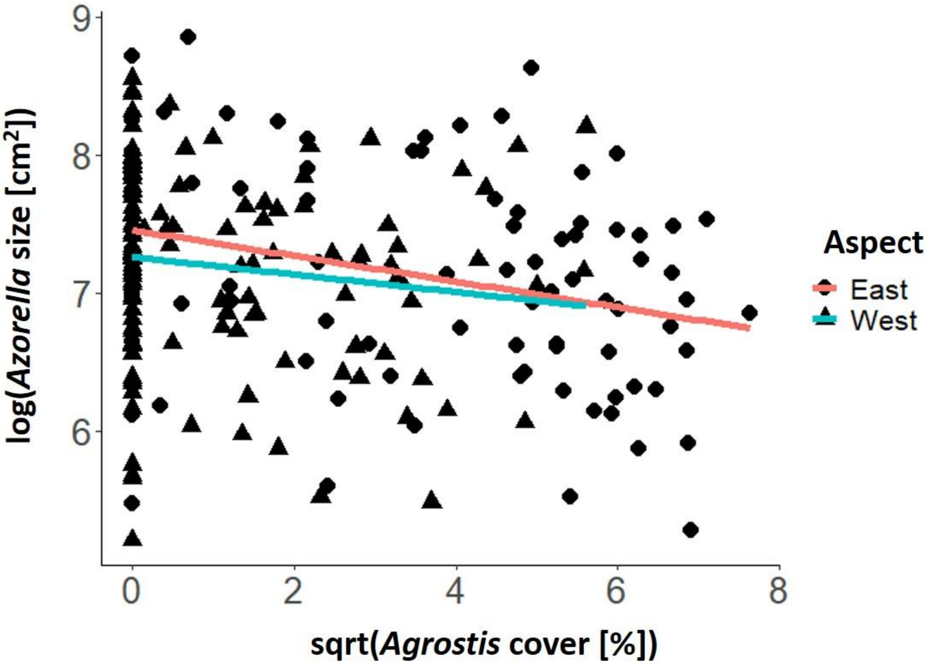

Figure S4. The relationship between *Azorella selago* and *Agrostis magellanica* cover on *Azorella* in relation to aspect (i.e. position of the plots on the eastern or western side of Marion Island) based on data from a single time period (2003). The negative relationship between *Agrostis* cover and *Azorella* size was significantly stronger on the eastern side of Marion Island than the western side (see also Table S1).

Table S5. Modelling the number of fruits and flower buds on *Azorella selago* using generalized linear mixed effects models. Standard deviation of random effect (1|Plot) for number of *A. selago* fruits: variance = < 0.001 and standard deviation = < 0.001; and number of flower buds on *A. selago*: variance = < 0.001 and standard deviation = < 0.001. *Azorella selago* size (in 2003) was included into each model as an offset variable. For both categorical variables (Altitude and Aspect) the order of factor levels is indicated (> = greater than, < = less than).

		Predictor variables (measurements from 2003)						
Response variables		**Intercept**	***Agrostis* cover (%)**	**Cover of other (%)**	**Altitude**	**Aspect**	***Agrostis* cover*Altitude**	***Agrostis* cover*Aspect**
Number of fruits	Estimate	-0.591	1.046	-0.110	H > M > L	W > E	-1.063	-0.062
	SE	0.344	1.689	0.072	-	-	1.689	0.030
	z	-1.720	0.620	-1.520	-	-	-0.630	-2.080
	p	0.086	0.536	0.128	**0.006**	0.310	0.529	**0.037**
		Intercept	***Agrostis* cover (%)**	**Cover of other (%)**	**Altitude**	**Aspect**	***Agrostis* cover*Altitude**	***Agrostis* cover*Aspect**
Number of flower buds	Estimate	-1.450	-2.843	-0.057	H > M > L	W > E	2.817	-0.029
	SE	0.330	1.670	0.063	-	-	1.671	0.026
	z	-4.390	-1.700	-0.910	-	-	1.690	-1.100
	p	**< 0.001**	0.089	0.364	**< 0.001**	**< 0.001**	0.060	0.270

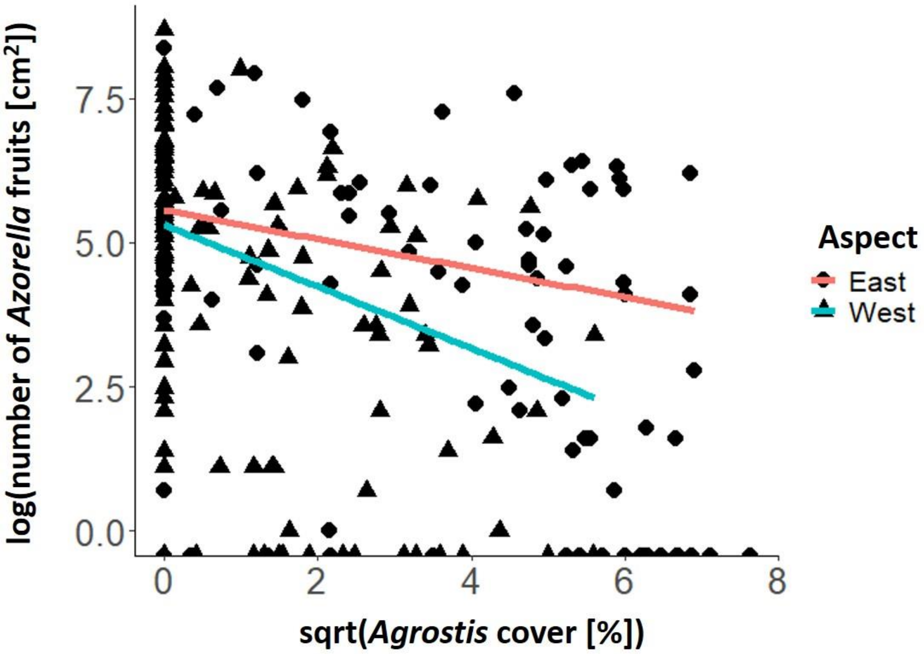

Figure S5. The relationship between the number of *Azorella selago* fruits and *Agrostis magellanica* cover *per Azorella* cushion plant in relation to aspect based on data from a single time period (2003). The negative relationship between *Agrostis* cover and number of *Azorella* fruits was significantly stronger on the western side of Marion Island than the eastern side (see also Table S1).

Text S1

Summary of the methodology utilized by Buwa (2007)

The research by Buwa (2007) has been published as MSc thesis (available from https://scholar.sun.ac.za/handle/10019.1/17743) but here I summarize the key study design points and findings relevant to my chapter. The broad aim of Buwa's (2007) experimental study was to examine the impact of *Agrostis magellanica* cover on *Azorella selago* within the dominant fellfield habitat type on sub-Antarctic Marion Island. Sampling was conducted at three sites (low-altitude, medium-altitude and high-altitude sites: 103 m a.s.l., 176 m a.s.l. and 375 m a.s.l.) on the eastern side of the island between April 2004 and April 2005. At each site, 30 medium-sized *A. selago* individuals with low densities of *A. magellanica* and 50 medium-sized *A. selago* individuals with high *A. magellanica* densities were randomly selected.

Eight treatments were applied randomly to the 80 *A. selago* cushion plants at each site during April-May 2004 and/or September-October 2004. Treatments consisted of 1) high density *A. magellanica* plots (control), 2) low density *A. magellanica* plots (control), 3) autumn thinned *A. magellanica* plots, 4) spring thinned *A. magellanica* plots, 5) autumn clipped *A. magellanica* plots, 6) spring clipped *A. magellanica* plots, 7) procedural control thinned plots (applied in autumn and spring) and 8) procedural control clipped plots (applied in autumn and spring). The thinning treatments (3 & 4) involved weeding *A. magellanica* individuals from 10 *A. selago* individuals by carefully pulling out *A. magellanica* individuals from each cushion plant. The roots and shoots of these individuals were weighed separately using a microbalance. The procedural control thinned plots (7) were applied to 5 cushion plants at each site; metal rods (2 cm in diameter) were inserted ten times into the northern sides of the cushion plants to simulate the action of weeding.

The clipping treatments (5 & 6) were also applied to 10 plants per site. Using scissors, *A. magellanica* individuals for this treatment were cut as close as possible to the surface of the cushion plants. This treatment was designed to assess the effect of shading by *A. magellanica* on *A. selago*. Again, a procedural control (8) was applied in each site to 5 *A. magellanica* individuals by cutting *A. magellanica* individuals close to the surface of the cushion plants in such a way that it caused minor abrasions to the surface of the plants.

At the low and middle altitude sites, phenological data (i.e. the occurrence and cover of flowers and buds) were recorded from the *A. selago* individuals from August 2004 to February 2005, and for the high-altitude site, phenological data were recorded from October 2004 to

February 2005 due to weather constraints. For cushion plants with high *A. magellanica* cover, bud and flower cover were recorded on the sections of the cushion plants that were not covered in grass.

Key findings

The main finding from Buwa's (2007) thesis was the impact of *A. magellanica* on *A. selago* is negative: the percentage of budding and flowering on *A. selago* was negatively related to *A. magellanica* cover. In addition, low grass density cushion plants had greater vitality than high grass density cushion plants.

Cushion plant vitality declined significantly with increasing altitude. Cushion plants from the high-altitude site had significantly more dead stem cover than the low- and mid- altitude sites. In contrast, there was no significant difference in the cover of buds on *A. selago* between the three sites. However, flower cover differed significantly between altitudes, with a significantly greater flowering percentage on *A. selago* at the high-altitude site than the mid- and low-altitude sites for the thinned treatment. In contrast, from the clipped treatments, flowering percentage was greater at mid- and high-altitude sites relative to low-altitude sites.

Budding percentage differed significantly between treatments, with low grass density cushion plants having a higher budding percentage than high grass density, autumn-thinned and spring-thinned cushion plants. Flowering percentage on *A. selago* also differed significantly between treatments. High grass density cushion plants had significantly lower flowering percentages than low grass density cushion plants and procedural-thinned cushion plants. Similar results were obtained for between-treatment comparisons in the clipped *A. magellanica* cushion plants.

References

Buwa, Z.S. (2007) The Interaction between a Keystone Plant Species and its Dominant Epiphyte on Marion Island: Climate Change Implications. MSc Thesis, Stellenbosch University, Cape Town, South Africa.

Vegetation cover declines with elevation on Marion Island. Image taken from the interior of the island.

Chapter 3:

Inter-specific facilitation mediates the outcome of intra-specific interactions across an elevational gradient

*In prep for submission to *Ecology*: Raath-Krüger, M.J., Schöb, C., McGeoch, M.A. & le Roux, P.C. *In prep*. Inter-specific facilitation mediates the outcome of intra-specific interactions across an elevational gradient.

Abstract

Where inter-specific facilitation favours the establishment of high densities of a beneficiary species, strong intra-specific competition may subsequently impede beneficiary performance and may ultimately reduce beneficiary fitness. Consequently, the negative influence of intra-specific competition between beneficiary individuals could potentially outweigh the positive influence of inter-specific facilitation when, for example, higher densities of a beneficiary are negated by the negative effect of crowding on beneficiary reproduction. The aim of this study was, therefore, to examine the impact of an inter-specific interaction on the outcome of intra-specific interactions within the context of plant-plant facilitation. I used the cushion-forming *Azorella selago* and a commonly co-occurring dominant perennial grass species, *Agrostis magellanica*, on sub-Antarctic Marion Island as a model system. I assessed the impact of an inter-specific interaction (between *Azorella* and *Agrostis*) on the outcome of intra-specific interactions (between *Agrostis* individuals), by testing if the impact of *Agrostis* density on *Agrostis* performance is mediated by its interaction with *Azorella*. Observational data from six altitudinal transects were complemented by experimental data. Experimentally reducing intra-specific *Agrostis* density had no effect on *Agrostis* performance. However, the effect of *Azorella* on *Agrostis* (i.e. the inter-specific interaction) was positive, and increasingly so under more severe conditions. Moreover, observational data showed that high *Agrostis* densities may favour conspecific performance, because *Agrostis* performance was significantly positively correlated with conspecific density, both on and away from *Azorella.* These data also suggested that the inter-specific interaction could mediate the outcome of the intra-specific interaction, as the effect of *Agrostis* density on *Agrostis* performance was dependent on whether the grass was growing on or away from *Azorella*. This highlights the importance of considering observational approaches in conjunction with experiments when examining plant-plant interactions, and suggests that, at least in this abiotically-severe environment, species may respond slowly to changes in some biotic interactions. Additionally, my findings suggest that facilitation, both within and between plant species, could matter more than intra-specific competition in some systems. More broadly, these results suggest that both positive inter- and intra-specific biotic interactions should be considered when examining spatial and temporal variation in species' performance.

INTRODUCTION

Biotic interactions may strongly shape ecological communities by affecting plant fitness, abundance, cover and survival (Cavieres *et al*., 2007; Lamb *et al*., 2009; Schöb *et al*., 2013; Zhang & Wang, 2016; Svanfeldt *et al*., 2017; Eurich *et al*., 2018; Kunstler *et al*., 2019). The impact of these interactions can vary considerably across spatial scales and may be strongly linked to environmental conditions (Bertness & Callaway, 1994; Schemske *et al*., 2009; Olsen *et al*., 2016; O'Brien *et al*., 2017). For example, at broad scales, the impact of biotic interactions varies across latitude, with higher predation rates in the tropics than temperate regions (Schemske *et al*., 2009; Roslin *et al*., 2017). Additionally, at finer scales variation in the impact of biotic interactions on species cover and richness has been observed across landscapes, i.e. across gradients of environmental severity (e.g. Mod *et al*., 2016). Biotic interactions are therefore potentially important in determining the structure and functioning of ecological communities, although predicting their impacts may be difficult as they may depend on local environmental conditions.

Inter-specific interactions are typically negative (Eurich *et al*., 2018). For example, if one species from a competitively interacting pair is experimentally removed, the other species may experience a competitive release resulting in increased performance (see e.g. Toumey & Kienholz, 1931; Eurich *et al*., 2018). Strong competition is also generally expected between individuals of the same species due to greater niche overlap within species than between species (e.g. Adler *et al*., 2018). For example, if individuals of the same species are grown in high-density vs. low-density stands, individuals from the low-density stands may perform better than the individuals from high-density stands (e.g. Tilman & Cowan, 1989; Kufel *et al*., 2018; but see in contrast, Leicht-Young *et al*., 2011). Thus, it is typically assumed that intra-specific interactions will also have negative outcomes, with, for example, self-thinning reducing conspecific abundance. Therefore, both negative inter- and intra-specific interactions may be important when examining plant species’ survival and performance.

While many studies have documented the impact of negative interactions (e.g. both intra- and inter-specific competition) on populations and communities (Tilman & Cowan, 1989; Stoll & Prati, 2001; Armitage & Jones, 2019; Warren *et al*., 2019), the importance of positive (e.g. facilitative) interactions has gained recognition in the last 20 years (Bruno *et al*., 2003; Zhang & Wang, 2016). Facilitative interactions are defined as interactions where the presence of certain species (i.e. benefactor species) can enhance the growth, reproduction and/or survival of other species (i.e. beneficiary species and/or individuals) by ameliorating the local microclimate, increasing resource availability, improving substrate stability, and/or providing associational defence from herbivores (Cavieres *et al*., 2006; Molenda *et al*., 2012; Schöb *et al*., 2013; Bonanomi *et al*., 2016; Hupp *et al*., 2017). Facilitation between species can be particularly important for ecological communities in environmentally-severe habitats (Bruno *et al*., 2003; Hupp *et al*., 2017; see also SGH: Bertness & Callaway, 1994). Moreover, facilitation has been observed intra-specifically (Eränen & Kozlov, 2008; Goldheim *et al*., 2008; Fajardo & McIntire, 2011; García-Cervigón *et al*., 2013; Zhang & Wang, 2016; Svanfeldt *et al*., 2017). For example, individuals of the same plant species can mitigate the impact of abiotic stress on one another (thereby benefitting one another) when growing in dense stands (e.g. Goldenheim *et al*., 2008; Zhang & Tielbörger, 2019). Irrespective of whether interactions are positive or negative, the outcome of biotic interactions may be influenced at both the inter- and intra-specific levels.

For example, if the facilitative effects of benefactor species change the composition of associated beneficiary species, this may have consequences for the interactions among the beneficiary species (e.g. Saccone *et al*., 2010; Zhang & Wang, 2016; Llambí *et al*. 2018). The effects of interactions among beneficiaries appear to mostly be competitive, with negative impacts on plant growth and survival (Aguiar & Sala, 1994; Schöb *et al*., 2013). However, the outcome of these interactions can also be positive where beneficiaries facilitate one another. For example, beneficiary species can benefit from enhanced pollination by attracting shared pollinators (e.g. Molina-Montenegro *et al*., 2008). Moreover, one species can facilitate other species through the competitive suppression of a third species (i.e. through indirect facilitation; Levine, 1999; Llambí *et al*. 2018). Adult plants can also have a positive effect on conspecific seedlings through the reduction of herbaceous competitors (e.g. through intra-specific facilitation; see Saccone *et al*., 2010). Beneficiary survival and/or performance is therefore dependent on the effect of the benefactor species and the effect of interactions among beneficiary species (inter-specific interactions) and/or individuals (intra-specific interactions) themselves.

When a benefactor facilitates beneficiaries (Fig. 1A.; see also, e.g., Cavieres *et al*., 2006; Molenda *et al*., 2012; Schöb *et al*., 2013; Bonanomi *et al*., 2016; Hupp *et al*., 2017), the density of beneficiaries may be higher in the presence of a benefactor species, and consequently, beneficiaries may experience stronger intra-specific competition (Fig. 1B; Tielbörger & Kadmon, 2000; García-Cervigón *et al*., 2013). Thus, by increasing the productivity and/or density of beneficiaries, inter-specific interactions could potentially mediate the outcome of interactions among beneficiaries (see e.g. Armas *et al.*, 2008; García-Cervigón *et al.*, 2013; Schöb *et al.*, 2013; Llambí *et al.* 2018). For example, the positive effect that a benefactor has on the abundance of beneficiaries may be negated by the negative effect of high conspecific density on beneficiary reproduction. Thus, even if beneficiaries reach high densities as a result of facilitation by a benefactor, unless the beneficiaries are also able to reproduce, the net effect of the benefactor on the beneficiaries will not be positive. Alternatively, facilitation by a benefactor could overwhelm the negative effects among beneficiaries, allowing beneficiaries a greater degree of co-existence (at the community-level) and/or higher fitness (at the species-level) than in the absence of the benefactor (Armas *et al.*, 2008; see also e.g. Feldman & Morris, 2011). For example, when facilitation is absent (e.g. in a semi-arid system), a stress-tolerant species may have a competitive advantage over another species (see Armas *et al.*, 2008). However, where both species are facilitated by a benefactor, they are more likely to coexist.

Here, I examine the impact of an inter-specific interaction (Fig. 1A; between a benefactor and a beneficiary species) on the outcome of intra-specific interactions (Fig. 1B & 1C). I use *Azorella selago* (*Azorella* hereafter), a widespread cushion plant, and a dominant perennial grass species, *Agrostis magellanica* (*Agrostis* hereafter) as a model system on Marion Island. Both experimental and observational approaches are used to assess the relationship between *Agrostis* density and *Agrostis* performance (i.e. intra-specific interactions), and how these interactions are modified by the interaction between *Azorella* and *Agrostis* (i.e. the inter-specific interaction). I ask three broad questions: 1) is the outcome of the inter-specific interaction between *Azorella* and *Agrostis* positive, and does the outcome of this interaction vary at the intra-individual level (i.e. within individual cushion plants: in line with Anthelme, *et al*., 2017; and see “facilitation in the halo” concept by Pescador *et al*., 2014)?; 2) is higher *Agrostis* density, due to the interaction with *Azorella*, correlated with poorer *Agrostis* performance?; and 3) will *Agrostis* performance increase if conspecific density is experimentally reduced? I expect the inter-specific interaction between *Azorella* and *Agrostis* to be positive (in agreement with le Roux & McGeoch, 2010; le Roux *et al*., 2013), and increasingly so on the edges of *Azorella* cushion plants as opposed to the centres of the cushion plants (see Anthelme *et al*., 2014). However, I expect the facilitative effect of *Azorella* on *Agrostis* (Fig. 1A) to increase the density of *Agrostis*, resulting in strong competition among *Agrostis* conspecifics. Consequently, *Agrostis* performance will be reduced (Fig. 1B), possibly even overwhelming the facilitative effect of *Azorella* on *Agrostis* (following, e.g., García-Cervigón *et al*., 2013). Alternatively, it is possible for interactions among *Agrostis* conspecifics to be facilitative (e.g. Goldenheim *et al*., 2008; Saccone *et al*., 2010; or weak relative to the impact of the inter-specific interaction), in which case, *Agrostis* performance may be improved by the interaction with *Azorella*, irrespective of the grass's density (Fig. 1C). Although interactions between beneficiaries that are a result of facilitation by benefactors are infrequently considered in empirical studies, they could have profound implications for communities (Schöb et al., 2013a; Llambí et al., 2018).

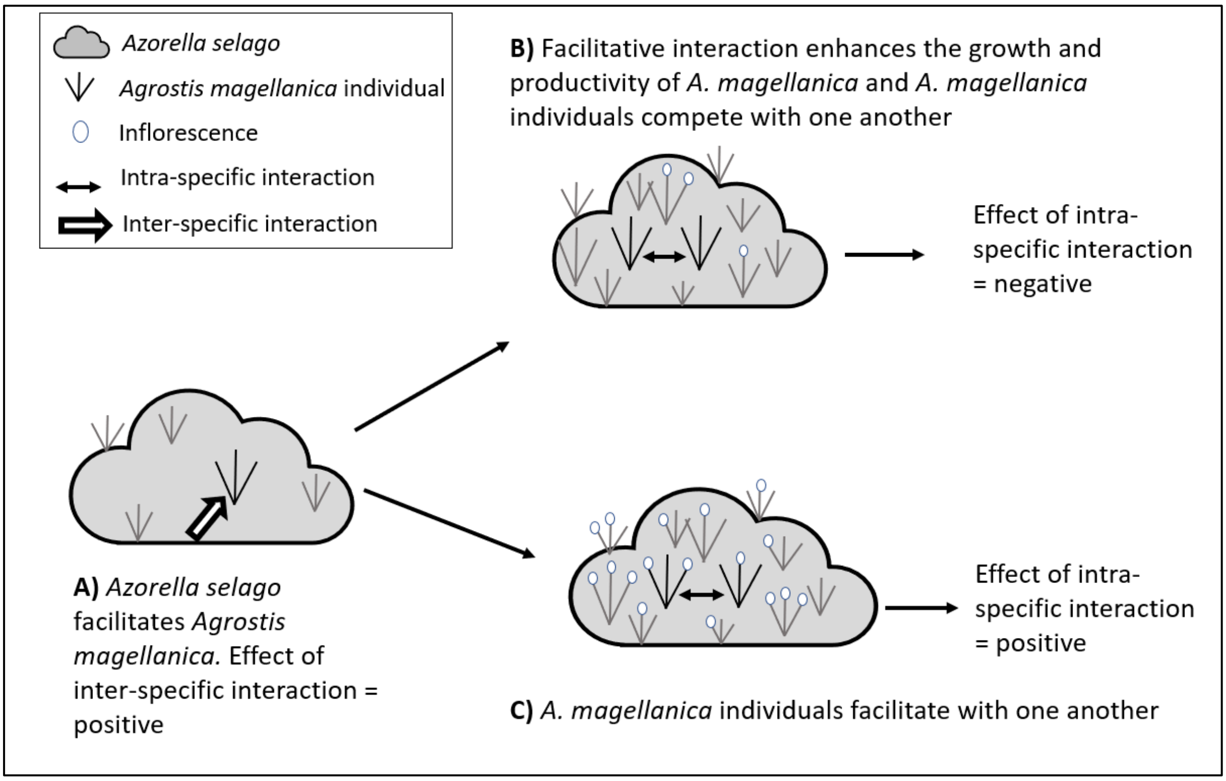

Figure 1. Visual representation of the hypotheses considered in this study: A, B) the facilitative effect of *Azorella selago* on *Agrostis magellanica* will result in competition among *A. magellanica* conspecifics which will reduce *A. magellanica* reproductive performance (i.e. net reduction in fitness); or A, C) the facilitative effect of *A. selago* on *A. magellanica* will indirectly result in increased intra-specific facilitation among *A. magellanica* conspecifics, improving *A. magellanica* reproductive performance.

METHODS

Study site and species

This study was conducted on sub-Antarctic Marion Island (46º54 S, 32º45 E; 290 km^2), which is located in the southern Indian Ocean (Chown & Froneman, 2008). Marion Island has a hyperoceanic climate, with low but very stable seasonal and daily temperatures, along with high precipitation and humidity, cloud cover on most days, and frequent strong winds (Smith & Steenkamp, 1990; le Roux, 2008). Altitude represents an important stress gradient on the island, as temperature and substrate stability decrease with elevation and wind speed increases (Goddard *et al*., unpublished data; Boelhouwers *et al*., 2003; le Roux & McGeoch, 2010).

The island supports 22 indigenous vascular plant species and approximately 200 bryophyte and lichen species (Smith, 1987; Greve *et al*., 2019). Here, I examine the interaction between the two most widespread vascular plants on Marion Island, *Azorella selago* Hook. (Apiaceae) and *Agrostis magellanica* (Lam.) Vahl. (Poaceae). *Azorella selago* is a cushion plant species (i.e. a compact, hemispherical species) occurring on multiple sub-Antarctic islands and in many habitat types on those islands. Due to its cushion growth form, *Azorella* ameliorates stressful environmental conditions (see Nyakatya & McGeoch, 2008; McGeoch *et al*., 2008), particularly in the cold, wind-exposed areas where the cushion plant is commonly found. Consequently, *Azorella* hosts an array of species, including invertebrates and other plant species (Huntley, 1971; Huntley, 1972; Barendse & Chown, 2001; Barendse *et al*., 2002; Hugo *et al*., 2004), which makes the plant an important ecosystem engineer and keystone species (Hugo *et al*. 2004). Indeed, cushion plants elsewhere have also been shown to positively impact other plant species (Badano & Cavieres, 2006a; Cavieres *et al*., 2007; Xu *et al*., 2010; Hupp *et al*., 2017; Yang *et al*., 2017).

Agrostis magellanica is a dominant perennial grass species on Marion Island and is the most common vascular plant species growing on *Azorella* (Huntley, 1971). *Agrostis magellanica* is found in most habitats on Marion Island, occurring up to 600 m above sea level (le Roux & McGeoch, 2008). The *Azorella* (benefactor)-*Agrostis* (beneficiary) interaction on Marion Island is positive (except at the lowest altitudes), where *Azorella* presence has been shown to alter *Agrostis* population structure and increase *Agrostis* reproductive output, biomass and abundance compared to surrounding areas where *Azorella* is absent (le Roux & McGeoch, 2010; le Roux et al., 2013). *Agrostis* is the dominant plant growing on *Azorella* (mean cover ±

SE = 18.5 ± 1.3 %; this study), with all other vascular plants combined (3.2 ± 0.5 %) and all bryophytes combined (5.3 ± 0.9 %) having much lower cover on *Azorella*. Because I am examining interactions within the most dominant plant species on *Azorella*, all the intra-specific interactions are also indirect interactions (*sensu* Armas *et al*. 2008).

Data collection

Observational study

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

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

Experimental study

For the experimental component of this study, three sites were sampled on the eastern side of the island. Three substrate types (i.e. cushion plant centre, cushion plant edge and soil) were sampled using 10 x 20 cm sampling quadrats (Fig. S1: Appendix S2). Data were collected separately from both the edges and the centres of cushion plants because recent work has showed that there is pronounced variation in facilitation within cushion plants (i.e. at the intra-individual level; see Anthelme *et al*. 2017). Data from cushion centres and cushion edges were collected from separate cushions, which were separated by a minimum distance of 0.5 m. For the cushion plant edges, the sampling quadrat was placed to cover the cushion's edge and surrounding soil (representing the area immediately affected by the cushion plant) approximately equally. For all substrate types, the percentage rock cover within the plot was visually estimated, and the percentage cover of other vascular plant species and bryophytes recorded. Cushion plant size was recorded by measuring the height of the cushion plant, maximum diameter and the diameter perpendicular to maximum diameter.

Prior to the implementation of the experimental treatment, *Agrostis* abundance was recorded within all sampling quadrats. Then, for each substrate type, samples were split by *Agrostis* density: high density (i.e. the plots with the highest two-thirds of *Agrostis* abundance values) and low density (i.e. the plots with the lowest third of *Agrostis* abundance) (Table S1: Appendix S2). Half of the high-density plots were randomly assigned to a thinned density *Agrostis* treatment (Table S2: Appendix S2), where *Agrostis* abundance was reduced to the average *Agrostis* abundance of the low-density treatment plots of that site and substrate type (Table S1: Appendix S2).

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

Data analysis

Observational study

Generalized linear mixed effects models (GLMMs) were used to model the total number of reproductive *Agrostis* individuals as a function of whether grasses were located on a cushion plant or the adjacent substrate (i.e. the inter-specific interaction of interest), *Agrostis* density (the intra-specific interaction of interest), and altitude (m a.s.l.; a proxy for environmental severity), and the three pair-wise interactions between these variables since these predictors may mediate each other's effects on *Agrostis* performance. The combined cover of other vascular plants and mosses were included into these models to account for the effect of the other, sub-ordinate species (mean combined cover across both *Azorella* and the adjacent substrate ± SE = 18.6 ± 1.68 %; range = 0 to 100 %). To account for the spatial structure of the data, a random effect of "pair" (representing each pair of cushion and adjacent substrate samples) nested within "transect" (representing the different transects along which samples were collected) was included in all models. Additionally, the proportion of the sampled area covered by rock was accounted for by including (1 - rock cover) as an offset variable, since large rocks reduce the potentially suitable area for *Agrostis* to grow. Therefore, data were analyzed using the following model:

$$\begin{aligned}
&Number\ of\ reproductive\ \text{Agrostis}\ individuals\ \sim\ Altitude + Location \\
&+\ \text{Agrostis}\ density + cover\ of\ other\ plants \\
&+ (Altitude\text{:}\ Location) + (Altitude\text{:}\ \text{Agrostis}\ density) + (Location\text{:}\ \text{Agrostis}\ density) \\
&+ (1|Transect/Pair) \\
&+ offset(\log\ of\ sample\ area) \qquad\qquad (eqn.\ 1)
\end{aligned}$$

Count data for number of reproductive individuals were zero-inflated but not overdispersed. Therefore, the model was run as a generalized linear mixed effects hurdle model using a truncated negative binomial distribution with a log-link function, implemented using the glmmTMB package (see Brooks *et al.*, 2017 for details) in R (R Core Team, 2018). Hurdle models involve two separate analyses (Rose *et al.*, 2006); one analysis assesses the positive (count) data with a linear model (conditional model), whereas the other compares samples with reproductive individuals to samples lacking reproductive individuals with a binary model (zero-inflation model).

Experimental study

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

RESULTS

Observational study

A total of 12’109 *Agrostis* individuals were sampled from paired cushion and soil plots along six altitudinal transects. The number of reproductive *Agrostis* individuals was significantly higher on *Azorella* than on adjacent soil substrate plots (Table 1; conditional model). The number of reproductive *Agrostis* individuals was also significantly positively related to conspecific density, with this increase in *Agrostis* performance with conspecific density being significantly greater on *Azorella* than on the adjacent soil (Fig. 2; Table 1: conditional model).

Table 1. Results from the mixed effects model testing the listed fixed and random effects against the total number of reproductive *Agrostis magellanica* individuals (from 252 samples, p < 0.001). The conditional model (standard negative binomial model; count data component of the model) and the zero-inflation model are presented here. Abbreviations: C = cushion, S = soil, A = altitude, L = location and D = density. Asterisks indicate interactions.

Conditional model					
Fixed effects	Level	Estimate	SE	z	p
(Intercept)	-	-5.823	0.277	-21.055	< **0.01**
Altitude	-	-0.001	0.001	-1.342	0.180
Location (Soil)	C > S	-1.077	0.468	-2.302	**0.021**
Agrostis density	-	-0.042	0.041	-1.027	0.304
Cover of other plants	-	-0.004	0.004	-0.875	0.381
Altitude*Location (Soil)	A*L(C) = A*L(S)	0.001	0.001	0.920	0.358
Altitude**Agrostis* density	-	0.001	0.000	2.832	**0.005**
Location (Soil)**Agrostis* density	D*L(S) < D*L(C)	0.128	0.057	2.227	**0.026**
Zero-inflation model					
Fixed effects	Level	Estimate	SE	z	p
(Intercept)	-	0.418	0.851	0.491	0.624
Altitude	-	-0.003	0.002	-1.431	0.152
Location (Soil)	-	-0.326	0.984	-0.331	0.740
Agrostis density	-	-1.565	0.788	-1.987	**0.047**
Cover of other plants	-	-0.005	0.008	-0.641	0.521
Altitude*Location (Soil)	A*L(C) > A*L(S)	0.006	0.003	2.091	**0.037**
Altitude**Agrostis* density	-	-0.001	0.001	-1.176	0.240
Location (Soil)**Agrostis* density	D*L(S) < D*L(C)	1.421	0.768	1.850	0.064
Random effects	Variance	SD			
Pair:Transect	0.139	0.373			
Transect	0.089	0.298			

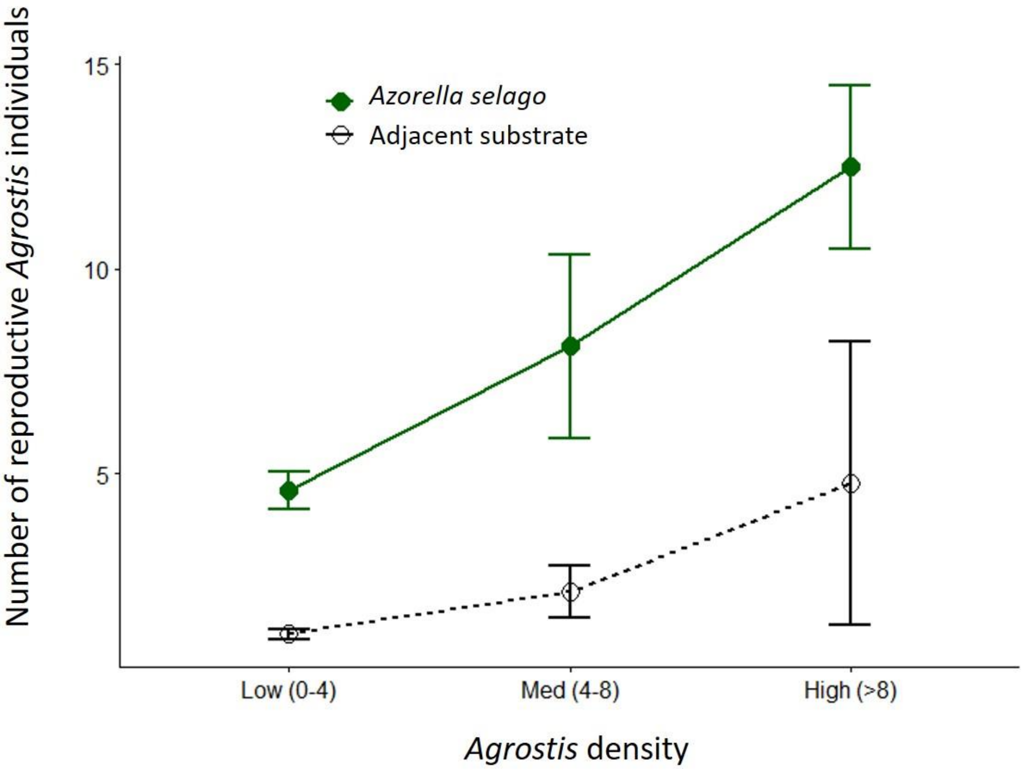

Figure 2. Mean (± SE) number of reproductive Agrostis magellanica individuals at low (0 - 4 individuals/cm^2), medium (4 - 8 individuals/cm^2) and high (> 8 individuals/cm^2) conspecific densities on and away from *Azorella selago*.

The positive effect of *Agrostis* density on the number of reproductive *Agrostis* individuals varied significantly with altitude (Table 1, Fig. 3). The number of reproductive *Agrostis* individuals increased significantly between low and middle altitudes across all *Agrostis* density categories. However, where *Agrostis* density was low, the number of reproductive *Agrostis* individuals decreased significantly between middle and high altitudes. The impact of *Agrostis* density on *Agrostis* performance, therefore, varied with altitude. The interaction between altitude and *Agrostis* density was significant (Table 1), where, at higher altitudes, there was generally a more positive effect (Fig 3).

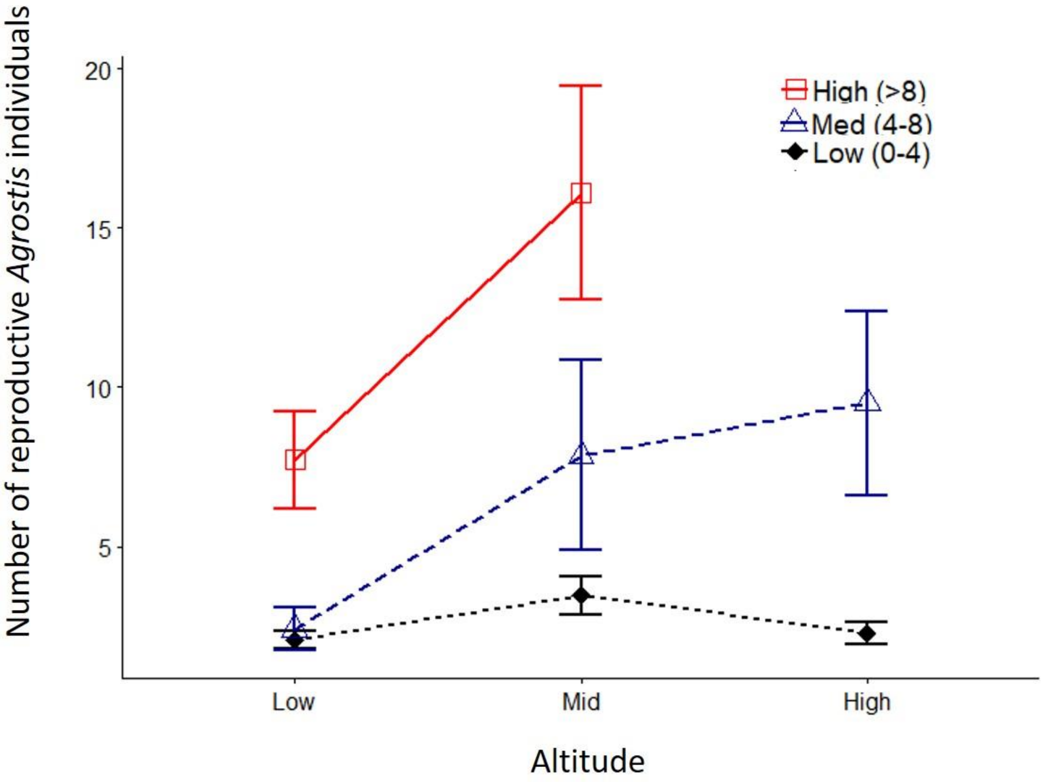

Figure 3. Mean (± SE) number of reproductive *Agrostis magellanica* individuals at low (0 - 4 individuals/cm^2), medium (4 - 8 individuals/cm^2) and high (> 8 individuals/cm^2) densities across the altitudinal range: low (18 - 160 m a.s.l.), mid (161 - 302 m a.s.l.) and high (307 - 535 m a.s.l.) altitudes. There were no reproductive *Agrostis* individuals at high altitudes when *Agrostis* density exceeded 8 individuals per unit area.

In contrast, the effect of *Azorella* on *Agrostis* (i.e. the inter-specific interaction) did not vary significantly across the altitudinal range; although, both the mean number of reproductive *Agrostis* individuals on *Azorella* and the difference in the mean number of reproductive *Agrostis* individuals on *Azorella* were greatest at mid altitudes (Fig. 4). Moreover, the occurrence of reproductive *Agrostis* individuals is correlated with *Agrostis* density and the interaction between altitude and *Agrostis* location (i.e. whether *Agrostis* is located on *vs.* away from *Azorella*), with a greater probability of observing reproductive *Agrostis* individuals on *Azorella* across all altitudes (Table 1; zero-inflation model).

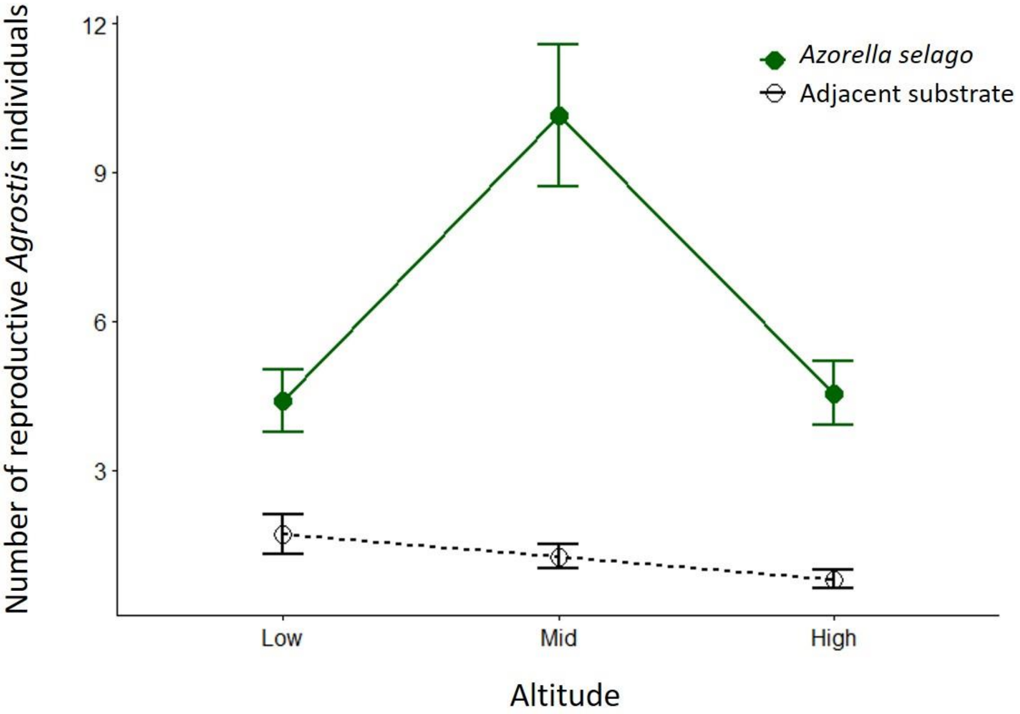

Figure 4. Mean (± SE) number of reproductive *Agrostis magellanica* individuals growing on *Azorella* cushion plants on the adjacent soil across an altitudinal gradient. Low altitude: ≤ 160 m a.s.l.), mid: 161-302 m a.s.l., high: > 307 m a.s.l.).

Experimental study

In the experiment, a total of 520 *Agrostis* individuals were monitored for a growing season. *Agrostis* individuals growing on the edge of *Azorella* plants were significantly heavier than *Agrostis* individuals in the centre of *Azorella* and on the adjacent substrate (Table 2; Fig. 5). Experimentally reducing *Agrostis* density had no significant effect on *Agrostis* shoot mass (Table 2). The other two *Agrostis* characteristics examined, maximum leaf height and basal diameter, were both not significantly related to either intra- or inter-specific interactions (Table S3; Table S4, Appendix S2).

Table 2. Results from the mixed effects model testing the listed fixed and random effects (treatment = high density *vs*. low density *vs*. thinned density) against the *Agrostis magellanica* shoot mass (g) at the end of the monitoring period (from n = 519 samples, p < 0.001). Abbreviations: L = low density, T = thinned density, H = high density, C = cushion, S = soil and E = cushion edge.

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

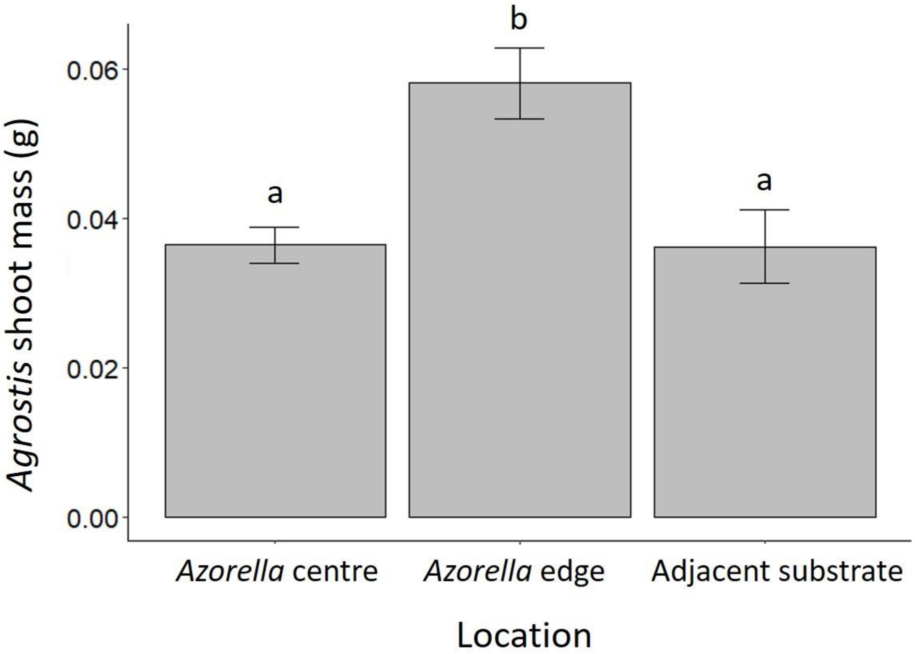

Figure 5. Mean (± SE) total *Agrostis magellanica* shoot mass (g) growing in the centre of *Azorella selago* cushion plants, on the edges of cushion plants and in the adjacent bare soil substrate.

DISCUSSION

Where facilitation increases beneficiary species density and/or size (e.g. Tielbörger & Kadmon, 2000), it is possible that the negative influence of competition between beneficiary individuals could outweigh the positive influence of inter-specific facilitation (Tielbörger & Kadmon, 2000; García-Cervigón *et al*., 2013; Schöb *et al*., 2013a). For example, facilitation by a benefactor can result in high densities of beneficiaries, but due to crowding beneficiaries may not be able to reach reproductive size. Here, I tested this idea by examining the impact of *Agrostis* density on conspecific performance within a facilitative system. From both the experimental and observational data, I observed (1) no evidence for intra-specific competition. Therefore, based on my results from both observational and experimental studies I have to reject my second hypothesis, i.e. that increasing beneficiary abundance would increase competition among the beneficiaries. Specifically, in terms of (2) the outcome of the intra-specific interaction (between *Agrostis* individuals) and (3) the impact of the inter-specific interaction on the outcome of the intra-specific interaction, I observed contradictory results between the experimental and mensuration components of this study.

First, for both the experimental and observational components of this study, the number of reproductive *Agrostis* individuals was on average higher on *Azorella* cushion plants than on the adjacent substrate, across the entire altitudinal range. Therefore, in agreement with previous findings, the inter-specific *Azorella-Agrostis* interaction positively affected *Agrostis* performance (le Roux & McGeoch, 2010 and le Roux & McGeoch, 2013). These results also mirror the generally positive impact of vascular plants in abiotically-severe environments from other studies, including the observed nurse effects of other cushion plant species in the same family as *Azorella,* i.e. *Bolax* spp. (e.g. Molina-Montenegro *et al*., 2000; Badano & Cavieres, 2006; Bonanomi *et al*., 2016; Hupp *et al*., 2017; Yang *et al*., 2017). Specifically, the strongest positive effect on *Agrostis* performance was observed on the edges of cushion plants. This is in agreement with Anthelme *et al*. (2017) who showed that facilitation by the congeneric cushion plant, *Azorella compacta*, was higher at the periphery of the cushion plant than at the centers of the cushion plants (see also Pescador *et al*'s., 2014 "facilitation in the halo" concept). The improved beneficiary performance on the periphery of cushion plants may be attributed to reduced root competition for resources (in line with the interpretation by Anthelme *et al*., 2017). Alternatively, the periphery of cushion plants may be associated with warmer temperatures and greater protection from strong winds (on the northern and leeward sides of cushion plants, respectively; Anthelme *et al*., 2017). Therefore, although benefactors may consistently positively impact associated beneficiaries, the magnitude of the impact of benefactors on beneficiary' performance can vary within individual benefactor plants.

Second, when examining the impact of *Agrostis* density on *Agrostis* performance (i.e. the impact of intra-specific interactions), I expected that *Azorella* could increase the density and productivity of *Agrostis* to such an extent that the *Agrostis* individuals would experience a reduction in their reproductive output. (Aguiar & Sala, 1994; García-Cervigón *et al*., 2013; Schöb et al., 2013a). However, I found no evidence for intra-specific competition. Instead, using a correlative approach, I show that *Agrostis* performance both on and away from *Azorella* was greatest at high conspecific densities (see e.g. Fajardo & McIntire, 2011; Zhang & Wang, 2016; Zhang & Tielbörger, 2019). These results can be interpreted in two ways, which are not necessarily mutually exclusive. First, the results from the observational study may reflect both *Agrostis* abundance and reproduction responding to an unmeasured variable. For example, *Agrostis* density and inflorescence production may both be positively related to *Azorella* compactness because compact cushion plants are typically associated with higher soil nutrient contents, more effective heat trapping and greater stability than more lax cushion plants (Schöb *et al*., 2013b; Jiang *et al*., 2017; Yang et al., 2017). However, in this study system there is no *a priori* data to suggest that density and fecundity are responding in the same way to an unmeasured variable. Second, these results may suggest that intra-specific interactions are positive, with greater *Agrostis* densities favouring conspecific performance (e.g. Saccone *et al*., 2010; Zhang & Tielbörger, 2019). Although ecological theory suggests that fecundity should be negatively affected by density (Feldman & Morris, 2011), I find no evidence for this. However, from my experiment, we see that reducing *Agrostis* density had no significant effect on *Agrostis* performance, suggesting neither facilitation nor competition within species. This difference between the experimental and observational study may be due to the monitoring only being conducted for one season after the experimental reduction of *Agrostis* density, potentially reflecting that the species may respond slowly to changes in this biotic interaction or preallocate some resources in the previous season. Nevertheless, intra-specific facilitation may be one of the potential mechanisms that explains the findings from my observational study. If the positive impact of *Agrostis* density on *Agrostis* performance is a reflection of intra-specific facilitation, it could suggest that *Agrostis* individuals shield one another from the strong winds (e.g. Zhang & Wang, 2016) and/or low temperatures (Eränen & Kozlov, 2008; Zhang & Wang, 2016; Zhang & Tielbörger, 2019; see also Svanfeldt *et al*., 2017), to a point where the positive effects of intra-specific facilitation outweigh the negative impacts of intra-specific competition (e.g. Fajardo & McIntire, 2011; García-Cervigón *et al*., 2013).

Alternatively, *Agrostis* individuals may have greater substrate stability when growing in dense clusters (although this is most likely to be more important on the adjacent substrate since *Azorella* already provides a stable substrate). Moreover, intraspecific facilitation can occur through the sharing of mycorrhiza (e.g. Teste & Simard, 2008), with *Agrostis* individuals growing in dense clusters potentially benefiting from shared mycorrhizae. Thus, there are several mechanisms that could drive positive intra-specific interactions.

Lastly, observational data suggest that the impact of *Agrostis* density on the number of reproductive *Agrostis* individuals may be dependent on (i.e. mediated by) the inter-specific interaction between *Azorella* and *Agrostis*. In other words, the effect of *Agrostis* density on *Agrostis* performance was dependent on whether *Agrostis* was growing on vs away from *Azorella*. Specifically, my results suggest that the potential positive effect that *Azorella* had on *Agrostis* abundance was not negated by a negative effect of high *Agrostis* density on the species' reproduction. However, these findings were not supported by the experimental study, as the impact of *Agrostis* density on *Agrostis* reproduction was not dependent on whether *Agrostis* was located on *Azorella* vs on the adjacent substrate. Contradictions between experimental and observational approaches have been documented from other studies, with, for example, Metz and Tielbörger (2016) observing contradictory findings in the outcome of plant-plant interactions between spatial, temporal and experimental approaches. Despite my contradictory results, my findings suggest that it is important to consider both intra- and inter-specific interactions when examining plant-plant interactions in relation to abiotic stress (e.g. García-Cervigón et al., 2013).

More broadly, this study reveals four issues that could be considered to improve our understanding of the impact of inter-specific interactions on the outcome of intra-specific interactions within the context of facilitation. First, the nature of the gradient being examined may be important (as suggested by Maestre *et al.*, 2009, albeit in a different perspective). Specifically, I hypothesize that intra-specific competition between plants will more likely outweigh the effects inter-specific facilitation along resource gradients, as opposed to along non-resource gradients (e.g. as in this study). Second, the outcome of biotic interactions could vary with individuals' ontogenetic stages (Eränen & Kozlov, 2008; le Roux *et al.*, 2013). I hypothesize that as *Agrostis* individuals grow, the effects of intra-specific interactions are likely to become more negative, potentially switching the relationship from intra-specific facilitation to intra-specific competition, with decreasing space or resources. Third, the strength and/or outcome of inter-specific facilitation might be related to the outcome of the intra-specific interaction. For example, different cushion plant species vary in their impact on associated beneficiary species (e.g. Hupp *et al.*, 2017), and therefore, intra-specific competition may be greater on cushion plants that have stronger facilitative effects. Fourth, while this study focusses on intra-specific interactions, I expect the observed results to be general to plant species that grow on cushion plants, especially in abiotically severe environments, with inter-specific interactions between beneficiaries also potentially being positive (although see Llambí *et al.*, 2018).

More generally, my results suggest that both positive inter- and intra-specific biotic interactions may be crucial for the performance and survival of plant species in extreme environments. Moreover, experimental approaches should be used in conjunction with observational data to accurately examine context-dependency in the outcome of inter- and intra-specific interactions. Within the context of facilitation, the overall performance and abundance of beneficiary species may be dependent on the combined effects of the benefactor species on the beneficiaries, the indirect interactions among beneficiaries themselves and the interaction of the benefactor and beneficiaries with their environment (e.g. Schöb *et al.*, 2013a; Llambí *et al.*, 2018). Indeed, while other recent research (e.g. García-Cervigón *et al.*, 2013) has highlighted the importance of intra-specific interactions, this study emphasizes that there are several mechanisms that could drive the outcome of intra-specific interactions, and both inter- and intra-specific interactions could be important to consider when understanding variation in species' performance and community processes.

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Appendix S2.

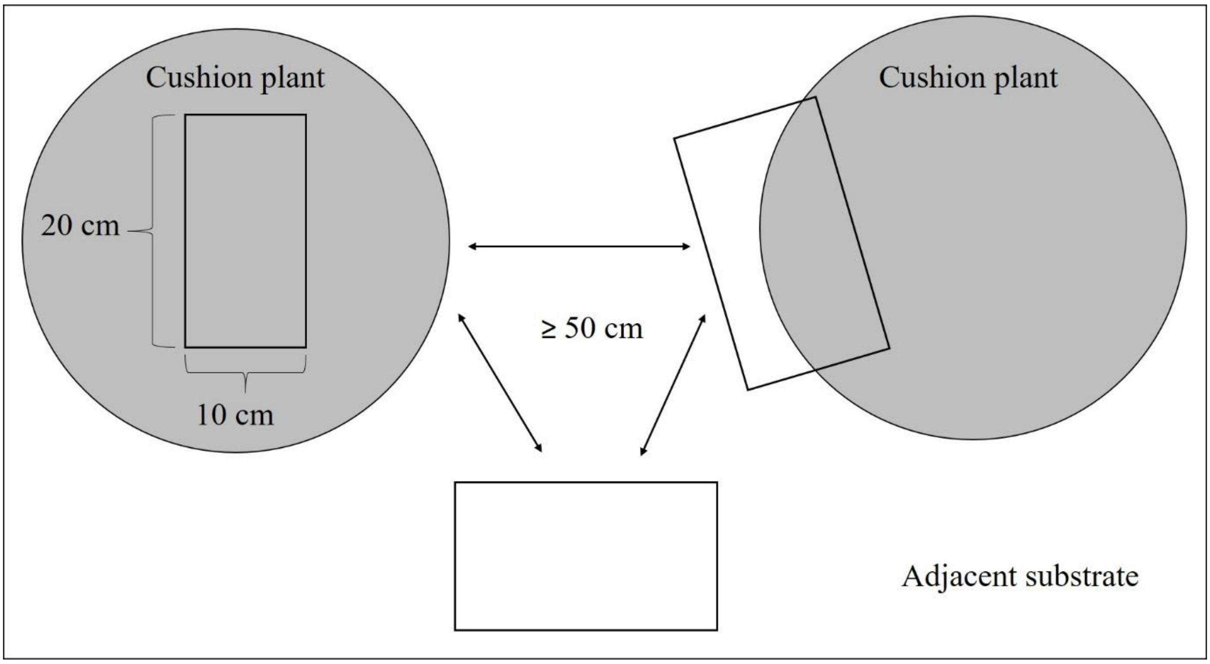

Figure. S1. Diagram illustrating the sampling location for the experimental component. Circles represent cushion plants and the rectangles are the 10 x 20 cm sampling plots.

Table S1. A) *Agrostis magellanica* abundance for each substrate type (*Azorella selago*, *Azorella* edge and Adjacent substrate) per site where plots were split to obtain the lowest third (33rd percentile of *Agrostis* abundance). B) Average *Agrostis magellanica* abundance per substrate type, site and *A. magellanica* density treatment [High = high density, Low = low density and Thin = thinned from high density to low density]. *Agrostis* abundance was recorded within a 10 x 20 cm sampling grid at each location and the minimum and maximum *Agrostis* abundances across all three sites were 5 and 84 *Agrostis* individuals per sampling area respectively.

A.	*Azorella selago*	Edge	Substrate	B.	*Azorella selago*			Edge			Substrate		
Site	*Agrostis* abundance at 33rd percentile			Site	Low	High	Thin	Low	High	Thin	Low	High	Thin
Site 1	23.3	23.5	11.4	Site 1	18.1	35.3	32.5	18.1	31.2	34.7	7.3	19.7	18.1
Site 2	24.2	24	10.5	Site 2	20	34	35	21.6	28.4	30.8	9.7	18.3	15
Site 3	36	33	12	Site 3	30.3	52.5	48.1	26.3	40.7	42.8	10	16.2	14.6

Table S2. Number of plots per substrate type (*Azorella*, *Azorella* edge and Adjacent substrate) and site (Skua Ridge 1, high site; Skua Ridge 2, Low site and Tafelberg) allocated to the different *Agrostis magellanica* density treatments [High = high density, Low = low density and Thin = thinned from high density to low density]

	Azorella selago			Edge			Soil		
	Low	High	Thin	Low	High	Thin	Low	High	Thin
Site 1	7	7	6	7	6	7	7	7	7
Site 2	7	7	7	7	7	6	7	6	7
Site 3	7	6	7	7	7	6	7	6	7

Table S3. Results from the mixed effects model testing the listed fixed effects and random effect (treatment = high density vs. low density vs thinned density) against the maximum *Agrostis magellanica* leaf height (mm) at the end of the monitoring period (2017) (n = 519 observations, p < 0.001). Abbreviations: L: low density, T: thinned density, H: high density, C: *Azorella* cushion, S: Adjacent substrate and E: *Azorella* cushion edge. Asterisks indicate interactions.

Fixed effects	Level	Estimate	SE	z	p
(Intercept)		12.31	1.99	6.2	< **0.01**
Treatment	H = T = L	–	–	–	> 0.05
Location	C = S = E	–	–	–	> 0.05
Initial size		0.71	0.04	19.194	< **0.01**
Treatment*Location		–	–	–	> 0.05
Random effect		Variance	SD		
Plot		18.76	4.33		

Table S4. Results from the mixed effects model testing the listed fixed effects and random effect (treatment = high density vs. low density vs thinned density) against the basal diameter (mm) at the end of the monitoring period (2017) (from n = 519 observations p < 0.001). Abbreviations: L: low density, T: thinned density, H: high density, C: *Azorella* cushion, S: Adjacent substrate and E: *Azorella* cushion edge. Asterisks indicate interactions.

Variable	Level	Estimate	SE	z	p
(Intercept)		9.425	1.872	5.036	< **0.01**
Treatment	L= H = T	–	–	–	0.443
Location	C = S = E	–	–	–	0.705
Initial size		0.713	0.037	19.194	< **0.01**
Treatment*Location		–	–	–	0.546
Random effect	Variance	SD			
Plot	0.142	0.377			

***Azorella selago* growing on a fellfield slope on Marion Island**

Chapter 4:

Positive plant-plant interactions expand the upper distributional limits of some vascular plant species

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Abstract

Biotic interactions can shape species' distributions through their impact on species' realized niches, potentially constraining or expanding the range of conditions under which species occur. I examine whether fine-scale plant-plant interactions scale up to shape broad-scale species' distributions, using *Azorella selago*, a widespread cushion plant that facilitates other species, and the rest of the vascular flora of sub-Antarctic Marion Island as a model system. I compared the upper elevational distributional limit of each species when growing on *vs* away from *A. selago* to test how the interaction with this cushion plant species affects species' ranges. Three out of 19 vascular plant species occurred at higher altitudes in the presence of *A. selago* than in the absence of *A. selago*: *Acaena magellanica* (+ 26 m higher), *Colobanthus kerguelensis* (+ 37 m higher), and *Lycopodium saururus* (+ 19 m higher). Therefore, *A. selago*'s fine-scale impacts scaled up to shape the distribution of a subset of the vascular flora of Marion Island. Plant-plant interactions thus have the potential to expand species upper distributional limits by increasing the niche space that a species can occupy, although the influence of these interactions may be strongly species-specific.

INTRODUCTION

Biotic interactions among species, which vary from competitive to facilitative, may strongly shape ecological communities (Bruno *et al.*, 2003; Armas *et al.*, 2011) and influence species-environment relationships (López *et al.*, 2018). As a result, biotic interactions may affect species' realized niches (He & Bertness, 2014; Jones & Gilbert, 2016; Filazzola *et al.*, 2018), and potentially constrain (via negative interactions) or expand (via positive interactions) a species' observed distribution (le Roux *et al.*, 2012, Jones & Gilbert, 2016). While the influence of abiotic conditions on species' distributions has been well documented, particularly at broad spatial scales (Pearson & Dawson, 2003), the impact of biotic interactions on species' distributions are still relatively poorly understood (e.g. López *et al.*, 2018; Louthan *et al.*, 2018), with few suitable datasets available to investigate the influence of inter-specific interactions on species' range limits.

Moreover, while most studies have focused on the impact of negative trophic interactions (e.g. competition, parasitism and predation) on species' distributions and range limits, fewer studies have examined the influence of positive interactions (e.g. facilitation between benefactor species and associated beneficiary species: Bruno *et al.*, 2003; He & Cui, 2015; Bulleri *et al.*, 2016; Filazzola *et al.*, 2018). This may reflect the assumption of the traditional niche model that a species' realized niche can only be smaller than its fundamental niche due to the negative impacts of biotic interactions on a species' niche volume (Soberón & Arroyo-Peña, 2017); or, more broadly, the assumption that competitive interactions most strongly shape ecological patterns (Ulrich *et al.*, 2017). However, empirical evidence suggests that positive interactions could potentially expand the realized niche of a species (Bruno *et al.*, 2003; He & Bertness, 2014; He & Cui, 2015; Filazzola *et al.*, 2018), although there is still a paucity of field-quantified data to explicitly test the impact of positive inter-specific interactions on species' occurrence patterns at broad scales across representative samples of assemblages (but see e.g. Badano & Cavieres, 2006; Badano & Marquet, 2008). Therefore, the prevailing view that species' distributions are determined by the physical environment and negative inter-specific interactions alone is changing, as evidenced by the growing recognition of the importance of including positive interactions into ecological theories of community structure and organization (Bertness & Callaway, 1994; Bruno *et al.*, 2003; Jones & Gilbert, 2016).

Both positive and negative biotic interactions can affect the fine-scale occurrence patterns of plant species (Armas *et al.*, 2011; le Roux *et al.*, 2012). It is, however, still unclear whether these fine scale interactions could scale up to shape species' distributions at broader extents. For plant species, this idea has been tested using species distribution modelling (Filazzola *et al.*, 2018), and there are recent studies showing that this may also be true for animals (He & Cui 2015; López *et al.*, 2018). Moreover, although few studies have tested how fine-scale biotic interactions may scale up, theoretical evidence suggests that positive fine-scale interactions could potentially expand species' distributions (López *et al.*, 2018).

Whereas the Stress Interactions-Abiotic Stress Hypothesis (SIASH) postulates that biotic interactions set species' range limits in more benign areas (Louthan *et al.*, 2015), positive plant-plant interactions (e.g. facilitation) are typically most frequent under stressful environmental conditions (Bruno *et al.*, 2003; Armas *et al.*, 2011). Indeed, positive interactions tend to increase in strength and frequency relative to negative interactions with increasing environmental severity (Stress Gradient Hypothesis [SGH]; Bertness & Callaway, 1994). This suggests that although the upper distributional limits of species are thought to be set by abiotic extremes in thermally-limited environments (Normand *et al.*, 2009; Ettinger *et al.*, 2011; Louthan *et al.*, 2015), positive interactions could potentially expand the upper altitudinal range limits of species further than in the absence of the interactions.

This study, therefore, examines whether fine-scale plant-plant interactions scale up to shape plant species' altitudinal distributions using field observations. I use *Azorella selago*, a widespread cushion plant (Appendix S3: Fig. S1), and the rest of the vascular flora of sub-Antarctic Marion Island as a model system. Because plant species on Marion Island are exposed to stressful abiotic conditions (especially with increasing altitude; see le Roux, 2008 for details) and available data provide evidence for *A. selago* facilitating some plant species (Appendix S3: Fig. S2), I specifically test if species' upper elevational distributions differ when growing in association or away from *A. selago*. I expect that, because *A. selago* ameliorates abiotic conditions locally, co-occurring with the cushion plant will allow species to grow in areas that would otherwise be abiotically unsuitable, and may potentially expand the species' upper distributional limits (e.g. Badano & Cavieres, 2006).

METHODS

Study site and species

Marion Island (46°55'S, 37°45'E) is a volcanic island located in the southern Indian Ocean. It possesses a hyper-oceanic climate, with low but very stable temperatures, along with high precipitation and humidity, cloud cover on most days and frequent strong winds (le Roux, 2008). A clear elevational gradient of increasing abiotic severity is evident on the island, with greater wind speeds and soil instability, and lower mean temperatures at higher elevations (le Roux, 2008). Consequently, plant species richness (le Roux & McGeoch, 2008b), cover (Smith *et al.*, 2001) and productivity (Smith, 2008) decline with elevation. There are 130 scoria cones (Appendix S3: Fig. S3) distributed across the island, which are geomorphologically active landforms due to their unconsolidated substrate and relatively steep slopes (Holness, 2004). Vegetation cover on these scoria cones decreases with elevation (see e.g. le Roux & McGeoch, 2008a).

Marion Island has experienced rapid climate change over the past 50 years, with temperature having risen by approximately 1.2 °C (le Roux & McGeoch, 2008b), rainfall having declined by *c.* 1000 mm p.a. and the interval between rainfall events having increased (le Roux & McGeoch, 2008c). Species altitudinal distributions have changed over the same period, with most species' upper altitudinal limits expanding (le Roux & McGeoch, 2008b).

Marion Island supports 22 indigenous and 17 alien vascular plant species (Greve *et al.*, 2019; Kalwij *et al.*, 2019). One of the most widespread vascular plant species in the sub-Antarctic is the compact, prostrate cushion plant, *Azorella selago* Hook. (Apiaceae) (*Azorella* hereafter). On Marion Island this species occurs in all vegetation types, from the interior of the island (*c*. 840 m a.s.l.) to sea level (le Roux & McGeoch, 2008b). As a consequence of its cushion growth form (Appendix S3: Fig. S1. A-B), *Azorella* ameliorates stressful conditions by locally modifying the physical environment (see Nyakatya & McGeoch, 2008).

The positive impacts of cushion plants on associated plants has been well documented (le Roux *et al*., 2013, Hupp *et al*., 2017). Cushion plants may moderate microclimatic conditions by ameliorating soil temperatures, increasing soil moisture, improving soil nutrient status and enhancing substrate stability (Nyakatya & McGeoch, 2008; Hupp *et al*., 2017). On Marion Island there are some data that demonstrate facilitation by *Azorella* (see le Roux & McGeoch, 2008a; Nyakatya & McGeoch, 2008; le Roux & McGeoch, 2010; le Roux *et al*., 2013). Additional data are available for other congeneric species which show strong facilitation in similar environments (Badano & Cavieres, 2006; Badano & Marquet, 2009). On Marion Island *Azorella* has a positive effect on the richness and total cover of vascular plant species (Buyens *et al*. in prep; see also Appendix S3: Fig. S2. A) and on the abundance of individual species (e.g. *Agrostis magellanica*, except at the lowest altitudes; see also le Roux & McGeoch, 2008a; le Roux & McGeoch, 2010). Additionally, *Azorella* has a significant positive effect on the richness, biomass and occurrence of invertebrate species (Hugo *et al*., 2004). This, along with the important role that *Azorella* plays in succession (Scott, 1985) on Marion Island, makes the species an ecosystem engineer and keystone species (Hugo *et al*., 2004).

Data collection

To compare the upper elevational limits of species on *vs* away from *Azorella*, the upper altitudinal boundaries of all vascular plant species were determined along 20 island-scale altitudinal transects (“broad-scale transects”; Appendix S3: Fig. S4), and 21 landform-scale altitudinal transects located on five scoria cones.

Data from 10 broad-scale transects were available from le Roux & McGeoch (2008b) and le Roux & McGeoch (unpublished data) and were supplemented by surveying 10 additional transects in 2016 - 2017. Transects were 5 m wide and ran from approximately 900 m a.s.l. (since the current upper limit to vascular plant growth is 840 m a.s.l.) down to sea level (following the methods of Huntley, 1970 and le Roux & McGeoch, 2008b). Each transect was sampled over 1 to 1.5 days. The altitude of the highest five individuals of all vascular plant species (alien and indigenous) was recorded using a hand-held GPS unit, both when growing on and away from *Azorella* cushions. Additionally, for a subset of transects, altitude was also recorded using a barometric altimeter and was extracted from a digital elevation model (DEM) (see Meiklejohn & Smith, 2008 for details). There were no significant differences between these three measurements of altitude (Appendix S3: Text S1). Therefore, altitudes recorded from the GPS were used. Only species recorded in five or more transects (N = 19) were considered for further analyses.

At the landform-scale, the altitude of the five highest individuals of all vascular plant species growing on and away from *Azorella* were recorded from twenty-one 5 m wide transects along scoria cones (i.e. “fine-scale transects”). Where possible, multiple transects were surveyed on different aspects of the same cone (i.e. typically in the cardinal or ordinal directions, as allowed by topography; five scoria cones samples in total). Four landform-scale transects were sampled in 2006, and an additional 17 transects were sampled in the 2016 - 2017. If the top of a sampled scoria cone was comprised of conglomerated scoria, the transect was started at a lower altitude where loose scoria was the main substrate to ensure the same substrate was sampled throughout the transect. Only species recorded in five or more transects (N = 13) were considered for further analyses.

Both fine- and broad-scale transects were surveyed during snow-free (or at least chiefly snow-free) conditions. All sampling was conducted in late summer or autumn and only mature individuals of each species were recorded. *Azorella* was abundant across both island-scale and landform-scale transects.

Data analysis

Both broad-scale and fine-scale data were analyzed using the average altitude of the five highest individuals growing on *vs* away from *Azorella* per transect (although using the altitude of the highest individual per transect gave similar results; Appendix S3: Table S1).

A one-sided Wilcoxon signed rank test was used to perform paired analyses contrasting species’ upper distributional limits with and without *Azorella* within each transect. One-sided analyses were used because I can only robustly test for changes in the upper distributional limits of species with my sampling design. While this sampling design provides accurate estimates of species' upper altitudinal limits, due to the cover of *Azorella* generally being well below 50% (Appendix S3: Fig. S5), it results in unequal sampling effort (i.e. a larger non-*Azorella* area is sampled than *Azorella*-covered area in each transect). Therefore, observations of species' upper limits being lower in the presence of *Azorella* relative to the absence of *Azorella* does not necessarily reflect the cushion plant having a negative effect on species' upper distributional limits, but could instead be a result of the difference in sampling effort (i.e. the paired test is biased towards negative differences because *Azorella* covers < 50% of the total area in my transects). Thus, any species occurring significantly more in the presence of *Azorella* than in its absence represents a very conservative test given this sampling bias.

Range expansion data of vascular plant species on Marion Island between 1966 and the 2000s were extracted from le Roux & McGeoch (2008b) and were used to test for a correlation between the impact of *Azorella* on species' current altitudinal limits and the rate of each species range expansion between the 1960's and the 2000's.

Additional analyses were performed to examine altitudinal variation in the mean cover and frequency of occurrence of species on *vs* away from *Azorella* using a separate dataset where altitudinal transects were sampled in a paired manner, recording the cover and frequency of occurrence of vascular plant species in the presence *vs* in the absence of *Azorella* along an elevational gradient (following the methods of le Roux & McGeoch, 2010) (adequate data were available for six species that occurred in > 15 plots).

Finally, to determine whether the species that occurred at higher altitudes in the presence of *Azorella* differed in functional trait expression from the other species, generalized linear mixed effect models (assuming a binomial distribution, and using species identity as a random effect) were used to test for differences functional trait values between the species that occurred at higher altitudes in the presence of *Azorella* and those species that did not. All continuous functional trait data that were available for Marion Island's angiosperm species were extracted from Mathakutha *et al*. in press; data from 14 species, with 17 to 55 replicates per trait per species, except for frost tolerance where there were data available from 13 species with 5 to 10 replicates per trait per species. All analyses were conducted in R v.3.3.3 (R Core Team, 2017).

RESULTS

Upper altitudinal limits for most species did not differ significantly in the presence and absence of *Azorella* at the island-scale (Table S2; Fig. 1). However, *Acaena magellanica* (Appendix S3: Fig. S1. C) and *Colobanthus kerguelensis* (Appendix S3: Fig. S1. D) occurred

26 m (p = 0.015) and 37 m (p = 0.034) higher in the presence of *Azorella* than in its absence, while *Lycopodium saururus* occurred 19 m (p = 0.058) higher in the presence of *Azorella* than in its absence (Appendix S3: Fig. S1. E). At fine-scales, *Azorella* had no significant impacts on the upper altitudinal limits of species (Appendix S3: Table S3). The current upper altitudinal range limits of species in the presence of *Azorella* was not correlated with the rate at which the species' upper range limits had shifted since the 1960's (r = 0.31, p = 0.254; Appendix S3: Fig. S6).

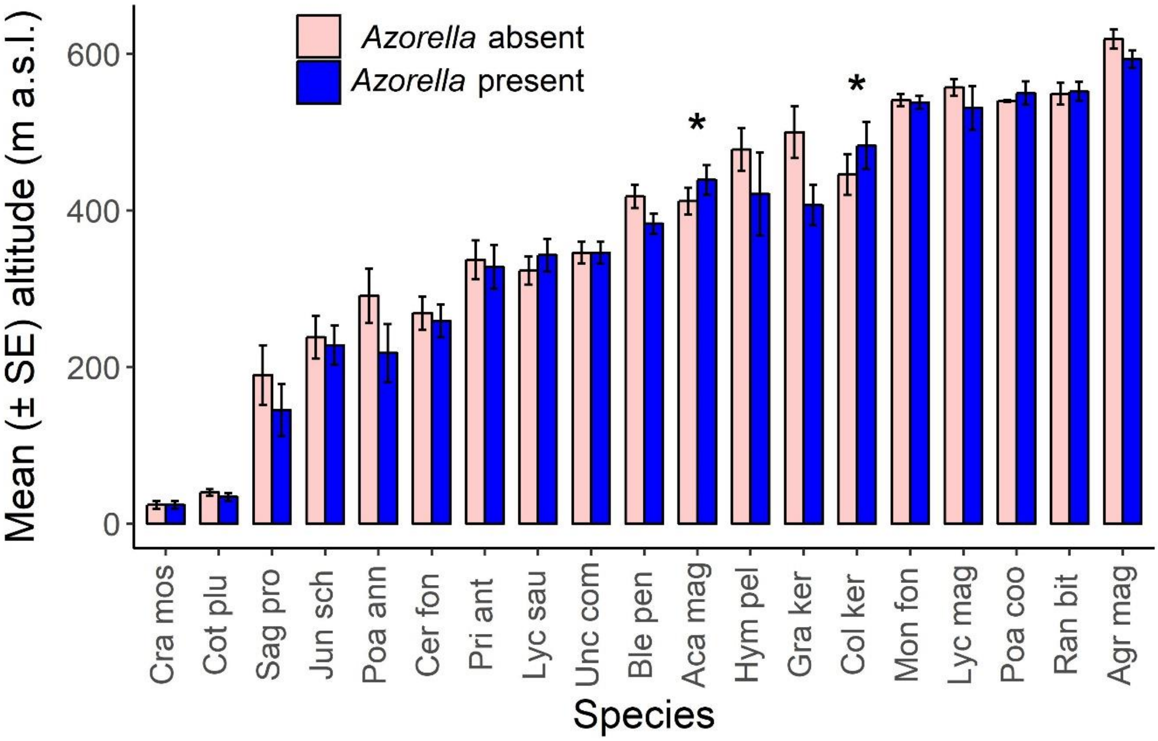

Figure 1. Mean (± SE) altitude (m a.s.l.) of vascular plant species growing on *vs* away from *Azorella selago* for the island-scale transects. See Table S1 for species name abbreviations. Species are ordered by their upper altitudinal limit on *A. selago* Asterisks indicate where differences in species upper distributional limits on vs. away from *A. selago* were significant.

The mean cover and frequency of occurrence of species on *vs* away from *Azorella* was not generally affected by the presence of *Azorella* (Appendix S3: Fig. S7; although cover of *Agrostis magellanica* was significantly higher on *Azorella* at several altitudes: Fig. S3 A). Similarly, the frequency of occurrence of individual species was generally similar on *vs* away from *Azorella* across the altitudinal range (Appendix S3: Fig. S8 A-E; only *Ranunculus biternatus* differed strongly in the altitude at which it had the highest frequency of occurrence on *vs* away from *Azorella*: Appendix S3: Fig. S8 F).

Analysis of species' functional traits showed that five of the six traits did not differ significantly between the species that occurred at higher altitudes in the presence of *Azorella* and those that did not (Appendix S3: Table S4). However, leaf area was significantly larger for the species that occurred at higher altitudes in the presence of *Azorella* compared to the other species, with *Acaena magellanica* having the largest leaves of any species on the island.

DISCUSSION

Facilitative interactions may allow species to occur in areas that are otherwise unfavorable (e.g. Armas *et al*., 2011; He & Cui, 2015). Thus, the range of environmental conditions (and the total range size) that a species occupies in the presence of a positive interaction may be larger than the conditions occupied by that species in the absence of that interaction (i.e. the realized niche may extend beyond the fundamental niche along some niche axes due to positive biotic interactions: see Bruno *et al*., 2003; le Roux *et al*., 2012; He & Bertness, 2014; Jones & Gilbert, 2016; Filazzola *et al*., 2018). In this study, I show that 3 out of 19 vascular plant species, i.e. the suffrutescent herb *Acaena magellanica*, the cushion-forming *Colobanthus kerguelensis* and the clubmoss *Lycopodium saururus* occurred at higher altitudes in the presence of *Azorella* than in the absence of *Azorella*. Additionally, out of the six species for which sufficient data were available, *Azorella* had a positive impact on the cover of one species, *Agrostis magellanica* (at mid-altitudes), and on the frequency of occurrence of another species, *Ranunculus biternatus* (at low and mid altitudes). At fine spatial scales such species-specific responses to cushion plants (e.g. higher cover and abundance; Alliende & Hoffmann, 1985; Hupp *et al*., 2017) and other benefactor plants (Iyengar *et al*., 2017; Filazzola *et al*., 2018) are common. Such species-specificity may be related to species traits (Schöb *et al*., 2017), with for example woody species tending to be more abundant on the adjacent substrate than on cushion plants (Alliende & Hoffmann, 1985). However, the only widespread woody plant species on Marion Island, *Acaena magellanica*, occurs at higher altitudes in the presence of *Azorella* than in its absence. Of the functional traits that were analyzed only leaf area differed significantly, with species that occurred at higher altitudes in the presence of *Azorella* having larger leaves than the other species. Because small leaf area is typically associated with stress-tolerance (Pérez-Harguindeguy *et al*., 2013) this suggests that the two plant species that occurred at higher altitudes in the presence of *Azorella* are possibly less stress-tolerant (i.e. stress-sensitive species may benefit more from facilitation than stress-tolerant species, in agreement with Liancourt *et al.*, 2017). Our results further reveal a mismatch between species which benefit from facilitation at fine and broad spatial scales. For example, *Agrostis magellanica* is strongly facilitated by *Azorella* at fine scales (Appendix S3: Fig. S2; le Roux & McGeoch, 2010; le Roux *et al.*, 2013) but the interaction with *Azorella* had no effect on the upper distributional limit of *Agrostis magellanica*. In contrast, *Acaena magellanica* is facilitated by *Azorella* at fine scales (Fig. S2: Appendix S3), and occurs at significantly higher altitudes in the presence of *Azorella* than in its absence.

Contrary to expectation, the interaction with *Azorella* had no impact on the upper altitudinal limit of most vascular plant species. This suggests that climatic conditions (and other abiotic factors) may be the main drivers of species' upper distributional limits (Normand *et al.*, 2009; Louthan *et al.*, 2015), regardless of the presence of positive interactions. Biotic interactions may, instead, be more important in determining range limits at the less stressful distributional boundary, as supported by studies that suggested an increase in the importance of biotic interactions for population-level processes with a decrease in abiotic severity (e.g. Louthan *et al.*, 2015; Louthan *et al.*, 2018; in contrast to with predictions of the SGH: Bertness & Callaway, 1994). Alternatively, perhaps the impact of the "benefactor" species on some other species is negative or the facilitative effect of the benefactor species collapses near other species' upper elevational limits (i.e. become neutral or competitive under extreme conditions: see Holmgren & Scheffer, 2010; Michalet *et al.*, 2014). Our *a priori* predictions assumed that *Azorella* has a consistent and positive effect on associated species at all altitudes. This assumption is in agreement with, for example, le Roux & McGeoch (2010) finding no evidence for facilitation collapse in this system. However, not all species were positively affected by *Azorella* at fine-scales, with the cushion plant having a significantly negative impact on the cover of the fern *Blechnum penna-marina* (Fig. S2: Appendix S3). These mechanisms may, therefore, all potentially contribute to the generally negligible impact of *Azorella* on species' upper distributional limits.

In this study I examined the occurrence of species on *vs* away from *Azorella* and could not determine if the populations growing on the adjacent substrate were self-sustaining or subsidized by individuals growing on *Azorella* cushion plants. At higher altitudes on Marion Island up to 95% of inflorescences produced by the grass *Agrostis magellanica* are from individuals rooted in *Azorella* (le Roux *et al.*, 2013). Therefore, even the distribution of a species growing away from *Azorella* may still be affected by facilitation by *Azorella* through individuals growing on *Azorella* subsidizing seed rain to the adjacent substrate. This may be a form of source-sink dynamics (Ferrer *et al*., 2015), where individuals on *Azorella* act as a net source of individuals, supporting a sink population on the adjacent substrate, which in turn, may allow a species to occur outside of its fundamental niche (Ferrer *et al*., 2015). A demographic approach would be necessary to understand if populations growing in the adjacent substrate can maintain themselves without seed input from facilitated individuals, and, therefore, to test if this is another potential mechanism through which fine-scale scale facilitation can affect species' distributions.

While other studies have suggested that positive biotic interactions could potentially expand species' distributions and altitudinal limits (Bruno *et al*., 2003; He & Bertness, 2014; He & Cui, 2015), this is the first study to explicitly test this idea using fine-scale field data collected across a continuous gradient. From an applied perspective my results can improve our understanding of how species' ranges shift in response to climate change. For example, if a benefactor species' range expands in response to warming, it could potentially "pull" associated beneficiary species up the elevational gradient by creating favourable micro-sites at higher altitudes which would otherwise still be unfavorable (see e.g. Travis *et al*., 2005). Indeed, it has been hypothesized that biotic interactions can mediate species' responses to climate change and the rate of climate-induced range shifts (HilleRisLambers *et al*., 2013). However, in this study, I found no correlation between the nature of the interaction with *Azorella* and the magnitude of the response to recent climate change. This suggests that biotic interactions may be important in determining the range limits of certain species, but overall may be relatively unimportant in influencing species range shifts (possibly due to, e.g., beneficiary species having more limited dispersal potential; Travis *et al*., 2005; Travis *et al*., 2013).

More broadly, there are at least four avenues of research that could further improve our understanding of how fine-scale biotic interactions scale up to affect species' range limits. First, I hypothesize that the degree to which a benefactor species expands a beneficiary species' range will be positively correlated with how strongly the benefactor species alters environmental conditions. For example, if one cushion plant species is able to modify the limiting factors more positively than another cushion plant (see e.g. Hupp *et al*., 2017), the former may allow greater range expansion into abiotically unsuitable conditions. Second, an experimental approach (e.g. Alexander *et al*., 2015) could be used in conjunction with observational data to measure niche expansion. For example, transplant experiments can be used to examine whether species are able to survive and reproduce at higher elevations than at their current elevational limits. Third, if biotic interactions are important for setting species' lower distributional limits (e.g. Ettinger *et al.*, 2011, and see SIASH hypothesis: Louthan *et al.*, 2015), these biotic interactions may also expand beneficiary species' lower distributional limits if a benefactor species provides additional resources, competition-free space and/or protection against herbivores (e.g. Holmgren & Scheffer, 2010). Fourth, relatedly, based on the ideas of Maestre *et al.* (2009), I hypothesize that the impact of biotic interactions on species' ranges may differ along resource versus non-resource gradients. For example, with declining resource availability, competition for a limiting resource may outweigh any effect of facilitation and, consequently, positive interactions may be less frequent (e.g. as predicted by Maestre *et al.*, 2009) and less likely to affect species' range limits. Therefore, niche expansion driven by positive biotic interactions is more likely under non-resource limited conditions. However, irrespective of these details, the importance of explicitly considering the influence of biotic interactions on species' range limits is clear because of the potential for biotic interactions to constrain or expand the range of conditions under which certain species can occur.

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Appendix S3.

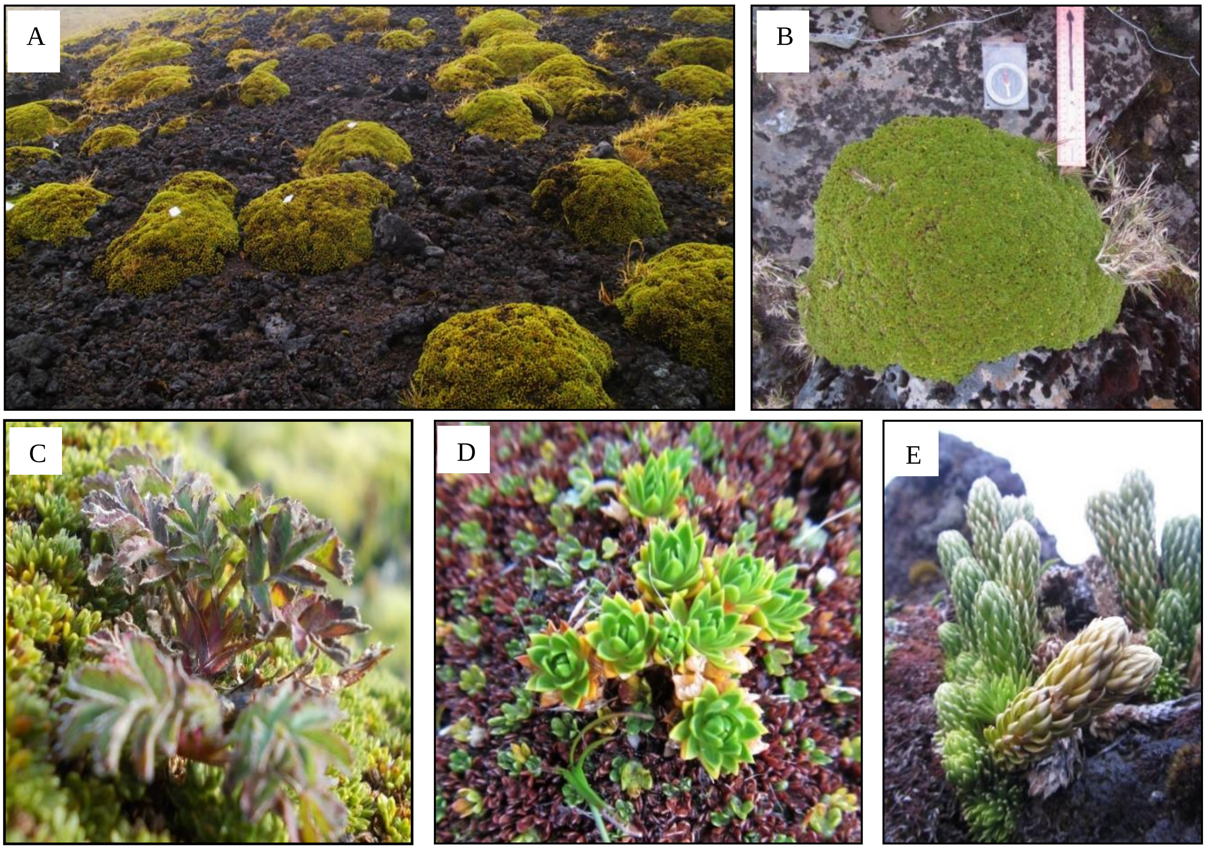


Figure. S1. A) *Azorella selago* Hook. (Apiaceae) cushion plants growing at mid-altitudes on Marion Island, B) An individual *A. selago* cushion plant with several *Agrostis magellanica* grasses growing on its edge (15 cm ruler included in the image for scale), C) *Acaena magellanica* (Rosaceae), growing on *A. selago*: Image taken by Christien Steyn, D) *Colobanthus kerguelensis* (Caryophyllaceae) growing on *A. selago* and E) *Lycopodium saururus* (Lycopodiaceae).

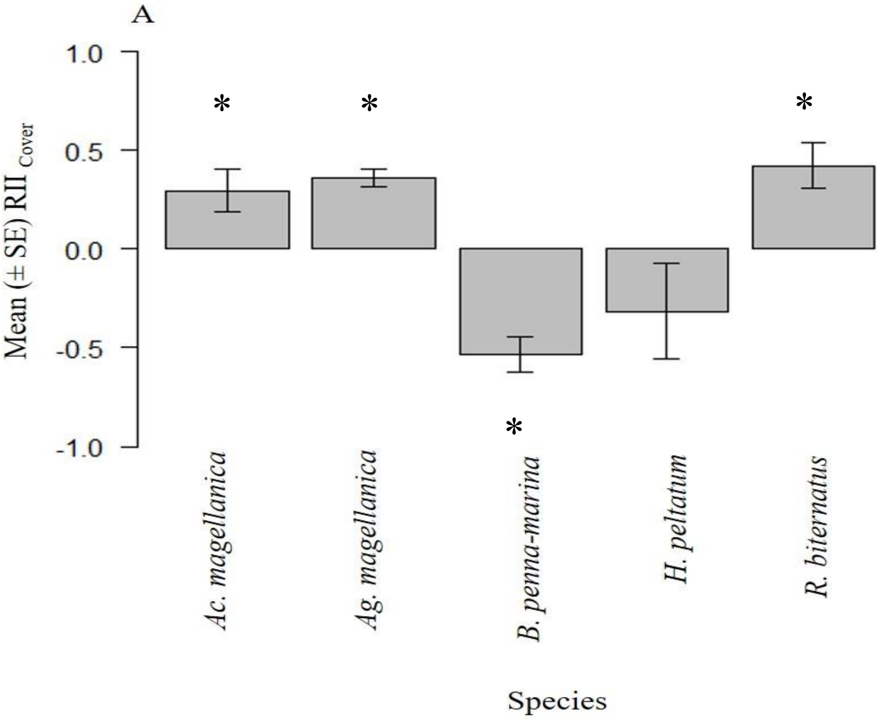


Figure S2. The Relative Interaction Index (RII) for the interaction between *Azorella selago* and five commonly co-occurring plant species. A) Mean (± SE) RII values for *Acaena magellanica*, *Agrostis magellanica*, *Blechnum penna-marina*, *Hymenophyllum peltatum* and *Ranunculus biternatus*, based on the cover of these species when growing on *A. selago* relative to the adjacent substrate. A generalized linear model with a binomial distribution revealed that the RII scores for three species were significantly greater than zero (indicted using asterisks; *Ag. magellanica* [z = 4.128, p-value = < 0.001], *Ac. magellanica* [z = 2.184, p-value = < 0.05], *R. biternatus* [z = 2.924, p = < 0.01]), while the mean RII score for *B. penna-marina* was significantly smaller than zero (z = -2.714, p = < 0.01), and the mean RII score for *H. peltatum* was not significantly different from zero (z = -1.155, p = 0.248).

Figure S3. Junior’s Kop, one of the surveyed scoria cones on the eastern side of Marion Island.

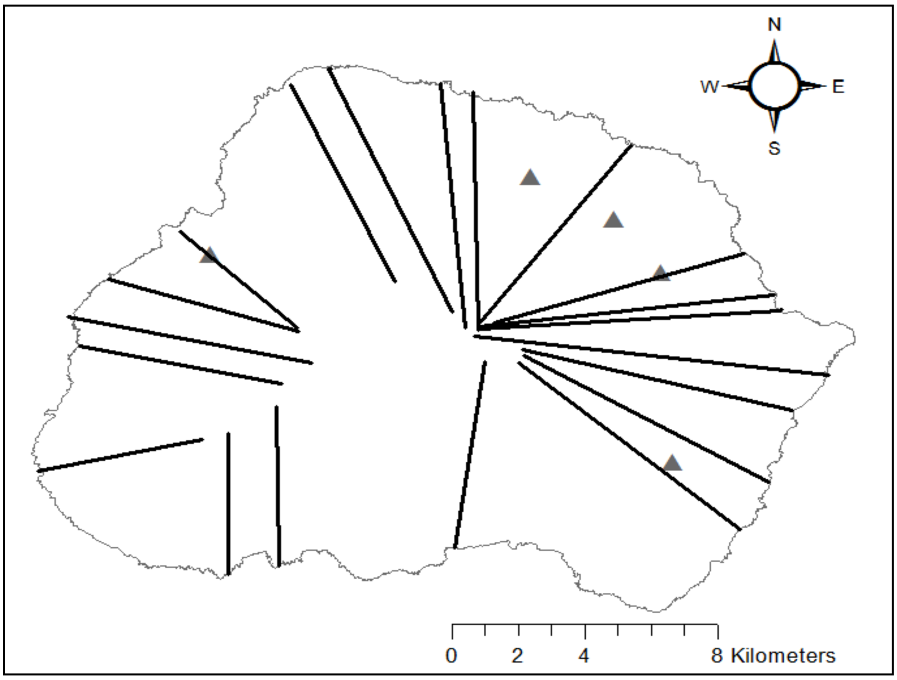


Figure S4. The approximate location of the island-scale altitudinal transects (represented by thick lines) and landform-scale altitudinal transects (surveyed scoria cones represented by triangles) surveyed on sub-Antarctic Marion Island.

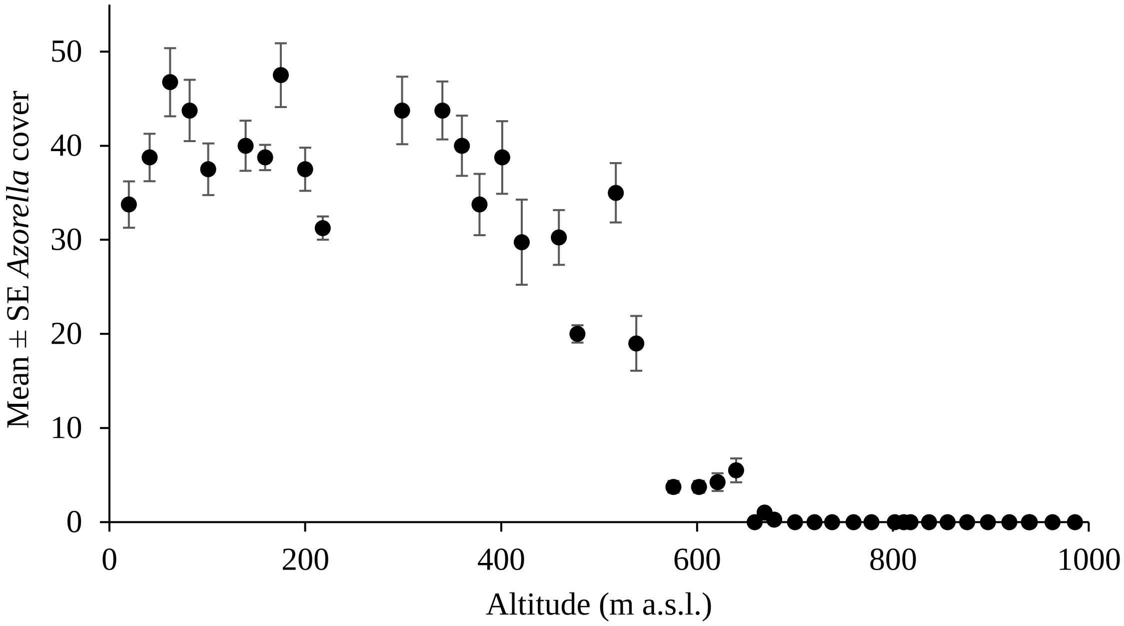


Figure S5. Mean (± SE) Azorella selago cover (%) at 20 m elevation intervals across four elevational transects.

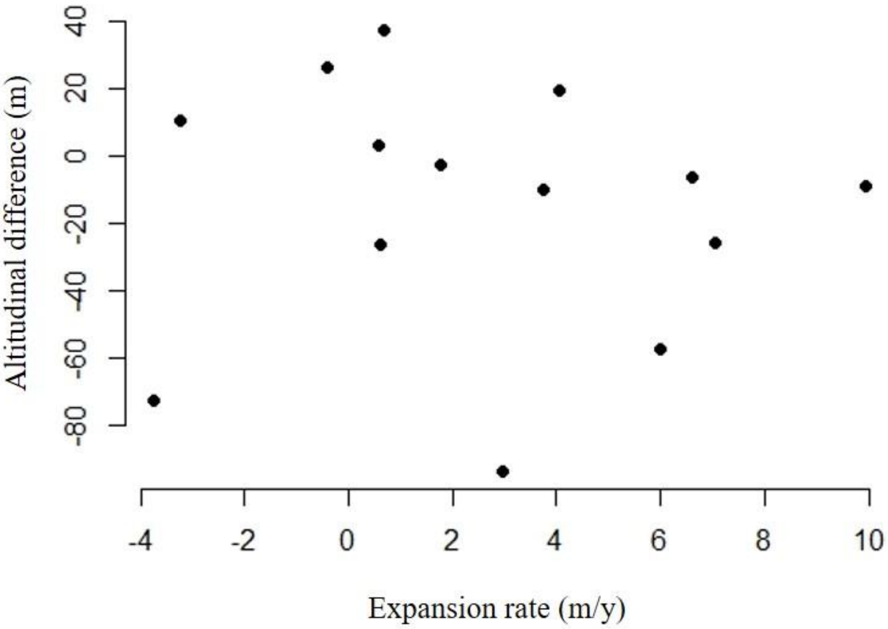


Figure S6. Scatterplot showing the relationship between the difference in species' upper altitudinal limits on and away from *Azorella selago* (positive values indicate species have a higher upper altitudinal limit when growing on *A. selago* than when growing on the adjacent substrate) and species' upslope expansion rates between 1966 and the 2000's in response to climate warming (data from le Roux and McGeoch 2008b). The current upper altitudinal range limits of species in the presence of *Azorella* was not correlated with the rate at which the species upper range limits had shifted since the 1960's (r = 0.31, p = 0.254).

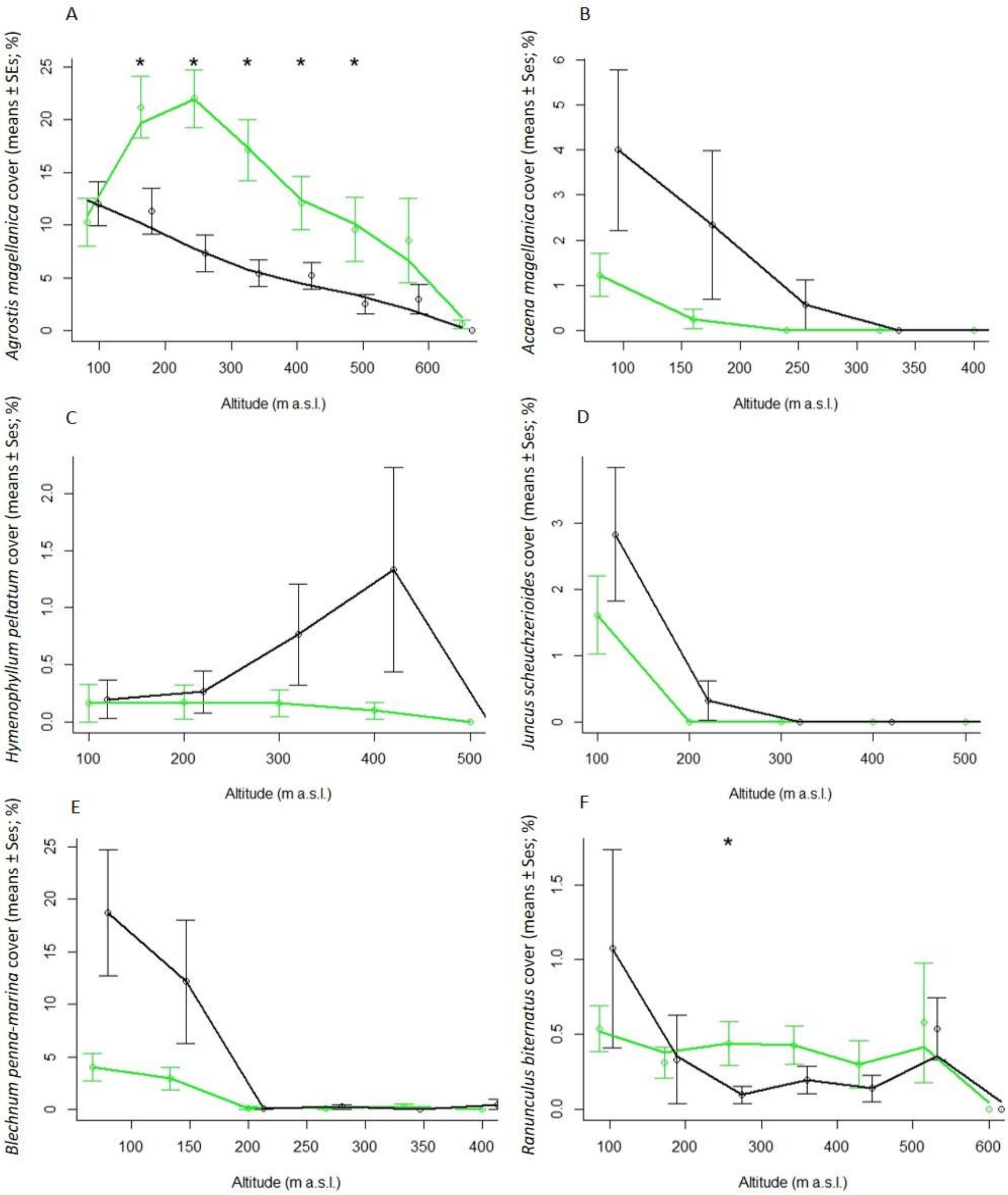


Figure S7. Variation in mean (± SE) cover (%) of A) *Agrostis magellanica* (n = occurring in 253 of 366 plots), B) *Acaena magellanica* (n = 20/366 plots), C) *Hymenophyllum peltatum* (n = 18/366 plots), D) *Juncus scheuchzerioides* (n = 19/366 plots), E) *Blechnum penna-marina* (n = 45/366 plots) and F) *Ranunculus biternatus* (n = 71/366 plots) across altitude, growing on (green line) *vs* away from (black line) *Azorella selago*. Asterisks indicate significant differences (as determined from two-sided Wilcoxon signed rank tests). For (A) and (F) loess lines are drawn to reflect the trends.

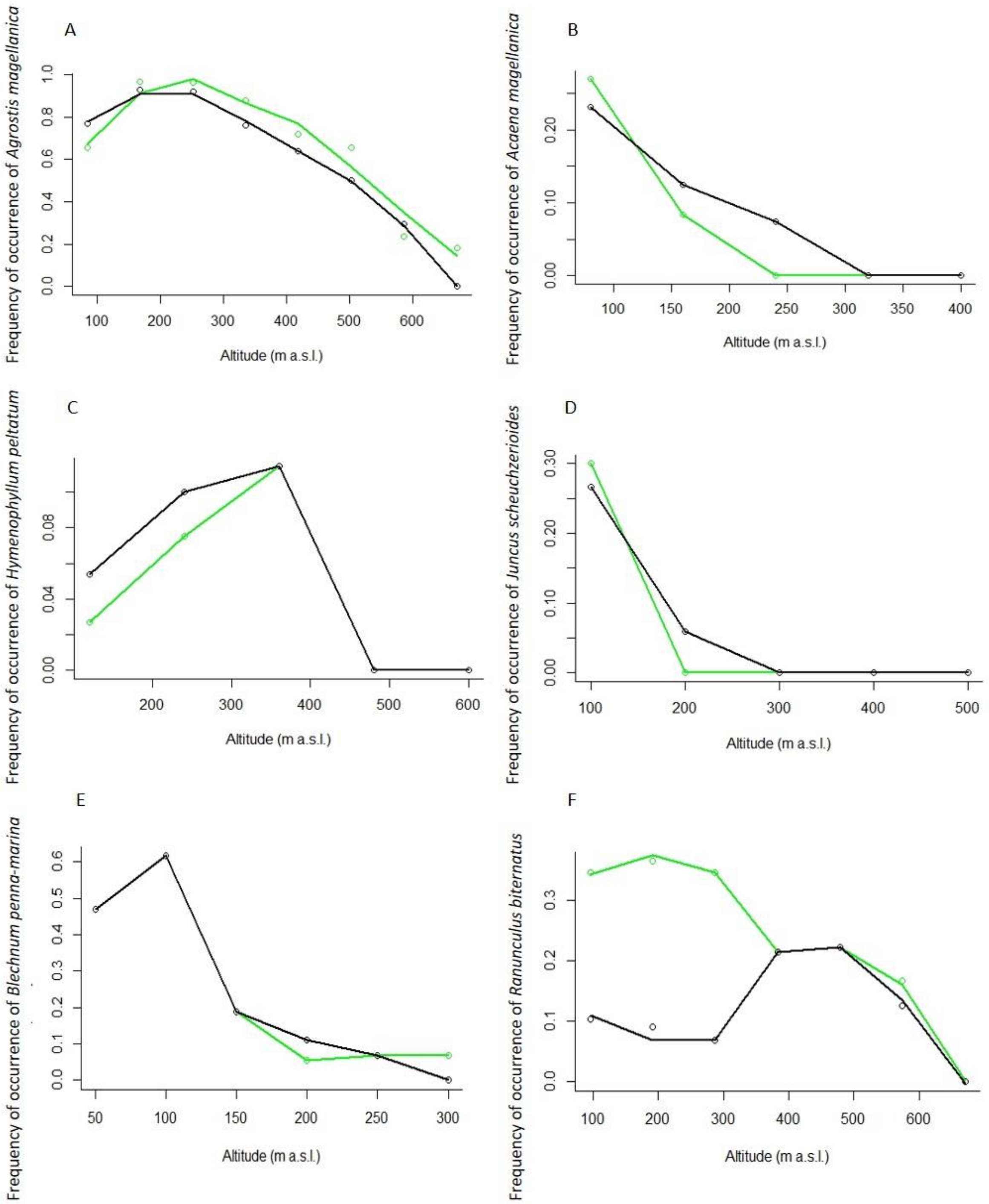


Figure S8. Variation in frequency of occurrence of A) *Agrostis magellanica* (n = occurring in 253 of 366 plots), B) *Acaena magellanica* (n = 20/366 plots), C) *Hymenophyllum peltatum* (n = 18/366 plots), D) *Juncus scheuchzerioides* (n = 19/366 plots), E) *Blechnum penna-marina* (n = 45/366 plots) and F) *Ranunculus biternatus* (n = 71/366 plots) across altitude growing on (green line) *vs* away from (black line) *Azorella selago*. For (A) and (F) loess lines are drawn to reflect the trends.

Table S1. Mean (± SE) altitude (m a.s.l.) of the highest occurring individual of each vascular plant species per transect growing on *vs* away from *Azorella selago* for the island-scale transects. Difference = difference in the mean upper altitudinal limit of species in the presence and absence of *A. selago* (limit in the presence of *A. selago* – limit in the absence of *A. selago*). n = number of transects for which paired data (i.e. altitude of species on and away from *A. selago*) were available. V = one-sided Wilcoxon signed rank test statistic. Species are sorted based on their upper altitudinal limit on *A. selago*.

	Azorella present	*Azorella* absent	Pairs			
Species	Mean ± SE (m a.s.l.)	Mean ± SE (m a.s.l.)	Present – Absent	n	V	P
Sagina procumbens	163 ± 35	190 ± 38	-27.32	19	66	0.999
Poa annua	200 ± 33	291± 35	-90.75	16	77	0.999
Juncus scheuchzerioides	228 ± 25	238± 27	-9.33	18	14	0.970
Crassula moschata	24 ± 5	24± 5	0.60	10	0	0.500
Cerastium fontanum	262 ± 22	272 ± 22	-9.94	17	28	0.993
Pringlea antiscorbutica	328 ± 28	337± 25	-9.17	6	4	0.789
Lycopodium saururus	339 ± 21	324 ± 18	15.45	20	53.5	0.085
Cotula plumosa	34 ± 5	40± 4	-6.07	14	44	0.995
Uncinia compacta	343 ± 14	346 ± 14	-3.45	20	7	0.819
Blechnum penna-marina	383 ± 13	419 ± 15	-35.65	20	103	0.999
Grammitis kerguelensis	414 ± 25	486 ± 35	-72.14	7	21	0.989
Hymenophyllum peltatum	421 ± 53	478 ± 27	-57.17	6	9	0.950
Acaena magellanica	439 ± 19	412 ± 17	26.40	20	8	0.015
Colobanthus kerguelensis	483 ± 30	446± 26	37.25	16	12	**0.034**
Lycopodium magellanicum	531 ± 28	557± 11	-26.15	20	37	0.453
Montia fontana	538 ± 8	541 ± 8	-2.55	20	9	0.709
Poa cookii	550 ± 15	540 ± 13	10.50	20	10	0.147
Ranunculus biternatus	552 ± 12	549 ± 14	3.16	19	2	0.395
Agrostis magellanica	591 ± 11	619 ± 12	-27.25	20	114.5	0.992

Table S2. Mean altitude of vascular plant species growing in the presence and absence of *Azorella selago* in 20 island-scale transects. Difference = difference in the mean upper altitudinal limit of species in the presence and absence of *A. selago* (limit in the presence of *A. selago* – limit in the absence of *A. selago:* Present - Absent). n = number of transects for which paired data (i.e. altitude of species in the presence and absence of *A. selago*) were available. V = one-sided Wilcoxon signed rank test statistic. Species are ordered by their upper altitudinal limit on *A. selago*. Significant and marginally significant p-values are bolded. The altitude of the highest individual across all transects on *Azorella* and away from *Azorella* (on *Azorella*/away from *Azorella*: Az/Away) is given in the last column for each species. The highest occurrence of *Azorella* across all the transects was at 765 m a.s.l.

	Azorella present	*Azorella* absent	Difference	Pairs			
Species	Mean ± SE (m a.s.l.)	Mean ± SE (m a.s.l.)	Present – Absent	n	V	p	Upper limit (Az/Away m a.s.l.)
Crassula moschata (Cra mos)	24 ± 5	24 ± 5	0.6	10	0	0.500	55/55
Cotula plumosa (Cot plu)	34 ± 5	40 ± 4	-6.1	14	36	0.995	57/60
Sagina procumbens (Sag pro)	145 ± 33	190 ± 38	-45.3	19	55	0.998	451/511
Poa annua (Poa ann)	218 ± 37	291 ± 35	-72.7	16	65	0.998	500/508
Juncus scheuchzerioides (Jun sch)	228 ± 25	238 ± 27	-9.3	18	14	0.971	392/421
Cerastium fontanum (Cer fon)	259 ± 21	269 ± 21	-9.9	18	36	0.995	411/411
Pringlea antiscorbutica (Pri ant)	328 ± 28	337 ± 25	-9.0	6	4	0.789	419/414
Lycopodium saururus (Lyc sau)	343 ± 21	323 ± 18	19.4	20	55.5	**0.058**	540/475
Uncinia compacta (Unc com)	346 ±14	346 ± 14	-0.6	20	3	0.605	437/437
Blechnum penna-marina (Ble pen)	383 ± 13	418 ± 15	-35.5	20	90	0.999	526/526
Grammitis kerguelensis (Gra ker)	407 ± 26	500 ± 33	-93.4	8	28	0.993	514/647
Hymenophyllum peltatum (Hym pel)	421 ± 53	478 ± 27	-57.2	6	9	0.949	555/571
Acaena magellanica (Aca mag)	439 ± 19	412 ± 17	26.4	20	8	**0.015**	581/504
Colobanthus kerguelensis (Col ker)	483 ± 30	446 ± 26	37.3	16	12	**0.034**	595/575
Lycopodium magellanicum (Lyc mag)	531 ± 28	557 ± 11	-26.2	20	37	0.453	633/633
Montia fontana (Mon fon)	538 ± 8	541 ± 8	-2.5	20	5.5	0.644	607/607
Poa cookii (Poa coo)	550 ± 15	540 ± 1	10.5	20	10	0.147	659/642
Ranunculus biternatus (Ran bit)	552 ± 12	549 ± 14	3.2	19	2	0.395	653/653
Agrostis magellanica (Agr mag)	593 ± 11	619 ± 12	-25.8	20	98.5	0.987	689/743

Table S3. Mean (± SE) altitude (m a.s.l.) of the highest occurrences, using the mean altitude of the five highest individuals, of vascular plant species growing on *vs* away from *Azorella selago* for the landform-scale transects. Difference = difference in the mean upper altitudinal limit of species in the presence and absence of *A. selago* (limit in the presence of *A. selago* – limit in the absence of *A. selago*). n = number of transects for which paired data (i.e. altitude of species on and away from *A. selago*) were available. V = one-sided Wilcoxon signed rank test statistic. Species are sorted based on their upper altitudinal limit on *A. selago*.

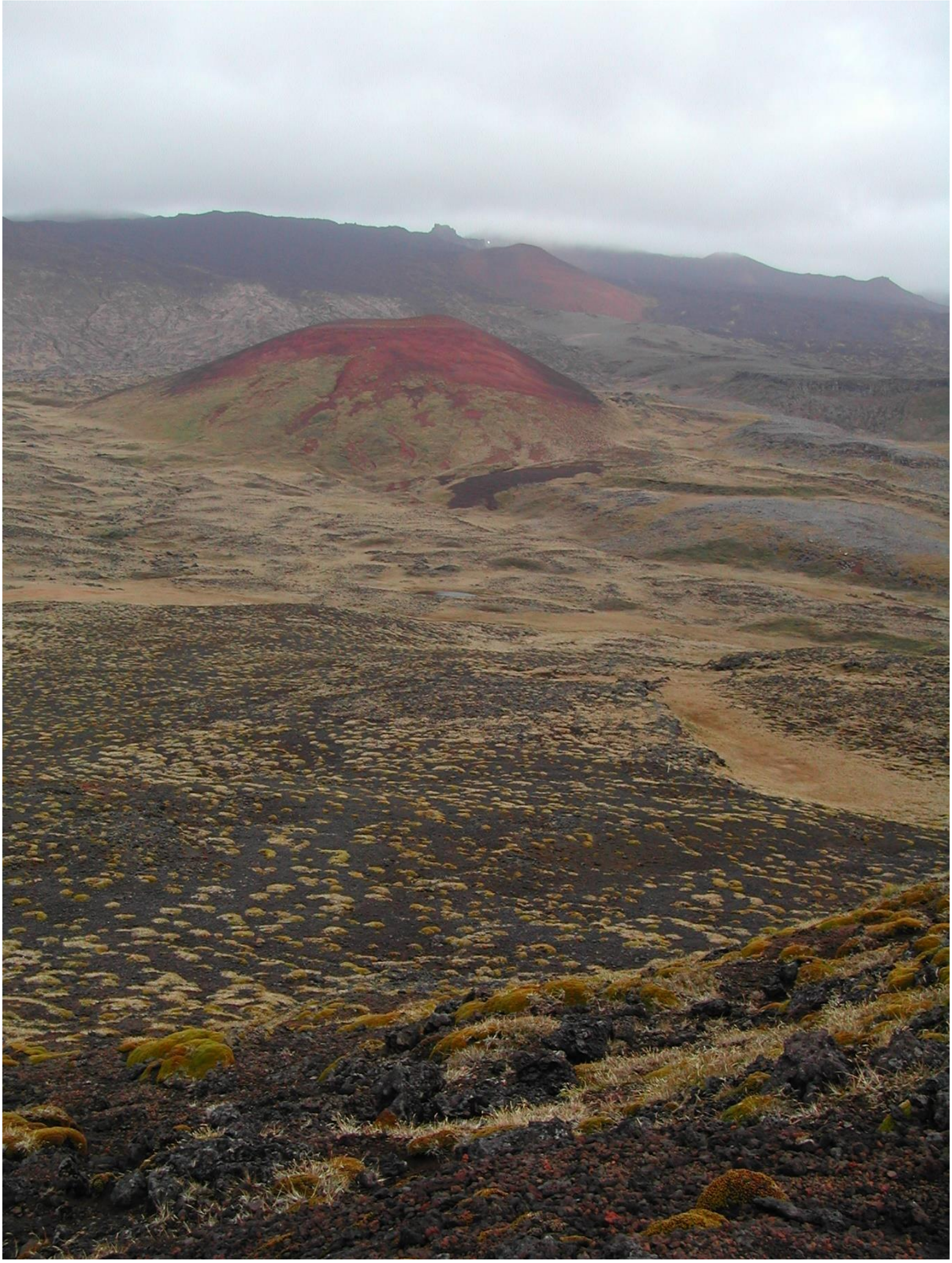
	Azorella present	*Azorella* absent	Difference	Pairs		
Species	Mean ± SE	Mean ± SE	Present - Absent	n	V	p
Uncinia compacta	208 ± 7	212 ± 8	-3.6	13	9	0.95
Pringlea antiscorbutica	219 ± 7	239 ± 9	-20.3	8	30	0.96
Lycopodium saururus	231 ± 7	224 ± 5	6.7	12	11	0.095
Lycopodium magellanicum	231 ± 8	230 ± 6	1.4	7	2	0.395
Poa cookii	232 ± 7	233 ± 8	-1.3	17	33	0.73
Acaena magellanica	238 ± 6	240 ± 6	-1.8	19	38	0.972
Grammitis kerguelensis	241 ± 15	256 ± 13	-15.3	8	15	0.985
Blechnum penna-marina	242 ± 5	255 ± 6	-13.2	20	101	0.991
Ranunculus biternatus	255 ± 6	252 ± 9	2.8	21	47	0.377
Colobanthus kerguelensis	261 ± 8	263 ± 10	-1.8	10	11	0.336
Montia fontana	261 ± 9	270 ± 9	-8.8	13	23.5	0.955
Cerastium fontanum	264 ± 10	277 ± 7	-13.2	5	10	0.979
Agrostis magellanica	273 ± 6	276 ± 5	-2.6	20	33.5	0.746

Table S4. Comparison of functional trait values (mean ± standard error) of all study species for which data were available from Marion Island (from Mathakutha et al. in press). Trait values were compared between the species that occurred at higher altitudes in the presence of *Azorella selago* ("Higher species") vs. the species that did not occur higher in the presence of *A. selago* ("No effect species"). n = the number of samples for which functional trait data were available. Leaf toughness was measured as force to puncture through a leaf, and frost tolerance was measured through electrolyte leakage after freezing.

Trait	Higher species	No effect species	p
Height (mm)	68.5 ± 6.7 (n = 75)	119.8 ± 5.1 (n = 420)	0.898
Leaf area (mm^2)	5302.6 ± 608.5 (n = 75)	519.4 ± 51.3 (n = 248)	**< 0.01**
Specific leaf area (mm^2 mg^{-1})	13.9 ± 0.8 (n = 72)	19.0 ± 0.6 (n = 234)	0.955
Leaf chlorophyll content (mg)	363 ± 9.1 (n = 114)	323.3 ± 4.8 (n = 299)	0.989
Leaf toughness (N)	0.1 ± 0.02 (n = 69)	1.1 ± 0.06 (n = 344)	0.955
Frost tolerance (µS g^{-1})	7005.28 ± 1551.38 (n = 13)	4767.91 ± 490.85 (n = 71)	0.945

Text S1

The altitude of the five highest occurring individuals of each vascular plant species growing on and away from *Azorella selago* were recorded using a handheld GPS unit. Additionally, for a subset of transects, altitude was also recorded using a barometric altimeter and was extracted from a digital elevation model (DEM). There were no significant differences between these three measurements of altitude, both broad scales and fine scale (DEM: t = 1.5, df = 410.99, p-value = 0.123; barometric altimeter: t = 0.997, df = 417.61, p = 0.319) and fine scales (DEM: t = 1.7, df = 410.99, p-value = 0.083; barometric altimeter: t = 0.997, df =417.61, p = 0.319). The absolute mean difference between attitudes from the GPS and DEM and from the GPS and the barometric altimeter were 9.76 and 5.1 m, respectively.



Scoria cone on Marion Island in the distance and *Azorella selago* cushion plants in the foreground.

Chapter 5:

General Conclusion

Biotic interactions may strongly influence the structure, functioning and stability of ecological communities (Schöb *et al.*, 2013; Zhang & Wang, 2016; Eurich *et al.*, 2018; Kunstler *et al.*, 2019). However, predicting the impacts of biotic interactions may be difficult because they can vary considerably both spatially (e.g. Bertness & Callaway, 1994; Zhang & Wang, 2016; Kunstler *et al.*, 2019) and temporally (e.g. Holzapfel & Mahall, 1999; Armas & Pugniare, 2009; Metz & Tielbörger, 2016). Despite a growing understanding of the spatio-temporal variability and species-specific nature of biotic interactions, there are still several issues that require clarification to improve predictions of the nature and strength of interactions and, therefore, to improve our understanding of species coexistence. Within the context of facilitation, many studies have documented the positive impact of benefactors on associated beneficiary species (Schöb *et al.*, 2013; Chen *et al.*, 2015; Hupp *et al.*, 2017). However, fewer studies have documented beneficiary feedback effects (i.e. the impact of beneficiary species and/or individuals on their benefactors: Holzapfel & Mahall, 1999; Lortie & Turkington, 2008; Schöb *et al.*, 2013; Schöb *et al.*, 2014a; García *et al.,* 2016; Bai *et al.*, 2018) and examined if interactions among beneficiaries are mediated by the benefactor (Aguiar & Sala, 1994; Schöb *et al.*, 2013). In addition, while it has been argued that abiotic variables primarily determine broad-scale range limits (Pearson & Dawson, 2003), theory suggests that biotic interactions can either expand (through positive interactions) or limit (through negative interactions) the total area in which a species can occur (He & Bertness, 2014; Filazzola *et al.*, 2018). However, few studies have tested this idea using empirical data. The broad aim of this thesis was therefore to examine the consequences of biotic interactions (both within species and bidirectionally between species) on species' performances and distributions, with a focus on these three research avenues. Using a combination of experimental and observational data, this study revealed several key findings related to plant-plant interactions.

The impact of *Agrostis magellanica* on *Azorella selago* is neutral

Beneficiary feedback effects have typically been documented using snapshot approaches (i.e. correlations within a single time period: e.g. Holzapfel & Mahall, 1999; Lortie & Turkington, 2008; but see García *et al.*, 2016). Many of these short-term studies have documented negative beneficiary feedback effects (Michalet *et al.*, 2011; Cranston *et al.*, 2012; Schöb et al., 2014b; García *et al.*, 2016; Michalet *et al.*, 2016; Llambí *et al.*, 2018). However, I show for the first time, using a long-term dataset, that beneficiary feedback effects can be neutral (Chapter 2). Therefore, in this study system the relationship between the benefactor species and the beneficiary species is commensalistic. However, I also highlight a methodological issue, as beneficiary feedback effects vary from neutral to negative depending on the benefactor performance metrics measured and depending on the type of approach used (i.e. between long-term observational approaches and snapshot approaches: Chapter 2; see also Schöb *et al*., 2014a; García *et al*., 2016). Therefore, to accurately assess the reciprocity of biotic interactions, studies need to consider maybe moving beyond contemporary snapshot approaches and short-term experiments (see e.g. Metz & Tielbörger, 2016)

Facilitation, both within and between species, may be more common than competition

Where facilitation by benefactor species increases the cover and/or density of beneficiary species (e.g., Tielbörger & Kadmon, 2000; Llambí *et al*., 2018), competition among beneficiary species may outweigh the positive impact of the benefactor species on beneficiary species' performance (Tielbörger & Kadmon, 2000; García-Cervigón *et al.*, 2013; Schöb *et al*., 2013). Therefore, facilitation by a benefactor could potentially mediate the outcome of interactions among beneficiaries (Schöb *et al.,* 2013). I confirm that the interaction between the benefactor and beneficiary species in my model study system is generally positive, and increasingly so under greater abiotic severity (Chapter 3). However, in contrast to expectations (Aguiar & Sala, 1994; Schöb *et al*., 2013), I show that benefactor-mediated intra-specific interactions among beneficiary individuals can also be positive (Chapter 3). Therefore, in certain systems, including the abiotically-severe sub-Antarctic habitat studied here, both inter- and intra-specific interactions have stronger positive than negative effects, suggesting a stronger influence of facilitation than competition. As a result, although the Stress Gradient Hypothesis (SGH) was originally formulated for inter-specific interactions, it may also apply to intra-specific interactions (in agreement with Fajardo & McIntire, 2011; Zhang & Wang, 2016; Svanfeldt *et al*., 2017).

The influence of positive plant-plant interactions on species range limits is strongly species-specific

Because strong inter-specific facilitative interactions can occur between benefactors and associated plants in abiotically-stressful environments, benefactors could allow species to occur in areas that are otherwise abiotically unfavourable (Chapter 4). Specifically, the fine-scale impacts of interactions could potentially scale-up to influence broad-scale species' distributions (see e.g. Bruno *et al.*, 2003; Araújo & Rozenfeld, 2014; He & Bertness, 2014; Filazzola *et al.*, 2018). Using field-quantified data, I show that a benefactor species can expand the upper altitudinal limits of some, but not all, vascular plant species in my sub-Antarctic study system (Chapter 4). However, predicting which species' upper altitudinal limits would be expanded upslope as a consequence of facilitation may be difficult because, for example, functional traits did not differ significantly between the species that occurred at higher altitudes in the presence of the benefactor and those that did not. Positive plant-plant interactions, therefore, have the potential to increase the niche space that certain species occupy, but the influence of these interactions may be strongly species-specific.

Implications of these findings for plant ecology

In this thesis, I show that plant-plant interactions, both within beneficiary species (i.e. at the individual-level) and between a benefactor and beneficiary species (i.e. at the species-level) are indeed positively related to beneficiary species' performance in this system (Chapter 3). In contrast, I demonstrate that beneficiary species may have no impact on benefactor species performance (Chapter 2). Finally, I also document that the impact of positive plant-plant interactions may scale up from the individual- and species-levels to the population- and community-levels (Fig. 1; see also Chapter 4). My findings have several ecological implications, particularly for our understanding of plant-plant interactions in abiotically stressful environments, not only at the individual- and species-levels (Chapter 2 - 3), but also at the community-level (Chapter 4).

The impacts of fine-scale biotic interactions do not always scale-up to influence broad-scale species' distributions

Plant-plant interactions typically positively affect the abundance and performance (e.g. reproductive effort) of species under increasingly stressful conditions (Chapter 2 - 3: He *et al.*, 2013). However, certain interactions only have fine-scale impacts on the species involved and do not scale up to affect broader community patterns (see e.g. Araújo & Rozenfeld, 2014). For example, from this thesis we see that even though *Azorella selago* has a positive impact on the abundance and performance of *Agrostis magellanica* (Chapter 3), *A. selago* has no impact on the upper distributional limit of *A. magellanica* (Chapter 4). Therefore, while benefactor species may positively impact the fine-scale performance and survival of beneficiary species, factors other than biotic interactions (e.g. dispersal potential; Travis *et al*. 2005, Travis *et al*. 2013) may more strongly drive broader community patterns. Discrepancies may therefore exist between the patterns and processes observed at fine and broad spatial scales, where facilitation impacts on species strongly at local scales but does not affect species' distributions.

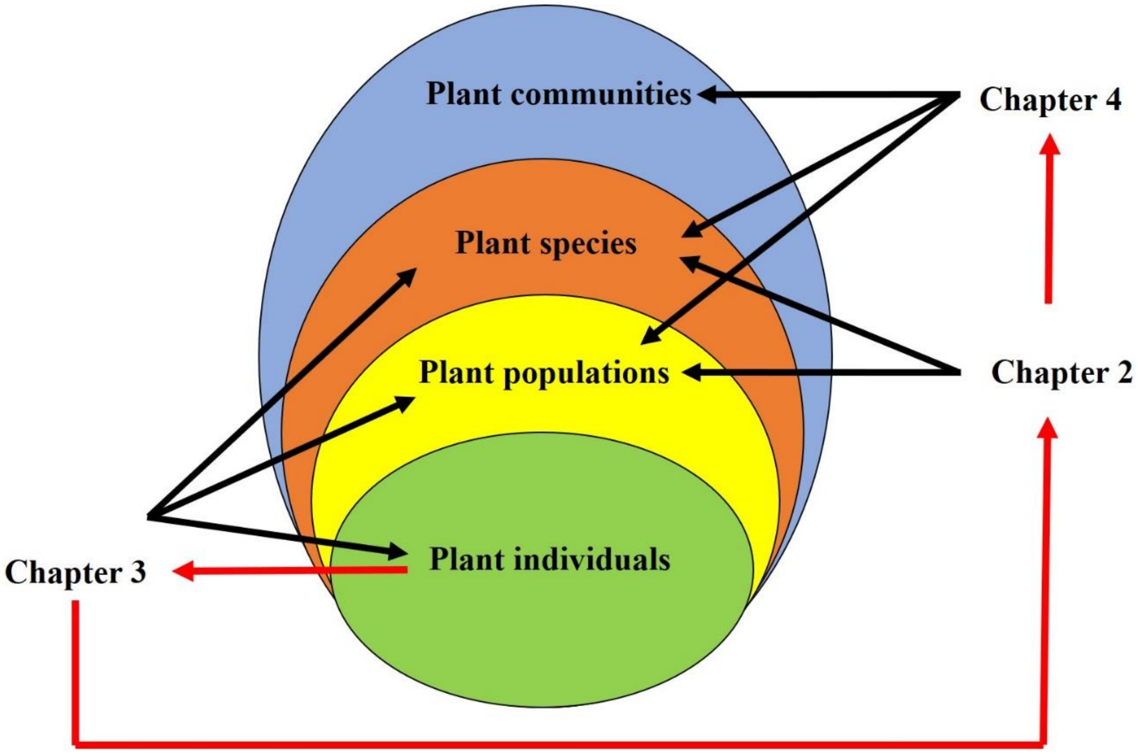


Figure 1. Schematic diagram representing the scaling up of the impacts of biotic interactions from the individual- and species- levels (Chapter 2, Chapter 3) to the population- and community-levels (Chapter 4).

Positive intra-specific interactions are maybe more important than previously assumed

A fundamental principle in ecology is that population density will generally negatively affect individual performance (Silvertown & Charlesworth, 2009). Density-dependent effects are therefore typically assumed to be negative, with strong competition expected between conspecific neighbours due to greater niche overlap within species than between species (Adler *et al*., 2018). However, density-dependent effects can also be positive (García-Cervigón *et al*., 2013), and my results suggest that *A. magellanica* performance, both in the presence and absence of *A. selago*, is positively related to conspecific density (Chapter 3). There are potentially several mechanisms driving these patterns. For example, because wind pollinated plants benefit more from high densities, *A. magellanica* will most likely be efficiently pollinated at high densities (Seifan *et al.*, 2014).

Additionally, while facilitation research (and related theories, such as the SGH; Bertness & Callaway, 1994) is often focused on variation in the outcome of inter-specific interactions along environmental gradients (i.e. between benefactor species and associated beneficiary species: Badano *et al.*, 2010; Anthelme *et al.*, 2017), I show that the outcome of intra-specific interactions among *A. magellanica* conspecifics growing on *A. selago* also vary with changing abiotic conditions (Chapter 3; see also Fajardo & McIntire, 2011; García-Cervigón *et al.*, 2013; Zhang & Wang, 2016; Svanfeldt *et al.*, 2017). Such benefactor-mediated interactions among beneficiaries have rarely been assessed within the context of facilitation (see Schöb *et al.*, 2013), but may have important consequences for the net outcome of biotic interactions. For example, my results suggest that benefactor-mediated interactions among beneficiaries can be positive. However, this may not be a general pattern and in other abiotically-stressful systems because benefactor-mediated interactions among beneficiaries could be negative. For example, if the intensity of facilitation by benefactors increases linearly along stress gradients, strong intra-specific competition among beneficiaries may eventually outweigh the positive impact of the benefactors on the beneficiaries (i.e. under extreme abiotic stress the net outcome of benefactor-beneficiary interactions may be negative). Therefore, the SGH should be further refined to include changes in intra-specific interactions along stress gradients, particularly within the context of facilitation (i.e. including benefactor-mediated interactions among beneficiary species and/or individuals).

Biotic interactions may mediate climate-driven range shifts

The global climate has changed considerably over the past 100 years (IPCC, 2014), with widespread ecological consequences (Parmesan, 2006). On Marion Island, specifically, the majority of vascular plant species' upper altitudinal limits have expanded upslope in response to warming (le Roux & McGeoch, 2008b). Understanding the interplay between biotic interactions and climate is important because biotic interactions can mediate species' responses to climate change (Blois *et al.*, 2013). For example, biotic interactions could either accelerate or impede species' range shifts (HilleRisLambers *et al.*, 2013). However, biotic interactions will only mediate climate-driven range shifts if they are able to influence the establishment and/or survival of species at their upper (Chapter 4) or lower range limits (see e.g. HilleRisLambers *et al*., 2013).

The stress gradient hypothesis also provides some insights into how biotic interactions could respond to climate change and, as a result, how biotic interactions could mediate climate-driven range shifts (e.g. Choler *et al*., 2001; He & Bertness, 2014). For example, species will most likely benefit from facilitation at the extreme ends of stress gradients, where the species are most stressed and environmental conditions are sub-optimal (e.g. at their upper altitudinal limits; Choler *et al*., 2001; Liancourt *et al*., 2005). Therefore, facilitation could allow species to establish and persist at these higher elevations by acting as a buffer against abiotic severity if plants in alpine systems migrate to higher elevations in response to warming (Cavieres *et al*., 2014). However, I expect that the impact of facilitation on beneficiary species' distributional limits in response to warming will differ between habitat specialists and habitat generalists. Therefore, on Marion Island, species like *Blechnum penna-marina* and *Grammitis kerguelensis* may be restricted to certain microhabitat conditions that *A. selago* cannot provide. In contrast, widespread generalists, including as *A. magellanica*, may benefit greatly from the interaction with *A. selago* (Chapter 3). Additionally, under benign conditions (i.e. at lower altitudes) positive biotic interactions may also be important for setting species distributional limits (see e.g. Ettinger *et al*., 2011; Louthan *et al*., 2015). For example, at lower altitudes, benefactors could provide additional resources and/or competition-free space for beneficiaries and, therefore, potentially expand species' lower distributional limits (Holmgren & Scheffer, 2010). In contrast, because competitive interactions (as an example of a negative biotic interaction) increase as abiotic stress decreases, competitive interactions may also contribute to determining species lower distributional limits (Kikvidze *et al*., 2005; HilleRisLambers *et al*., 2013). Both positive and negative biotic interactions therefore have the potential to influence species' upper and lower range limits (Chapter 4).

Climate change alters the outcome of biotic interactions

In addition to biotic interactions mediating climate change impacts, changing environmental conditions may also reciprocally alter biotic interactions (Blois *et al*., 2013). For example, one could speculate that the impact of beneficiary species on their benefactors may shift from neutral (Chapter 2) to negative if beneficiary species' cover increases in response to warming (Schöb *et al*., 2014a). Consequently, beneficiary species would compete more strongly with their benefactors under warmer conditions. Moreover, the impact of benefactor species on associated beneficiary species could shift from positive (Chapter 3) to negative if, under climate warming, there is facilitation release (Anthelme *et al*., 2014). Thus, under different scenarios of changing conditions, shifting outcomes of plant-plant interactions could indirectly limit one or both of the interacting species' performance and, as a result, distribution. It is, therefore, important to understand how benefactor-beneficiary species interactions will change in response to climate change, especially if the species involved in the interaction are dominant and/or widespread (Chapter 2), because a shift in the balance of such an interaction will likely drive changes in community-wide vegetation patterns.

Contrary to these predictions, in this thesis, I found that the current upper altitudinal limits of species in the presence of *A. selago* are not correlated with the rate at which the species' upper range limits had shifted in response to warming on Marion Island. Therefore, I found no relationship between the nature of the interaction with a benefactor and the magnitude of the response to recent climate change (Chapter 4). This result suggests that although biotic interactions may be important in determining the range limits of certain species, they may be relatively unimportant in influencing species range shifts in response to climate change (possibly due dispersal limitation of the beneficiary species; Travis *et al*. 2005, Travis *et al*. 2013).

The impacts of beneficiary feedback effects are context-dependent

Beneficiary feedback effects appear to be context-dependent, and this context-dependency has largely been unexplored (but see Schöb *et al*., 2014b). For example, beneficiary feedback effects can vary with beneficiary species richness (Schöb *et al*., 2014b), and, therefore, in more species rich systems it may be expected that beneficiary feedback effects will shift between negative, neutral (Chapter 2) and positive as the complexity of reciprocal interactions increases (e.g. as demonstrated by Llambí *et al*., 2018). Therefore, the outcome of beneficiary feedback effects may be different in more complex multi-species systems than in the relatively species-poor sub-Antarctic fellfield. Additionally, beneficiary feedback effects may differ depending on the type of environment in which a benefactor-beneficiary interaction is examined and the type of gradient along which species interactions are assessed (i.e. resource vs. abiotic gradients: Maestre *et al*., 2009). For example, in a sub-Antarctic system, I show that beneficiary feedback effects can be neutral in the long-term (Chapter 2); however, it could be expected that long-term beneficiary feedback effects will be more negative in arid environments (Michalet *et al*., 2016). Therefore, while I have documented that long-term beneficiary feedback effects are neutral in a species-poor and abiotically-severe system, more studies are needed to test the broader generality of this finding (particularly in species-rich and/or water-stressed environments).

Methodological limitations and future perspectives

In this thesis, there are some methodological issues that need to be noted. First, while correlative approaches can be advantageous (and pragmatic), they have some methodological limitations, including specifically their inability to reveal mechanistic relationships (Metz & Tielbörger, 2016). For example, I observed contradictory results between experimental and observational data (Chapter 3), where observational data revealed a positive relationship between *A. magellanica* density and *A. magellanica* performance both in the presence and absence of *A. selago*; however, experimentally thinning *A. magellanica* had no effect on conspecific performance over a single growing season. To overcome this problem, future studies should consider using experimental data, especially when collected over multiple seasons, in conjunction with observational data. While correlative approaches have some advantages (including fewer logistical issues), carefully designed experiments could be useful to confirm (or refute) findings from purely observational data. Future studies could, therefore, consider measuring niche expansion using transplant experiments (see e.g. Alexander *et al*., 2015) to test whether beneficiary species will be able to reproduce and survive at higher altitudes than at their current elevational limits.

Relatedly, although my study design provided an accurate estimate of species' upper distributional limits, a larger non-*Azorella* area was sampled compared to *Azorella*-covered area in each transect because *A. selago* cover was generally well below 50 % within each transect (Chapter 4). Therefore, any species that were recorded at a lower altitude in the presence of *A. selago* does not necessarily reflect a negative impact of *A. selago* on the species, but rather represents an unequal sampling effort (Chapter 4). Future studies could therefore consider using experimental and observational data to examine the influence of biotic interactions on species' lower distributional limits in addition to the influence of biotic interactions on species' upper distributional limits (see e.g. Ettinger *et al*., 2011; Louthan *et al*., 2015). Additionally, future studies employing observational approaches should also control for sampling bias in systems where plant cover and productivity declines with elevation.

Lastly, when examining beneficiary feedback effects (Chapter 2), I observed contradictory results between benefactor performance measures based on the type of approach used (i.e. a long-term repeated measures approach vs. snapshot approaches). While beneficiary feedback effects are typically documented using snapshot approaches and/or correlations over a single time period (Holzapfel & Mahall, 1999; Lortie & Turkington, 2008), experimental approaches may be especially valuable for understanding the causal relationship between interacting species (Metz & Tielbörger, 2016). In this thesis, however, a long-term repeated measures approach was more practical for assessing the impact of *A. magellanica* on *A. selago* because *A. selago* is a slow-growing species (le Roux & McGeoch, 2004) and may, therefore, respond slowly to changes in biotic interactions (i.e. highlighting the value of long-term datasets; see also Metz & Tielbörger, 2016). However, future studies could consider examining the bidirectional nature of biotic interactions by explicitly comparing snapshot approaches with long-term observational and/or long-term experimental approaches across a range of ecological systems where facilitation is prominent.

Conclusion

Although the unidirectional effect of biotic interactions (e.g. the impact of one species on another) has received much attention, considering the bidirectionality of biotic interactions (i.e. the impact of each of the interacting species and/or individuals on the other) may highlight important consequences for the net performance of all the species involved (Schöb *et al.*, 2013; Schöb *et al.*, 2014b; García *et al.*, 2016; Michalet *et al.*, 2016; Llambí *et al.*, 2018). Here I build on this existing framework and reveal three broad insights: 1) despite the predominant attention traditionally devoted to negative interactions in ecological theory, considering positive inter-specific interactions, as well as examining intra-specific interactions and the bidirectional nature of inter-specific interactions, could be key in improving our understanding of contemporary and future plant community dynamics; 2) to fully understand how fine-scale biotic interactions (i.e. influencing species' performance) scale up to affect species' distributions, we need to examine the context-dependency and reciprocity of these interactions, both at the inter- and intra-specific levels; and 3) to predict the impacts of global environmental change on species, we need a more complete understanding of the complexity of biotic interactions and species-specific responses.

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