CHAPTER 10

SPATIAL VARIATION IN THE TERRESTRIAL BIOTIC SYSTEM

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‘Space’ has been referred to as ‘the final frontier for ecological theory’ (Kareiva 1994). Indeed, a spatial approach to documenting and modeling variation in populations, communities and species diversity has dominated ecology for the last few decades, and resulted in significant advances in understanding (e.g. island biogeography (MacArthur & Wilson 1967), metapopulation dynamics (Hanski 1991; Tilman *et al.* 1997), and macroecology (Gaston & Blackburn 2000)). We now appreciate not only that ecological pattern and process is scale dependent, but that multiscale approaches are necessary to understand the hierarchical nature of mechanisms underlying the patterns we observe (Usher & Booth 1986; Wiens 2000; Schneider 2001; McGeoch & Price 2004). Integrating the findings from a range of hierarchical spatial scales is therefore an effective tool for generating hypotheses and identifying the scale dependent nature of pattern and mechanism in any biotic system (Bellehumeur & Legendre 1998; Noda 2004).

The islands of the Southern Ocean provide particularly convenient platforms for such an approach because terrestrial habitat boundaries are well defined, the islands are comparatively small and species poor, have only a few key alien species, and low levels of natural migration and human-mediated introductions (Bergstrom & Chown 1999). Furthermore, both plant and invertebrate taxa are particularly well-known for Marion Island (Gremmen 1981; Crafford *et al.*

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1986; Chown *et al.* 2002). Spatial pattern in the terrestrial biota on Marion is likely to be a synthetic consequence of strong gradients along with patchiness in patterns of climate, geomorphology and nutrient availability (Gremmen 1981; Blake 1996; Smith & Steenkamp 2001). For example, colonization of the island by winged insects (such as the fairly recent arrival of *Plutella xylostella* (Lepidoptera: Plutellidae) and other air-borne propagules, is predicted to occur on the leeward side of the island, deposited there as a consequence of dominant wind and airflow patterns (Chown & Avenant 1992). The effect of nutrient availability, soil properties and altitude in structuring the terrestrial habitat is particularly clear in the plant community (Gremmen 1981; Smith & Steenkamp 2001; Gremmen & Smith 2008). Indeed, vegetation community type, together with abiotic variables, play an important role in structuring the most speciose faunal component on the Prince Edward Islands, i.e. the invertebrates.

Although *c.* 23 habitats grouped into seven habitat complexes exist on Marion Island (Smith *et al.* 2001), a clear distinction can be made between the vegetated (supporting vascular plants) and epilithic (areas between vascular cushion plants in fellfield, rocky shores, and lava outcrops) biotopes (Chown 1989). For example, the largely cryptogam-feeding, ectemnorhine weevils on the island are more speciose and abundant in the epilithic than vegetated biotope (Chown 1989, 1997). By contrast, mite and springtail abundance and richness are greater in vegetated than in epilithic habitats (Mercer *et al.* 2000; Barendse & Chown 2001). The invertebrate fauna certainly responds fairly strongly to qualitative differences between habitat types (Crafford & Scholtz 1987; Chown 1990), with several habitat-specific species and distinct differences in community composition (Hänel 1999; Barendse & Chown 2000; Mercer *et al.* 2000; Gabriel *et al.* 2001; Barendse *et al.* 2002). For example, although there is some species overlap, lower shore, upper shore and inland mite communities differ significantly (Mercer *et al.* 2000). The microarthropod communities associated with several of the dominant vascular plant species on the island are also distinct, not only in terms of some habitat specificity, but also in the relative abundances of species (Hugo *et al.* 2006). In general, arthropod densities are much higher in habitats typically characterized by vascular vegetation than in those that are not (Hänel 1999; Gabriel *et al.* 2001; Barendse *et al.* 2002). Although competitive interactions are considered unimportant in the invertebrate communities on the island, both mite and springtail communities cluster distinctly into a dozen or more plant community associations (Gabriel *et al.* 2001; Barendse *et al.* 2002; Hugo *et al.* 2006). In general, biotic interactions, at least in the plant community, are considered more prevalent and important at speciose lower altitudes, replaced by abiotic variables with an increase in elevation and concomitant decline in diversity (although altitudinal gradients are not always linear, see later discussion) (le Roux 2004; see also Körner 2003). Finally, as discussed elsewhere in this book (Chown *et al.* 2008; De Villiers & Cooper 2008), introduced and invasive species (plants, invertebrates and *Mus musculus*) are beginning to alter terrestrial biodiversity patterns, by

changing local species richness, abundance and taxonomic diversity (Chown & Language 1994; Gremmen *et al.* 1998; Chown *et al.* 2002).

In this chapter we focus on one component of the terrestrial biota on Marion Island, and adopt a multiscale approach to understanding the processes driving spatial variation in this terrestrial system. We use *Azorella selago* Hook. (Apiaceae), a characteristic and keystone plant species on the island, as a model. This species is well suited for an examination of spatial variation because it is abundant and widely distributed on the island, plants have a discrete physical boundary, and are host to several other plant and invertebrate species. Furthermore, *A. selago* has been the focus of a research programme aimed at understanding not only spatial variation in the terrestrial system, but also the likely impact of climate change on the biota of Marion Island (Hugo *et al.* 2004; le Roux 2004; le Roux & McGeoch 2004; le Roux *et al.* 2005; McGeoch *et al.* 2006; le Roux & McGeoch 2008). Here we explore variation in this species, and the epiphytes and arthropods associated with it, within and across three spatial scales: (i), fine scale patterns within individual plants (plant scale), (ii) mesoscale variation across stands or patches of plants (landscape scale) and (iii) island-wide variation associated with the altitude gradient on the island and island aspect (the island scale).

10.1 The model

Its remarkable growth form immediately attracts the attention of visitors to the islands, not only as an outstanding example of adaptation to the harsh environment, but also as a welcome cushion for the weary explorer of these rugged, tractless islands. Huntley (1972)

Azorella selago (or the ‘cushion plant’) is widely distributed in the sub-Antarctic (from southern South America to Heard Island) and is the member of a genus dominant in the region (Gremmen 1981). It is long-lived with a hemispherical, cushion growth form (Huntley 1972; Frenot *et al.* 1993) (cushion growth forms are considered to reduce wind stress and heat and moisture loss: Ashton & Gill 1965; Huntley 1971; Körner 2003) (Plate 10.1a). Individual plants, or cushions, have a central taproot, from which stems arise radially and branch dichotomously (Frenot *et al.* 1993). The plant’s root system is well developed with extensive shallow, horizontal roots and shorter sub-vertical roots. The latter root type only produces rootlets in fine-textured soil caps and enables the plant to extract efficiently, patchily-distributed soil nutrients (Frenot *et al.* 1998). Leaves of the plant are small, tough and lobed, with petioles that form a sheath around the stem, and the plant surface is hard and compact, with the leaves tightly packed and stems generally growing close together (Orchard 1989) (Plate 10.1a, d).

On Marion Island, *A. selago* is found in a wide range of plant communities, and may take the form of small plants interspersed amongst dominant grasses, to fairly regularly dispersed, isolated cushions in fellfield habitat (Gremmen 1981) (Plate 10.1 b, c). Although *A. selago* occupies as little as 10% of the surface area

of the habitat even where it is dominant (Barendse & Chown 2001), it is a conspicuous component of the vegetation (Gremmen 1981), and one of only six species that contribute significantly to the islands' standing crop (Smith 1978a). Indeed, *A. selago* is considered a keystone species on Marion Island for several reasons. It is ubiquitous (Huntley 1972; Smith *et al.* 2001) and has the greatest altitudinal range of any vascular plant on the island (from sea-level to 840 m a.s.l.). In fellfield habitat it is the dominant vascular species, where it occurs in virtual monocultures interspersed with the cryptogam-dominated epilithic biotope (Huntley 1972; Frenot *et al.* 1993). It is a pioneer and plays an important role in succession (Scott 1985; Frenot *et al.* 1998), as it colonizes loose scoriaceous slopes, recent lava flows and the forelands of retreating glaciers (Huntley 1972; Frenot *et al.* 1998). Indeed, it is strongly associated with geomorphological processes, such as terrace formation and soil accumulation in fellfield landscapes (see e.g. Selkirk 1998; Boelhouwers *et al.* 2000). Cushions add significantly to the microhabitat heterogeneity of fellfield. For example, the species retains senescent leaves that decompose to form a rich, moist, humus-like collection of organic material inside the plant (Huntley 1971). This trait, in common with cushion plants elsewhere, enables individuals to recycle their own nutrients, leading to a local accumulation of nutrients in otherwise poor soils (Nuñez *et al.* 1999; Körner 2003; le Roux & McGeoch 2004). Cushion plants (including South American *Azorella* species) have also been shown to alter local soil moisture and temperature (Cavieres *et al.* 1998; Cavieres *et al.* 2002; Arroyo *et al.* 2003).

In addition to its interaction with the abiotic environment, *A. selago* increases heterogeneity and patchiness in fellfield habitats by hosting diverse epiphyte (Huntley 1972; Brancaloni *et al.* 2003) and invertebrate communities (Barendse & Chown 2001; Hugo *et al.* 2004). As many as 20 vascular, and at least 17 non-vascular species have been recorded growing epiphytically on *A. selago* (Table 10.1) (le Roux 2004). *Azorella selago* also facilitates the growth of other vascular plants at higher altitudes, where some species are limited to growing epiphytically on cushions (Huntley 1972; see also Alliende & Hoffmann 1985; Nuñez *et al.* 1999; Cavieres *et al.* 2002 for other cushion plant species). In addition, nine of Marion Island's 16 springtails, and 26 of its known 69 mite species are found in association with *A. selago* (Table 10.2, Chown *et al.* 2002), and the plant is thought to have acted as a refugium for arthropods during Neogene glaciations (Barendse *et al.* 2002). Microarthropod (springtail and mite) density in cushions greatly exceeds that of surrounding soils (Barendse & Chown 2001).

Table 10.1 Epiphytic plant species recorded on *Azorella selago* on Marion Island (from Huntley 1971, 1972; le Roux 2004; M.J. Nyakatya & Z. Buwa, personal observation). The list of epiphytic bryophytes and lichens remains incomplete. * Introduced species.

	Species	Family
Vascular plants	<i>Acaena magellanica</i>	Rosaceae
	<i>Agrostis magellanica</i>	Poaceae
	<i>Blechnum penna-marina</i>	Polypodiaceae
	<i>Callitriche antarctica</i>	Callitrichaceae
	<i>Cerastium fontanum</i> *	Caryophyllaceae
	<i>Colobanthus kerguelensis</i>	Caryophyllaceae
	<i>Cotula plumosa</i>	Asteraceae
	<i>Crassula moschata</i>	Crassulaceae
	<i>Hymenophyllum peltatum</i>	Hymenophyllaceae
	<i>Juncus scheuchzerioides</i>	Juncaceae
	<i>Lycopodium magellanicum</i>	Lycopodiaceae
	<i>Lycopodium saururus</i>	Lycopodiaceae
	<i>Montia fontana</i>	Portulacaceae
	<i>Poa annua</i> *	Poaceae
	<i>Poa cookii</i>	Poaceae
	<i>Poa pratensis</i> *	Poaceae
	<i>Pringlea antiscorbutica</i>	Brassicaceae
	<i>Ranunculus bitermatus</i>	Ranunculaceae
	<i>Sagina procumbens</i> *	Caryophyllaceae
	<i>Ucinia compacta</i>	Cyperaceae
Bryophytes: Mosses	<i>Andreaea</i> sp.	Andreaeaceae
	<i>Blindia magellanica</i> (as <i>B. coutecta</i>)	Seligeriaceae
	<i>Brachythecium rutabulum</i>	Brachytheciaceae
	<i>Breutelia integrifolia</i>	Bartramiaceae
	<i>Campylopus subnitens</i>	Dicranaceae
	<i>Ditrichum</i> sp. (<i>D. conicum</i> ?)	Ditrichaceae
	<i>Ptychomnion densifolium</i> (as <i>P. ringianum</i>)	Ptychomniaceae
	<i>Racomitrium</i> sp. (<i>R. lanuginosum</i> ?)	Grimmiaceae
	<i>Sanionia uncinata</i>	Amblystegiaceae
Bryophytes: Liverworts	<i>Blepharidophyllum densifolium</i>	Scapaniaceae
	<i>Clasmatocolea humilis</i>	Geocalycaceae
	<i>Jamesoniella</i> sp. (<i>J. colorata</i> ?)	Lophoziaaceae
	<i>Jensenia pisicolor</i>	Pallaviciniaceae
	<i>Lophocolea randii</i>	Geocalycaceae
	<i>Marchantia berteriana</i>	Marchantiaceae
Lichen	<i>Cladonia</i> sp.	Cladoniaceae

Table 10.2 Invertebrate species collected from *Azorella selago* cushions (Barendse & Chown 2001; Hugo *et al.* 2004). Abbreviations (Abrev.) used elsewhere in the chapter.

Acari	Abrev.	Collembola	Abrev.
Acari sp1	Aca1	Arthropleona	
Acari sp3	Aca3	<i>Tullbergia bisetosa</i>	Tbis
Acari sp4	Aca4	<i>Isomotoma marionensis</i>	Imar
Mesostigmata		<i>Cryptopygus dubius</i>	Cdub
<i>Rhodacaridae</i> sp.	Rhod	<i>Cryptopygus antarcticus travei</i>	Cant
<i>Dendrolaelaps</i> sp.	Dend	<i>Cryptopygus caecus</i>	Ccea
<i>Cilibidae</i> sp.	Cili	<i>Isotomurus cf. palustris</i>	Ipal
Prostigmata		Symphyleona	
Prostigmata sp1		<i>Megalothorax</i> sp.	Mega
<i>Nanorchestes</i> sp.	Nano	<i>Sminthurinus granulosus</i>	Sgra
<i>Eupodes minutus</i>	Emin	<i>Sminthurinus tuberculatus</i>	Stub
<i>Rhagidia</i> sp.	Rhag		
<i>Ereynetes macquariensis</i>	Emac	Psocoptera	
<i>Tydeus</i> sp.	Tyde	<i>Antarctopsocus jeanneli</i>	
<i>Bdellodes</i> sp.	Bdel	Thysanoptera	
<i>Eryngiopus</i> sp.	Eryn	<i>Apterothrips apteris</i>	
<i>Balaustium</i> sp.		Hemiptera	
<i>Pygmephoridae</i> sp.		Aphididae	
Cryptostigmata		Coleoptera	
<i>Oribatidae</i> sp1	Orib	<i>Ectemnorhinus</i> spp.	
<i>Liochthonius australis</i>	Laus	<i>Bothrometopus parvulus</i>	
<i>Maquarioppia striata</i>	Mstri	<i>Bothrometopus elongatus</i>	
<i>Austroppia crozetensis</i>	Acro	<i>Halmaeusa atriceps</i>	
<i>Halozetes fulvus</i>	Hful	Diptera	
<i>Podocarus auberti</i>		<i>Limnophyes minimus</i>	
<i>Domatorina marionensis</i>	Dmar	Lepidoptera	
<i>Magellozetes antarcticus</i>		<i>Pringleophaga marioni</i>	
Astigmata		<i>Embryonopsis halticella</i>	
<i>Schwiebea talpa</i>	Stal	Araneae	
<i>Algophagus</i> spp.	Alg1,2	<i>Prinerigone vagans</i>	
		Earthworms	
		Enchytraeid worms	

Spatial variation in *A. selago* thus has a considerable effect on the structure, composition and functioning of fellfield ecosystems, that constitute approximately half of Marion Island's surface area (Smith *et al.* 2001; Gremmen & Smith 2008). Therefore, documenting and understanding this variation is important, and increasingly so given the rapid rates of environmental change on the Prince Edward Islands (Bergstrom & Chown 1999; Chown *et al.* 2001; Smith 2002; le Roux *et al.* 2005; McGeoch *et al.* 2006; le Roux & McGeoch 2008).

10.2 The plant

At first glance, the surfaces of *A. selago* cushions appear fairly homogenous. However, closer inspection reveals these surfaces to be complex, with stems interspersed with epiphytes and patches of dead and decaying plant tissue (Plate 10.1 a, d). Along with vertical changes in cushion structure, this within-plant variation in morphology and tissue quality has several implications, including an effect on the plant's ability to survive strong winds and freezing (Ashton & Gill 1965; Cavieres *et al.* 2002; le Roux 2004). For example, the hemispherical shape so characteristic of *A. selago*, not uncommonly degrades to form crescents in older cushions, with the crescent generally advancing towards the dominant wind (Huntley 1972). Indeed, plant microclimate varies with aspect (i.e. side of the cushion), and temperatures tend to be warmest on the northern side (Fig. 10.1a), exposed to the highest solar radiation and warm, north-westerly winds (Schulze 1971). Cushion aspects are also exposed to different levels of frost-heave activity, as evidenced by differential erosion and sorting on the windward and leeward sides (J.C. Boelhouwers, personal communication). Microclimatic conditions vary not only with aspect, but also with depth inside the cushion. Temperatures inside the plant are significantly buffered, with higher minima and lower maxima than ground surface temperatures (Fig. 10.2, Nyakatya 2006, see also Chown & Crafford 1992). The difference in temperature between the plant surface and 10 cm below the surface can be as high as 2.0°C on average, with the surface warmest at 15h00 in summer and the plant interior warmest at 19h00 (Fig. 10.1). By contrast, in winter, temperature inside the plant is comparatively static, whereas the plant surface warms by 2.0°C during the day (Fig. 10.1). Therefore, cushions encompass not only structural, but also microclimatic variability that is a product of wind direction, strength and moisture content, as well as exposure (Chown & Crafford 1992). Along with within-plant heterogeneity in morphology and tissue quality, cushions thus form a microcosm of potential habitats for other species.

Figure 10.1 Thermal and biotic differences associated with different *Azorella selago* cushion aspects on Skua Ridge. a) Temperatures 10 mm below cushion surface, b) cover of epiphytic *Agrostis magellanica*, c) abundance of microarthropods (data from Hugo *et al.* 2004).

Figure 10.2 Mean hourly temperatures ($n = 10$ days and 4 cushions) recorded inside and adjacent to *Azorella selago* plants in a) winter and b) summer (error bars removed for clarity). Positions: ground surface, just beneath plant surface, and 50 mm and 100 mm beneath plant surface.

Within-plant temperature profiles are associated with significant differences in the distribution of both epiphytes and microarthropods. For example, on Skua Ridge (Table 10.3), the highest abundance of the dominant epiphyte, *Agrostis magellanica*, occurs on the sheltered south-east quarter of the plant (Fig. 10.1b). At the same site, mites and springtails are most abundant on the cooler, south-easterly side (Fig. 10.1c). The magnitude of this abundance difference in this case is pronounced, and amounts to a difference of 13 000 to 21 000 individuals m^{-2} (Hugo *et al.* 2004). This is a remarkable difference over such a small spatial scale, and suggests a distinct preference by the microarthropods for the southern sections of the cushion. However, the precise area of preference is dependent to some extent on the position of the site on the island, as a likely consequence of slope, exposure and topography (Hugo *et al.* 2004). The

positive association of individuals as a consequence of a common preference for microhabitat quality is not unusual in arthropods (McGeoch & Chown 1997), and indeed species abundance distributions frequently reveal hot and cold density spots at multiple spatial scales (Gaston 2003; McGeoch & Price 2004). Within-plant microarthropod abundance may, however, also be driven by epiphyte abundance rather than temperature. Microarthropod community structure was found to differ (driven by higher abundances rather than differences in species richness) between areas of the plant with high epiphyte cover in comparison with those with no epiphytes (Hugo *et al.* 2004). However, there appears to be little difference in temperature in parts of the plant with and without epiphyte cover (Hugo *et al.* 2004). Leinaas *et al.* (unpublished data) also found evidence of vertical stratification of microarthropods in *A. selago*. Total and species-specific abundances in the springtails declined over a 8 cm descent into the plant, and the lower strata were dominated by eudaphic species (Leinaas *et al.*, unpublished data), similar to that detected in moss turfs in Antarctica (Usher & Booth 1984). Therefore, significant within-plant variation in microarthropod abundance occurs, that is both a consequence of epiphyte load and apparently of spatial variation in abiotic factors within cushions. Such local scale variation has been documented previously for communities in the Arctic (Coulson *et al.* 2003), and moss turves in the Antarctic (Usher & Booth 1984; Usher & Booth 1986).

At this fine scale, patterns are thus dominated by species responses to microclimate and resource quality, and the interspecific interactions that occur as a result. *Azorella selago* provides a favourable, yet in itself heterogeneous microhabitat for epiphytes, springtails and mites, with *A. magellanica* adding a level of heterogeneity for the microarthropods.

10.3 The landscape

One cannot fail to be struck by the uniform expanses of grey and black lava fellfield encountered when rising to 150 m a.s.l. and above on the island (Plate 10.1b, c). *Azorella selago* cushions dot the landscape like a chequerboard, each plant an island in a sea of cryptogam-covered lava. The physical structure of such a landscape cries out for island-biogeographic and metapopulation interpretation (see also Tepedino & Stanton 1976; Hertzberg 1997). The questions that arise, therefore, are what is the extent of variation in cushion morphology and spatial structure across stands of plants, and to what extent does this explain patterns of epiphyte and microarthropod community structure?

As outlined in the previous section, variation in microtopography and aspect alter the abiotic conditions to which cushions are exposed, which in turn to some extent determines between-plant variation in growth form and compactness (see also Jumpponen *et al.* 1999; Sage & Sage 2002; Kleier & Rundel 2004). Cushion size, however, appears to have only a weak effect on cushion temperature, supporting the proposition that the prostrate growth form reduces temperature variability (Hugo *et al.* 2004; Nyakatya & McGeoch

2008). Shading results in etiolation, loss of compactness and larger leaves, typical of plant responses to shading (Plate 10.1e; see also Bergstrom *et al.* 1997; le Roux *et al.* 2005). However, for *Azorella*, where cushion compactness is considered to be an adaptation to harsh environmental conditions (Huntley 1972), this effect may alter cushion longevity (although this has to date not been determined). While hemispherical cushions are common, and perhaps most conspicuous, several other cushion shape categories may be distinguished across the landscape, i.e. crescent (e.g. Huntley 1972), elongated (see vegetation-banked terraces: Selkirk 1998; Holness 2003), semicircular and irregular. In addition, on some parts of the island, often in association with seepages and drainages, cushions coalesce to form extensive mats (Gremmen 1981) (e.g. at the eastern base of First Red Hill, and Watertunnel Valley (Meiklejohn, personal communication).

Table 10.3 Stands of *Azorella selago* in xeric fellfield on Marion Island that are being used for long-term monitoring of population changes in this species, and the arthropods and epiphytes associated with it. Results presented in this chapter were obtained largely from data collected from these stands. Each stand is demarcated with four marker poles and numbered metal tags in some *A. selago* cushions.

Plot	Position 46°South	Position 37°East	Altitude (m a.s.l.)	Aspect	Lava type	Cushion density (m ⁻²)	Closest landmark
Tafelberg							
Low	52.749'	49.651'	176	Flat	Black	1.100	Junior's Kop
Middle	53.276'	48.125'	375	Flat	Grey	0.137	Tafelberg
High	53.670'	47.293'	588	South	Black	0.260	First Red Hill
Stony Ridge							
Low	54.917'	51.435'	176	Flat	Grey	0.901	Stony Ridge
Middle	54.608'	49.062'	380	Flat	Grey	0.299	Tate's Hill
High	54.059'	47.978'	620	South	Black	0.146	Halfway Kop
Swartkop							
Low	55.789'	36.481'	216	N/East	Black	1.081	Skuinskop
Middle	55.818'	37.225'	415	Flat	Black	1.188	Stevje
High	56.195'	37.520'	575	Flat	Black	0.493	Bakkerkop
Mixed Pickle							
Low	52.574'	38.539'	222	N/East	Black	1.551	Neville
Middle	53.224'	38.858'	375	Flat	Black	1.124	Halfmaankop
High	53.839'	39.268'	600	Flat	Black	0.368	Saalrug
Skua Ridge							
Low	52.033'	50.283'	100	Flat	Grey	-	Skua Ridge

Cushion densities on the island generally range from 0.13-1.55 m² (Table 10.3). In some stands, cushion size has been found to be spatially structured with, for example, cushions up to approximately 8.0 m apart significantly similar in size (Fig. 10.3). The only significant explanatory variables found to date for cushion size across stands are the size and distance of nearest neighbouring cushions. In the stands examined, cushions were neighboured by individuals of a similar size (i.e. forming patches of similar size cushions), but larger cushions were always further apart than smaller ones (le Roux & McGeoch 2004). This suggests regular competitive exclusion of individuals in stands; a process thought to be important in this species due to its extensive root system (Frenot *et al.* 1998). Therefore, it appears that while cushion height is constrained by wind and exposure (le Roux 2004), cushion diameter may be constrained by intraspecific competition.

The distribution of *A. selago* plant size and growth rate on the island is right-skewed, with the majority of plants ranging from 0.40 to 1.15 m in diameter (Fig. 10.4). The growth rate of plants ranges between 0.7 to 21.0 mm per year (le Roux & McGeoch 2004). Growth rate is not related to plant height, and there is no clear relationship between variability in growth rate and plant size (le Roux & McGeoch 2004). Plant size and growth rate also differ significantly between sites on the island (le Roux 2004; le Roux & McGeoch 2004; Nyakatya 2006) (see following section). Using the phytometric model developed by Frenot *et al.* (1993), age estimates for *A. selago* were also found to be right-skewed (le Roux & McGeoch 2004) (Fig. 10.4). Mean plant ages range from 26 to 41 years, and the oldest plants sampled ranged between 55 and 96 years (le Roux & McGeoch 2004) (Fig. 10.4).

Cushion size and age on the island are only loosely related, and appear to be more a function of local stand characteristics than environmental gradients (le Roux & McGeoch 2004). Indeed, *Azorella* is thought to have infrequent, periodic establishment pulses, associated with periods or patches of mild and infrequent soil freezing, combined with suitable substrate conditions (Wickens 1995; Kleier & Rundel 2004; le Roux 2004). While a large proportion of the variability in cushion characteristics could not be explained (le Roux 2004), variation in soil moisture and nutrients, wind exposure and snow cover due to topographical and microclimatic variation are known to be important determinants of plant performance in high altitude and latitude communities (Frenot *et al.* 1993; Callaghan & Carlsson 1997; Jumpponen *et al.* 1999; Körner 2003). The frequency of cushions < 0.29 m in diameter on the island is significantly lower than cushions in intermediate size classes (Fig. 10.3), suggesting not only infrequent establishment, or high juvenile mortality, but possibly spatially-patchy recruitment sites. Episodic establishment is characteristic of many polar and sub-polar species (including *Azorella* species), and it is likely that *A. selago* has pulsed recruitment in response to irregular and/or unpredictable conditions, probably including mild and infrequent soil freezing, combined with suitable substrate conditions (Wickens 1995; Kleier &

Rundell 2004; le Roux 2004). Thus, in terms of cushion morphology, sufficient variability apparently exists at the landscape scale to potentially generate spatial patterns in diversity and community structure amongst the cushion inhabitants.

Figure 10.3 Correlograms of Moran's I-values, depicting spatial structure in the a) maximum diameter of *Azorella selago* cushions, b) the abundance of epiphytic *Agrostis magellanica* on cushions, c) abundances of the cushion-dwelling mite, *Dendrolaelaps* sp., and d) springtail, *Cryptopygus dubius*, at sites near Mixed Pickle Cove. Bonferoni-corrected overall significance of correlograms provided in frames. Significant, positive I-values denote positive spatial autocorrelation in that distance class (i.e. values of the variable in question are significantly more similar to each other than expected by chance over that distance). Filled symbols indicate significant spatial autocorrelation in that distance class. Note differences in distance scales between a, b and c, d.

Figure 10.4 Frequency distributions of *Azorella selago* cushion a) maximum diameter ($n = 738$), b) height ($n = 738$), c) growth rate ($n = 527$) and d) estimated cushion age ($n = 738$) (with permission from le Roux & McGeoch 2004).

Several plant species are found growing epiphytically (including vascular and non-vascular species) on *A. selago* across the island (Table 10.1). By far the most dominant of these (in terms of biomass on cushions) is the grass *A. magellanica*. Nonetheless, most cushions on the island are host to a range of epiphyte species, particularly mosses (Fig 10.5, Table 10.1). Vascular plants, such as *A. magellanica* and *Ranunculus bitermatus*, and other non-vascular species such as liverworts and lichens are commonly found on cushions. Indeed, the strongest spatial structure found across plants within a stand was in the dominant epiphyte (Fig. 10.3b), suggesting seed dispersal away from established grass clumps onto adjacent cushions generates patchiness in the distribution of this species across stands of *A. selago* (at least at medium to high altitudes where *A.*

magellanica is less common off cushions). Larger cushions also tend to support both more individual grasses, as well as total coverage by this grass (le Roux & McGeoch 2004).

Virtually all cushions are occupied by at least four springtail and one mite species, whereas the prevalence of other members of the microarthropod assemblage associated with *A. selago* is lower (Fig. 10.5). However, surprisingly little spatial or deterministic structure in the microarthropod community is apparent at the landscape scale (Hugo *et al.* 2004), and the abundances of only one mite and one springtail species are spatially autocorrelated, inconsistently so, across stands (Fig. 10.3c, d). No spatial structure is apparent in either total abundance or richness across any of 13 stands (Table 10.3) examined on the island. There is some evidence that cushions with large proportions of dead and decaying stem and leaf material are associated with greater microarthropod abundances (Hugo 2006). Nonetheless, cushion size and isolation have little effect on microarthropod species richness, abundance and, consequently, community structure (Hugo *et al.* 2004; Hugo 2006). These findings are comparable to studies on springtails in tussock patches in the Arctic, where total vegetation cover (as a percentage of the total area) and patch quality are more important predictors than patch size and isolation (Hertzberg 1997; Ims *et al.* 2004). However, previous studies (Barendse & Chown 2001; Barendse *et al.* 2002) have shown that the same species of microarthropods occur both in the cushions and in the epilithic matrix (albeit at far lower densities) within which they are embedded. Elsewhere (short-grass prairie), larger cushions (species from the Fabaceae and Polemoniaceae) have been found to support more species and individuals in total (Tepedino & Stanton 1976), but here there is no difference per unit area of cushions of different sizes. These results are therefore consistent with the view that microarthropods move freely between cushions and the surrounding matrix in fellfield habitat. The generally similar temperatures and moisture contents of different-sized cushions are also consistent with this view.

At the scale of the landscape, therefore, patterns in *A. selago* variability appear to be driven largely by historical events (i.e. plant recruitment), intraspecific competition that structures cushion size and dispersion, and microtopography that alters cushion exposure to wind and light. While most plants are host to epiphytes, the size and distribution of cushions is a significant determinant of the distribution of *A. magellanica* in mid-altitude fellfield habitat. By contrast, cushion characteristics appear to play comparatively little role in structuring the microarthropod assemblage at this scale.

Figure 10.5 Percentage of sampled cushions occupied by a) epiphyte species ($n = 600$), b) springtail and c) mite species ($n = 431$) (Hugo 2006; Nyakatya 2006). Moss = mosses; Agro = *Agrostis*; Ranu = *Ranunculus*; Live = liverworts; Lich = lichens; Fung = fungi; Lyco = *Lycopodium*; Blec = *Blechnum*; Acac = *Acaena*. See Table 10.2 for arthropod species abbreviations.

10.4 The island

Across Marion Island, spatial variation in *A. selago*, and its inhabitants, is likely to be driven by island-wide patterns of climatic and geomorphological variation, as well as interspecific competition at lower, more plant-species rich altitudes. Island-scale abiotic patterns include strong altitude-linked declines in temperature and solar radiation with increases in wind speed, precipitation and freeze-thaw frequency (Fig. 10.6). However, soils at higher altitudes are poorly developed, and mineral-poor, with low water retention capacity (Smith 1978b). Furthermore, these abiotic gradients are not necessarily equally pronounced on the eastern and western sides of the island. The western side of the island is directly exposed to the dominant north-westerly winds, and is more frequently cloudy than the eastern side (Schulze 1971). We have shown, for example, that *A. selago* is exposed to greater temperature variation, and that summers are significantly warmer and winters cooler on the eastern than the western side of the island (Fig. 10.7a, Nyakatya & McGeoch 2008). The western side of the island thus appears to be more temperate, whereas the east is more extreme.

Figure 10.6 Idealized representation of altitudinal gradients in abiotic variables and plant cover on Marion Island (based on Huntley 1971; Schulze 1971; Blake 1996; Smith *et al.* 2001; Boelhouwers 2003; Holness 2003; J.A. Deere, unpublished data; Nyakatya 2006) (from le Roux 2004).

Figure 10.7 General linear model interaction plots showing mean ($\pm$ s.e.) summer temperature a), cushion surface area b), trichome density c) and stomatal density d) recorded across altitudes and on different sides of Marion Island (see Table 10.3 for stand details). Diamonds (600 m a.s.l.), squares (380 m a.s.l.), circles (200 m a.s.l.).

Fellfield habitat occurs on both black and grey lava substrate on the island, and although the older grey lava stands have better developed soils, they are more nutrient poor than the geologically younger, black lava substrates (Smith 1977, 1978b). Indeed, substrate type does appear to have an effect on cushion size and density, with cushions significantly smaller and present in higher densities on black than on grey lava (Nyakatya 2006). In addition, *A. magellanica* densities tend to be higher on *A. selago* in grey than in black lava fellfield (Nyakatya 2006). This suggests that *A. selago* size and establishment patterns are to some extent related to soil structure and nutrient availability.

Azorella selago is found from sea level to approximately 750 m a.s.l. (although isolated individuals have been observed at higher elevations), and several altitudinal and aspect-related morphological and phenological trends are apparent in the species. For example, cushions at low altitudes undergo autumnal senescence earlier than high altitude plants, as do cushions on the eastern side of the island (Nyakatya 2006). This suggests a possible degree-day (time taken to accumulate a number of heat energy units) threshold for autumnal senescence, with a more rapid accumulation of heat energy units over summer at low altitudes and in the east than the converse. While *A. selago* cushions on the eastern side of the island tend to be larger than those on the

west, cushion size is inconsistently related to altitude (Fig. 10.7b). Growth rate does not appear to be related to altitude, and surprisingly also not to island side (Nyakatya 2006). By contrast, leaf characteristics show clear altitudinal and aspect differences. Leaves are larger on the east and towards mid- and high altitudes, whereas trichome density is highest on the western side of the island and at higher altitudes (Fig. 10.7c) (le Roux 2004; Nyakatya 2006). Stomatal density is also highest in the east, decreasing towards higher altitudes (Fig. 10.7d). Therefore, while phenology and leaf characteristics appear to be comparatively plastic, cushion size and growth rate respond less strongly to island-scale environmental variation, with local site characteristics apparently more important.

Patterns of epiphyte abundance and cover are also strongly related to altitude (Fig. 10.8). The abundance and proportional cover of *Agrostis magellanica* peaks at mid-altitudes, although maximum abundance and cover (as well as the altitude at which this was attained) differs between gradients on different parts of the island (le Roux 2004). A mid-elevation abundance peak in this species has also been recorded from Macquarie Island (Bergstrom *et al.* 1997). The proportion of cushion surface covered by other vascular epiphyte species (i.e. excluding *A. magellanica*) is also related to altitude, and declines strongly with increasing elevation (Fig. 10.8). Other vascular epiphytes include mainly *Blechnum pennamarina*, *Acaena magellanica* and *Cotula plumosa*, that together cover on average 2.6% of cushion surfaces (with a maximum cover of nearly 50% on some cushions). Non-vascular epiphyte species richness peaks at higher altitudes (on average > 350 m a.s.l.) and declines rapidly towards sea level (Fig. 10.8). By contrast, vascular epiphyte species richness is highest at sea-level, declining gradually with increasing altitude. On Marion Island, epiphyte species richness thus peaks at mid-altitudes. Epiphytes also appear to be more frequent on cushions on the eastern than western side of the island (Nyakatya 2006). This form of taxon and locality-specific richness and abundance difference has been documented across other high latitude, altitudinal gradients (Andrew *et al.* 2003).

Of all vascular plant species on the Prince Edward Islands, *A. selago* supports amongst the highest diversity of microarthropods (Hugo *et al.* 2006). A total of 22 mite species and nine springtail species have been recorded in *A. selago* cushions from across the island, with the majority of these species having island-wide distributions (Hugo *et al.* 2006) (Table 10.2). However, in some cases contrary to findings at the plant-scale, neither cushion surface area, plant height, percentage dead tissue or percentage grass cover appear to explain observed patterns in species richness or abundance at the island scale. Nonetheless, the microarthropods do respond to both altitude and position on the island. The difference between the eastern and western sides of the island are generally more marked than those across altitude (Fig. 10.9, Hugo 2006). Mean abundance and richness of microarthropods is significantly higher in cushions on the west, with a weak, yet significant decline towards higher

altitudes (Fig. 10.9, Hugo 2006). While these general patterns are clear, the responses of springtails and mites are somewhat different. The abundance of virtually all springtail species are uniformly highest at low to mid altitudes on the western side of the island, whereas the responses of individual mite species are far more heterogeneous (Hugo 2006). The abundances of some mite species peak in the east and some even towards high, rather than low altitudes (Hugo 2006). The abundances of the introduced springtail, *Isotomurus cf. palustris*, and mite, *Cillibidae* sp., are also higher on the west than the east. Nonetheless, the richness and abundance of introduced species in the *Azorella* microarthropod community is consistently low, and these are the only two recorded in any significant abundance in this community (see Chown *et al.* 2002

Figure 10.8 Altitudinal variation in the species richness (mean $\pm$ s.e.) of a) all epiphytes, b) non-vascular epiphytes, and c) vascular epiphytes on *Azorella selago* cushions (Ie Roux 2004).

for list of indigenous and invasive species). The relative abundances of the dominant species in the community do not change significantly across altitude, although there are some rank abundance changes amongst the less abundant mite and springtail species. *Eupodes minutus* dominates the mite community by at least 75% in all cases (Hugo 2006). Generally, the springtail *Cryptopygus dubius* prefers higher altitudes, whereas *Isomotoma marionensis* is dominant at mid-altitudes. In the mite community *Austroppia crozetensis* appears to prefer lower altitudes, whereas *Schwiebea talpa* prefers higher altitudes. By contrast, the rank abundance of springtail species is clearly different between the eastern and western sides of the island, with *I. marionensis* replacing *C. dubius* as the dominant species on the western side (Hugo 2006).

Figure 10.9 Microarthropod abundance (a) and species richness (b) per core sample across 12 stands (see Table 10.3) at low, medium and high altitudes on Marion Island. Closed symbols = east and open = west of island.

Spatial variability in *A. selago* and its epiphyte and arthropod inhabitants across Marion Island is therefore driven at least partly by island-side and altitude-related climatic differences, as well as by differences in grey and black lava fellfield substrates. Interestingly, many of the plant variables responded similarly, with contrasts between high altitude-west and low altitude-east sites. This raises the question of what abiotic environmental conditions high altitudes and the western side of the island share? Cloudy conditions are more frequent, temperature ranges lower (Nyakatia & McGeoch 2008; see also Slabber & Chown 2004) and precipitation probably higher at high altitudes and on the western side of the island, whereas the reverse is true for low altitude and eastern areas. The findings thus support the significance of abiotic drivers of terrestrial diversity patterns at intermediate and high altitudes on Marion Island.

10.5 Apparent mechanisms

The multiscale patterns in *A. selago* and its associated fauna and flora described here suggest several mechanisms important to the structure and maintenance of this system on Marion Island. In addition, some of these hypotheses are supported by work done on sub-Antarctic systems and *Azorella* species elsewhere. Nonetheless, as the hypotheses that we outline here are largely derived from mensurate rather than manipulative approaches, most remain to be tested.

First, characteristics of cushion morphology and survival correlate with microclimatic and microtopographic features. Local site conditions (such as substrate and soil properties) appear to be important for episodic seedling establishment, as well as eventual cushion size and density. The structure and dispersion patterns in *A. selago* populations across the landscape also imply intra-specific competition. Leaf morphology varies strongly with climatic differences associated with both aspect and altitude, such as radiation, precipitation and temperature fluctuations. Indeed, east-west differences emerge as a particularly important correlate with pattern in this system, often stronger than elevation. More detailed, quantitative information on meteorological differences between these two sides of the island are thus needed to explore potential mechanisms underlying these aspect-related differences.

Azorella selago contributes significantly to plant species diversity at intermediate altitudes, by hosting, particularly vascular, species that are unable to otherwise establish at these altitudes. Nonetheless, the altitudinal range of these species remains narrower than that of *A. selago*, as a likely consequence of wind and temperature (e.g. Pammenter *et al.* 1986). Indeed, wind appears to be responsible for both within- and across-cushion distribution patterns of the dominant epiphyte, *A. magellanica*. Epiphytes increase within-cushion heterogeneity and resource diversity for the microarthropod community. In some cases they also appear to alter patterns of cushion decay and longevity.

Microarthropod community patterns change along both vertical and horizontal gradients in cushion microclimate, as well as in relation to the within-cushion

distribution of *A. magellanica*. Microhabitat preferences and selection by mites and springtails appears to be an important determinant of fine-scale patterns in the distribution and abundance of these taxa. The absence of landscape-level structure in the abundance or distribution of microarthropods suggests that rates of immigration and emigration exceed birth and death rates at the scale of individual cushions. Indeed, given the size and dispersal abilities of the species involved (Marshall & Chown 1995), habitat selection across a stand is unlikely. At the same time, however, cushion quality is often fairly homogeneous across stands and this is possibly also an explanation for the lack of spatial or deterministic structure in the microarthropod community at this scale. Neither island biogeography nor metapopulation dynamics offer satisfactory explanations for this system, because dispersal likely exceeds local population growth rates. However, abiotic patterns associated with both altitude and aspect do explain the island-wide richness and abundance patterns in the microarthropods. The temperate, moist, western side of the island apparently provides more suitable conditions for these species than the comparatively extreme, dry conditions on the east.

10.6 Implications of environmental change

Given the current rapid rate of environmental change on the Prince Edward Islands (as a consequence of both climate change and species invasion) (Smith & Gremmen 2001; Smith 2002; Frenot *et al.* 2005; Sumner *et al.* 2004), and observed changes elsewhere in the Antarctic (see Kennedy 1995; McGeoch 2006; le Roux & McGeoch 2007), some impact on the structure and functioning of this model system may be expected. Contrary to evidence from lower altitude communities (Chown & Gaston 2000; Gabriel *et al.* 2001; Chown *et al.* 2002; Gaston *et al.* 2003; Frenot *et al.* 2005), the system appears largely unaffected by introduced species, with only one introduced plant species (*Sagina procumbens*) commonly recorded to date on *A. selago*. Also, only two introduced microarthropods occur in *A. selago* cushions and in comparatively low numbers (see also Barendse & Chown 2001). Gabriel *et al.* (2001) showed that the introduced, warm and moist sites with high levels of organic material are preferred by the introduced springtails, whereas their presence was negligible in cold, fellfield areas. Nonetheless, given the warming trend on the Prince Edward Islands, it would be wise to monitor the presence and abundance of introduced species associated with *A. selago* and fellfield habitats.

Climate change is predicted to significantly alter patterns of primary productivity, nutrient cycling, vegetation succession and habitat structure on Marion Island (Smith & Steenkamp 1990; Smith *et al.* 2001; le Roux & McGeoch 2008). While Smith *et al.* (2001) do not predict a successional change in fellfield under continued warming and drying, mesic fellfield may become more xeric. Nonetheless, should climate change bring about an increase in the shading of cushions at low altitudes by rapidly growing vascular species (introduced or otherwise), slow-growing *A. selago* is likely to be negatively affected

(le Roux 2004). The results of experimental manipulation of precipitation (Plate 1f) suggest that ongoing drying of the island will increase stem senescence and interact with wind patterns to result in a directional die back and degradation of cushions (le Roux 2004; le Roux *et al.* 2005) (Fig. 10.10a). Under current climate change trends on Marion Island, the strongest community-level predictions for the microarthropod community include a dramatic decline in abundance and biomass under reduced precipitation (McGeoch *et al.* 2006; see also Convey *et al.* 2002, 2003), although increased temperatures are predicted to affect springtail abundances positively (Coulson *et al.* 1996; Hodkinson *et al.* 1996; Convey *et al.* 2002, 2003). In the same experiment mentioned above, springtail abundance and biomass were significantly negatively affected by drying of the cushion environment (Fig. 10.10b). However, species responses are likely to be idiosyncratic, both within and across mite and springtail taxa (McGeoch *et al.* 2006). Indeed, an ongoing decline in precipitation is likely to have dramatic effects, particularly on the desiccation-sensitive springtail component of this community (McGeoch *et al.* 2006; le Roux & McGeoch 2008).

Species interactions are of course predicted to be highly sensitive to climate change, and at the same time far more complex to understand than direct effects on particular species (Sudgen 1992; McGeoch 2006). Therefore, interactions between *A. selago* as host, its epiphytes and microarthropods are likely to be altered by any direct change to one of these components. For example, while temperature amelioration may increase cushion coverage by *A. magellanica*, the decline in precipitation may curb this response (le Roux 2004). Also, the loss of microarthropods from decomposer communities has been shown to alter the composition of decomposer microflora, and to change soil quality and respiration processes (Moore *et al.* 1988; Teuben & Verhoef 1992; Taylor *et al.* 2004). This is likely to be equally true on Marion Island, because nitrogen availability is low, nutrient turnover and decomposition rates are slow, and microarthropods constitute a disproportionately large component of the decomposer community (Smith & French 1988; Smith & Steenkamp 1990; Hopkin 1997; Robinson *et al.* 2004). The complexities of such interactions, as well as the testing of mechanism underlying the multiscale patterns observed, therefore form important future research priorities for this system.

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Figure 10.10 Effects of simulated climate change on *Azorella selago* and the springtails that occupy it. a) Unequal distribution of autumnal senescence across *A. selago* cushions exposed to reduced rainfall conditions (modified from le Roux *et al.* 2005). Quarters not sharing a common letter are significantly different ($P = 0.001$). NW = north-western quarter; NE = north-eastern; SE = south-eastern; SW = south-western. b) Springtail biomass (mean $\pm$ s.e.) in control cushions and under reduced rainfall conditions (Dry) and its associated procedural control (Proc. Con.), and increased shading (Shade) (modified from McGeoch *et al.* 2006). Treatments not sharing a common letter are significantly different ($P < 0.05$).

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