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Fine scale variation in microarthropod communities inhabiting the keystone species *Azorella selago* on Marion Island

Received: 20 November 2003 / Revised: 25 February 2004 / Accepted: 26 February 2004 / Published online: 22 April 2004
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Abstract Invertebrates contribute significantly to nutrient cycling on sub-Antarctic islands and thus their distribution patterns are of considerable interest. Few studies have, however, investigated the deterministic nature of fine-scale patterns in arthropod communities. This study investigated the relationship between the fine-scale distribution and abundance of mites (Acari: Arachnida) and springtails (Collembola: Hexapoda) in *Azorella selago* Hook. f. (Apiaceae) on Marion Island, and plant size, isolation, within-plant variability and epiphyte load. Microarthropod abundances were significantly higher on the southern, cold, dry, less frequently wind-blown sides of plants. Abundances were also significantly higher in association with the dominant epiphyte, a likely consequence of increased resource availability. No effects of cushion size or isolation on abundance or species richness were found. This study thus demonstrates that fine-scale variation in the microarthropod community is deterministic, a likely consequence of biotic and abiotic factors, and therefore of importance in the context of rapid climate change.

Introduction

Indigenous terrestrial vertebrates are largely absent on the sub-Antarctic islands, where invertebrates constitute the only herbivores and detritivores (Burger 1985; Tréhen et al. 1985; Chown et al. 2002). They contribute significantly to ecosystem functioning, often taking the role of keystone species (Smith and Steenkamp 1992a, b). For this reason, and because of the isolated nature of the islands and their considerable endemism, patterns in the distribution and abundance of invertebrates on sub-Antarctic islands, and the mechanisms underlying them, have long been of interest (reviewed in Gressitt 1970; Chown et al. 2002).

The large majority of these studies have until recently been concerned with biogeographic patterns in the wider distribution of species across the sub-Antarctic. Most early works were largely concerned with patterns of occupancy across islands (Gressitt 1970; Abbott 1974) and many studies continue to be done at this scale (Chown et al. 1998, 2001). It is only more recently that investigations of the abundance and distribution of species across habitats on individual islands have become more common. The impetus for these studies have not only arisen from a need to understand ecosystem structure and functioning on the islands (Davies 1973; Bellido and Cancela da Fonseca 1988; Barendse et al. 2002), but also to determine the likely effects of invasive species on local patterns and processes (Hänel and Chown 1998; Gabriel et al. 2001).

One consistent finding amongst the large majority of these studies is substantial variation in invertebrate abundance and occupancy within particular plant communities (Mercer et al. 2000; Gabriel et al. 2001; Barendse et al. 2002). Indeed, this kind of variation has come to be considered characteristic of both sub-Antarctic and Antarctic terrestrial invertebrate communities (Usher and Booth 1984, 1986). Few studies have determined whether or not small-scale spatial variation in occupancy and abundance is either largely random or

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influenced by more deterministic processes (see Coulson et al. 2003 for an Arctic example). Such studies are particularly important in the context of the rapid climate changes that are taking place on the sub-Antarctic islands (Bergstrom and Chown 1999; Smith 2002), and their apparent influence on alien, invasive species (Barendse and Chown 2000). Climate change is likely, not only to have direct effects on indigenous invertebrate communities (Davies and Melbourne 1999), but also to affect interactions between indigenous and invasive species, to the benefit of the latter (Walther et al. 2002).

One of the most striking cases of within-habitat variation in invertebrate occupancy and abundance is that of Marion Island fellfield habitats characterized by the cushion-forming plant *Azorella selago* Hook. f. (Apiaceae). Arthropod abundance in individual *Azorella selago* cushions can be an order of magnitude higher than in the surrounding matrix (that comprises soil, stones, lichens, bryophytes, and soil flora) (Barendse and Chown 2001; Barendse et al. 2002). When documenting this considerable variation, Barendse and Chown (2001) suggested that the *Azorella selago* cushions form climatically benign, nutrient-rich resource islands relative to the remaining fellfield (see also Huntley 1972), implying that they act as a keystone species in this habitat. Whilst they noted that the cushions have a considerable influence, despite occupying only 10% of investigated fellfield surface area, they largely ignored the fact that these cushion "islands" vary markedly in size, occur at various densities, and often carry a heavy load of epiphytes, especially the grass *Agrostis magellanica* (Lam.) Vahl. (Gremmen 1981). Therefore, variation in the abundance or occupancy of arthropods within *Azorella selago* cushions has never been examined.

Therefore, in this study, we investigated fine-scale variation in the distribution and abundance of microarthropods in *Azorella selago* cushions on Marion Island specifically to determine: (1) if community structure is related to cushion size and density, (2) whether there are consistent patterns of within-plant variability in microarthropod community structure, (3) if community structure is influenced by the dominant epiphyte, *Agrostis magellanica*, and (4) whether any of these patterns are related to temperature in the cushion and cushion moisture content. These last variables are of particular significance given the reported rapid warming and drying on Marion Island (Smith 2002).

Materials and methods

Study sites

The study was conducted during late summer (April–May 2002 and 2003) on Skua Ridge (46°52'S, 37°50'E, 100 m a.s.l.) and on Stony Ridge (46°54'S, 37°51'E, 175 m a.s.l.) on the eastern side of Marion Island. These two sites are typical grey lava fellfield areas (Gremmen 1981; Barendse and Chown 2001). Fellfield soil contains

little organic matter or plant nutrients, and has a low water-retention capacity compared with other soils on the island (Gremmen 1981). The vegetation in these areas consists mainly of mosses and lichens, in addition to the characteristic *Azorella selago* (Gremmen 1981).

Sampling

Microarthropods were sampled from cushions using an O'Connor split corer (inside diameter of core = 70 mm, height = 70 mm, surface area = 0.0039 m²). Core samples (including surface leaves and underlying decomposing plant material) were taken of four different cushion-size classes (maximum diameter of cushion) determined by a preliminary survey of cushion-size distributions at the sites. Cushions were assigned to one of four size classes: small (20–40 cm in diameter), medium (60–80 cm), medium-large (100–120 cm) and large (140–160 cm). Ten cushions per size class were selected randomly from an area of 100 m² and one core sample taken from the centre of each cushion at each site. The distances from each cushion to its five nearest neighbours were measured as an estimate of cushion isolation and density. The number of individual grasses of *Agrostis magellanica* (Lam.) Vahl. on these cushions was also counted as an estimate of epiphyte load.

To examine microarthropod community variability within cushions, 20 additional, randomly selected cushions in the 100- to 120-cm size class were sampled (at each site) by taking three core samples from each selected cushion. Ten randomly selected cushions were sampled in an east-west direction and the other ten cushions in a north-south direction. The lateral cores were taken midway between the centre core and the cushion perimeter, with the absolute distance between cores dependent on cushion size. North-south and east-west coring could not be done simultaneously on single cushions, because cushions in large size classes tended to become irregular in shape and smaller cushions could not accommodate more than three samples per cushion. The maximum diameter, width and height of each sampled cushion were measured and the number of individual grasses of *Agrostis magellanica* (Lam.) Vahl. on each cushion was also counted.

To further examine the effect of *Agrostis magellanica* on the microarthropod community, ten cushions were sampled with, and ten without any *Agrostis magellanica* on Stony Ridge (there were no cushions without grasses on Skua Ridge). Smaller cushions were selected (20 to 40-cm size class) because cushions larger than this generally supported at least some *Agrostis magellanica* individuals. All cores at a site were taken within 4 days of each other and the period between sampling the two sites was 10 days.

Mites and springtails were extracted from the cushion cores using a MacFadyen high-gradient extraction protocol of 2 days at 25°C followed by 2 days at 30°C (Barendse and Chown 2001; Barendse et al. 2002).

Although the efficacy of high gradient extraction has come under renewed discussion (Andre et al. 2002), any error is likely to be consistent across all samples. Microarthropod species were identified to the lowest possible taxonomic level (usually species), counted and stored in 99% ethanol at the University of Stellenbosch.

Temperature and moisture content

Temperature was recorded inside *Azorella selago* cushions on both Skua Ridge and Stony Ridge, as an indication of the temperature range experienced by microarthropods. "Ibutton" dataloggers (DS1921 Thermochron iButton, Dallas, diameter = 1.5 cm) were inserted between stems in the top 1.0 cm of cushions and were set to record temperature every 5 min for four successive days per site. Dataloggers were calibrated against temperatures recorded in a water bath (LTD 20 Grant Instruments, Cambridge, UK) programmed to hold each of five successive temperatures for 2 h. The loggers were always within $\pm 0.2^\circ\text{C}$ of the water-bath temperature.

To determine if temperature differed with respect to cushion size, ten cushions per size class at both sites were selected randomly from an area of 100 m² and a datalogger inserted into the centre of each cushion. To determine temperatures on different cushion sides, dataloggers were inserted in the N, E, S and W quadrants of ten randomly selected cushions in the 100- to 120-cm size class at both sites. The effect of *Agrostis magellanica* on cushion temperature was determined by inserting one datalogger in an area of this epiphytic grass and another about 5 cm distant on the same cushion in an area lacking grass. This was done for five cushions on Stony Ridge.

The influence of cushion size, logger direction in cushions, and the influence of *Agrostis magellanica* on temperature were investigated using hourly temperature recordings. The full data set was not used because of temporal autocorrelation (see Housemann et al. 2002). To investigate the influence of cushion size on temperature, an analysis of variance (ANOVA) with cushion-size class as the categorical factor was used. The influence of within-plant variability (or logger direction) on temperature was assessed by calculating the mean temperature for the four logger directions (N, S, E, W), and the difference from the mean was then calculated for each direction. These values were then used in a repeated measures ANOVA with temperature of the different directions as dependent variable and cushion as categorical predictor. Multiple comparison tests (Tukey's honest significant difference) were used to identify temperature differences between cushion-size classes and directions in cushions. The differences in temperature between areas with and without the epiphytic *Agrostis magellanica* were analysed using ANOVA with position (in and out of grass area) and cushion (five cushions used) as predictors.

Cushion moisture content was also measured. A circular core (inside diameter of core = 35 mm, height = 35 mm) was taken from each area in the cushion where dataloggers were inserted. The cores were weighed and dried at 60°C and then weighed again. Differences in moisture content in different cushions sizes, directions and areas with and without grasses were analysed with ANOVA (and Tukey's honest significant difference).

Stevenson screen dry-bulb temperatures, humidity, wind direction, wind speed and pressure measurements, recorded every 5 min, were obtained from the meteorological station (46°54'S, 37°45'E; South African Weather Bureau, Marion Island) for the days of temperature monitoring in the field and for the days preceding microarthropod sampling. The weather station is located about 1 km to the south of Skua Ridge and about 4 km to the north of Stony Ridge. Hourly wind-direction data from 1998 to 2002 were used to determine prevailing wind direction over a longer time period. Mean (\pm SE) Stevenson screen temperatures, humidities and wind speeds were calculated for the periods over which N, E, S, and W winds were blowing during the study period.

Analyses

Generalized linear models (McCullagh and Nelder 1989) were used to determine the relationship between species richness and abundance (separate models for each of these dependent variables) in *Azorella selago* cushions and the explanatory variables. A Poisson error distribution was assumed for species richness and abundance of microarthropods, a logarithmic link function used in all the models described here, and deviance used as a measure of goodness of fit (Collett 1991).

The first models constructed (1) included site, cushion-size class and mean distance to the five nearest neighbouring cushions. Thereafter, models to examine the relationship between richness and abundance and other explanatory variables were constructed individually for each of the two sites, because in this first model the difference between sites was found to be highly significant. Therefore, site-specific models were constructed to examine within-plant variability (2) in species richness and abundance (using core direction: N, E, S, W and cushion centre). The mean species richness and arthropod abundance for all core samples taken from each cushion was calculated. The difference from the cushion mean was then calculated for each core sample and these differences used in the model. Tabulated means for within-cushion variability thus represent the differences in species richness or abundance at each direction in the cushion from mean richness or abundance. This approach was used in favour of repeated measures to permit the simultaneous comparison of all compass directions across sampled cushions.

Site-specific models were also constructed for epiphyte load (3). Two sets of models were used: (a) using data on the number of *Agrostis magellanica* on all cushions on which core samples were taken from the centre of the cushion ($n=60$), as well as (b) comparing an additional set of ten cushions with this epiphyte and ten without. In (a), the maximum diameter of cushions was added to the models because cushion diameter and number of *Agrostis magellanica* were not independent.

Weighted marginal means and their 95% confidence intervals were used to establish differences between means (non-overlapping confidence limits taken as weighted means significantly different at $P < 0.05$, Sokal and Rohlf 1995) for the models described here.

Differences in microarthropod community structure between sites, cushion-size classes and cushions with and without epiphytic grass, were examined using cluster analysis based on group averaging and Bray-Curtis similarity measures (Primer v5, Clarke and Gorley 2001). Abundance data were fourth root transformed and standardized prior to analysis (to weight common and rare species equally) (Clarke and Warwick 1994). Analysis of similarity (ANOSIM) was used to test for significant differences between the communities of different cushion-size classes and in cushions with and without grass (Clarke and Warwick 1994). This is a non-parametric permutation procedure applied to rank similarity matrices underlying sample ordinations, that calculates a global R -statistic. The

closer a significant global R is to one, the more distinct the differences between those communities (Clarke and Warwick 1994).

Results

Cushion size and isolation

Thirty species (19 mites and 11 springtails) and 41,689 individuals were collected from the samples (Appendix). Cushion size and nearest neighbour distance did not contribute significantly to explaining either species richness or abundance (Tables 1 and 2). By contrast, mean species richness (S) and abundance (N) were significantly different between sites, being greater on Skua Ridge than Stony Ridge (Tables 1 and 2). Similarly, the arthropod communities in different cushion-size classes could not be distinguished (Global $R=0.06$; $P > 0.05$), whereas the communities differed significantly between sites (Global $R=0.34$; $P < 0.001$). Therefore, in all further analyses, the two sites were considered separately. These patterns remained the same when mites and springtails were analysed independently. Indeed, only minor differences in the response of mites and springtails were found throughout and the two groups were thus treated together.

The only significant effect of cushion size on temperature was found at Skua Ridge, where the lowest temperatures were recorded in small cushions (Table 3).

Table 1 Model fit and contribution of explanatory variables to the generalized linear models for species richness (S) and abundance (N) (NND Nearest neighbour distance, Max maximum)

	df	Deviance/df	Explanatory variable/factor	df	χ^2	P
1. Cushion size and isolation						
S	74	0.33	NND	1	0.01	0.940
			Site	1	13.41	< 0.001
			Size class	3	0.72	0.870
N	74	1.00	NND	1	3.58	0.060
			Site	1	34.10	< 0.001
			Size class	3	7.86	0.05
2. Within-plant variability						
Skua Ridge						
S	55	1.09	Core direction	4	6.13	0.190
N	55	1.09	Core direction	4	20.11	< 0.001
Stony Ridge						
S	55	1.09	Core direction	4	4.40	0.350
N	55	1.09	Core direction	4	20.20	< 0.001
3. Epiphyte load (<i>Agrostis magellanica</i>)						
a. All cushions						
Skua Ridge						
S	57	0.36	<i>A. magellanica</i>	1	0.21	0.640
			Max. diameter	1	0.12	0.730
N	57	1.00	<i>A. magellanica</i>	1	0.10	0.750
			Max. diameter	1	0.08	0.780
Stony Ridge						
S	57	0.40	<i>A. magellanica</i>	1	2.86	0.090
			Max. diameter	1	2.92	0.090
N	57	0.98	<i>A. magellanica</i>	1	9.12	< 0.001
			Max. diameter	1	3.17	0.080
b. Cushions with and without						
S	1	0.27	With/without <i>A. magellanica</i>	1	1.61	0.210
N	1	1.00	With/without <i>A. magellanica</i>	1	4.68	0.030

Table 2 Species richness (*S*) and abundance (*N*) of microarthropods (mean ± SE): (1) on Skua and Stony Ridge, (2) in different cushion-size classes at both sites, (3) in different directions in cushions (difference from mean across all directions), and (4) in areas with and without the epiphyte, *Agrostis magellanica* (statistics provided in Table 1)

Site and cushion size	Mean <i>S</i> ± SE	Mean <i>N</i> ± SE
1. Site		
Skua Ridge	15.18 ± 0.35 ^a	235.68 ± 14.41 ^a
Stony Ridge	12.13 ± 0.32 ^b	145.70 ± 6.97 ^b
2. Cushion sizes		
Medium large	14.2 ± 0.62	208.9 ± 22.01
Medium	13.7 ± 0.51	206.2 ± 20.18
Large	13.3 ± 0.68	174.65 ± 15.85
Small	13.4 ± 0.52	173.00 ± 16.57
3. Direction		
Skua Ridge		
East	0.80 ± 0.75	74.20 ± 18.42 ^a
South	0.93 ± 0.90	23.50 ± 24.55 ^{ab}
Centre	-0.13 ± 0.31	-4.10 ± 10.64 ^b
North	-0.97 ± 0.82	-30.70 ± 25.97 ^b
West	-0.50 ± 0.61	-34.60 ± 13.25 ^b
Stony Ridge		
South	0.67 ± 0.58	45.13 ± 16.06 ^a
West	0.30 ± 0.28	23.03 ± 12.82 ^{ab}
East	0.30 ± 0.64	5.73 ± 18.31 ^{ab}
Centre	-0.32 ± 0.40	-11.67 ± 6.94 ^b
North	-0.63 ± 0.54	-35.97 ± 13.63 ^b
4. <i>Agrostis magellanica</i>		
With	12.2 ± 0.61	132.4 ± 10.62 ^a
Without	10.3 ± 0.50	105.3 ± 7.04 ^b

Different letters (superscript) indicate a significant difference of $P < 0.05$ (see Table 1)

Table 3 Temperature (°C) (mean ± SE) in: (1) different cushion-size classes, (2) directions in cushions (difference from mean across all directions), and (3) in areas with and without *Agrostis magellanica* on Skua Ridge and Stony Ridge (SST Stevenson screen temperature)

	Skua Ridge	Stony Ridge
1. Size class		
	$F_{3,3716} = 5.16$, $P < 0.001$	$F_{3,3756} = 1.12$, $P > 0.05$
Small	4.79 ± 0.08 ^a	7.42 ± 0.12
Medium	5.11 ± 0.08 ^b	7.27 ± 0.11
Medium large	5.20 ± 0.08 ^b	7.13 ± 0.11
Large	5.14 ± 0.08 ^b	7.31 ± 0.11
SST	5.30 ± 0.10	7.58 ± 0.22
2. Direction in cushion		
	$F_{3,2484} = 99.79$, $P < 0.001$	$F_{3,2790} = 270.36$, $P < 0.001$
North	0.21 ± 0.01 ^a	0.64 ± 0.05 ^a
East	-0.05 ± 0.01 ^b	0.81 ± 0.05 ^a
South	-0.11 ± 0.02 ^c	-0.88 ± 0.05 ^b
West	-0.05 ± 0.01 ^b	-0.58 ± 0.04 ^c
3. <i>Agrostis magellanica</i>		
		$F_{1,934} = 2.50$, $P = 0.11$
With		7.26 ± 0.14
Without		6.93 ± 0.16

Different letters (superscript) indicate a significant difference between means of $P < 0.001$

Cushion size had no significant effect on moisture content on either Skua Ridge ($F_{3,36} = 0.24$, $P = 0.87$) or Stony Ridge ($F_{3,36} = 0.21$, $P = 0.89$).

Within-plant variability

Species richness did not vary significantly with direction (cushion centre, N, W, S and E), although abundance was highest in the S and E cores on Skua Ridge, and S and W cores on Stony Ridge (Tables 1 and 2). There was also a significant difference in temperature between directions in the cushion, i.e. generally higher temperatures on the N and E sides at both sites (Table 3), while core moisture content did not vary with direction (Skua Ridge: $F_{3,36} = 0.48$, $P = 0.70$; Stony Ridge: $F_{3,36} = 2.37$, $P = 0.09$).

Wind from the south on Marion Island was generally colder and drier than winds from other directions during the study period (Table 4). The predominant wind direction during coring was from the E, W and SW and, during microclimate recordings, from SE, SW and W. However, data over a 5-year period showed that dominant winds blew more than 50% of the time from the NNW. Therefore cushions are more often exposed to a wet, warm north wind than a cold and dry south wind.

Epiphyte load

Microarthropod abundance was significantly related to the numbers of *Agrostis magellanica* epiphytes on a cushion on Stony Ridge, but not on Skua Ridge (Table 1). Species richness was not related to *Agrostis magellanica* numbers at either of the sites (Table 1). The comparison of cushions with and without *Agrostis magellanica* yielded similar results in that species richness was not affected by the presence of *Agrostis magellanica*, yet abundance was significantly greater where the grass was present (Tables 1 and 2). Moreover, community structure differed significantly between cushions with and without *Agrostis magellanica* (Global $R = 0.51$, $P < 0.001$, Fig. 1).

Temperature was not significantly different between areas with *Agrostis magellanica* and areas without the grass (Table 3), although there were significant differences in temperature between the five cushions measured (Full model: $F_{5,934} = 2.64$, $P = 0.02$; cushion effect $F_{4,934} = 2.67$, $P < 0.03$; grass effect $F_{1,934} = 2.50$, $P = 0.11$). Core moisture content of the cushions was also unaffected by *Agrostis magellanica* ($F_{1,8} = 0.24$, $P = 0.64$).

Discussion

Cushion size and isolation had little effect on microarthropod species richness, abundance and, consequently, community structure. Hertzberg et al. (2000) have suggested that patch size and isolation become significant correlates of abundances and occupancy when the proportion of suitable habitat declines to less than 30% of the landscape, and *Azorella selago* often occupies as little as 10% of the fellfield surface (Barendse and Chown 2001). The absence of an effect of patch size and isolation

Table 4 Stevenson screen temperature (*SST*), humidity and wind speed (mean \pm SE) when wind is blowing from different directions

Wind direction	Number of observations	Temperature (<i>SST</i>) \pm SE ($^{\circ}$ C)	Humidity \pm SE (%)	Wind speed \pm SE (m/s)
North	365	5.72 \pm 0.07	89.70 \pm 0.45	3.24 \pm 0.07
East	317	6.23 \pm 0.12	90.82 \pm 0.55	3.86 \pm 0.11
South	345	4.80 \pm 0.09	76.91 \pm 0.48	7.42 \pm 0.31
West	1,205	7.17 \pm 0.05	85.12 \pm 0.33	20.89 \pm 1.02

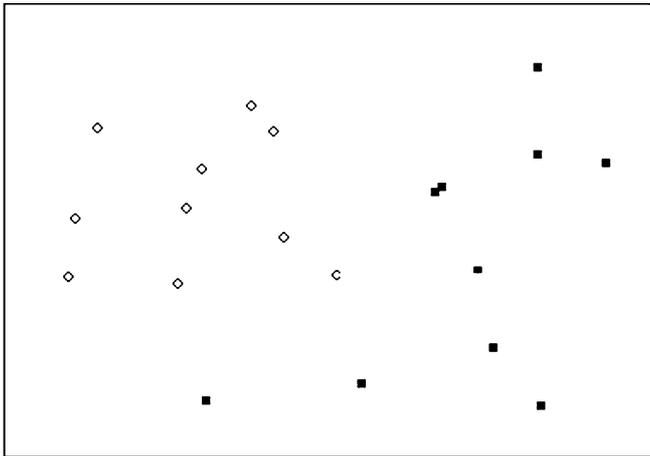


Fig. 1 Non-metric multi-dimensional scaling (*MDS*) ordination of the abundance of microarthropods in cushions with and without the epiphytic grass, *Agrostis magellanica* (unfilled circle with, filled square without). (Global $R=0.51$; $P<0.001$; stress = 0.21)

might therefore appear unusual. However, previous studies (Barendse and Chown 2001; Barendse et al. 2002) have shown that the same species of microarthropods occur both in the cushions and in the matrix (albeit at far lower densities) within which they are embedded. Elsewhere larger cushions support more species and individuals in total (Tepedino and Stanton 1976), but here there was no difference per unit area of cushions of different sizes. Our results therefore support the tenet that microarthropods move freely between cushions and the surrounding matrix, although this has yet to be verified. The generally similar temperatures and moisture contents of different-sized cushions also support this view. Although small cushions had significantly lower temperatures than the other cushion sizes on Skua Ridge, a maximum difference of 0.4°C in mean temperatures does not initially seem biologically meaningful. However, given that this difference was at temperatures of ca. $13\text{--}14^{\circ}\text{C}$, i.e. towards the upper thermal limit for development of some of the springtail species (S. Slabber and S.L. Chown, unpublished data), cushion-size related variation in abiotic conditions does deserve further exploration (see Sinclair 2001 for the rationale).

By contrast with the lack of variation between cushions as a consequence of size and nearest neighbour distance, there was a significant effect of *Agrostis magellanica* presence on the abundance of the microarthropods. The influence of *Agrostis magellanica* suggests that variation between cushions is not merely a conse-

quence of stochastic processes (Haydon et al. 1993; Ives and Klopfer 1997). Rather, the presence of the epiphytic grass has a pronounced effect on microarthropod abundance, with an increase in the numbers of epiphytic plants associated with an increase in arthropod abundance at least at the less-vegetated site on Stony Ridge (see also Coulson et al. 2003 for an Arctic example of the effects of single plants on arthropod abundance). For springtails, and possibly for mites, this effect of *Agrostis magellanica* can be readily explained. *Agrostis magellanica* roots have more mycorrhizae than those of *Azorella selago* (Smith and Newton 1986). Thus, cushions with *Agrostis magellanica* epiphytes are not only likely to have a greater abundance of fungal resources, but also a different fungal community composition. Given that many springtails feed exclusively or partly on fungi (Hopkin 1997; Bakonyi et al. 2002), and that feeding on mixed resources considerably enhances their performance (Scheu and Folger 2004), the increase in abundances found as a consequence of epiphyte presence is likely a consequence of both a greater abundance and greater diversity of fungal resources. The significant relationship between epiphyte load and abundance for Stony Ridge, a site much less-vegetated and with a generally lower plant cover than Skua Ridge, also provides support for this hypothesis. The greater total abundance of microarthropods on Skua Ridge may similarly be explained by the high density of *Agrostis magellanica* at this site. Resource quality or quantity is thus the likely explanation for these differences found, particularly as there were no differences in temperature or moisture content associated with *Agrostis magellanica*.

The significant and sizeable within-cushion direction effect on arthropod abundance further complicates the picture. On Skua Ridge, abundances on the southern and eastern sections of the cushion were generally 20–25% higher compared with northern and western sides, while on Stony Ridge the generally higher abundance on the southern section of the cushion was even more pronounced, amounting to a difference of 13,000–21,000 individuals m^{-2} . This is a remarkable difference over such a small spatial scale, and suggests a marked preference of the arthropods for the southern sections of the cushion, with the precise area of preference dependent to some extent on the position of the site. The positive association of individuals as a consequence of a common preference for microhabitat quality is not unusual in arthropods (McGeoch and Chown 1997) and, indeed, species abundance distributions frequently

reveal hot and cold density spots at multiple spatial scales (Gaston 2003; McGeoch and Price 2004).

Precisely why arthropods prefer the southern side of the cushions cannot be determined at present. However, temperature variation within the cushions, and the nature of the overall climate at Marion Island provide several hypotheses for this variation. Northwesterly winds tend to be the warmest and wettest on Marion Island (Table 4; Schulze 1971), and given the island's position, north-facing aspects tend to receive most solar radiation. In consequence, southerly aspects are colder and generally drier than others, and this is reflected in the cushion temperature data. Moreover, northwestern aspects tend to receive most of the onshore winds (Table 4; Schulze 1971; Gremmen 1981), with turbulence depositing material on the leeward side (Warren Wilson 1959; Chown and Avenant 1992). Because high windspeeds, as are characteristic of Marion Island (Schulze 1971), disrupt the boundary layer (Campbell and Norman 1998), and consequently contribute to the drying power of the air (Berjak 1979; Klok and Chown 1998), microarthropods, which are generally not particularly resistant to desiccation (Sømme 1995; Hopkin 1997), might prefer to avoid the windward side of cushions. Despite more pronounced wetting by rainfall on the northwestern side of cushions (see above), moisture did not vary with direction within the cushion. Thus, the effect of boundary layer disruption by wind on desiccation might be more significant for springtail distributions, given a lack of spatial variation in cushion moisture status, than the direction of rainfall receipt. Deposition of detritus on the leeward side of cushions might also enhance nutrient content of this part of the cushion. Usher (1969) and Usher and Booth (1986) showed that the distribution of springtails tends to be highly aggregated, and suggested that springtails aggregate in microenvironments that are suitable, either in terms of microclimate or resource availability. Indeed, both mechanisms appear to play a role in the microarthropod community associated with *Azorella selago*, and deserve further exploration.

In conclusion, this study has demonstrated significant within-plant variation in microarthropod abundance that is both a consequence of epiphyte load and apparently of spatial variation in abiotic, or perhaps biotic 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 and Booth 1984, 1986), but not for the sub-Antarctic. If the variation within cushions is a consequence of variation in temperature, then the rapid increase in temperature at Marion Island, as a consequence of global climate change (Smith 2002), might not only mean broader scale redistribution patterns (Bergstrom and Chown 1999; Walther et al. 2002), but also a fundamental change in abundance-structure at local scales. Furthermore, an indirect effect of climate change on microarthropod communities via any effect on the distribution and abundance of *Agrostis magellanica* is possible.

Acknowledgements The Department of Environmental Affairs and Tourism, South Africa, provided the financial and logistic support for this research. Marion Island Meteorological Station data were provided by the South African Weather Bureau. S.L.C. is supported by the USAID Capacity Building Programme for Climate Change Research. This is a SCAR RiSCC contribution.

Appendix

Acari (mites) and Collembola (springtails) species collected in *Azorella selago* cushions on Skua Ridge and Stony Ridge

Acari	Collembola
Acari sp3	Suborder: Arthropleona
Suborder: Mesostigmata	<i>Tullbergia bisetosa</i> Börner
Rhodacaridae sp.	<i>Isotoma marionensis</i>
	Déharveng
<i>Dendrolaelaps</i> sp.	<i>Cryptopygus dubius</i>
	Déharveng
Cilibidae sp. ^a	<i>Cryptopygus antarcticus</i>
	<i>travei</i> Déharveng
Suborder: Prostigmata	<i>Cryptopygus caecus</i>
	Wahlgren
Prostigmata sp1	<i>Isotomurus cf. palustris</i>
	(Müller) ^a
<i>Nanorchestes</i> sp.	<i>Isotomurus</i> sp.
<i>Eupodes minutus</i> (Strandtmann)	Suborder: Symphypleona
Rhagidia sp.	<i>Megalothorax</i> sp. ^a
<i>Ereynetes macquariensis</i> Fain	<i>Sminthurinus tuberculatus</i>
	Delamare et al.
<i>Tydeus</i> sp.	<i>Sminthurinus granulatus</i>
	Enderlein
<i>Bdellodes</i> sp.	<i>Sminthurinus</i> sp.
Suborder: Cryptostigmata	
Oribatidae sp1	
<i>Liochthonius australis</i> Covarrubias	
<i>Maquarioppia striata</i> (Wallwork)	
<i>Austroppia crozetensis</i> (Richters)	
<i>Halozetes fulvus</i> Engelbrecht	
<i>Dometorina marionensis</i>	
van Pletzen and Kok	
Suborder: Astigmata	
<i>Swiebea talpa subantarctica</i> Fain	
<i>Algophagus</i> sp.	

^aIntroduced species; Pugh (1994) and Gabriel et al. (2001)

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