

# The abundance structure of *Azorella selago* Hook. f. on sub-Antarctic Marion Island: testing the peak and tail hypothesis

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**Abstract** Understanding the spatial distribution of organisms and the factors underlying it are key questions in ecology. Two competing hypotheses exist about the form of spatial variation in abundance. The abundant centre hypothesis suggests that abundance is highest in the centre of a species' range and declines towards the range margins. By contrast, the peak and tail spatial pattern in abundance posits that several high abundance areas exist across a species range. Here, we test these competing hypotheses by surveying the abundance of the keystone plant species *Azorella selago* Hook. f. (Apiaceae) across sub-Antarctic Marion Island on a regular spatial grid. We also examine several factors that might explain variation in abundance. *Azorella selago* occurs between ca. 30 and 850 m above sea level, with sharp discontinuities in abundance at ca. 30 m and at 667 m a.s.l. The survey and analyses revealed a complex abundance structure with patches of high abundance alternating with areas of low abundance or absence, providing support for the peak and tail hypothesis, but with some support for the abundant centre idea too. Variation in abundance was best explained by a model including the negative effects of elevation and of closed vegetation. Our work provides support for the peak and tail

pattern of spatial variation in abundance, which has profound importance for understanding the mechanisms underlying the spatial distribution of abundance and other macroecological regularities.

**Keywords** Abundance · Abundant centre hypothesis · Cushion plant · Range limits · Spatial aggregation

## Introduction

Two of the most fundamental ecological characteristics of any species are its distribution and abundance. Much of ecology has focussed on understanding not only the determinants of species abundances and population sizes, but also how these translate into spatial variation in sites occupied (occupancy) and eventually the distribution ranges that characterise all species (McGeoch and Gaston 2002; Gaston 2003; Samaniego and Marquet 2013). Indeed, spatial variation in the distribution of individuals at multiple scales and the aggregation of individuals is considered central to a unified theory of macroecology, prompting calls for a better understanding of it (McGill 2010).

Early theory suggested that spatial variation in abundance typically assumes a Gaussian form, sometimes known as the 'abundant centre hypothesis', such that a species reaches its highest densities at the centre of its geographic range with density gradually declining towards the range edge (Brown 1984). Later work showed that spatial patterning is more intricate, demonstrating that environmental gradients (such as those associated with topographic variation) result in a spatially variable abundance structure, which is not typically Gaussian (e.g. Sagarin and Gaines 2002a, b; McGeoch and Price 2004).

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Rather, abundance more usually follows a peak and tail pattern with several (1–5) peaks of very high abundance, which rapidly and smoothly drop off to a long tail of abundance one to two orders of magnitude lower than the peaks (McGill and Collins 2003). Clearly, these alternatives depend to some extent on spatial scale, but as McGill and Collins (2003) note: ‘Although a symmetric pattern with the peak in the centre (i.e. Gaussian) is not uncommon...it is also common to find asymmetric, non-centred and multi-peaked distributions’.

The number of studies that has sought to empirically examine these contrasting ideas remains rather limited (e.g. Murphy et al. 2006; Samis and Eckert 2007; Lee et al. 2009). Moreover, several of these studies are complicated either by the use of presence only data or by the use of existing data records collated from multiple sources, rather than direct, systematic surveys (see discussion in Sagarin and Gaines 2002b; Sagarin et al. 2006). In consequence, much remains to be understood about the spatial distribution of individuals, including the prevalence and pattern of aggregation, and the ubiquity of the peak and tail pattern. Such a situation is unhelpful because geographic patterns in species abundance form an important basis for understanding population- and community-level dynamics in space and time (McGill 2010).

Here, we contribute to current understanding of species abundance structure across environmental gradients by quantifying the distribution and abundance of a vascular plant species, *Azorella selago* Hook. f. (Apiaceae), across an entire, self-contained area within its overall geographic range (sub-Antarctic Marion Island), and by examining the extent to which the peak and tail hypothesis or Gaussian alternatives best suit the patterns found. *Azorella selago* is an important constituent of sub-Antarctic plant communities, and one of the major contributors to the aerial cover and standing crop of Marion Island’s vegetation (McGeoch et al. 2008). It is a long-lived perennial (le Roux and McGeoch 2004) and a pioneer species in fellfield communities and deglaciated areas (Huntley 1970; Frenot et al. 1993). Here, it stabilises loose substrates (Hausmann et al. 2009a) and has been shown to act as a nurse plant. At least sixteen vascular and seventeen non-vascular epiphytic plants are positively associated with *A. selago* cushions (le Roux and McGeoch 2008b, 2010; Hausmann et al. 2010; le Roux et al. 2013a), which also form an important habitat for many invertebrate species (Barendse and Chown 2001; Hugo et al. 2004; McGeoch et al. 2006). *Azorella selago* is also common in all habitat complexes on the island, occurring from sea level to approximately 840 m a.s.l. (Hedding 2006; le Roux and McGeoch 2008a). As a consequence of its significance in the terrestrial ecosystem and its wide distribution on the island, it forms an ideal species for testing the extent to which a peak and tail pattern

applies, and for documenting spatial variation in abundance given the implications of such variation for other macroecological patterns (McGill 2010).

Therefore, in this study we specifically do the following: first, we describe patterns in the distribution of the species across the island. Second, we use these data to test whether the predictions of the abundant centre or peak and tail hypotheses are met, so enabling us to determine which of these two hypotheses can be rejected. Third, we test the idea that the abundance structure of this keystone species on Marion Island is correlated with particular environmental variables, notably vegetation type, substrate type, aspect, slope or elevation as a proxy for abiotic variation in conditions (see le Roux 2008).

## Materials and methods

### Study site and species

Field work was conducted on Marion Island (46°54’S, 37°45’E) from April 2005 to May 2006. The volcanic, basalt island has a surface area of ca. 300 km<sup>2</sup>, rises to 1230 m a.s.l. and has an oceanic climate with a mean annual temperature of ca. 6.5 °C, total annual precipitation of ca. 1900 mm, generally high humidity and strong winds (see Chown and Froneman 2008 for an overview). It has two major biomes: tundra, which predominates in lowland areas, and polar desert, restricted to high elevations (above ca. 650 m a.s.l.). Species richness of plants and invertebrates is low and only seven vegetation complexes (subdivided into twenty-three vegetation communities) have been recorded on the island (Gremmen 1981; Gremmen and Smith 2008).

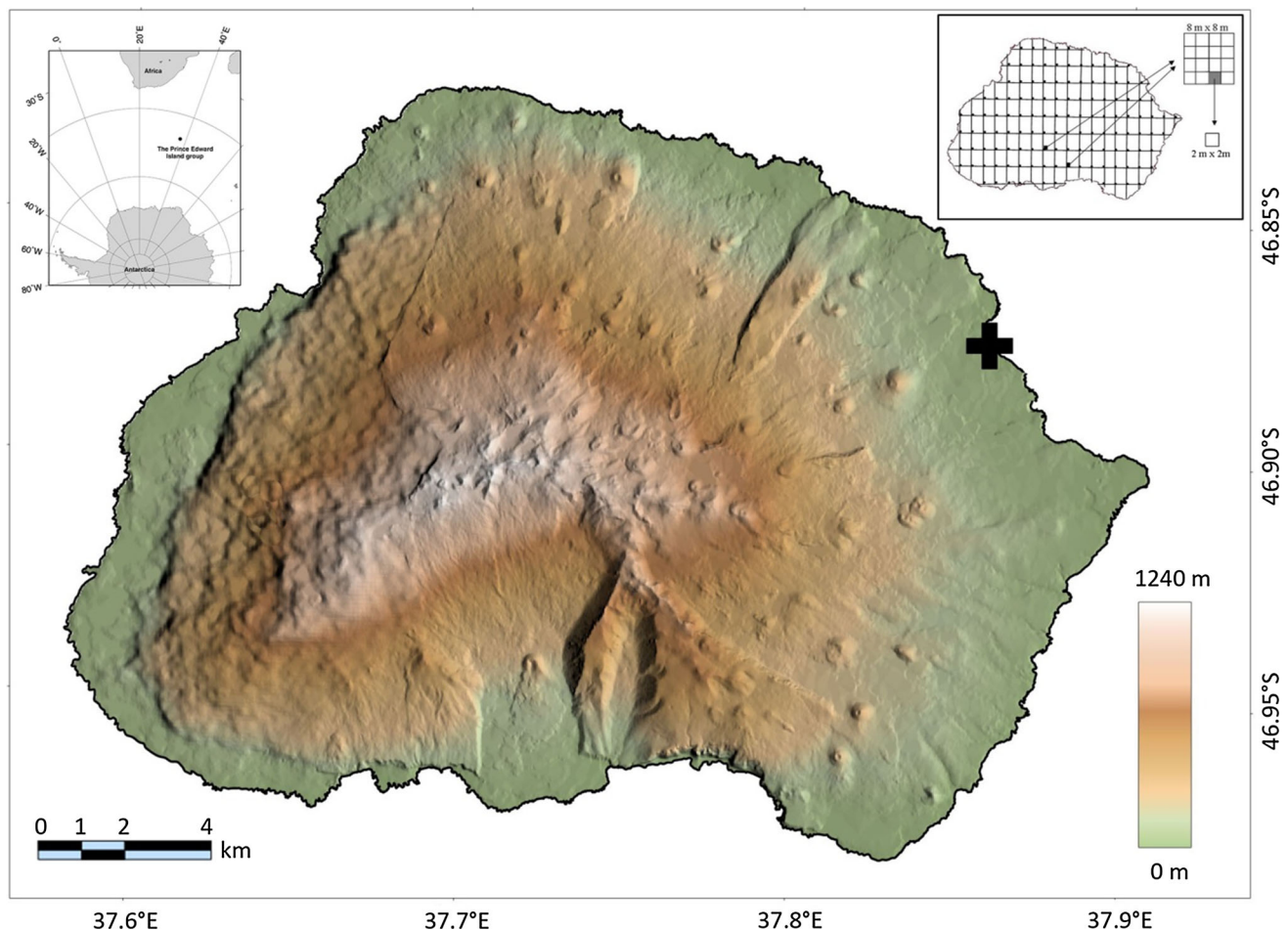
*Azorella selago* is slow growing (Frenot et al. 1993), and cushion age has been estimated to be between 30 and 80 years for single cushions of ca. 40 cm in diameter (cushions vary in size from ca. 7 to 141 cm) (le Roux and McGeoch 2004). The species has two distinct growth forms: discrete cushions and large, continuous mats (Frenot et al. 1993; Mortimer et al. 2008). In both growth forms, the leaves and stems of the plant typically grow tightly against each other to create hard, compact surfaces varying in height and diameter (le Roux and McGeoch 2004). In the discrete cushion growth form, cushions grow as spatially isolated individuals that are mainly surrounded by bare ground and rocks (le Roux and McGeoch 2004; le Roux et al. 2005). The mat growth form comprises flat, continuous expanses of plant material and often, though not exclusively, occurs in association with seepages as well as drainages (Gremmen 1981). Single, continuous mats may extend over areas as large as 30 × 40 m. Genetic evidence suggests that mats might either be single, continuous

cushions or a series of cushions that have merged (Mortimer et al. 2008). For analysis, we counted mats as single cushions (mats were less than 2 m across) because without genetic analysis it is difficult to discern whether one or more individuals are involved, but single individuals do form mats.

### Field sampling

Count data for *A. selago* were obtained using a system of grid cells placed systematically across Marion Island on a minute-by-minute basis following Raunkiær (1934) (Fig. 1). Gridline intersection points were used as sampling sites, given the systematic sampling approach adopted, constituting a total of 124 sites across the entire island (Fig. 1). An 8 m × 8 m plot (subdivided into sixteen 2 m × 2 m quadrats to obtain a measure of occupancy for each plot) was positioned at each site, and the number of *A. selago* cushions was counted in each 2 m × 2 m

quadrat (i.e. 16 quadrats per plot). Although this method provides a measure of cushion density (number of plants per 64 m<sup>2</sup> plot), for convenience from here on we refer to the number of plants counted as cushion abundance. Intersection points were pre-programmed into a hand-held GPS (Garmin E-trex Vista-C<sup>®</sup> with a barometric altimeter which was calibrated at least once a day at known altitudes). No sites were compromised by position (i.e. in an inaccessible position) or by human activity, which is restricted to the scientific station occupying a very small area (about 500 × 500 m, see Chown and Froneman 2008). At each site, the following were recorded: vegetation type (also named vegetation complexes), volcanic lava type or substrate, aspect (i.e. the direction in which a slope faces) and GPS coordinate (4-m accuracy). The main vegetation types (named vegetation complexes by Smith et al. 2001; Gremmen and Smith 2008) recorded across the island were as follows. Fellfield (comprising open vegetation dominated by cushion-forming mosses and *A. selago*),



**Fig. 1** Location and topography of, and the sampling design used on Marion Island. The left-hand inset indicates the position of the island in the Southern Ocean. The right-hand inset indicates the sites placed at 1-min gridline intersection points, with one 8 m × 8 m plot

(square box) at each site, divided into 16, 2 × 2 m quadrats. The large cross indicates the position of the scientific station, and the shading indicates topographic variability

mire (which includes a variety of both wet and dry mires dominated by the grass *Agrostis magellanica*, and in which *A. selago* can be found), slope (which incorporates habitats dominated by *Blechnum penna-marina* and at times *Acaena magellanica*, again including individuals of *A. selago*) and polar desert (from which vascular vegetation is largely missing except for occasional *A. selago* cushions at its lower elevations). For substrate type, we used the broad classification of lava types on the island: black lava, grey lava and scoria (Boelhouwers et al. 2008), along with closed vegetation as a class because in that case the underlying substrate is dominated by a peat layer (Gremmen and Smith 2008). Aspect was divided into eight categories corresponding to compass points, but also included the category flat, which does not have an aspect (see Online Resource 1 for the classes for each of the non-spatial variables). Of the 124 sites, 110 were physically surveyed. Of the remaining 14 sites, anecdotal data were obtained for three based on observations by geomorphological researchers (i.e. the researchers documented whether or not *A. selago* was present, in these cases it was not), and the remainder were surveyed using oblique aerial photography (i.e. aerial photography taken at an angle, and in this case from a slow-moving Bell 212 helicopter) (see le Roux et al. 2013b). The aspect of the sites that were not physically visited was estimated using a topographic map (obtained from the Chief Directorate: Surveys and Mapping, Cape Town). The elevation of these sites was estimated to the nearest 10 m using the Marion Island digital elevation model (originally from the Chief Directorate: Surveys and Mapping; corrected by Hedding 2006).

## Analysis

The GPS coordinates as well as abundance data were converted to a shapefile and plotted in ArcGIS<sup>TM</sup> 9.1 to produce a map of the distribution and abundance of *A. selago* across Marion Island. Two macroecological relationships were quantified to examine whether the species follows standard expectations for abundance and occupancy, i.e. a right-skewed abundance frequency distribution and the existence of an occupancy–abundance relationship (i.e. a positive relationship between the number of individuals at a site and the number of sub-sites occupied by those individuals, see He and Gaston 2000), so assessing whether the current spatial scale of analysis is in keeping with macroecological expectations (discussed in Gaston and Blackburn 2000). The abundance frequency distribution was examined using both untransformed data and  $\log_{(10)}$  transformed data using abundance per  $8 \times 8$  m plot (see Gaston and Blackburn 2000). To investigate the relationship between plant occupancy (measured as a count of the number of  $2 \times 2$  m quadrats occupied per plot, see

He and Gaston 2000) and abundance (measured as total abundance per  $8 \times 8$  m plot), zero values were first removed and the relationship was examined by fitting a generalised linear model assuming quasi-Poisson errors because of overdispersion (Crawley 2013: 580) and conducted in R v. 2.15.1 (R Core Team 2012). The relationship was illustrated with a plot of  $\log_{(10)}$  abundance against occupancy.

The individuals of a species within its geographic range can be distributed in either of three statistically different ways, i.e. random, uniform or aggregated (Coomes et al. 1999). To determine whether the distribution of *A. selago* across Marion Island was non-random, and if so if it was even or aggregated (two alternative hypotheses), we quantified the patterns of aggregation using the  $8 \times 8$  m plot data and a spatially implicit measure of aggregation, Morisita's index ( $I_m$ ), where  $I_m < 1$  indicates a uniform dispersion and  $I_m > 1$  an aggregated dispersion (Hui et al. 2010). Morisita's index is independent of total count, mean abundance and number of grid squares sampled, but is dependent on the mean number of samples in the sampled area. The significance of the deviation of  $I_m$  from 1 was assessed by calculating the Chi-square statistic. A high  $\chi^2$  value, greater than the critical value at the specified degrees of freedom, indicates that the value for Morisita's index is statistically significantly different from 1 (Hamill and Wright 1986). We then used geostatistical prediction, by kriging, as a spatially explicit approach to illustrating the form of the distribution of individuals across the island (Rossi et al. 1992). Specifically, universal kriging (Zimmermann and Zimmermann 1991) was used to identify areas of high and low *A. selago* abundance. The interpolation was performed using ArcGIS<sup>TM</sup> 9.1 Geostatistical Analyst.

Several suggestions have been made for the ways in which tests for understanding the abundance structure of species ranges should be undertaken. For example, Sagarin et al. (2006) suggested that the balance point (which is the centroid of the range) should be sought, rather than the intersection of the longest perpendicular axes as suggested by Brown (1984), when testing for an abundant centre distribution. Here, we calculated the balance point of the range using Sagarin et al.'s (2006) approach and the  $8 \times 8$  m plot data, but with the realisation that for a two-dimensional distribution across a steep environmental gradient such a null model is unlikely to be realistic. Rather, as a null hypothesis, an abundant centre distribution for Marion Island, which has an approximately central peak elevation, would be more torus-like, with low abundances at the altitudinal limits and high abundances at mid-elevation. Should such a distribution be collapsed to a single dimension, a quadratic, unimodal relationship with elevation might be expected. The more complex, two-



dimensional distribution should readily be visible as a mid-elevation band of high abundance. We tested whether this is the case by undertaking polynomial regression of abundance against altitude in R v. 2.15.1, increasing the number of degrees from 1 (a standard linear model) to 3. We then compared the fits of the models against each other using an ANOVA approach (Crawley 2013) and plotted the predictions of the best fit onto the abundance by altitude data. In addition, we used quantile regression, as implemented in the *quantreg* library in R v. 2.15.1, with a tau setting of 0.90, to examine the form of the change in the highest abundance of plants with altitude, and plotted this outcome on the data too.

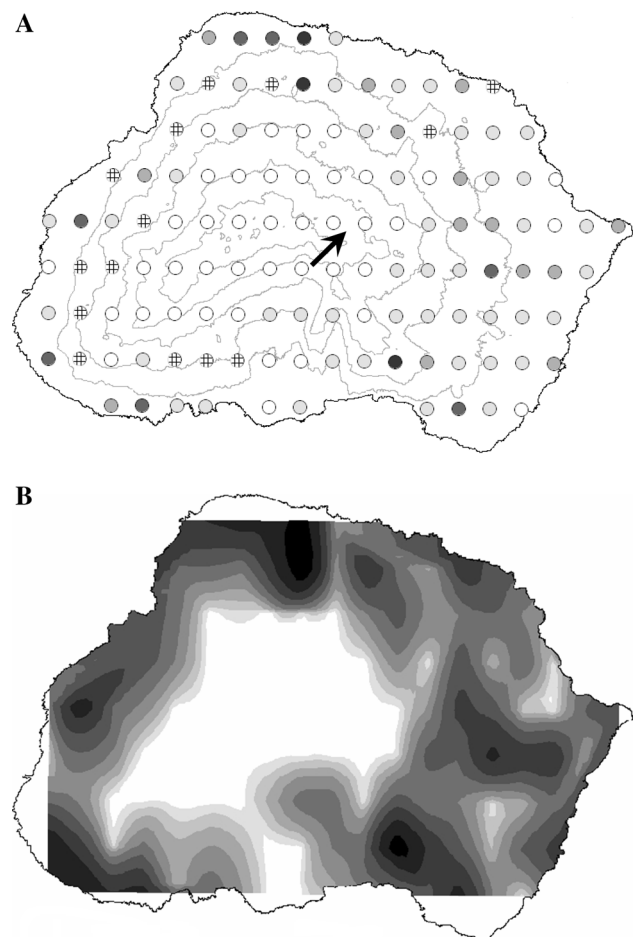
To examine the form of the spatial abundance patterns, we plotted the interpolated distribution obtained from the kriging (see above). We then sought to determine whether a consistent relationship nonetheless exists between abundance and latitude, longitude, vegetation type, substrate type and aspect using the  $8 \times 8$  m plot data on abundance. Several methods exist for examining the factors to which abundance may be most strongly related (Legendre and Legendre 1998; Zuur et al. 2009; Crawley 2013). Because absence data, i.e. zeros, were included, we used a two-part or hurdle model (Zuur et al. 2009: 271) as implemented in the *pscl* package of R (Jackman 2012). Here, a binomial model is first used to model the probability that a zero value is observed. That is, what circumstances determine whether an individual is likely to be present or absent? These may be very different to the circumstances that determine abundance once conditions for presence are met (Zuur et al. 2009: 273). In consequence, they need to be assessed first and separately from the circumstances that might determine abundance variation. Thereafter, the factors influencing abundance variation are assessed—that is one has to get over a ‘hurdle’ to do so, explaining the name of the models (Zuur et al. 2009: 273). To examine the factors influencing abundance variation, either a truncated Poisson or truncated negative binomial model is used to model the nonzero observations. We used a likelihood ratio test, as implemented in the R package *lmtree* (Zeileis and Hothorn 2002) to examine which of the latter was most appropriate and therefore used the truncated negative binomial. The independent data were abundance, and the dependent data were categorical based on the classes for vegetation type, aspect and substrate, and continuous data for elevation, latitude and longitude.

## Results

A total of 3578 discrete *A. selago* cushions was recorded, and the estimated cushion density was  $6.48 \text{ m}^{-2}$  ( $\pm 0.68$  SE) in sites occupied by discrete cushions. Of the occupied

sites, 83 % were occupied by discrete cushions and 17 % by mats (Fig. 2a). The species was absent in the centre of the island (Fig. 2a). Discrete cushion abundance ranged from 1 to 208 cushions per plot with an altitudinal range of between 30 and 667 m a.s.l. Three sites had abundances greater than 150 cushions per plot, situated on the south-east and north sides of the island (Fig. 2a).

Most plots included 1–50 cushions, and the abundance frequency distribution (at the plot scale) was clearly right-skewed (Shapiro–Wilk  $W = 0.7648$ ;  $p < 0.0001$ ; skewness = 1.7558; kurtosis = 3.1328) (Online Resource 2). Log-transforming the data did not fully normalise it, and indeed, the distribution became left-skewed (Online

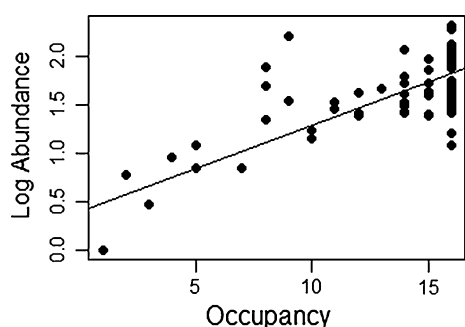


**Fig. 2** a Distribution of *Azorella selago* abundance across Marion Island. The clear circles represent areas where *A. selago* was absent; ● = cushion abundance of 1 to 50 cushions per plot; ● = 51 to 100 cushions; ● = 101 to 150 cushions; ● = 151 to 210 cushions per plot. The cross-hatched circles are sites with *A. selago* mats. The arrow indicates the balance point of the range (see text for detail). b The interpolated pattern of abundance of *A. selago* across Marion Island. The white areas represent sites where *A. selago* was absent and the black areas represent sites where cushion abundance was >150 cushions per plot

Resource 2) (Shapiro–Wilk  $W = 0.7604$ ;  $p < 0.0001$ ; skewness =  $-0.0156$ ; kurtosis =  $-1.8605$ ). As expected, log abundance and occupancy were strongly and positively related (generalised linear model,  $t = 4.304$ ,  $p < 0.0001$ ) (Fig. 3).

Morisita's index was significantly greater than 1.0 ( $I_m = 1.72$ ), and the calculated  $\chi^2$  value was greater than the critical value at  $p < 0.05$ . Thus, the abundances of *A. selago* across plots were significantly aggregated. The spatially explicit, geostatistical description of *A. selago* abundance illustrated clear patchiness in the distribution and abundance of *A. selago* across Marion Island, with four to five clear, high density peaks distributed around the island (Fig. 2b). The balance point of the range was found to be at approximately  $46^{\circ}54.300'S$ ,  $37^{\circ}45.300'E$  (Fig. 2a), though clearly this point reflects the geography of the island rather than an area of high abundance or occupancy. By contrast, a significant third-order polynomial relationship between abundance and altitude (Table 1; Fig. 4) provided statistical evidence in support of a peak in abundance between 200 and 300 m a.s.l. (the ANOVA indicated a better fit than either the first-order or second-order polynomials,  $p < 0.03$  in all cases). Although the highest absolute abundances in any one plot were found between ca. 300 and 400 m (Fig. 4), the 0.90 quantile regression indicated that, typically, maximum abundances declined almost linearly with altitude (Table 1).

In the initial hurdle model, neither aspect nor vegetation type had significant effects in the model and were therefore excluded. However, the model without these terms had a larger Akaike information criterion value than the one retaining them (AIC 734.2 vs. 715.5); thus, the outcome of the latter is considered here (see Online Resource 3 for the full model outcome). Elevation was the only significant term accounting for zero values in the binomial model ( $z = -2.429$ ,  $p = 0.0152$ ), with abundance declining at



**Fig. 3** Relationship between  $\log_{10}$  abundance (per  $8 \times 8$  m quadrat) and occupancy of *Azorella selago* on Marion Island. The fitted line is that of an ordinary least squares regression ( $\log_{10}$  abundance =  $0.089 \times$  occupancy +  $0.390$ ,  $r^2 = 0.635$ ,  $F_{(1,67)} = 119.3$ ,  $p < 0.0001$ ) and is for illustrative purposes only

the higher elevations (Fig. 4). By contrast, weak negative relationships were found with both spatial variables (latitude  $z = -2.104$ ,  $p = 0.035$ ; longitude  $z = -2.361$ ,  $p = 0.018$ ), and a marked negative influence of substrates dominated by closed vegetation ( $z = -2.967$ ,  $p = 0.003$ ) on *A. selago* abundance was found.

## Discussion

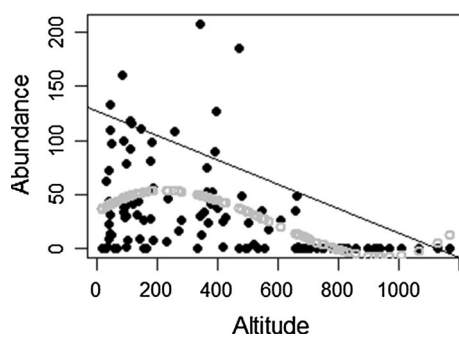
This study provides the first quantification of the abundance structure for a plant species, *A. selago*, across its entire geographic range on a small sub-Antarctic island. While the analysis is partial in the sense that it does not cover the full range of *A. selago* (which occurs on several Southern Ocean islands) (Nicolas and Plunkett 2012), it is complete in the sense that it covers the full local distribution of the species on an island typically separated by hundreds of kilometres from the nearest patches of the same species (with the exception of the 22 km distant and adjacent Prince Edward Island—Chown and Froneman 2008—which was inaccessible owing to its strict conservation status).

*Azorella selago* was absent at the centre of the island, and abundance was consistently high (i.e. typically more than 20 cushions per plot) below a threshold elevation of 667 m a.s.l. Moreover, no gradual increase or decline in abundance with elevation was found. Rather, a sharp increase in abundance was observed at the coastal range edge (ca. 5 m) and an abrupt stepped decline at 667 m. These findings are inconsistent with a balance point of range expectation (Sagarin et al. 2006). By contrast, the expectation of a mid-elevational peak if the two-dimensional torus expectation was to be collapsed into one dimensional had some support. The significant third-order polynomial indicated high abundances on average between 200 m and 300 m a.s.l., and the absolute maximum abundances were found at elevations somewhat higher than this, even though the quantile regression suggested strong declines in maximal abundance with elevation. Thus, the areas about midway along the 660-m elevational range occupied by the species on Marion Island tend to have the highest abundances (Fig. 4). Nonetheless, high abundance was patchy and most common at both exposed low and mid-elevational sites. Large areas of low abundance or absence were located at the highest elevations as illustrated by the two-dimensional kriging interpolation.

In consequence, these findings provide some support for an abundant centre distribution hypothesis for *A. selago* on Marion Island, but illustrate that it is not continuous and symmetric as has previously been suggested (see overview in McGill and Collins 2003). Rather, 4–5 abundance peaks were found, with abundances at these peaks typically an

**Table 1** Outcomes of a third-order polynomial regression of *Azorella selago* abundance on altitude, and of a quantile regression ( $\tau = 0.90$ ) of abundance on altitude

	Estimate	SE	<i>t</i>	<i>p</i>
Polynomial regression				
Intercept	32.6	10.6	3.08	0.003
Altitude	0.204	0.1	2.04	0.044
Altitude <sup>2</sup>	−0.0005	0.00022	−2.6	0.012
Altitude <sup>3</sup>	0.0000003	0.0000001	2.4	0.017
$R^2 = 0.196, F_{(3,106)} = 9.83, p < 0.0001$				
	Coefficient	SE	<i>t</i>	<i>p</i>
Quantile regression				
Intercept	127.6	17.7	7.2	<0.0001
Altitude	−0.112	0.02	−5.1	<0.0001

**Fig. 4** Relationship between altitude (m) and abundance (per  $8 \times 8$  m quadrat) of *Azorella selago* on Marion Island. The grey dots are predicted values from a third-order polynomial, while the black line is a 90 % quantile regression line (see Table 1). Note the absence of the species at the highest elevations

order of magnitude greater than those in low abundance areas. This finding provides support for the hypothesis of a peak and tail pattern considered most common for species at larger geographic extents (McGill and Collins 2003). Moreover, individual abundance was clearly spatially aggregated, in keeping with patterns found for a range of other species (McGill 2010). A preponderance of mats on the western side of the island (and an absence of mats at high elevations) supported this overall pattern, though the factors driving mat formation were not explicitly investigated. Indeed, we did not focus on the spatial distribution of cover, though doing so is clearly an important next step in understanding the ecological significance of the abundance variation we documented. Likewise, at smaller spatial scales, with finer resolution, other patterns of spatial variance in abundance may be found (see, e.g. Born et al. 2012), though we are of the view that at the scale and resolution of our study, other approaches, such as transects, will reveal similar patterns.

Nonetheless, it might be argued that the abundance and distribution characteristics of this species across a

relatively small, mountainous island, are unusual, given that the species is more widely distributed across the region (Nicolas and Plunkett 2012). However, two lines of evidence suggest that this is not the case. First, the abundance frequency distribution was typical of what has been found for many continental species across a wide range of taxonomic groups (Gaston and Blackburn 2000; McGeoch and Gaston 2002). Second, a strong, positive intraspecific relationship between abundance and occupancy was found, which is also typical of many species across a wide range of scales (Hui and McGeoch 2007). In consequence, in most ways the macroecology of *A. selago* is typical, therefore supporting the strength of the evidence concerning the absence of an abundant centre distribution.

What environmental factors might be responsible for the complex patterns shown by *A. selago* is not entirely clear. The distribution, heterogeneity and availability of suitable habitat attributes are important factors underpinning species abundance and distribution patterns (Brown 1984; Caughley et al. 1988; Lee et al. 2009), but biotic factors may also play a role. Overall, it seems that some factors associated with elevation determine the range limits, as indicated by altitude being the only significant term accounting for zero values in the binomial model. By contrast, abundance generally declines slightly, but significantly to the south-east, perhaps reflecting the cooler, drier conditions in this quadrant of the island (see Chown and Froneman 2008). Closed vegetation also tends to reduce abundance, in keeping with experimental findings where shading of cushions leads to poor performance and etiolation (le Roux et al. 2005). Thus, the cushions themselves may be poor competitors with species that form closed canopies (Huntley 1972), though such an hypothesis requires explicit testing.

At lower elevations, the range limit is abrupt. It seems likely that salt spray, which may be discharged many metres inland because of rough ocean conditions

(Gremmen 1981), limits the distribution of the species and its abundance at coastal sites. It has long been observed that areas exposed to salt spray on the island support separate communities dominated by halophilic species such as *Crassula moschata* and *Cotula plumosa* (Gremmen 1981; Smith et al. 2001). By contrast, interactions among individuals of the cushion plant itself, which play an important role as nurse plants in ameliorating abiotic disturbance and likely providing nutrients, may interact with other factors to set upper limits to distribution (le Roux and McGeoch 2008b; Nyakatia and McGeoch 2008; Haussmann et al. 2009a, b, 2010).

The most significant of the latter factors is likely one that has to do with the known sensitivity of *A. selago* to low light conditions, resulting in etiolation, cushion disruption and eventual death (Huntley 1972; le Roux et al. 2005). The most likely explanatory factor in this regard is permanent snow cover. At present, no permanent snow line exists on the island (Sumner et al. 2004). By contrast, in the 1960s the permanent snow line was found at approximately 650 m a.s.l., although by the late 1970s it had already receded to c. 950 m a.s.l. (Hall 1980; Sumner et al. 2004). Although the highest elevation recorded for *A. selago* is currently 840 m (Hedding 2006), its abundance and distribution are relatively sparse above 650 m. While the average altitudinal extent of the species has increased with warming at the island, it has been one of the slowest responders (le Roux and McGeoch 2008a), likely reflecting its slow growth and recruitment only under a relatively restricted set of conditions (le Roux and McGeoch 2004) and relatively low dispersal distances (Born et al. 2012). In consequence, it seems likely that the historical snow line is responsible for current distribution limits. Low recruitment, small dispersal distances and the need for intraspecific facilitation in ensuring survival, by overcoming substrate movement, frost creep and needle ice (Haussmann et al. 2009a, b; 2010), are then likely to have slowed responses to changing climatic conditions, leaving current distributional limits at the historical snow line.

Alternative explanations should also be considered. Although a threshold in the abundance of species as shown by *A. selago* may indicate a sudden change in abiotic conditions (Caughley et al. 1988), thresholds may also arise along shallow gradients where other factors such as competition come into play (Case and Taper 2000). However, with the possible exception of competition along drainage lines at lower elevations, and in warm, moist areas that favour mire formation (see Gremmen 1981; Yeloff et al. 2007), competition between *A. selago* species and other plants at high elevations and in exposed areas seems unlikely. At least on Marion Island, the converse is true, with *A. selago* facilitating the establishment of other individuals and other species which grow epiphytically on the

cushions (le Roux and McGeoch 2008b; McGeoch et al. 2008; le Roux et al. 2013a). Moreover, at the highest elevations, virtually no epiphytes are found (le Roux and McGeoch 2008b) and no other plant species are evident except for a very poorly developed interstitial cryptogam flora (Gremmen 1981). Similarly, although one weevil species feeds on live *A. selago*, the only herbivore known to use live material of this species, its abundance and consumption rates are too low to effect a reduction in plant viability (Crafford and Chown 1991). Alternatively, the severity of environmental conditions at the highest elevations may be the sole driving factor for abundance variation above 600 m and for range limits. These alternatives require explicit investigation.

What factors influence the peak and tail distribution pattern are much more difficult to ascertain without further analysis. Clearly, mid-elevational sites that are largely free from closed vegetation are important, and limited dispersal distances and some absence of needle ice and frost creep are also important. Specific recruitment requirements may also play a role. Further work will be required to determine which of these factors, along with history, are most significant, or how they interact. Comparison with current distribution patterns on nearby Prince Edward Island may also be important to determine whether extensive burrowing by invasive house mice into the cushions on Marion Island (Phiri et al. 2009) has played a role in affecting the spatial pattern of abundance, given that mice are absent on Prince Edward Island, and this difference between the islands can substantially alter macroecological patterns (Treasure and Chown 2014).

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## References

- Barendse J, Chown SL (2001) Abundance and seasonality of mid-altitude fellfield arthropods from Marion Island. *Polar Biol* 24:73–82
- Boelhouwers JC, Meiklejohn KI, Holness SD, Hedding DW (2008) Geology, geomorphology and climate change. In: Chown SL, Froneman PW (eds) *The Prince Edward Islands. Land-sea interactions in a changing ecosystem*. Sun Press, Stellenbosch, pp 65–96
- Born C, le Roux PC, Spohr C, McGeoch MA, van Vuuren BJ (2012) Plant dispersal in the sub-Antarctic inferred from anisotropic genetic structure. *Mol Ecol* 21:184–194
- Brown JH (1984) On the relationship between abundance and distribution of species. *Am Nat* 124:255–279



- Case TJ, Taper ML (2000) Interspecific competition, environmental gradients, gene flow, and the coevolution of species' borders. *Am Nat* 155:583–605
- Caughley G, Grice D, Barker R, Brown B (1988) The edge of the range. *J Anim Ecol* 57:771–785
- Chown SL, Froneman PW (eds) (2008) The Prince Edward Islands. Land-sea interactions in a changing ecosystem. Sun Press, Stellenbosch
- Coomes DA, Rees M, Turnbull L (1999) Identifying aggregation and association in fully mapped spatial data. *Ecology* 80:554–565
- Crafford JE, Chown SL (1991) Comparative nutritional ecology of bryophyte and angiosperm feeders in a sub-Antarctic weevil species complex (Coleoptera: Curculionidae). *Ecol Entomol* 16:323–329
- Crawley MJ (2013) The R book, 2nd edn. Wiley, Chichester
- Frenot Y, Gloaguen JC, Picot G, Bougère J, Benjamin D (1993) *Azorella selago* Hook. used to estimate glacier fluctuations and climatic history in the Kerguelen Islands over the last two centuries. *Oecologia* 95:140–144
- Gaston KJ (2003) The structure and dynamics of geographic ranges. Oxford University Press, Oxford
- Gaston KJ, Blackburn TM (2000) Pattern and process in macroecology. Blackwell Science, Oxford
- Gremmen NJM (1981) The vegetation of the subantarctic islands Marion and Prince Edward. Junk Press, The Hague
- Gremmen NJM, Smith VR (2008) Terrestrial vegetation and dynamics. In: Chown SL, Froneman PW (eds) The Prince Edward Islands. Land-sea interactions in a changing ecosystem. Sun Press, Stellenbosch, pp 215–244
- Hall K (1980) Late glacial ice cover and paleotemperatures on sub-Antarctic Marion Island. *Paleogeogr Paleoclimatol Paleoecol* 29:243–254
- Hamill DN, Wright SJ (1986) Testing the dispersion of juveniles relative to adults: a new analytic method. *Ecology* 67:952–957
- Hausmann NS, Boelhouwers JC, McGeoch MA (2009a) Fine scale variability in soil frost dynamics surrounding cushions of the dominant vascular plant species (*Azorella selago*) on sub-Antarctic Marion Island. *Geogr Ann* 91:257–268
- Hausmann NS, McGeoch MA, Boelhouwers JC (2009b) Interactions between a cushion plant (*Azorella selago*) and surface sediment transport on sub-Antarctic Marion Island. *Geomorphology* 107:139–148
- Hausmann NS, McGeoch MA, Boelhouwers JC (2010) Contrasting nurse plants and nurse rocks: the spatial distribution of seedlings of two sub-Antarctic species. *Acta Oecol* 36:299–305
- He F, Gaston KJ (2000) Occupancy-abundance relationships and sampling scales. *Ecography* 23:503–511
- Hedding DW (2006) Geomorphology and geomorphological responses to climate change in the interior of sub-Antarctic Marion Island. MSc Thesis, University of Pretoria
- Hugo EA, McGeoch MA, Marshall DJ, Chown SL (2004) Fine scale variation in microarthropod communities inhabiting the keystone species *Azorella selago* on Marion Island. *Polar Biol* 27:466–473
- Hui C, McGeoch MA (2007) Capturing the “droopy-tail” in the occupancy-abundance relationship. *Ecoscience* 14:103–108
- Hui C, Veldtman R, McGeoch MA (2010) Measures, perceptions and scaling patterns of aggregated species distributions. *Ecography* 33:95–102
- Huntley BJ (1970) Altitudinal distribution and phenology of Marion Island vascular plants. *Tydskrif Natuurwet* 10:225–262
- Huntley BJ (1972) Notes on the ecology of *Azorella selago* Hook. f. *J S Afr Bot* 38:103–113
- Jackman S (2012) pscl: classes and methods for R developed in the political science computational laboratory, Stanford University. Department of Political Science, Stanford University. Stanford, California, R package version 1.04.4. <http://pscl.stanford.edu/>
- le Roux PC (2008) Climate and climate change. In: Chown SL, Froneman PW (eds) The Prince Edward Islands. Land-sea interactions in a changing ecosystem. Sun Press, Stellenbosch, pp 39–64
- le Roux PC, McGeoch MA (2004) The use of size as an estimator of age in the subantarctic cushion plant, *Azorella selago* (Apiaceae). *Arct Antarct Alp Res* 36:509–517
- le Roux PC, McGeoch MA (2008a) Rapid range expansion and community reorganization in response to warming. *Global Change Biol* 14:2950–2962
- le Roux PC, McGeoch MA (2008b) Spatial variation in plant interactions across a severity gradient in the sub-Antarctic. *Oecologia* 155:831–844
- le Roux PC, McGeoch MA (2010) Interaction intensity and importance along two stress gradients: adding shape to the stress-gradient hypothesis. *Oecologia* 162:733–745
- le Roux PC, McGeoch MA, Nyakatyia MJ, Chown SL (2005) Effects of a short-term climate change experiment on a sub-Antarctic keystone plant species. *Global Change Biol* 11:1628–1639
- le Roux PC, Shaw JD, Chown SL (2013a) Ontogenetic shifts in plant interactions vary with environmental severity and affect population structure. *New Phytol* 200:241–250
- le Roux PC, Ramaswiela T, Kalwij JM, Shaw JD, Ryan PG, Treasure AM, McClelland GTW, McGeoch MA, Chown SL (2013b) Human activities, propagule pressure, and alien plants in the sub-Antarctic: tests of generalities and evidence in support of management. *Biol Conserv* 161:18–27
- Lee JE, Janion C, Marais E, Van Vuuren BJ, Chown SL (2009) Physiological tolerances account for range limits and abundance structure in an invasive slug. *Proc R Soc B* 276:1459–1468
- Legendre L, Legendre P (1998) Numerical ecology. Elsevier, Amsterdam
- McGeoch MA, Gaston KJ (2002) Occupancy frequency distributions: patterns, artefacts and mechanisms. *Biol Rev* 77:311–331
- McGeoch MA, Price PW (2004) Spatial abundance structures in an assemblage of gall-forming sawflies. *J Anim Ecol* 73:506–516
- McGeoch MA, le Roux PC, Hugo EA, Chown SL (2006) Species and community responses to short-term climate manipulation: microarthropods in the sub-Antarctic. *Austral Ecol* 31:719–731
- McGeoch MA, le Roux PC, Hugo EA, Nyakatyia MJ (2008) Spatial variation in the terrestrial biotic system. In: Chown SL, Froneman PW (eds) The Prince Edward Islands. Land-sea interactions in a changing ecosystem. Sun Press, Stellenbosch, pp 245–276
- McGill BJ (2010) Towards a unification of unified theories of biodiversity. *Ecol Lett* 13:627–642
- McGill BJ, Collins M (2003) A unified theory for macroecology based on spatial patterns of abundance. *Evol Ecol Res* 5:469–492
- Mortimer E, McGeoch MA, Daniels SR, Jansen van Vuuren B (2008) Growth form and population genetic structure of *Azorella selago* on sub-Antarctic Marion Island. *Antarct Sci* 20:381–390
- Murphy HT, van der Wal J, Lovett-Doust J (2006) Distribution of abundance across the range in eastern North American trees. *Global Ecol Biogeogr* 15:63–71
- Nicolas AN, Plunkett GM (2012) Untangling generic limits in *Azorella*, *Laretia*, and *Mulinum* (Apiaceae: Azorelloideae): insights from phylogenetics and biogeography. *Taxon* 61:826–840
- Nyakatyia MJ, McGeoch MA (2008) Temperature variation across Marion Island associated with a keystone plant species (*Azorella selago* Hook. (Apiaceae)). *Polar Biol* 31:139–151
- Phiri EE, McGeoch MA, Chown SL (2009) Spatial variation in structural damage to a keystone plant species in the sub-Antarctic: interactions between *Azorella selago* and invasive house mice. *Antarct Sci* 21:189–196
- Raunkiaer C (1934) The life forms of plants and statistical plant geography. Oxford University Press, Oxford

- R Core Team (2012) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0, <http://www.R-project.org/>
- Rossi RE, Mulla DJ, Journel AG, Franz EH (1992) Geostatistical tools for modeling and interpreting ecological spatial dependence. *Ecol Monogr* 62:277–314
- Sagarin RD, Gaines SD (2002a) Geographical abundance distributions of coastal invertebrates: using one-dimensional ranges to test biogeographic hypotheses. *J Biogeogr* 29:985–997
- Sagarin RD, Gaines SD (2002b) The ‘abundant centre’ distribution: to what extent is it a biogeographical rule? *Ecol Lett* 5:137–147
- Sagarin RD, Gaines SD, Gaylord B (2006) Moving beyond assumptions to understand abundance distributions across the ranges of species. *Trends Ecol Evol* 21:524–530
- Samaniego H, Marquet PA (2013) Range structure analysis: unveiling the internal structure of species ranges. *Theor Ecol* 6:419–426
- Samis KE, Eckert CG (2007) Testing the abundant centre model using range-wide demographic surveys of two coastal dune plants. *Ecology* 88:1747–1758
- Smith VR, Steenkamp M, Gremmen NJM (2001) Terrestrial habitats on sub-Antarctic Marion Island: their vegetation, edaphic attributes, distribution and response to climate change. *S Afr J Bot* 67:641–654
- Sumner PD, Meiklejohn KI, Boelhouwers JC, Hedding DW (2004) Climate change melts Marion Island’s snow and ice. *S Afr J Sci* 100:395–398
- Treasure AM, Chown SL (2014) Antagonistic effects of biological invasion and temperature change on body size of island ectotherms. *Divers Distrib* 20:202–213
- Yeloff D, Mauquoy D, Barber K, Way S, van Geel B, Turney CSM (2007) Volcanic ash deposition and long-term vegetation change on Subantarctic Marion Island. *Arct Antarct Alp Res* 39:500–511
- Zeileis A, Hothorn A (2002) Diagnostic checking in regression relationships. *R News* 2:7–10
- Zimmermann DL, Zimmermann MB (1991) A comparison of spatial semivariogram estimators and corresponding ordinary kriging predictors. *Technometrics* 33:77–91
- Zuur AF, Ieno EN, Walker NJ, Saveliev AA, Smith GM (2009) *Mixed effects models and extensions in ecology with R*. Springer, New York