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. We 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. We 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.

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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 and Bertness 2014, Jones and 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 and Gilbert 2016). While the influence of abiotic conditions on species' distributions has been well

documented, particularly at broad spatial scales (Pearson and Dawson 2003), the impact of biotic interactions on species' distributions is still relatively poorly understood (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 and 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 and 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 and Bertness 2014, He and 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 and Cavieres 2006, Badano and Marquet 2009). 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 and Callaway 1994, Bruno et al. 2003, Jones and 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 modeling (Filazzola et al. 2018), and there are recent studies showing that this may also be true for animals (He and 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 and 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. We use *Azorella selago*, a widespread cushion plant (Appendix S1: 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 S1: Fig. S2), we specifically test if species' upper elevational distributions differ when growing in association or away from *A. selago*. We 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 (Badano and 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 and McGeoch 2008*b*), cover (Smith et al. 2001), and productivity (Smith 2008) decline with elevation. There are 130 scoria cones (Appendix S1: 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 (le Roux and McGeoch 2008*a*).

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

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, *A. selago* Hook. (Apiaceae; *Azorella* hereafter). On Marion Island, this species occurs in all vegetation types, from the interior of the island (~840 m a.s.l.) to sea level (le Roux and McGeoch 2008*b*). As a consequence of its cushion growth form (Appendix S1: Fig. S1A, B), *Azorella* ameliorates stressful conditions by locally modifying the physical environment (Nyakatya and McGeoch 2008).

The positive impacts of cushion plants on associated plants have 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 and McGeoch 2008, Hupp et al. 2017). On Marion Island, there are some data that demonstrate facilitation by *Azorella* (Nyakatya and McGeoch 2008, le Roux and McGeoch 2008*a*, 2010, le Roux et al. 2013). Additional data are available for other congeneric species which show strong facilitation in similar environments (Badano and Cavieres 2006, Badano and Marquet 2009). On Marion Island, *Azorella* has a positive effect on the richness and total cover of vascular plant species (I. P. R. Buyens et al., *in preparation*; see also Appendix S1: Fig. S2A) and on the abundance of individual species (e.g., *Agrostis magellanica*, except at the lowest altitudes; see also le Roux and McGeoch 2008*a*, 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 S1: Fig. S4), and 21 landform-scale altitudinal transects located on five scoria cones.

Data from 10 broad-scale transects were available from le Roux and McGeoch (2008*b*) and P. C. le Roux and M. A. 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 and McGeoch 2008*b*). Each transect was sampled over 1–1.5 d. The altitude of the highest five individuals of all vascular plant species (alien and indigenous) was recorded using a handheld GPS unit, both when growing on and away from *Azorella* cushions (Data S1). Additionally, for a subset of transects, altitude was also recorded using a barometric altimeter and was extracted from a digital elevation model (see Meiklejohn and Smith 2008 for details). There were no significant differences between these three measurements of altitude (Appendix S1: 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* was 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 (Data S1). 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 S1: 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 we can only robustly test for changes in the upper distributional limits of species with our 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 S1: 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* do 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., our paired test is biased toward negative differences because *Azorella* covers <50% of the total area in our 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 and McGeoch (2008*b*) 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 1960s and the 2000s.

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 and 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 17–55 replicates per trait per species, except for frost tolerance where there were data available from 13 species with 5–10 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 (Appendix S1: Table S2; Fig. 1). However, *Acaena magellanica* (Appendix S1: Fig. S1C) and *Colobanthus kerguelensis* (Appendix S1: Fig. S1D) 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 S1: Fig. S1E). At fine scales, *Azorella* had no significant impacts on the upper altitudinal limits of species (Appendix S1: Table S3). The current upper altitudinal range limits of species in the presence of *Azorella* were not correlated with the rate at which the species' upper range limits had shifted since the 1960s ($r = 0.31$, $P = 0.254$; Appendix S1: Fig. S6).
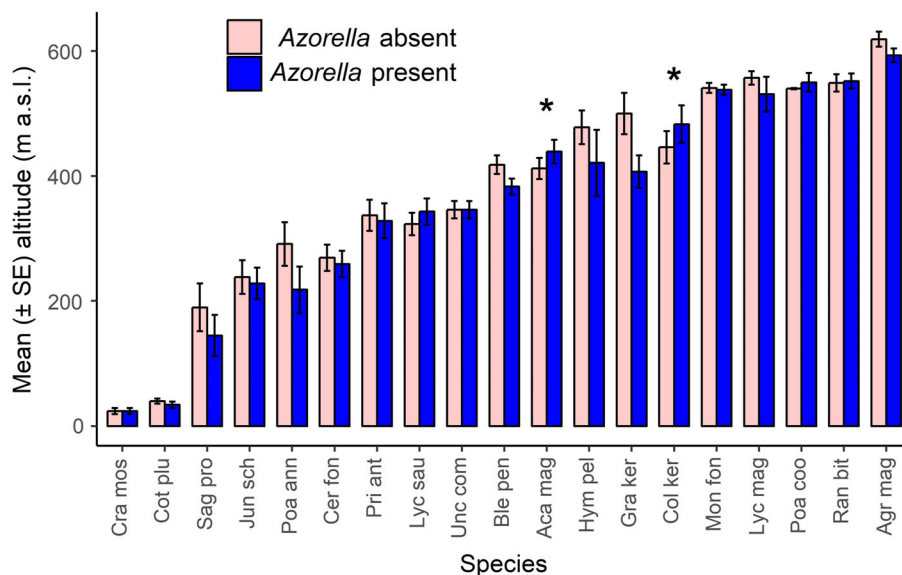
Fig. 1. Mean (±standard error) altitude (m a.s.l.) of vascular plant species growing on vs. away from *Azorella selago* for the island-scale transects. See Appendix S1: Table S1 for species name abbreviations. Species are ordered by their upper altitudinal limit on *A. selago*.

The mean cover and frequency of occurrence of species on vs. away from *Azorella* was not generally affected by the presence of *Azorella* (Appendix S1: Fig. S7; although cover of *Ag. magellanica* was significantly higher on *Azorella* at several altitudes; Appendix S1: Fig. S7A). Similarly, the frequency of occurrence of individual species was generally similar on vs. away from *Azorella* across the altitudinal range (Appendix S1: Fig. S8A–E; only *Ranunculus biternatus* differed strongly in the altitude at which it had the highest frequency of occurrence on vs. away from *Azorella*: Appendix S1: Fig. S8F).

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 S1: 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 *Ac. 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 (Armas et al. 2011, He and 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 and Bertness 2014, Jones and Gilbert 2016, Filazzola et al. 2018). In this study, we show that 3 out of 19 vascular plant species, that is, the shrub *Ac. magellanica*, the cushion-forming *C. kerguelensis* and the clubmoss *L. 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, *Ag. magellanica* (at mid-altitudes), and on the frequency of occurrence of another species, *R. biternatus* (at low and mid-altitudes). At fine spatial scales, such species-specific responses to cushion plants (e.g., higher cover and abundance; Alliende and Hoffmann 1985, Hupp et al. 2017) and other nurse 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 and Hoffmann 1985). However, the only widespread woody plant species on Marion Island, *Ac. 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 *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, *Ag. magellanica* is strongly facilitated by *Azorella* at fine scales (Appendix S1: Fig. S2; le Roux and McGeoch 2010, le Roux et al. 2013), but the interaction with *Azorella* had no effect on the upper distributional limit of *Ag. magellanica*. In contrast, *Ac. magellanica* is facilitated by *Azorella* at fine scales (Appendix S1: Fig. S2) 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, 2018; in contrast to with predictions of the SGH: Bertness and 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 and 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 and 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* (Appendix S1: Fig. S2). These mechanisms may, therefore, all potentially contribute to the generally negligible impact of *Azorella* on species' upper distributional limits.

In this study, we examined the occurrence of species on vs. away from *Azorella* and could not determine whether 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 *Ag. magellanica* are from individuals rooted with *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 whether populations growing in the adjacent substrate can maintain themselves without seed input from facilitated individuals, and, therefore, to test whether 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 and Bertness 2014, He and 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, our 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 favorable micro-sites at higher altitudes, which would otherwise still be unfavorable (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, we 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, 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, we 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 (Hupp et al. 2017), the former may allow greater range expansion into abiotically unsuitable conditions. Second, an experimental approach (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 (Holmgren and Scheffer 2010). Fourth, relatedly, based on the ideas of Maestre et al. (2009), we hypothesize that the impact of biotic interactions on species' ranges may differ along resource vs. 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.

Acknowledgments

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Supporting Information

Additional Supporting Information may be found online at: http://onlinelibrary.wiley.com/doi/10.1002/ecs2.2820/full