

**Spatial patterns in the microarthropod community
associated with *Azorella selago* (Apiaceae)
on the sub-Antarctic Prince Edward Islands**

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Dissertation presented for the degree of Doctor of Philosophy (Forestry and
Natural Resource Sciences) at the University of Stellenbosch



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December 2006

Declaration

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

Signature: _____

Date: _____

ABSTRACT

The spatial distribution of animals and plants at different scales is a central theme in ecology. Knowledge of biodiversity distribution is essential, especially with the current threat of climate change and invasion by alien species. Since the impact of climate change and alien species will be, and has already been pronounced in polar regions, information on the current spatial distributions of biota in these regions is critical to predict the consequences of climate change and alien species on the future survival, distribution and abundance of indigenous biota. This study was conducted on the sub-Antarctic Prince Edward Islands (consisting of Marion Island and Prince Edward Island), which have experienced rapid climate changes over the past 50 years. Additionally, a number of alien plant, vertebrate and invertebrate (also microarthropod) species have been introduced to these islands. Since microarthropods (mites and springtails) play an essential role in decomposition and mineralization of plant material on the islands, the loss of microarthropods from decomposer communities might have disastrous results for ecosystem processes. Therefore it is essential to know the current distributions of microarthropods in order to predict future distributions patterns in reaction to climate change and invasive species. In this study, the spatial distribution of mites and springtails inhabiting the cushion plant *Azorella selago* Hook, were examined at different scales of observation. Firstly, the microarthropod community was examined at a fine scale. The relationship between microarthropod species richness and abundance and plant size, isolation, within-plant variability, grass cover and microclimate variables were investigated. Thereafter, the spatial variability of microarthropod abundances was examined within stands of plants, with statistical methods using varying degrees of locational information to determine if microarthropod abundance is random, regular or aggregated at this scale. Further, the spatial variability of microarthropod communities in *A. selago* at different altitudes and on different sides of Marion Island, i.e. island-wide scale, was examined. The last scale of observation was the island-wide scale, in which microarthropod assemblages were compared between Marion Island and Prince Edward Island, as well as in different plant species. Microarthropods showed spatial heterogeneity within *A. selago* plants (higher abundances in eastern and southern sides of

plants), island-wide (lower springtail abundance on the eastern side of the island and at high altitudes) and between islands (more alien species on Marion Island). In contrast, microarthropod abundance was not spatially heterogeneous within a stand of plants, i.e. mostly randomly distributed. The possible mechanisms responsible for these patterns differ between scales, and range from temperature and nutrient availability at the within plant and island wide scale to alien species between islands. Climate change is likely to alter these distribution patterns of microarthropods, either directly (unfavourable climate for indigenous species growth, development and dispersal) or indirectly (favouring alien microarthropod species; increase in grass cover on *A. selago* plants may alter community structure). The information presented here, is essential for predicting the possible impacts of climate change on microarthropods in fellfield ecosystems on sub-Antarctic islands.

OPSOMMING

Die ruimtelike verspreiding van diere en plante op verskillende skale is 'n sentrale tema in ekologie. Kennis van die verspreiding van biodiversiteit is belangrik, veral met die huidige bedreiging van klimaatsverandering en indringerspesies. Omdat die impak van klimaatsverandering en indringerspesies in die poolstreke alreeds duidelik is en nog meer so sal word, is inligting oor die huidige ruimtelike verspreiding van biota in hierdie streke noodsaaklik. Hierdie studie is op die sub-Antarktiese Prins Edward-eilande (bestaande uit Marion Eiland en Prins Edward Eiland) uitgevoer, waar die klimaat vinnig verander het oor die afgelope 50 jaar. Bykomend is 'n aantal indringer plant, vertebraat en invertebraat (ook mikroartropood) spesies op die eilande ingebring. Omdat mikroartropoda (myte en springsterte) 'n baie belangrike rol in ontbinding en mineralisering van plantmateriaal op hierdie eilande speel, sal die verlies van mikroartropoda uit die ontbindingsgemeenskap rampspoedige gevolge vir die prosesse in die ekosisteem hê. Kennis van die huidige verspreiding van mikroartropoda is dus noodsaaklik om die toekomstige verspreidingspatrone, asook oorlewing en volopheid van inheemse spesies in reaksie op klimaatsverandering en indringerspesies, te voorspel. In hierdie studie is die ruimtelike verspreiding van myte en springsterte wat in die kussingplant *Azorella selago* Hook voorkom, op verskillende ruimtelike skale ondersoek. Eerstens is die mikroartropood gemeenskap op 'n klein skaal ondersoek. Die verwantskap tussen mikroartropood spesies rykheid en volopheid en plantgrootte, isolasie, binne-plant variasie, gras bedekking en mikroklimaat faktore is ondersoek. Daarna is die ruimtelike variasie van mikroartropood volopheid binne in 'n plantstand ondersoek deur gebruik te maak van metodes wat verskillende grade van ligging data gebruik. Dit is gedoen om uit te vind of mikroartropood volopheid lukraak, reëlmatig of versameld verspreid is. Verder is die ruimtelike verspreiding van mikroartropood gemeenskappe in *A. selago* op verskillende hoogtes bo seespieël en op verskillende kante van Marion Eiland ondersoek. Laastens is die mikroartropood gemeenskap op Marion Eiland en Prins Edward Eiland, asook die gemeenskap in verskillende plant spesies vergelyk. Mikroartropoda is ruimtelik heterogeen verspreid binne-in *A. selago* (meer individue in die oostelike en suidelike kante van plante), asook regoor Marion Eiland (minder springstert individue aan die ooste kant van die eiland asook minder op hoë hoogtes bo seespieël) en tussen eilande

(meer indringerspesies op Marion Eiland). In teenstelling hiermee is mikroartropood volopheid ruimtelik homogeen oor 'n plantstand, dus meestal lukraak verspreid. Die meganismes wat moontlik vir hierdie patrone verantwoordelik is wissel van temperatuur en voedselbeskikbaarheid op die binne-plant en oor die eiland skaal tot indringerspesies op die tussen-eiland skaal. Klimaatsverandering mag waarskynlik mikroartropood verspreidingspatrone direk (ongunstige klimaat vir inheemse spesies se groei, ontwikkeling en verspreiding), of indirek verander (indringer spesies word begunstig; toename in grasbedekking bo-op *A. selago* mag die gemeenskapstruktuur van mikroartropoda verander). Hierdie inligting is belangrik vir die voorspelling van die moontlike impak van klimaatsverandering op mikroartropoda in klipveld ekosisteme op sub-Antarktiese eilande.

It is not so very important for a person to learn facts. For that he does not really need a college. He can learn them from books. The value of an education in a liberal arts college is not the learning of many facts, but the training of the mind to think, something that cannot be learned from textbooks.

- Albert Einstein, 1921, on Thomas Edison's opinion that a college education is useless; quoted in Einstein: His Life and Times by P. Frank

ACKNOWLEDGEMENTS

The work presented here, represent four years of my life in which I not only grew intellectually, but also gained experience, have been to places and made friends, which I never could have done otherwise. Therefore, I am grateful and indebted to many people and organizations.

I thank my supervisor, Prof. Melodie McGeoch, for her patience, motivation and support during my time on Marion Island and in Stellenbosch. She taught me to work hard but most of all to question and to think about everything. I also thank my co-supervisor, Prof. Steven Chown, for invaluable advice academically and personally. I thank Dr Mick Marshall and Dr Penny Greenslade for all taxonomic assistance.

A special thanks to my parents, sister and family for encouragement and support. I am grateful to the Marion 58 team, for making the year on Marion Island an unforgettable experience. Wilna Wilkinson, Mawhethu Nyakatya and Beneke de Wet for carrying heavy samples and equipment and help with fieldwork, sometimes in adverse weather conditions. Many thanks also to all my friends in Stellenbosch, laughing with me in good times and giving a supporting shoulder through rough times especially Erika Nortje, Sarette Slabber, Peter Le Roux, Cang Hui and Monean Heynes. I also thank my colleagues and friends for valuable discussion, help with analyses and comments on manuscripts, especially Ruan and Antoinette Veldtman and Peter Le Roux.

This research was conducted as part of the Biocomplexity and Change project, under the auspices of the South African National Antarctic Programme (SANAP) of the Department of Environmental Affairs and Tourism (DEAT). I thank DEAT for logistic support and the National Research Foundation and University of Stellenbosch for financial support.

Finally I want to thank the Lord, without nothing is possible, for "...in Him we live and move and exist..." Acts 17:28

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GENERAL INTRODUCTION

“It is argued that the problem of pattern and scale is the central problem in ecology, unifying population biology and ecosystem science, and marrying basic and applied ecology.” Levin 1992

“Although these patterns are increasingly well documented, understanding why they exist constitutes one of the most significant intellectual challenges to ecologists and biogeographers.” Gaston 2000

The spatial distribution of animals and plants at different scales is a central theme in ecology (Cornell and Lawton 1992; Levin 1992; Lawton 1999; Schneider 2001; Krawchuk and Taylor 2003). Indeed, it has been stated that multiscale approaches in ecological studies need to become a primary focus of research since spatial patterns of species abundances and responsible mechanisms vary across scales of observation (Wiens 1989; Hurlbert 1990; Gaston 2000; McGeoch and Gaston 2002; Krawchuk and Taylor 2003; Fischer et al. 2004). Dominant ecological processes change across scale (i.e. local, regional or global), with the consequence that different sets of processes account for spatial variation of organisms at different scales (McGeoch 1995; Benedetti-Cecchi 2001; Anderson et al. 2004; Fischer et al. 2004). Knowledge of patterns and processes in animal and plant communities from fine to broad scales will contribute to improved explanation and prediction in ecology (Levin 1992; Gardner 1998; Benedetti-Cecchi 2001; Harte et al. 2005), encourage sufficient sampling designs and contribute in conservation planning and management processes (Gardner 1998; Thomas et al. 2001).

An important basis for understanding community variation across scales is knowledge of the spatial distribution of species ranges, abundances and biomasses at a specific scale of observation (Underwood and Chapman 1996). Insect and soil arthropod populations rarely show random spatial distributions (Brown et al. 1995; Ettema and Wardle 2002). The non-random spatial distributions of species abundances are a result of the interaction of several factors, including environmental conditions (microclimate, weather, the availability, quality and distribution of nutrients and habitat), biotic processes (predation, competition, dispersal, attraction or repulsion by conspecifics, attraction to olfactory cues, physiological tolerances, life

history), disturbance, disease, topography, history of habitat and stochastic temporal variation (Ricklefs 1987; Cornell and Lawton 1992; Ricklefs and Schluter 1993; Speight et al. 1998; Thomas et al. 2001; Perry et al. 2002; McGeoch and Price 2004; Paris 2004). Typically, evolutionary and biogeographical history dominates in determining spatial patterns at the regional scale, while biotic interactions (e.g. competition) determine local scale distribution patterns of species (Noda 2004). However, larger scale processes such as climate, long distance dispersal and metapopulation patch dynamics may also influence distribution patterns of communities at local scales (Cornell and Lawton 1992; Ricklefs and Schluter 1993; Chown et al. 2002; Sandin and Johnson 2004).

Current human-induced environmental changes, such as climate changes and the introduction of exotic species, are an additional, important factor determining the current distributions of species in most parts of the world (Gaston 2000; Frenot et al. 2005). For example, climate change is altering species distribution patterns (Walther et al. 2002; Parmesan and Yohe 2003; Root et al. 2003), often with idiosyncratic responses of species to altered temperature or precipitation (Root et al. 2003; Thomas et al. 2004, McGeoch et al. in press). In general, particularly in the northern hemisphere, where species ranges are shifting, they are moving poleward (Parmesan et al. 1999; Walther et al. 2002; Parmesan and Yohe 2003) or to higher elevations (Fielding et al. 1999; Parmesan and Yohe 2003). It has been stated that species at high latitudes might be able to endure the direct effects of climate change, but indirect effects such as interactions with exotic species (which are favoured by climate change) may dominate species responses to climate change (Callaghan et al. 2004; Frenot et al. 2005). The introduction of exotic animal and plant species changes the abundance and distribution of indigenous species, resulting in the disruption of community structure and local species extinction (Dennis and Shreeve 1991; Pitelka 1994; Williamson 1996; Root et al. 2003; Thomas et al. 2004; but see Gurevitch and Padilla 2004). Thus, an understanding of the current regional and local distribution patterns of species (Heaney 2001; Walther et al. 2002; Sanders et al. 2003) is important to predict the likely impacts of climate change and exotic species on future patterns (Peterson et al. 2002; Thomas et al. 2004). In fact, the monitoring of communities to determine the impact of anthropogenic environmental changes is considered a priority in ecological research (Kingsolver et al. 1993).

Southern Ocean islands are ideal for examining the effects of climate change and exotic species on the spatial variability of biota (Smith and Steenkamp 1990; Smith 2002; see also Vitousek 2002). Ecosystems on sub-Antarctic islands are remote, relatively closed systems with an abiotically harsh environment and with relatively low species richness (Smith and Steenkamp, 1990). The species on these islands have evolved under cool humid conditions largely in the absence of competitors and are therefore often particularly sensitive to climate change (warming and drying) and to competition with exotic species (Smith and Steenkamp, 1990). In fact, it is predicted that climate change and the introduction and establishment of exotic species will both have a major impact on the natural distribution patterns of the indigenous biota on these islands (Smith and Steenkamp 1990; Davies and Melbourne 1999; Smith et al. 2001; Frenot et al. 2005). Information on the current spatial distributions of biota and the drivers of these patterns on sub-Antarctic islands is thus critical to predict the consequences of climate change and exotic species on the future distribution and abundance of indigenous biota on these islands.

Sub-Antarctic Marion Island, which lies about 1770 km south of South Africa in the Southern Ocean (Fig.1) (Hänel and Chown 1999), has experienced rapid climate changes over the past 50 years. Mean annual air temperature has increased with more than 1.2 °C and mean annual precipitation has decreased with more than 500 mm (Smith 2002). Additionally, a number of exotic plant, vertebrate and invertebrate species have been introduced to Marion Island (Chown et al. 2002; Frenot et al. 2005). In this study, the possible effects of climate change and exotic species on the microarthropod community inhabiting the cushion plant *Azorella selago* Hook, were examined.

Mite and springtail (for convenience collectively called microarthropods) distribution and abundance are limited by factors such as temperature and moisture (Ferguson and Joly 2002). Springtails have varying degrees of tolerance to dehydration (respiration actually occurs across the cuticle and not through a tracheal system, Hopkin 1997; Hertzberg and Leinaas 1998; Convey 2001). Although, springtails have evolved behavioral and physiological ways to reduce the rate of water loss, as evident from their occurrences in deserts and polar regions, they have to periodically return to available water to rehydrate, unless they are in a desiccation-resistant phase (Hopkin 1997; Convey et al. 2003). Mites, on the other hand, are more limited by temperature than by moisture (Convey et al. 2003). It has also been found

on Marion Island that exotic springtail species were more abundant in warm moist vegetated sites, compared to indigenous species, which had higher abundances in cold drier fellfield sites (Gabriel et al. 2001). Therefore, increasing temperature and decreasing rainfall can have both a direct (responses related to insect physiology, tolerance, behaviour) and indirect (favouring exotic species) effect resulting in altered spatial distribution of microarthropods (Gonzalez and Descamps-Julien 2004) and new communities with different species compositions (Callaghan et al. 2004). Since mite and springtail communities seem to be very sensitive to climate change, they are ideal to use in climate change studies.

The objective of this research was to investigate spatial patterns in microarthropod distributions in the keystone plant species, *Azorella selago*, at multiple scales on Marion Island, i.e., within-plant, within stand, island-wide and across islands. Information presented in this study provides insight into the scale at which the influence of climate change and exotic species on the distribution patterns of the indigenous community will be the most pronounced.

Study system

The Prince Edward Islands

The Prince Edward Islands lie about 1770 km south of South Africa in the Southern Ocean (Fig. 1) (Hänel and Chown 1999). Marion Island (46°54'S; 37°45'E) (Fig. 2a) covers approximately 290 km² and rises to 1230 m above sea level, while the smaller Prince Edward Island (46°38'S; 37°57'E) (Fig 2b), 19 km to the northeast, is about one seventh the size and reaches 650 m above sea level (Hänel and Chown 1999). Marion Island is the older of the two islands and was extensively glaciated at the end of the Pleistocene and during the early Holocene with some remnants still evident (Scott 1985; Hänel and Chown 1999; KI Meiklejohn personal communication).

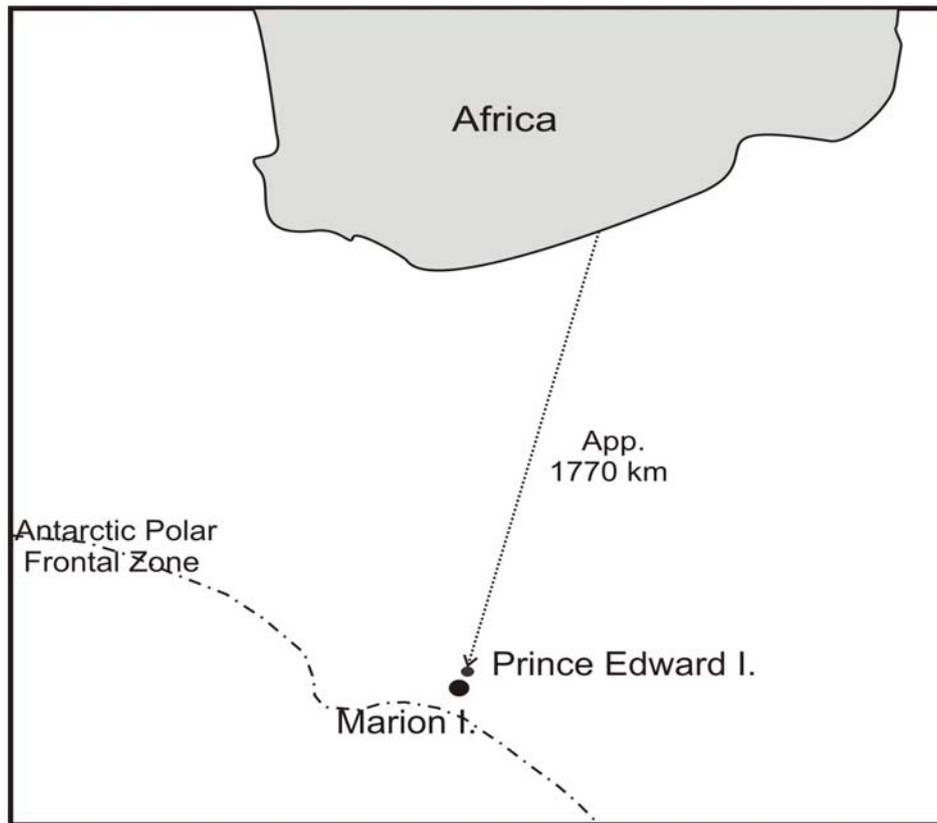
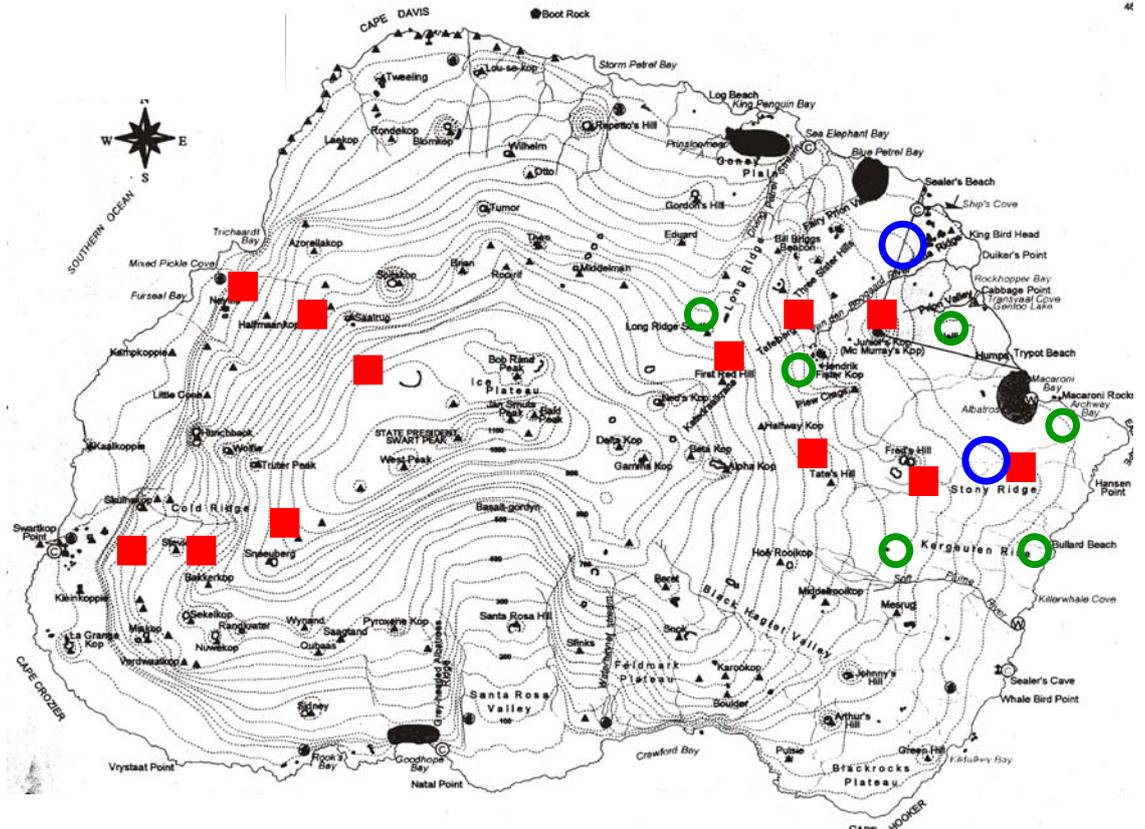


Fig. 1. Location of Marion Island and Prince Edward Island (redrawn from Hänel and Chown 1999)

a)



b)

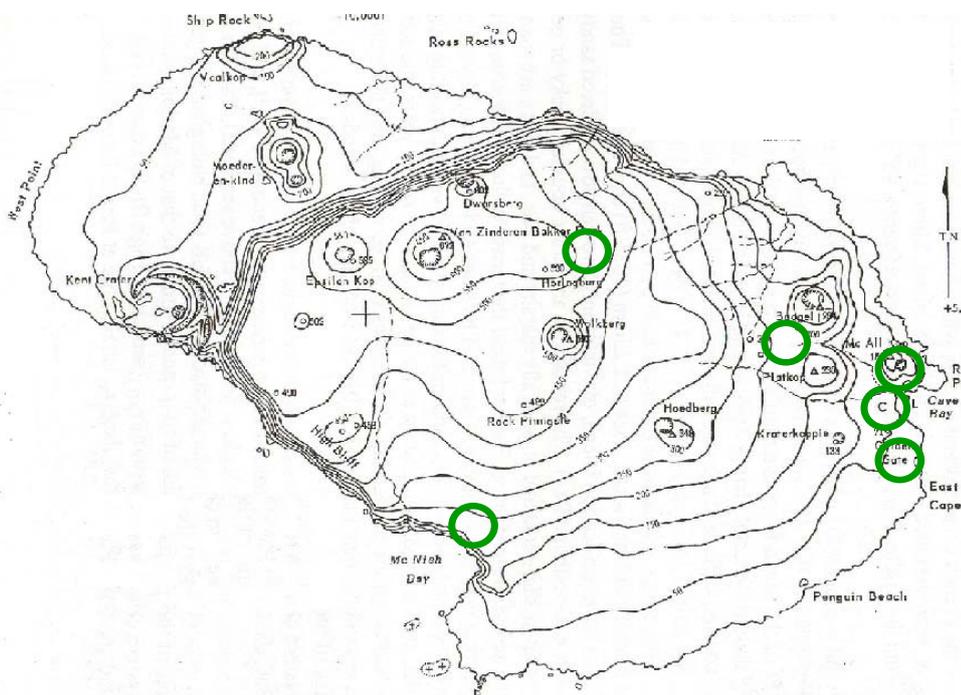


Fig. 2. Study sites on a) Marion Island and b) Prince Edward Island. Sample areas used for analyses in the different chapters are indicated as blue circles (Chapter 2), red squares (Chapter 3 and 4) and green circles (Chapter 5) (Scale: Marion Island: 6 mm = 1000 m; Prince Edward Island: 15 mm = 1000 m) (maps from Hänel and Chown 1999).

The climate on Marion Island is oceanic, with mean annual temperature of 5.7 °C, mean annual rainfall 1900 mm and a high degree of cloudiness (Hänel and Chown 1999; Smith 2002). Mean air, soil and within plant temperatures decrease with an increase in altitude (Blake 1996; Boelhouwers 2003; Nyakatya et al. unpublished). The air temperature lapse rate is approximately 4 °C every 1000 m (Klok and Chown 2003). Wind speed is highest at high altitudes and rainfall peaks at mid-altitudes (Blake 1996). Freeze-thaw events are more frequent at mid-altitudes, but at high altitudes these events occur for longer periods with deeper soil freezing (Boelhouwers 2003). Additionally, the western side of the island is thought to be colder than the eastern side (Schulze 1971; Gremmen 1981) and also receives more rain and stronger more frequent wind due to its exposure to the dominant westerly winds (Schulze 1971; Gremmen 1981). Prince Edward Island's climate is thought to be broadly similar (weather data is not available), although it might have a milder local climate and experiences drier weather than Marion Island, due to different size, topography, elevation and the absence of permanent ice (Crafford and Scholtz 1987).

The biotas of the islands have probably originated by colonization from several sources and arrived via ocean currents (Coulson et al. 2002a; Hodkinson et al. 2004), mainly with the circumpolar current, on driftwood (Van Zinderen Bakker 1971) or kelp rafts (Smith 2002), but also via wind and airflows (Chown and Avenant 1992; Greenslade et al. 1999; Coulson et al. 2002b; Pugh 2003) and by animals, mainly birds (Falla 1960; Van Zinderen Bakker 1971; Lebedeva and Krivolutskij 2004). It has already been shown that some indigenous springtail species originally established at the southeastern side of Marion Island (Kildalkey Bay) (Marike Myburgh, personal communication), probably through active upwelling of the ocean on the leeward side of the island (Ansorge and Lutjeharms 2000) or windflow patterns (Chown and Avenant 1992). Furthermore the biota has been modified considerably by local speciation (Chown et al. 2002) resulting in a number of endemic species on the islands (e.g. 5% of Marion Island's plant species is endemic) (Hänel and Chown 1999). Additionally, a number of exotic animal and plant species has been introduced to Marion Island since the first humans arrived in the early 1800s (Deharveng 1981; Hänel and Chown 1999; Pugh 1994), e.g. it is thought that exotic springtail species have also been introduced at Kildalkey Bay by sealers in the early 1800s (Marike Myburgh, personal communication). Furthermore, a permanent occupied research station was established in 1948 with consequent more ship visits and higher risk of

introducing exotic species (Chown et al. 1998). Introduced and naturalized exotic species on Marion Island include 13 vascular plant species, one mammal species (house mouse) and 18 invertebrate species most of which occur in vegetated areas at low altitudes and in human impacted areas (Frenot et al. 2005). Prince Edward Island, on the other hand, has few naturalized exotic species (three vascular plant species and one invertebrate species; Frenot et al. 2005) and is now a Special Nature Reserve with a strict permitting system, limiting visits to four days once a year for six persons (Anon. 1996; Cooper et al. 2003) to reduce the risk of introductions.

The plant: *Azorella selago* Hook.

The landscape of Marion Island can be divided into the vegetated biotope (areas dominated by vascular vegetation) and epilithic biotope (fellfield, rock faces, rocky shores and polar desert areas) (Chown et al. 2002). Fellfield (Fig. 3) occupies approximately 46 % of the island surface, consisting of black (Fig. 3a) or grey (Fig. 3b) basalt and some vegetation including mainly mosses, lichens and *Azorella selago* (Fig. 4) (Huntley 1972; Gremmen 1981). Fellfield soil contains little organic matter or plant nutrients and has low water-retention capacity compared to other soils on the island (Gremmen 1981).

The cushion plant *Azorella selago* (Apiaceae, previously called Umbelliferae) (Fig. 4) is widespread in the sub-Antarctic - from southern South America across to Heard Island (Gremmen 1981). On Marion Island it occurs from sea level to 850 m a.s.l. (DW Hedding, personal communication). *Azorella selago* is one of only six species that contribute significantly to the island's standing crop and is considered a keystone species in the fellfield of Marion Island (Smith 1978). It is a long-lived (Le Roux and McGeoch 2004) pioneer plant species and occurs in varying sizes and densities in the fellfield soil (Huntley 1972; Frenot et al. 1993). Cushion growth forms reduce wind stress (due to the streamlined shape) and heat and moisture loss (due to the compact growth) (Ashton and Gill 1965, Huntley 1971), and therefore can *A. selago* survive in fellfield areas of Marion Island where climate conditions are harsh.

Azorella selago plants have a well-developed root system, which consists of a central taproot and extensive shallow horizontal roots and shorter sub-vertical roots (Frenot et al. 1993). Stems, on which the leaves are attached, arise from the central taproot (Frenot et al. 1993). The leaves are small, tough and lobed, with petioles that

form a sheath around the stem (Orchard 1989). The leaves are tightly packed and the stems grow close together so that the plant surface is hard and compact (Orchard 1989). Cushion growth stops in the austral autumn, retaining the old leaves, which form a rich humus like collection of organic matter inside the plant (Huntley 1971). The inside of cushion plants has higher humidity (Cavieres et al. 1998) and buffered temperatures (higher minimum and lower maximum temperatures) compared to the fellfield soil (Nyakatya et al. unpublished). Therefore, the cushion interior presents an ideal microenvironment for microarthropods and epiphytes and is considered to be 'islands' presenting more resources and favourable microclimate in the fellfield soil (Huntley 1972; Barendse and Chown 2001; Chown et al. 2002). Indeed microarthropods reach higher abundances in the cushions compared to the surrounding fellfield (Barendse and Chown 2001).

A wide variety of plant species grow epiphytically on *Azorella selago* (Gremmen 1981; Le Roux 2004). At least 16 vascular and 17 non-vascular species have been recorded growing on *A. selago* over its altitudinal range (Le Roux 2004). These epiphyte species are not obligatory epiphytes and grow independently from cushion plants at lower altitudes. The most common species that grows epiphytically on *A. selago* is the grass, *Agrostis magellanica* (Lam.) Vahl (Fig. 4), which occurs from sea level up to 500 m, peaking in abundance and cover in the middle of its altitudinal range, i.e. 200 to 300 m a.s.l. (Le Roux 2004). *Agrostis magellanica* modifies the microhabitat within a cushion by rooting within the cushion. *Agrostis magellanica* roots host more mycorrhizae hyphae than *A. selago* roots (Smith and Newton 1986) and therefore may present additional niches and food resources for microarthropods (Seastedt 1984).

a)



b)



Fig. 3. *Azorella selago* cushion plants growing in a) black and b) grey lava fellfield areas.



Fig. 4. *Azorella selago* cushion plant with the grass, *Agrostis magellanica*, growing epiphytically on it. The matchbox next to the plant gives an indication of plant size.

The microarthropod community

Because of the low abundance of herbivores on Marion Island, essentially all plant productivity becomes dead organic material and most of the energy and nutrient circulation occurs through the detritus system (Smith and Steenkamp 1990). Since mites and springtails are mainly detritivores, algivores or fungivores (Hopkin 1997), they play an essential role in decomposition and mineralization of plant material (Seastedt 1984). Predacious microarthropods in the microarthropod assemblage in *A. selago* are scarce with possibly only two predacious mite species, namely *Bdellodes* sp. and *Rhagidia* sp. (Krantz 1978). Sixteen springtails species and 69 mite species occur on Marion Island and of these 8 springtails and 22 mite species have been found in *A. selago* (Table 1) (Barendse and Chown 2001; Gabriel et al. 2001; Chown et al. 2002). Although there is uncertainty about the invasive status of some species (see species lists in Gabriel et al. 2001; Chown et al. 2002; Frenot et al. 2005), approximately ten alien microarthropod species have been recorded on Marion Island (following Chown et al. 2002) of which two occur in *A. selago* (Table 1) (Barendse and Chown 2001; Gabriel et al. 2001).

Studies on invertebrates on Prince Edward Island have been scarce and include species descriptions and occurrences (Crafford et al. 1986; Marshall et al. 1999; Marshall et al. 2003). Ecological studies involving invertebrates on Prince Edward Island include a study on the effect of mice predation on weevil assemblages and body sizes (Chown and Smith 1993) and a comparison of weevil assemblages and weevil and moth biomasses between Prince Edward Island and Marion Island (Crafford and Scholtz 1987; Chown 1992). Previous studies of microarthropods on Marion Island have compared species richness, abundance and biomass between habitat types (Barendse and Chown 2001; Gabriel et al. 2001), assessed habitat specificity for mites (Mercer et al. 2000; Barendse et al. 2002), determined body size distributions (Mercer et al. 2001), investigated seasonality (Barendse and Chown 2001) and studied the effect of experimental drying and warming (McGeoch et al. in press). The research reported in this thesis thus presents the first results of microarthropod species richness, abundance and community structure at multiple scales on the Prince Edward Islands. The scales of observation used here comprise within plant, between plants, island-wide and between Marion Island and Prince Edward Island, i.e., moving from fine to regional scale.

Table 1. Acari (mite) and Collembola (springtail) species found on Marion Island. Species found in *Azorella selago* are indicated with * and introduced and established exotic species are indicated with # (Barendse and Chown 2001; Gabriel et al. 2001; Chown et al. 2002).

ACARI

Mesostigmata

Rhodacaridae sp. *

Parasitiphis brunneus (Kramer)

Dendrolaelaps sp. *

Cillibidae sp. *#

Davacarus gresitti Hunter

Metastigmata

Ceratixodes uriae White

Ixodes pterodromae Arthur

Cryptostigmata

Oribatidae sp1 *

Liochthonius australis Covarrubias *

Liochthonius fimbriatissimus (Hammer)

Hermanniella sp.

Allodamaeus sp.

Macquarioppia striata (Wallwork) *

Austroppia crozetensis (Richters) *

Alaskozetes antarcticus (Michael)

<i>Ornithodoros capensis</i> Neumann	<i>Alaskozetes bouvetøyaensis</i> Van Pletzen and Kok
<u>Prostigmata</u>	<i>Halozetes belgicae</i> (Michael)
<i>Nanorchestes</i> sp. *	<i>Halozetes crozetensis</i> (Richters)
<i>Eupodes minutus</i> (Strandtmann) *	<i>Halozetes edwardensis</i> Van Pletzen and Kok
<i>Rhagidia</i> sp. *	<i>Halozetes fulvus</i> Engelbrecht *
<i>Peregrinacarus reticulatus</i> Bartsch #	<i>Halozetes marinus devilliersi</i> Engelbrecht
<i>Werthella tera</i> Bartsch	<i>Halozetes marionensis</i> Engelbrecht
<i>Halacarellus parilis</i> Bartsch	<i>Podocarus auberti</i> Grandjean *
<i>Halacarellus novus</i> (Lohmann)	<i>Dometorina marionensis</i> Van Pletzen and Kok*
<i>Halacarellus robustus</i> Lohmann	<i>Zygoribatula subantarctica</i> Van Pletzen and Kok
<i>Lohmannella gaussi</i> Lohman	<i>Totobates marionensis</i> Van Pletzen and Kok
<i>Isobactrus magnus</i> (Lohmann)	<i>Antarctozetes crozetensis</i> (Richters)
<i>Rhombognathus auster</i> Bartsch	<i>Ceratozetes gausii</i> (Richters)
<i>Rhombognathus apsteini</i> Lohmann	<i>Magellozetes antarcticus</i> (Michael) *
<i>Rhombognathus gresitti</i> Newell	<i>Porokalumma rotunda</i> (Wallwork)
<i>Ereynetes macquariensis</i> Fain *	<u>Astigmata</u>
<i>Tydeus (Pertydeus)</i> sp. *	<i>Schwiebea talpa subantarctica</i> Fain *
<i>Bdellodes</i> sp. *	<i>Algophagus</i> sp. *
<i>Disparipes antarcticus</i> Richters #	<i>Algophagus antarcticus antarcticus</i> Hughes
<i>Neopygmephorus</i> sp. #	<i>Algophagus antarcticus laticollaris</i> Fain
<i>Eryngiopus</i> sp. *	<i>Algophagus semicollaris</i> Fain
<i>Balaustium</i> sp. *	<i>Hyadesia halophila</i> Fain
<i>Pygmephoridae</i> sp.*	<i>Hyadesia kerguelenensis</i> Lohmann
	<i>Hyadesia subantarctica</i> Fain
	<i>Neohyadesia microtrichia</i> Marshall, O'Connor and Pugh
	<i>Neocalvolia travei</i> Fain
	<i>Neocalvolia</i> sp.
	<i>Austranoetus kerguelenensis</i> Fain
	<i>Glycyphagus domesticus</i> (de Geer) #

COLLEMBOLAArthropleona*Friesea tilbrooki* Wise*Ceratophysella denticulata* (Bagnall) #*Hypogastrura viatica* (Tullberg) #*Tullbergia bisetosa* Börner **Folsomotoma marionensis* Déharveng **Isotoma notabilis* Schäffer #*Cryptopygus dubius* Déharveng **Cryptopygus antarcticus* Déharveng **Cryptopygus caecus* Wahlgren **Cryptopygus tricuspis* Enderlein*Isotomurus cf. palustris* Müller * #*Pogonognathellus flavescens* (Tullberg) #Symphyleona*Megalothorax* sp. **Katianna* sp.*Sminthurinus granulatus* Enderlein **Sminthurinus tuberculatus* Delamamare,
Deboutteville and Massoud *

Study sites, sampling, sample sizes and sampling representivity

Twelve plots consisting of 36 *Azorella selago* plants (cushions > 0.15 m) each were selected on three altitudinal levels in four different areas on Marion Island (red squares, Fig. 2a). For convenience the three plots, high, middle and low, in each area of the island are referred to as transects. Two transects were on the eastern side (First Red – Tafelberg – Juniors Kop = Tafelberg transect; Halfway Kop – Fred's Hill - Stony Ridge = Stony Ridge transect) and two were situated on the western side (Halfmaankop – Neville – between Neville and Mixed Pickle cove = Mixed Pickle transect; Sneekop – Stevie – Skuinskop = labelled Swartkops transect for convenience) of Marion Island (Fig. 2a). These transects were located in typical grey or black lava fellfield (grey lava = Tafelberg, Fred's Hill, Stony Ridge; black lava = First Red, Juniors Kop, Halfway Kop, Mixed Pickle transect and Swartkops transect). Plant material (and dead plant material) in black lava fellfield generally has a higher mineral content, especially higher calcium and nitrogen than plants growing in grey lava fellfield (Smith 1977). On the other hand, grey lava soil has a higher organic carbon content (Smith 1977). Black lava fellfield areas could not be found for all sites, since large areas on the eastern side are covered only in grey lava. It was

assumed that the difference in other factors, such as temperature and rainfall, were more important determinants of microarthropod distribution patterns between sites than the differences in mineral and organic contents of black and grey lava. The low altitude plots were between 150 and 250 m a.s.l., middle altitude plots between 350 and 450 m a.s.l. and the high altitude plots between 500 and 600 m a.s.l.. Additionally, one plot on Skua Ridge and one on Stony Ridge (both grey lava sites) between 100 and 200 m a.s.l. were established where 60 plants at Skua Ridge and 80 plants at Stony Ridge were randomly chosen in an area of 100 x 100 m (blue circles, Fig. 1a). Microarthropods were also collected in different plant species on the southeastern side of Marion Island and at various locations on Prince Edward Island (green circles, Fig. 2a and b).

Sampling was mostly done using an O'Connor split corer (inside diameter of core = 70 mm, height = 70 mm, surface area = 0.0039 m²). Although the coring method is the usual and most effective method to sample microarthropods on Marion Island, it damages a part of the plant. It was observed that cored plants recovered from this damage after approximately three years. However, at low altitudes (especially at Skua Ridge) mice burrowed into these damaged areas. This burrowing could result in the dieback of the plant. Reassessment of the coring method at low altitudes is therefore needed. The time from sampling to extraction of microarthropods at Marion Island base station differ (transit times of samples from Tafelberg and Stony Ridge < 12 hours, transit times from Mixed Pickle and Swartkops between 12 and 24 hours), but care was taken to keep samples at field temperature to prevent microarthropods from reproducing or dying due to warmer temperatures in bags. Indeed, the patterns observed in this study are unlikely to be an artefact of the transporting of the samples, since one would expect either fewer individuals or more juveniles from samples with longer transit times. However, this was not the case (more individuals and fewer juveniles, Chapter 3) and therefore the patterns observed are a true indication of microarthropod abundances across the island. The microarthropods (mites and springtails) were extracted from the cores using a MacFadyen high-gradient extraction protocol of two days at 25 °C and two days at 30 °C (Southwood 1980; Barendse and Chown 2001; Barendse et al. 2002; Hugo et al. 2004). Although the efficacy of high gradient extraction has been debated (Andre et al. 2002), any error is likely to be consistent across samples. Furthermore, extraction efficiency varies with species and substratum type, and comparisons between similar habitats and species will thus be

reliable. Microarthropod specimens were identified to the lowest possible taxonomic level (usually species), counted and stored in 99 % ethanol at the University of Stellenbosch.

An important aspect in ecological studies is to obtain adequate representative samples to compare species richness or community structure between sites (Cao et al. 2002; Magurran 2004). This study is conducted on Marion Island, which is relatively species poor (total mite species = 69, total springtail species = 16) and some species reveal habitat specificity (Barendse et al. 2002). For example, the mite species *Halacarellus* is restricted to littoral habitats (Barendse et al. 2002) and the springtail *Pogonognathellus flavescens* only occurs in *Poa cookii* (Gabriel et al. 2001). Therefore only a small proportion of the known species on Marion Island do occur in *Azorella selago*. Therefore, a descriptive method, rather than species accumulation curves, is appropriate to estimate sampling representivity. Until now, only two studies have examined microarthropod species richness in *Azorella selago* plants. Barendse and Chown (2001) found 33 % of all known microarthropod species on Marion Island in *A. selago* (480 samples), where springtails represented 50 % of total springtail species and mites 29 % of total mite species. Gabriel et al. (2001) also found 50 % of springtails known on the island in *A. selago* plants (240 samples). Similar observations were found in this study. Springtails represented 56 % of total springtails species and the mites 32 % of total mite species on Marion Island (431 samples). Microarthropod species represented 37 % of total species on Marion Island. Therefore, species richness inside plants stayed relatively constant between studies, demonstrating that the sampling here was representative of species found in *A. selago* plants.

Thesis outline

The objective of this research was to investigate spatial patterns of microarthropod (mite and springtail) abundance, species richness and community structure in the keystone plant species, *Azorella selago* on the Prince Edward Islands, Marion Island in particular. A multiscale approach (within-plant, between plants, island-wide and between islands) to the investigation of these patterns was adopted. Additionally, because species often respond idiosyncratically to environmental factors such as plant characteristics and microclimate (Krawchuk and Taylor 2003; McGeoch et al. in press), patterns of individual species were also investigated.

Each chapter is presented as a research paper and consequently some of the methods and references overlap. The first chapter deals with the microarthropod community at a fine scale, i.e. within plants. The relationship between species richness and abundance of microarthropods and plant size, isolation, within-plant variability, epiphyte (*Agrostis magellanica*) load and microclimate variables are investigated. The second chapter examines the spatial distribution of microarthropods at a local scale (i.e. within stands of plants). Spatial variability is investigated using spatially non-explicit, semi-explicit and explicit methods to determine if microarthropod abundance and species richness have random, regular or aggregated distributions at this scale. This chapter also highlights the importance of using more than one statistical method to investigate spatial heterogeneity in communities. Chapter three deals with the distribution of microarthropods in plants at an island-wide scale. The spatial variability of microarthropod communities in *Azorella selago* along an altitudinal gradient (different temperatures) and on different sides of Marion Island (different moisture regime) is examined. The temperature gradient and difference of moisture regime can be seen as an approximate analogue for future climates, making predictions of future species distributions possible. Chapter 4 presents an extensive list of microarthropod species on Prince Edward Island. Microarthropod species richness, abundance and community structure are compared between Prince Edward Island and Marion Island and between four major habitat types (and associated plants), namely mire (*Sanionia uncinata*, *Jamesoniella colorata*, *Blepharidophyllum densifolium*), slope (*Acaena magellanica*, *Blechnum pennamarina*), biotically influenced (*Cotula plumosa*, *Crassula moschata*, *Poa cookii*) and fellfield habitat (*Azorella selago*, fellfield soil). The effect of exotic species on microarthropod community structure is also considered in this chapter. Finally, in the general synthesis, the patterns and processes at the four different spatial scales in this study are summarized and the importance of multiple scale studies highlighted. The possible impacts of climate change and alien species on microarthropod distribution patterns on Marion Island and Prince Edward Island are also discussed.

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CHAPTER 1

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

(Published: Hugo et al. 2004. *Polar Biology* 27:466-473)

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 1992 a, 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 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 (Bergström 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 *A. 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 *A. 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 *A. 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, *A. magellanica*, and (4) whether any of these patterns are related to temperature in the cushion and cushion moisture content. These latter 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 center 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 100-120 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, 10 cushions were sampled with, and 10 without any *A. magellanica* on Stony Ridge (there were no cushions without grasses on Skua Ridge). Smaller

cushions were selected (20-40 cm size class) because cushions larger than this generally supported at least some *A. magellanica* individuals. All cores at a site were taken within four days of each other and the period between sampling the two sites was ten days.

Mites and springtails were extracted from the cushion cores using a MacFadyen high-gradient extraction protocol of two days at 25 °C followed by two 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 specimens 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, U.S.A., diameter = 1.5cm) were inserted between stems in the top 1.0 cm of cushions and were set to record temperature every five minutes for four successive days per site. Data loggers were calibrated against temperatures recorded in a water bath (LTD 20 Grant Instruments, Cambridge, U.K.) programmed to hold each of five successive temperatures for two hours. The loggers were always within ± 0.2 °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 data logger inserted into the center of each cushion. To determine temperatures on different cushion sides, data loggers were inserted in the N, E, S and W quadrants of ten randomly selected cushions in the 100-120 cm size class at both sites. The effect of *Agrostis magellanica* on cushion temperature was determined by inserting one data logger 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 Houseman 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 difference in temperature between areas with and without the epiphytic *A. magellanica* were analyzed using ANOVA with position (in and out of grass area) and cushion (5 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 data loggers 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 analyzed with ANOVA (and Tukey's honest significant difference).

Stevenson screen dry-bulb temperatures, humidity, wind direction, wind speed and pressure measurements, recorded every five minutes, 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 1998-2002 were used to determine prevailing wind direction over a longer time period. Mean (\pm s.e.) 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 these models described below, 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 10 cushions with this epiphyte and 10 without. In (a) the maximum diameter of cushions was added to the models because cushion diameter and number of *A. 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 above.

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). 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 1.1 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 1.1 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). 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 center, 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 1.2 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 five-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.

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)

	d.f.	Deviance/d.f.	Explanatory variable/factor	d.f.	χ^2	<i>P</i>
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 \pm standard error) (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. Different letters (superscript) indicate a significant difference of $P < 0.05$ (see Table 1)

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

Table 3. Temperature (°C) (mean ± standard error) 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. Different letters (superscript) indicate a significant difference between means of $P < 0.001$. (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>A. magellanica</i>		$F_{1,934} = 2.50, P = 0.11$
With		7.26 ± 0.14
Without		6.93 ± 0.16

Table 4. Stevenson screen temperature (SST), humidity and wind speed (mean ± standard error) when wind is blowing from different directions

Wind direction	Number of observations	Temperature °C (SST) ± SE	Humidity (%) ± SE	Wind speed (m/s) ± SE
North	365	5.72 ± 0.07	89.70 ± 0.45	3.24 ± 0.07
East	317	6.23 ± 0.12	90.82 ± 0.55	3.86 ± 0.11
South	345	4.80 ± 0.09	76.91 ± 0.48	7.42 ± 0.31
West	1205	7.17 ± 0.05	85.12 ± 0.33	20.89 ± 1.02

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 1.3a). Species richness was not related to *A. magellanica* numbers at either of

the sites (Table 1.3a). The comparison of cushions with and without *A. magellanica* yielded similar results in that species richness was not affected by the presence of *A. magellanica*, yet abundance was significantly greater where the grass was present (Tables 1.3b and 2). Moreover, community structure differed significantly between cushions with and without *A. magellanica* (Global R = 0.51, $P < 0.001$, Fig. 1).

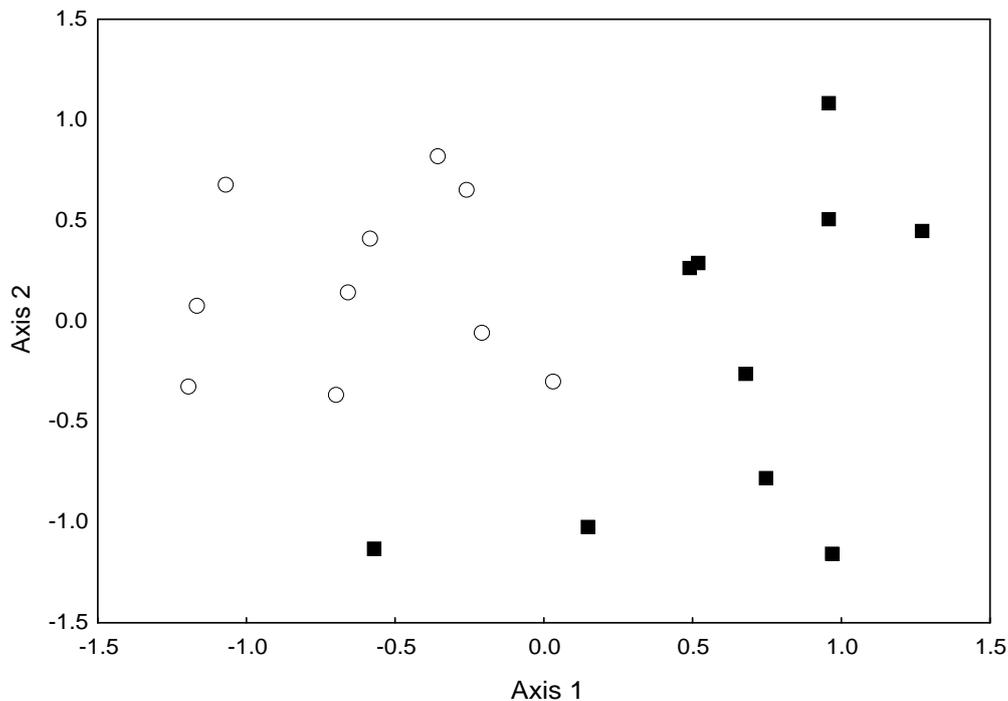


Fig. 1. Non metric multi-dimensional scaling (MDS) ordination of the abundance of microarthropods in cushions with and without the epiphytic grass, *Agrostis magellanica* (○ = with, ■ = without). (Global R = 0.51; $P < 0.001$; Stress = 0.21).

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 *A. 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 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 the cushions and between the cushions and the surrounding matrix, although this has yet to be verified on individuals. 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 c. 13 – 14 °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 *A. magellanica* suggests that variation between cushions is not merely a consequence 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 *A. magellanica* can be readily explained. *Agrostis magellanica* roots have more mycorrhizae than those of

A. selago (Smith & Newton 1986). Thus, cushions with *A. 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 *A. 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 *A. 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 to 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. North-westerly 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 reflected in the cushion temperature data. Moreover, north-western 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 north-western 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 *A. selago*, and deserve further exploration.

In conclusion, this study has demonstrated significant within-plant variation in microarthropod abundance that is both 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 (Bergström 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.

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Appendix. Acari (mites) and Collembola (springtails) species collected in *Azorella selago* cushions on Skua Ridge and Stony Ridge (# introduced species; Pugh 1994; Gabriel et al. 2001).

Acari	Collembola
Acari sp.3	<u>Suborder: Arthropleona</u>
<u>Suborder: Mesostigmata</u>	<i>Tullbergia bisetosa</i> Börner
Rhodacaridae sp.	<i>Folsomotoma marionensis</i> Déharveng
<i>Dendrolaelaps</i> sp.	<i>Cryptopygus dubius</i> Déharveng
Cillibidae sp.#	<i>Cryptopygus antarcticus travei</i> Déharveng
<u>Suborder: Prostigmata</u>	<i>Cryptopygus caecus</i> Wahlgren
Prostigmata sp.1	<i>Isotomurus cf. palustris</i> (Müller)#
<i>Nanorchestes</i> sp.	<u>Suborder: Symphypleona</u>
<i>Eupodes minutus</i> (Strandtmann)	<i>Megalothorax</i> sp.#
Rhagidia sp.	<i>Sminthurinus tuberculatus</i> Delamare et al.
<i>Ereynetes macquariensis</i> Fain	<i>Sminthurinus granulatus</i> Enderlein
<i>Tydeus</i> sp.	
<i>Bdellodes</i> sp.	
<u>Suborder: Cryptostigmata</u>	
Oribatidae sp.1	
<i>Liochthonius australis</i> Covarrubias	
<i>Maquarioppia striata</i> (Wallwork)	
<i>Austroppia crozetensis</i> (Richters)	
<i>Halozetes fulvus</i> Engelbrecht	
<i>Domatorina marionensis</i> van Pletzen & Kok	
<u>Suborder: Astigmata</u>	
<i>Schwiebea talpa subantarctica</i> Fain	
<i>Algophagus</i> sp.	

CHAPTER 2

Aggregation patterns in the microarthropods associated with *Azorella selago* (Apiaceae) on Marion Island

Introduction

The spatial distribution of species is a fundamental ecological property (Taylor 1984; Lam et al. 2002). Individuals rarely show random spatial distributions, but are generally unevenly spread across locations, and are most often aggregated (Legendre and Fortin 1989; Brown et al. 1995; Speight et al. 1998; Ettema and Wardle 2002; Kendal 2002; Perry et al. 2002). Furthermore, this spatial heterogeneity (sensu Wiens 2000) in the distribution of individuals is scale dependent (Cornell and Lawton 1992; Levin 1992; Lawton 1999; Schneider 2001; Ettema and Wardle 2002; Krawchuk and Taylor 2003), i.e. dependent on the scale of observation or grain of the study (Dungan et al. 2002; McGeoch and Gaston 2002). Scale dependence in ecological pattern is commonly a result of scale-specific ecological processes, such as fine scale movement patterns of individuals and strong, broad-scale environmental gradients (Levin 1992; O'Neill and King 1998; Krawchuk and Taylor 2003). Patterns observed at particular spatial scales may thus be used to infer particular mechanisms, such as environmental heterogeneity (i.e., climate, resource distribution) or intrinsic species characteristics (i.e., dispersal, behaviour) (Taylor 1984; Wiens 2000; Thomas et al. 2001; Ettema and Wardle 2002; Ims et al. 2004; McGeoch and Price 2004).

The spatial heterogeneity of arthropods has long been documented across a wide array of scales (Taylor 1984; Gaston and Lawton 1988; Kendal 2002). At both fine and local scales, studies include both single arthropod species as well as guild and community distributions. For example, Lam et al. (2002) showed that overwintering leaf beetles were aggregated across plants in soybean fields and woodland habitat; Maudsley et al. (2002) showed that predatory arthropods were aggregated at particular heights in English hedgerows, and Giller and Doube (1994) found significant intraspecific aggregation of dungbeetles across dung pads in a subtropic pasture. One group of arthropods for which heterogeneity has been extensively studied is the microarthropods, i.e. mites (Acari) and springtails (Collembola). Their distribution patterns have been examined in agricultural environments (Athanasassiou et al. 2003; Kanal 2004), in forests (Usher 1969; Burgess et al. 1999) as well as in Arctic

(Hertzberg 1997; Hertzberg et al 2000; Coulson et al. 2003; Callaghan et al. 2004; Ims et al. 2004) and Antarctic habitats (Usher and Booth 1984; 1986; Sinclair 2001). Microarthropods in Arctic tussocks and in Antarctic moss turves showed highly aggregated distributions both within and across turves (Usher and Booth 1984, 1986; Hertzberg et al. 2000; Ims et al 2004). Aggregation in mites and springtails is generally attributed to life history characteristics, mobility and micro-scale variation in habitat quality, as well as aggregation pheromones and stochastic, historical events causing mortality (Hertzberg et al. 2000; Ims et al. 2004). Regardless of the mechanism involved, studies to date thus suggest that intraspecific aggregation is pervasive, in both microarthropods and other taxa.

However, the large majority of microarthropod aggregation studies have adopted spatially implicit (*sensu* Wiens 2000) approaches to quantifying this heterogeneity, such as the variance-mean ratio (Greig-Smith 1964), Morisita's index (Morisita 1962), Taylor's power law (Taylor 1961) and k of the negative binomial distribution (Pielou 1977). These measures are spatially implicit as they are statistical measures of the combined variation across sampling points, and neither include nor provide any information on the spatial pattern of heterogeneity. Rather, they represent properties of the frequency distribution of counts, and are thus referred to as measures of statistical variance heterogeneity (Perry et al. 2002; Veldtman 2004; Veldtman and McGeoch 2004). Spatially explicit measures (both fully and semi-explicit), on the other hand, explicitly incorporate the physical locality of sampling points, or x-y coordinates, when quantifying spatial heterogeneity. Spatially semi-explicit measures provide information on the distances over which spatial heterogeneity occurs, whereas fully spatially explicit measures also provide information on the position of spatial heterogeneity within the study area (Wiens 2000, Veldtman 2004). Examples of semi-explicit and explicit measures include spatial autocorrelation measures (spatially semi-explicit, Legendre and Legendre 1998; Veldtman 2004) and Spatial Analysis by Distance Indices (fully spatially explicit, Wiens 2000; Veldtman 2004).

Indeed, a spatially explicit approach to quantifying distribution patterns in ecology has been shown to be important (Perry 1995, Perry 1998a, 1998b; Veldtman 2004; Veldtman and McGeoch 2004). Veldtman and McGeoch (2004) showed, for example, that the outcomes and conclusions drawn on the basis of spatially implicit and explicit measures of aggregation and spatial density dependence differ in both form and significance (see also Veldtman 2004). In fact, it has been argued that more

than a single method is essential to describe the spatial distribution patterns of individuals and species (Hurlbert 1990; Dale et al. 2002; Liebhold and Gurevitch 2002; Perry et al. 2002; Veldtman and McGeoch 2004).

The aim of this study was therefore to investigate the spatial heterogeneity of microarthropod abundance on sub-Antarctic Marion Island, using three methods that incorporate increasing degrees of spatial information, i.e. spatially implicit, semi-explicit and explicit (sensu Veldtman 2004, Veldtman and McGeoch in prep.). Assemblage and intraspecific spatial heterogeneity patterns in the abundances of mites and springtails across stands of *Azorella selago* Hook (Apiaceae) plants on the island are examined. The microarthropods associated with *A. selago* are considered to move freely between them (Barendse and Chown 2001; Hugo et al. 2004, Chapter 1), and the scale of the study, i.e. distributions across plants within stands of plants, is thus considered appropriate (Kampichler 1990; Hertzberg 1997; Ims et al. 2004). Within-plant spatial heterogeneity in the distribution of microarthropods in this system has previously been examined (Hugo et al. 2004). Here, the results of the three approaches to quantifying spatial heterogeneity across stands of plants (i.e. spatially implicit, semi-explicit and explicit) are compared, and it is determined whether plant characteristics are able to explain any spatially non-random patterns in species abundance found.

Material and methods

Study sites and species

Marion Island (46°54'S; 37°45'E) lies about 1770 km south of South Africa, covers an area of 290 km² and rises to an altitude of 1230 m a.s.l. (Hänel and Chown 1999). The climate is oceanic, with mean annual temperature 5.7 °C, mean annual rainfall approximately 1900 mm, a high degree of cloudiness and strong westerly winds (Schulze 1971; Hänel and Chown 1999; Smith 2002). However, temperature, rainfall and cloudiness show considerable variation across Marion Island (Blake 1996; Schulze 1971, Nyakatya et al. in prep).

The cushion plant, *Azorella selago*, occurs across Marion Island from sea level to about 850 m a.s.l. (DW Hedding, personal communication). It is the dominant vascular plant in fellfield areas and grows in various shapes, sizes and plant densities (Gremmen 1981; Le Roux 2004). The temperatures inside *A. selago* plants are buffered in comparison with air temperature around the plant (Le Roux et al. 2005).

Additionally, plants retain old dead leaves, which form a rich, moist, humus like collection of organic matter inside the plant (Huntley 1971). *Azorella selago* plants are thus thought to provide a more favourable microclimate and source of nutrients for mites and springtails than the exposed epilithic biotope of fellfield soils in which the plant grows (Barendse and Chown 2001). Furthermore, *A. selago* hosts a variety of epiphyte species of which the grass, *Agrostis magellanica* (Lam.) Vahl., is dominant (Gremmen 1981; Le Roux 2004). *Agrostis magellanica* is found epiphytically on *A. selago* up to approximately 500 m a.s.l., reaching peak densities at c. 250 m a.s.l. (Le Roux 2004).

Twelve stands each consisting of 36 *Azorella selago* plants (plants > 0.15 m) were selected at three altitudes in four different ‘transects’ on Marion Island. Six stands were on the western side (Halfmaankop – Neville – between Neville and Mixed Pickle cove = labelled Mixed Pickle transect; Sneeuokop – Stevie – Skuinskop = labelled Swartkops transect for convenience) and six were on the eastern side (First Red – Tafelberg – Juniors Kop = Tafelberg transect; Halfway Kop – Fred’s Hill - Stony Ridge = Stony Ridge transect) of the island. (see General Introduction for maps and Chapter 3, Table 1 for locational information). The low altitude stands were between 150 and 250 m a.s.l, middle altitude stands between 350 and 450 m a.s.l and the high altitude stands between 500 and 600 m a.s.l.. Each *A. selago* plant was digitally photographed from above at a height of approximately 1 m. Image analysis (software: SigmaScan Pro 5.0, Illinois, USA) (Anonymous 1999) was used on these photographs to determine plant size (surface area = m²), percentage dead tissue (brown or black stem or leaf areas on the plant surface) and percentage of the plant surface covered by the epiphytic grass, *Agrostis magellanica* (Table 1). The relative position of each individual plant within a stand was determined using a Nikon Total Station DTM350 Theodolite (Nikon Corporation, Tokyo, Japan), with an accuracy of 10 mm in three dimensions (Anonymous, 2001).

Table 1. Microarthropod species richness (S) and abundance (N), plant size, % dead tissue in the plant and % grass (*Agrostis magellanica*) cover at three altitudes along four transects on Marion Island (n = 36, except Mixed Pickle high n = 35).

Stand	Mean S \pm SE	Total S	Mean N \pm SE	Total N	Plant size (m ²) \pm SE	Median % dead tissue (range)	Median % grass cover (range)
Tafelberg							
Low	13.94 \pm 0.27	23	204.19 \pm 9.45	7351	0.19 \pm 0.02	13.64 (42.94)	11.39 (23.70)
Middle	12.89 \pm 0.34	22	261.08 \pm 10.45	9399	0.89 \pm 0.15	3.62 (15.47)	7.22 (35.31)
High	12.89 \pm 0.33	24	224.36 \pm 12.82	8077	0.15 \pm 0.02	2.97 (29.95)	0
Stony Ridge							
Low	13.75 \pm 0.33	28	275.33 \pm 12.62	9912	0.30 \pm 0.04	3.04 (25.72)	13.63 (55.35)
Middle	9.67 \pm 0.35	23	172.19 \pm 14.38	6199	0.26 \pm 0.05	3.81 (26.05)	4.89 (13.43)
High	12.50 \pm 0.44	27	203.39 \pm 11.78	7322	0.24 \pm 0.05	2.43 (27.88)	0
Mixed Pickle							
Low	16.69 \pm 0.40	29	349.56 \pm 16.43	12584	0.21 \pm 0.27	4.08 (28.82)	7.55 (22.69)
Middle	18.39 \pm 0.36	30	316.83 \pm 10.87	11406	0.15 \pm 0.02	6.56 (44.63)	0 (11.42)
High	15.26 \pm 0.32	22	300.17 \pm 13.62	10506	0.16 \pm 0.02	6.00 (24.94)	0 (2.73)
Swartkops							
Low	16.17 \pm 0.33	29	322.92 \pm 11.09	11625	0.13 \pm 0.01	5.31 (19.12)	6.46 (26.93)
Middle	15.89 \pm 0.43	27	290.00 \pm 14.70	10440	0.14 \pm 0.02	6.09 (13.50)	0 (0.44)
High	14.53 \pm 9.00	27	285.86 \pm 15.47	10291	0.13 \pm 0.03	0.88 (14.14)	0 (1.65)

Sampling

Microarthropods were sampled between November 2002 and February 2003, coinciding with peak abundances observed during summer (Barendse and Chown 2001). Sampling was done using an O'Connor split corer (inside diameter of core = 70 mm, height = 70 mm, surface area = 0.0039 m²). Core samples were taken from all 36 plants in each stand (except in the Mixed Pickle high altitude stand where one plant was too small to sample). Although the time from sampling to extraction of microarthropods at the base station differed (transit times of samples from Tafelberg and Stony Ridge < 12 hours, transit times from Mixed Pickle and Swartkops between 12 and 24 hours), care was taken to keep samples at field temperature to prevent microarthropods from reproducing or dying due to warmer temperatures in bags. The microarthropods (mites and springtails) were extracted from the cores using a MacFadyen high-gradient extraction protocol of two days at 25 °C and two days at 30

°C (Southwood 1980; Barendse and Chown 2001; Barendse et al. 2002; Hugo et al. 2004). Although the efficacy of high gradient extraction has been debated (Andre et al. 2002), any error is likely to be consistent across samples. Microarthropod specimens were identified to the lowest possible taxonomic level (usually species), counted and stored in 99 % ethanol at the University of Stellenbosch.

Analysis

Spatial heterogeneity of mite and springtail abundance and individual species abundances were quantified using three different approaches, representing an increase in the degree of spatial information used (Veldtman 2004). These included measures of (i) statistical heterogeneity (implicit methods i.e., spatial positions of plants relative to each other are not considered), (ii) spatial abundance structure or spatial autocorrelation (semi-explicit) and (iii) spatial non-randomness (explicit) (Veldtman 2004). The results of the three methods regarding spatial heterogeneity in the data were quantitatively compared between stands.

i. Statistical heterogeneity

The variance-mean ratio and Morisita's index were used as implicit measures to describe the statistical heterogeneity of mite and springtail and individual species abundances in each stand. The variance-mean ratio (s^2/\bar{x}) represents a regular distribution if < 1 , Poisson (random) distribution if $= 1$ and aggregated distribution when > 1 (Hurlbert 1990; Dale et al. 2002). Although the variance-mean ratio is universal and has been used in numerous works, Hurlbert (1990) argued that it is not a good measure of departure from a Poisson distribution, since a variance-mean ratio of one could be one of a number of other distributions than the Poisson distribution (see also Pielou 1974 and Ducarme and Lebrun 2004). Nonetheless, we use the variance-mean ratio here for comparison with the other indices. Hurlbert (1990) suggested the Morisita's index as a superior alternative. The Morisita's index also uses variances and means, but the mathematical properties differ and consequently result in different outcomes. The Morisita's index is given as follows:

$$I_M = (X/X-1) (1/\bar{x}) (s^2/\bar{x} + \bar{x} - 1)$$

where X is total abundance (Morisita 1959, 1962; Dale et al. 2002). This index indicates a regular distribution of individuals across samples when $I_M < 1$; $I_M = 1$

represents a random distribution, and $I_M > 1$ an aggregated distribution (Morisita 1959). The test of significant departure from random for the variance-mean ratio is:

$$\chi^2 = (Q_s - 1) (s^2 / \bar{x})$$

where Q_s is the number of sample sites (Stiteler and Patil 1971; Hurlbert 1990). The disadvantage of Morisita's Index is the lack of an associated test of significance (Stiteler and Patil 1971). However, the significance test for the variance-mean ratio may also be used for the Morisita's index (Stiteler and Patil 1971). Therefore, for 36 plants (sample sites), a variance-mean ratio and Morisita's index value larger than 1.44 are significant larger than one at $P < 0.05$.

The variance-mean ratio and Morisita's index were also calculated for individual species abundances when the absolute abundance of the species was more than five. Rare species were designated as those species with an occupancy of less than 33 % in a stand (see: iii Spatial non-randomness below for rationale).

For comparison with the results of Usher and Booth (1984), Taylor's Power Law was used as a third implicit method in this study. Usher and Booth (1984) used Taylor's Power Law to determine the horizontal distribution patterns of mite and springtail abundances and individual species abundances in Antarctic moss turves. Taylor's power law assumes a relationship between the mean (\bar{x}) and variance (s^2) as follows:

$$s^2 = a \bar{x}^b$$

where a and b are population parameters (Taylor 1961). Parameter b is an index of distribution of abundances, where $b < 1$ represent a regular pattern, $b = 1$ a random pattern and $b > 1$ an aggregated distribution pattern (Taylor 1961; Elliot 1983; Usher and Booth 1984). The b parameters were calculated by simple linear regression of the natural logarithm of variance of abundances in stands against the natural logarithm of the mean density of abundances in a stand (Taylor 1961). The intercept of the regression equation is parameter a while the slope is parameter b . The goodness of fit for the linear model was evaluated by the coefficient of determination (R^2) (Quinn and Keough 2002). Student's t-test was used to determine if the slope (b) of regression lines were significantly different from one (Elliot 1983; Usher and Booth 1984). Taylor's Power Law was thus calculated for mite and springtail and individual species abundances across plants within stands, and the parameter b taken as the slope of the

line regressing mean abundance against its variance across the 12 stands of plants (i.e., $n = 12$).

ii. Spatial structure

The spatial dependence of mite and springtail and individual species abundances between plants was quantified using spatial autocorrelation analysis (SAAP version 4.3) (Wartenberg 1989). Moran's I and all-directional correlograms were used to identify scales of variation in abundance (Legendre and Fortin 1989; Legendre and Legendre 1998; Dale et al. 2002; McGeoch and Price 2004). Overall correlogram significance was determined by comparing each distance class to a Bonferroni corrected α -level (Legendre and Legendre 1998; Veldtman 2004).

Total springtail and mite abundance and individual species (common species, i.e., species with a minimum occupancy of 12 plants across each stand, see iii Spatial non-randomness for rationale) abundance data were analysed in two ways. First, analyses were conducted using an equal number of point pairs (pairs of plants i.e. pairs of localities) in each distance class in all stands (63 point pairs per distance class, Fig. 1a) (Underwood and Chapman 1996; Ducarme and Lebrun 2004). The optimal number of distance classes was determined using Sturge's rule (Legendre and Legendre 1998). The formula for Sturge's rule is given as follows:

$$\text{Number of classes} = 1 + 3.3 \log_{10}(m)$$

where m is the number of distances in one of the triangular matrices (Legendre and Legendre 1998). In this study $m = 630$, so that the number of distance classes = 10. This resulted in equal statistical power across all distance classes (Lloyd et al. 2005), but in a low plant density, which is not biologically meaningful (Appendix 1). Therefore, in order to obtain a larger plant density, a fixed distance was chosen to compare correlograms of the different stands (Appendix 1). The fixed distance was chosen as the largest distance in a distance class as analysed with the first method. The largest distance (3.2 m) in a distance class was observed for Tafelberg middle stand and was therefore chosen as the distance in the fixed distance method. The size and significance of Moran's I values in distance classes with sufficient point pairs ($> 1\%$, thus 6.3 point pairs of total point pairs) were then examined (Legendre and Legendre 1998). However, since the number of point pairs differs for each distance class between stands, different statistical power exists for each distance class in a stand (Appendix 1, Fig. 1b). Since it is likely that microarthropods are able to move

between plants (Hugo et al. 2004) and probably to the closest neighbouring plant, it is biologically meaningful to use a high plant density (i.e., more than 2 plants) in the first distance class. The fixed distance of 3.2 m, therefore, provided plant densities in the 1st class that were biological meaningful. The equal point pairs on the other hand, resulted in lower plant density per distance class, but with equal statistical power in distance classes in all stands. Comparison of the outcomes of these two methods provides insight into the scale of variation of microarthropods in cushion plants.

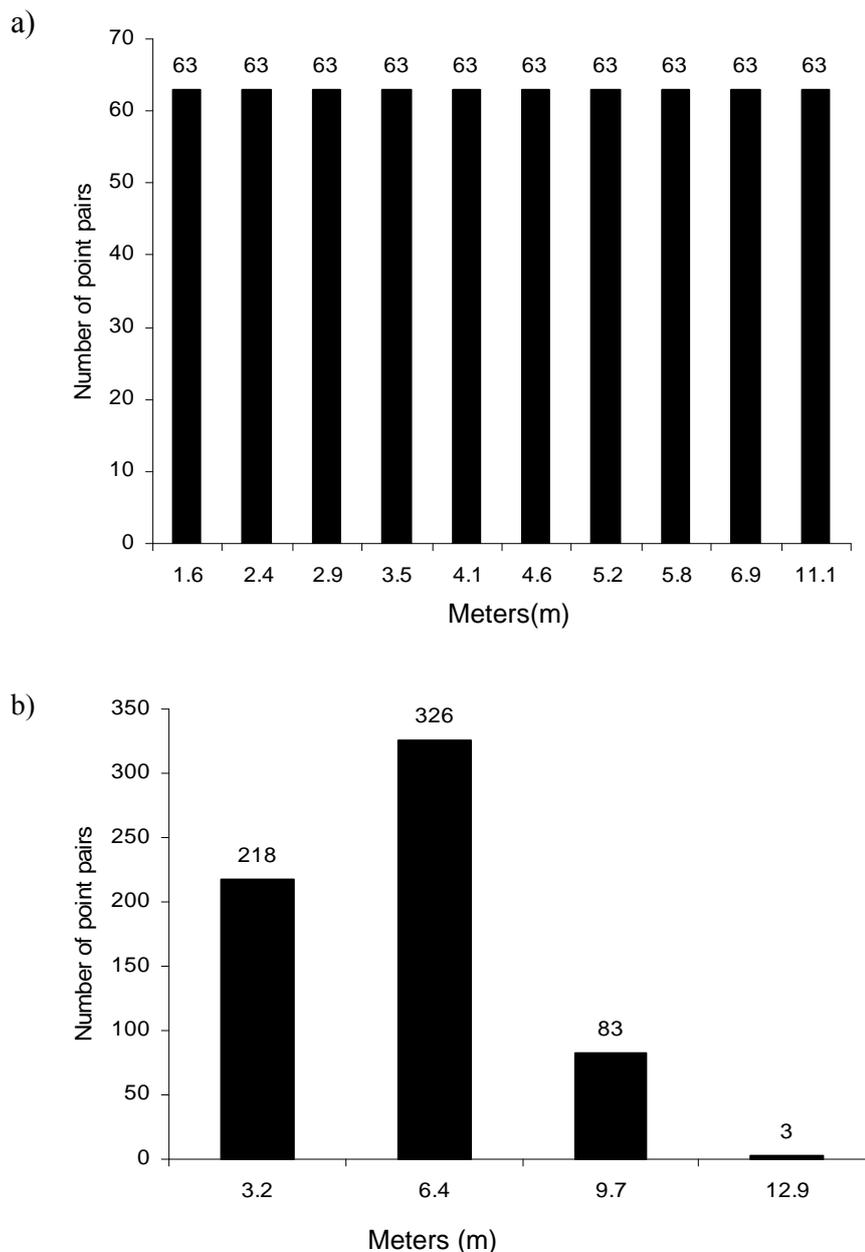


Fig. 1. The number of plant (point) pairs in different distance classes for a) equal number of point pairs ($n = 63$) and b) fixed distance (3.2 m) for Tafelberg high altitude stand.

iii. Spatial non-randomness

Patterns of spatial non-randomness (explicit approach) in mite and springtail abundance and individual species abundances were examined using Spatial Analysis by Distance IndicEs (SADIE) (Perry 1995; Dale et al. 2002). The basis of SADIE methodology is the quantification of spatial patterns in a sampled population by measuring the distance to regularity (that is the total number of moves which individuals in each sample must make so that all sample units have the same number of individuals) (Perry 1995). The overall index of spatial aggregation (I_a) indicates the spatial arrangements of counts relative to each other and is calculated by dividing the distance to regularity by the average distances of randomisations of the sample counts (Perry 1995; Perry et al. 1999; Perry and Dixon 2002). The index of aggregation indicates a spatially random distribution if $I_a = 1$, aggregated spatial distribution of individuals if $I_a > 1$, and a spatially regular distribution if $I_a < 1$ across the sample area (Perry et al. 1999). An additional index, v , defines and quantifies the clustering pattern within the sample area, with v_j and v_i indicating the presence of gaps or patches respectively (Perry et al. 1999). Significant mean negative (v_j) values thus indicate that the sample unit contributes to clustering as a member of a gap, and significant mean positive (v_i) values indicate that the sample unit contributes to clustering as a member of a patch (Perry et al. 1999).

Species with a minimum occupancy of 33 % (12) plants in a stand were used in the individual species analyses. Although it has been shown that for detection of significant spatial clustering, at least 16 % of samples should be greater than zero (Korie et al 2000), this is recommended for regular sampling points (e.g., grid). Here we used random sampling and therefore a more conservative approach was followed (Veldtman 2004). Thus, for analyses of total abundance 31 species were used, but only 20 species, i.e. common species, were used in individual species analyses.

Plant characteristics and microarthropod spatial heterogeneity

To examine if microarthropod abundance was spatially associated with plant characteristics, i.e., plant area, % dead tissue and grass (*Agrostis magellanica*) cover the spatial association statistic in SADIE was used. Individual species association analyses were also conducted when significant clustering was present in both the species and the plant characteristic. The correlation of two sets of clustering indices that share spatial references provide an index of association (X), and a probability of

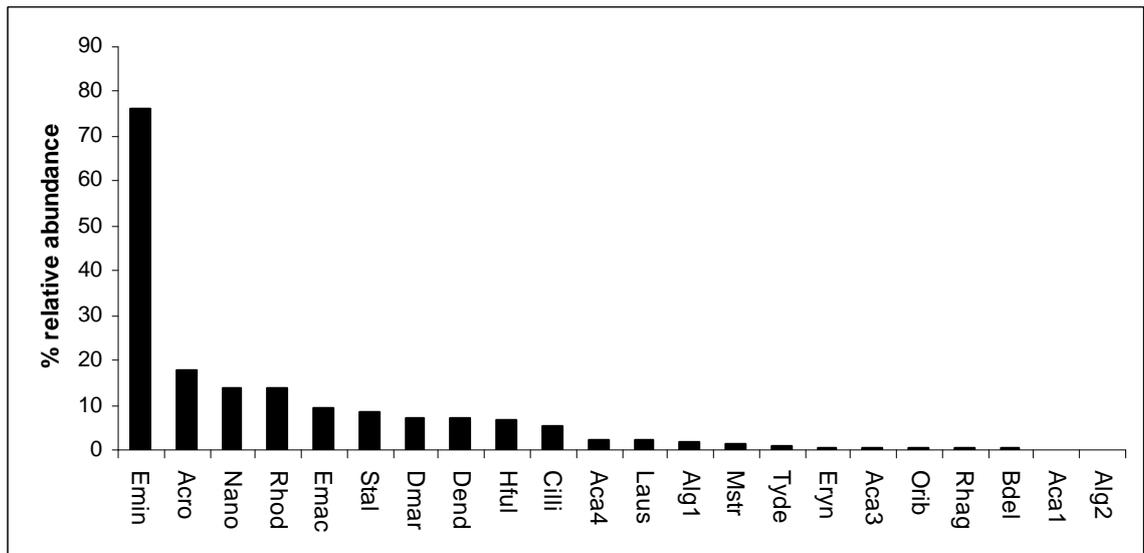
association (P) (Perry 1998a). The significance of associations is determined by comparing X to critical values for the randomised distribution of overall association, using the 97.5th and 2.5th centiles for a desired 95 % confidence interval (Perry and Dixon 2002) as well as the maximum critical value (derived from the 153 simulations) (Veldtman 2004). All aggregation and spatial association statistics were calculated with SADIE Shell v. 1.21 software (<http://www.iarc.bbsrc.-ac.uk/pie/sadie>; Winder et al. 2001; Perry and Dixon 2002). For visual presentation of spatial non-randomness and association, red-blue plots were generated with Arcview 3.1 (Perry et al. 1999; Winder et al. 2005).

Corrections to statistical significance values for multiple comparisons, such as Bonferroni tests (Holm 1979; Rice 1989) or the False Discovery Rate (Garcia 2004) were not performed, because the objectives of this study were largely exploratory, and not hypothesis-based, i.e. to determine general patterns in the spatial distributions of microarthropods and to compare the outcomes of alternative approaches to quantifying spatial heterogeneity (see rationale in Cabin and Mitchell 2000).

Results

A total of 31 species (22 mite and 9 springtail) and 115111 individuals were collected across the 12 stands. Mixed Pickle mid-altitude stand had the most species (30 species) and the low altitude stand in this transect the highest mean abundance per plant (349.56 individuals/sample) (Table 1). The lowest species richness was found at the Tafelberg middle stand (22 species) and the lowest mean abundance per plant at Stony Ridge middle stand (172.19 individuals/sample). Total species richness varied from 5 to 23 species per plant and total abundance varied from 23 to 612 individuals per plant. The mite species *Eupodes minutus* constituted 40 % of all individuals sampled and 76 % of all mite individuals (Fig. 2a). The most abundant springtail species was *Folsomotoma marionensis*, which constituted 35 % of all springtail individuals (Fig. 2b).

a)



b)

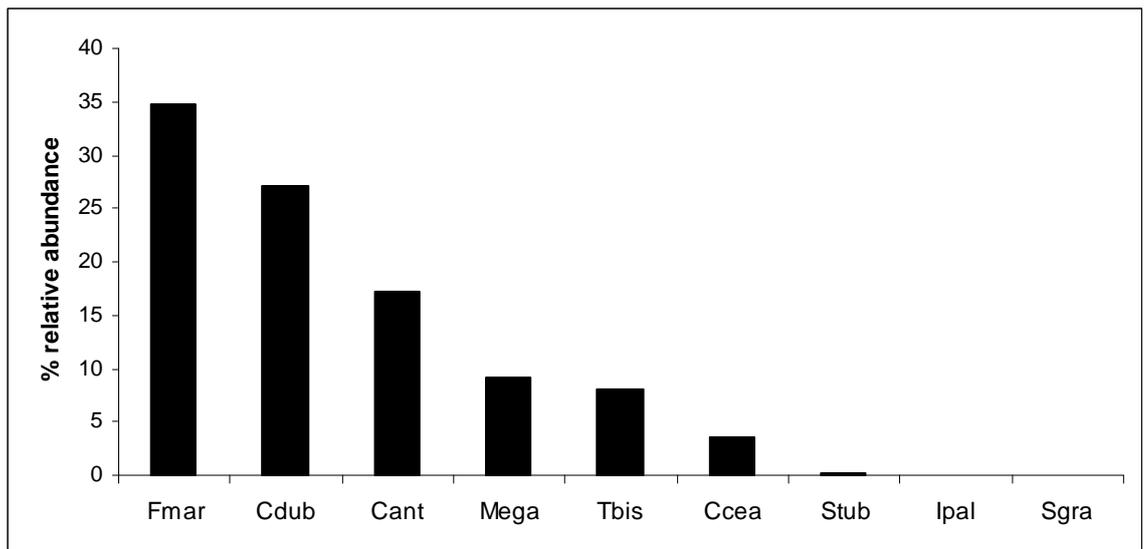


Fig. 2. Relative abundances (%) of a) mite and b) springtail species across all stands. All mite species other than the dominant *Eupodes minutus* are expressed as a percentage of total mite individuals excluding *E. minutus*. Species abbreviations in Table 3.

i. Statistical heterogeneity

The variance-mean ratio was significantly > 1.0 (individuals aggregated) for mite and springtail abundance in all stands (Table 2). In contrast, the Morisita index (I_M) was not significantly different from 1.0 for mite or springtail abundance in any stands, except in the Stony Ridge middle stand where springtail abundance was significantly aggregated (Table 2). For individual species across the 12 stands, the

variance-mean ratio was significantly greater than 1.0 in 73 % of cases, while the values of the Morisita's index for species abundances were greater than 1.0 in 63 % of cases (Fig. 3). Common species were aggregated in 93 % of cases using the mean-variance ratio, whereas only 60 % were significantly aggregated with the Morisita's index (Fig. 4). Rare species were significantly aggregated in 46 % of cases using the variance-mean ratio and 87 % of cases with Morisita's index. Where species abundances were not aggregated, the distributions were not significantly different from random (VMR and $I_M \sim 1$).

Table 2. Variance-mean ratio (VMR) and Morisita Index (I_M) of mite and springtail abundance at three altitudes along four transects on Marion Island (VMR for all mite and springtail abundances significantly > 1 , $P < 0.01$; significant I_M value > 1 , $P < 0.01$ indicated with *).

	Mites		Springtails	
	VMR	I_M	VMR	I_M
Tafelberg				
High	17.14	1.12	30.54	1.32
Middle	11.80	1.07	13.59	1.12
Low	11.76	1.10	7.24	1.07
Stony Ridge				
High	19.36	1.14	22.19	1.30
Middle	24.91	1.22	35.01	1.54*
Low	12.40	1.07	23.80	1.20
Mixed Pickle				
High	9.05	1.06	24.06	1.13
Middle	5.03	1.03	16.19	1.09
Low	15.35	1.09	25.89	1.13
Swartkops				
High	15.60	1.10	26.54	1.18
Middle	7.29	1.04	36.10	1.24
Low	7.77	1.05	15.70	1.08

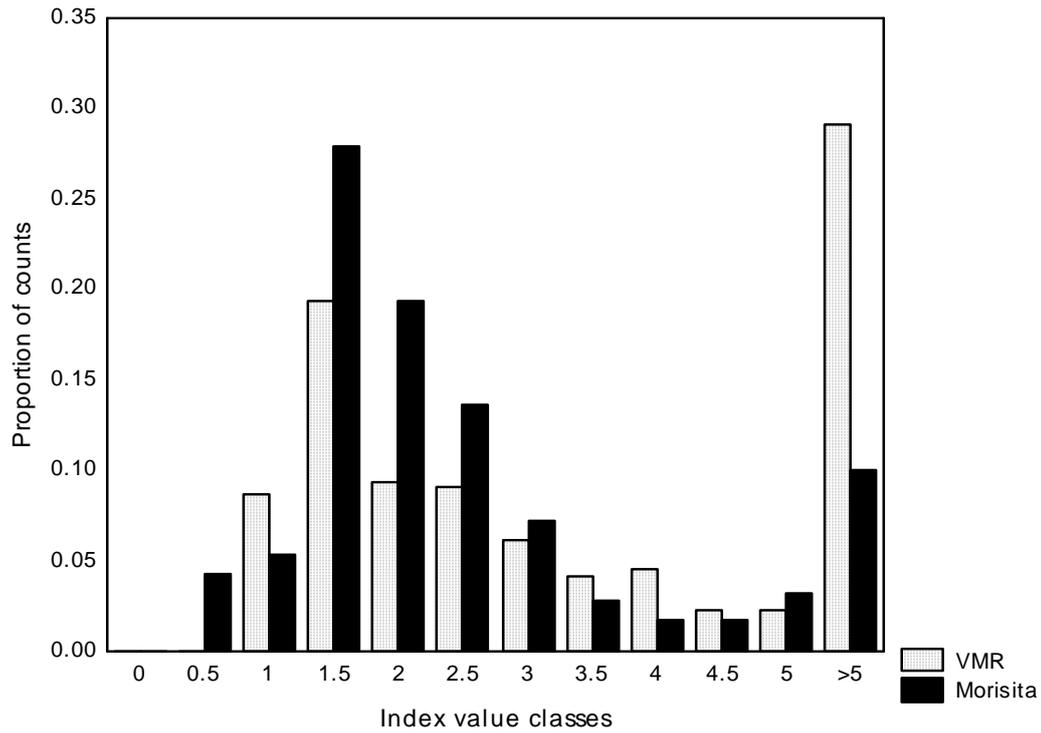


Fig. 3. Frequency distributions of the variance-mean ratio (VMR) and Morisita's index for individual species abundances (VMR $n = 307$; Morisita's $n = 278$). Index values were separated into classes with 0.5 intervals starting from -0.5 .

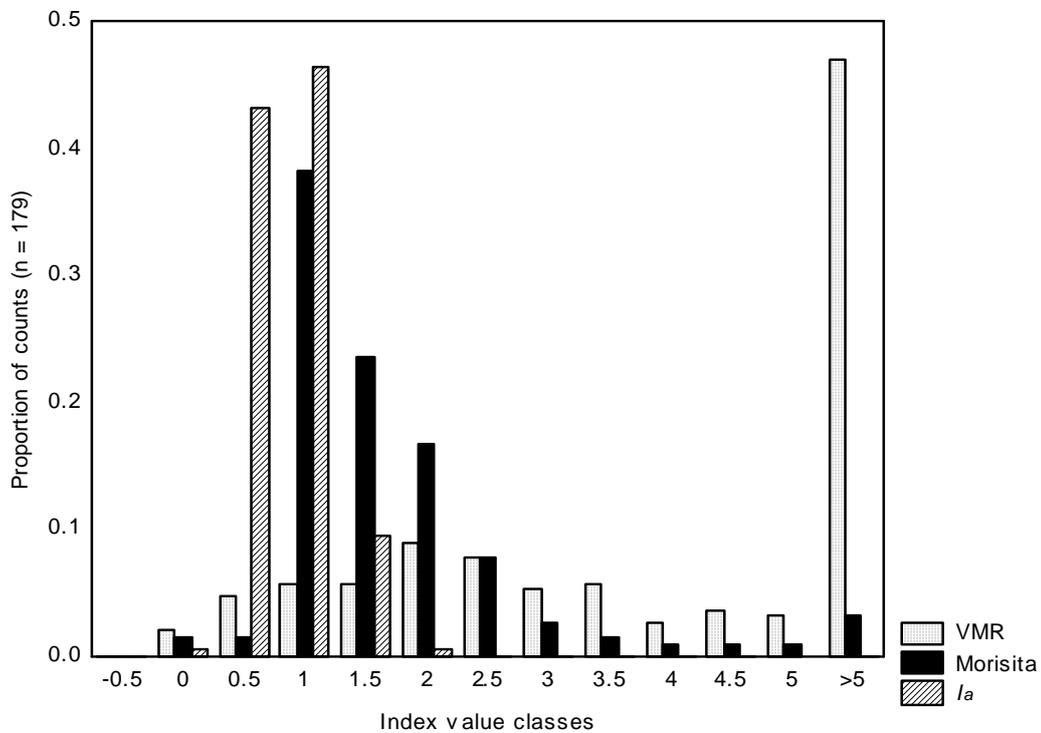


Fig. 4. Frequency distributions of the variance-mean ratio (VMR), Morisita index and the spatial aggregation index (I_a) for individual species abundances (common species) ($n = 179$). Index values were separated into classes with 0.5 intervals starting from -0.5 .

Taylor's power law did not provide a good fit for the relationship between mean and variance of total mite and springtail abundance (Table 3). Mite abundance was significantly smaller than one, indicating a regular distribution, while springtail abundance was randomly distributed ($b \sim 1$) (Table 3). Furthermore, for individual species abundances, Taylor's power law provided a good fit for the relationship between the mean and variance, and in all except one case the coefficient of determination (R^2) was greater than 60 % (Table 3). The exception was *Eupodes minutus*, the most abundant species, where R^2 was only 0.26 (Table 3). The b values of Taylor's power law regressions for individual species abundances were only significantly different from 1.0 for *E. minutus*. Therefore, using Taylor's power law, all species were identified as having random distributions, except *E. minutus* where the distribution was regular (Table 3). In general the b value decreased with increasing abundance of individuals ($F_{1,28} = 12.27$, $P = 0.001$, $R^2 = 0.28$) (Fig. 5).

Table 3. Estimates of b in Taylor's power law, $s^2 = a \bar{x}^b$ (where s^2 is the sample variance and \bar{x} is the sample mean). (* = significantly different from null model $b = 1$ at $P < 0.05$, Student's t test).

Species	Abbr.	$b \pm SE$	R^2	Abundance
Mite abundance		$-0.17 \pm 1.09^*$	0.002	60124
Springtail abundance		0.97 ± 0.38	0.39	55145
<i>E. minutus</i>	Emin	$0.15 \pm 0.07^*$	0.26	45824
<i>Rhodacaridae</i> sp.	Rhod	0.71 ± 0.06	0.93	1968
<i>Dendrolaelaps</i> sp.	Dend	0.66 ± 0.12	0.76	1005
Cillibidae sp.	Cill	0.77 ± 0.07	0.92	796
<i>Nanorchestes</i> sp.	Nano	0.61 ± 0.07	0.87	2005
<i>E. macquariensis</i>	Emac	0.74 ± 0.10	0.83	1349
<i>L. australis</i>	Laus	0.49 ± 0.07	0.83	294
<i>Tydeus</i> sp.	Tyde	0.88 ± 0.05	0.98	110
<i>Bdellodes</i> sp.	Bdel	0.99 ± 0.07	0.98	33
<i>Eryngiopus</i> sp.	Eryn	0.78 ± 0.04	0.98	77
Oribatid sp.1	Orib	0.78 ± 0.06	0.95	53
<i>A. crozetensis</i>	Acro	0.34 ± 0.08	0.63	2571
<i>H. fulvus</i>	Hful	0.55 ± 0.05	0.92	926
<i>D. marionensis</i>	Dmar	0.79 ± 0.03	0.98	1008
<i>S. talpa</i>	Stal	0.53 ± 0.08	0.81	1234
<i>Algophagus</i> sp.	Alg1	0.77 ± 0.06	0.95	257

<i>M. striata</i>	Mstr	0.77 ± 0.05	0.96	163
<i>Rhagidia</i> sp.	Rhag	0.96 ± 0.06	0.97	40
Acari sp.1	Aca1	0.70 ± 0.10	0.92	17
Acari sp.3	Aca3	0.83 ± 0.06	0.95	58
Acari sp.4	Aca4	0.90 ± 0.04	0.98	335
<i>T. bisetosa</i>	Tbis	0.54 ± 0.09	0.75	4473
<i>F. marionensis</i>	Fmar	0.65 ± 0.11	0.78	19134
<i>C. dubius</i>	Cdub	0.61 ± 0.09	0.82	14948
<i>C. antarcticus</i>	Cant	0.79 ± 0.18	0.63	9456
<i>C. caecus</i>	Ccea	0.67 ± 0.08	0.87	1941
<i>Megalothorax</i> sp.	Mega	0.69 ± 0.08	0.88	5075
<i>I. palustris</i>	Ipal	0.42 ± 0.12	0.84	18
<i>S. tuberculatus</i>	Stub	0.64 ± 0.08	0.90	431
<i>S. granulosus</i>	Sgra	1.05 ± 0.01	0.99	7

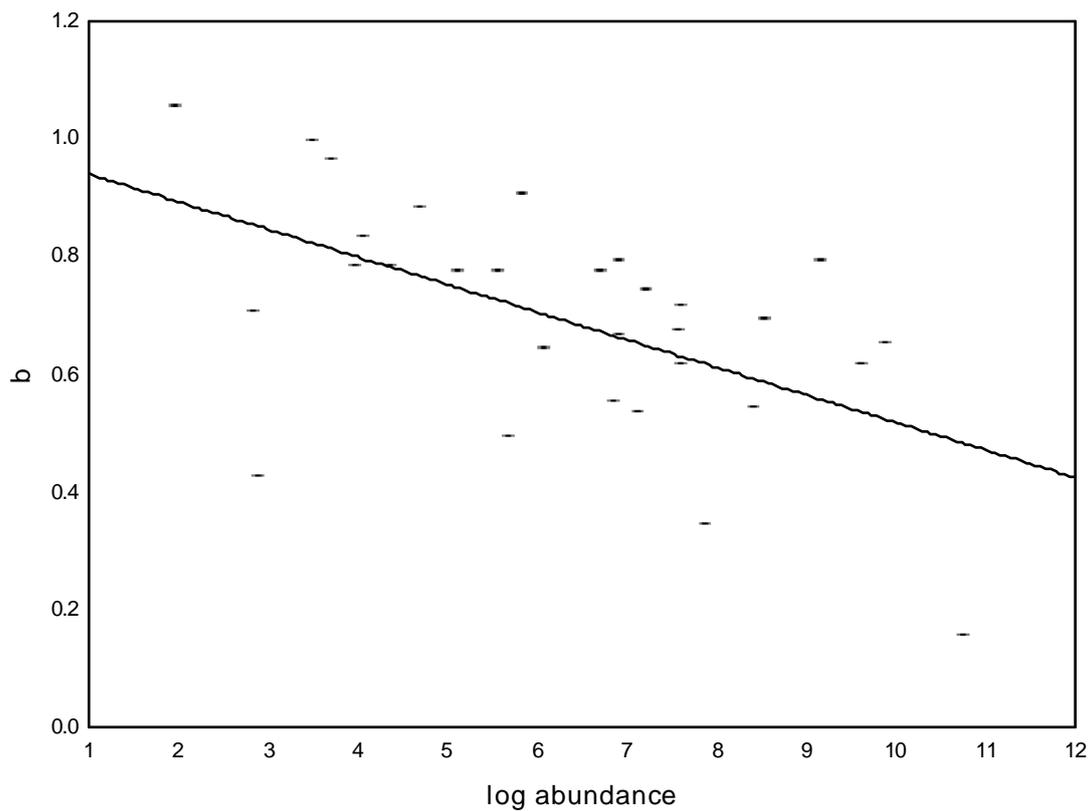


Fig. 5. The interspecific relationship between parameter b in Taylor's Power Law and species abundance ($F_{1,28} = 12.27$, $P = 0.001$, $R^2 = 0.28$).

ii. Spatial structure

The spatial structure of springtail and mite abundance varied between stands (Appendix 2). Using equal number of point pairs (method 1), overall correlogram significance appeared in 17 % of cases. Significant positive Moran's I values for the first distance class were present only for springtail abundance in the Stony Ridge middle stand (Appendix 2). Using the fixed distance method (method 2), overall correlogram significance appeared in two out of 24 cases (8 %) with only one case coinciding with that of method 1. Significant positive Morans' I values for the first distance class were again only present for springtail abundance in the Stony Ridge middle stand (Appendix 2).

In the equal point pairs method (1), significant correlograms for common individual species appeared in 22 out of a possible 179 cases (12 %), while with fixed distance method (2), 28 (16 %) of the cases were significant (Table 4), with 10 % overlap of significant cases between the two methods. In the first method 16 cases of species had significant positive Moran's I value for the first distance class, and for the second method 24 species with significant Moran's I values in the first distance class were observed (Table 4). Spatial structure for the same species was observed with both methods. *Cryptopygus caecus* and *Nanorchestes* sp. had spatial structure in 40 % of the stands and *C. dubius* in 25 % of stands (calculated with results from the fixed distance method, Table 4).

Mite and springtail abundance did not have spatial structure in the first distance class, i.e., abundances in samples were thus independent between samples at the distance in the first distance class, e.g. 1.1 m for Mixed Pickle middle (equal point pairs, Appendix 1) or greater than 3.2 m (fixed distance method), except for springtails in Stony Ridge middle, where autocorrelation occurred at smaller distances. Additionally, a few individual species, e.g., *Cryptopygus caecus*, *Nanorchestes* sp. and *C. dubius* had spatial structure at a distance less than 3.2 m (Table 4).

Table 4. Mite and springtail species showing significant spatial non-randomness and significant spatial structure (determined by the overall correlogram significance P; fixed distance = 3.2 m for all distance classes in all stands) at three altitudes along four transects on Marion Island (significant positive Moran's I value at the first distance class indicated by *, ** and *** denoting significance at $P < 0.05$, 0.01 and 0.001 level respectively).

Species	Spatial structure		Spatial non-randomness		
	Correlogram P	Moran's I	Species	I_a	P
Tafelberg					
High					
<i>C. caecus</i>	<0.001	0.21***	<i>C. caecus</i>	1.56	0.01
			<i>C. dubius</i>	1.36	0.05
Middle					
<i>C. caecus</i>	0.04	0.07	<i>C. caecus</i>	1.83	0.01
<i>T. bisetosa</i>	0.003	0.26*	<i>C. antarcticus</i>	1.51	0.04
<i>H. fulvus</i>	<0.001	0.58***	<i>H. fulvus</i>	1.91	0.002
Low					
<i>C. dubius</i>	0.002	0.06**	-		
Stony Ridge					
High					
<i>E. minutus</i>	0.01	0.11*	<i>C. dubius</i>	1.36	0.05
			<i>C. caecus</i>	1.56	0.01
Middle					
<i>Dendrolaelaps</i> sp.	0.001	0.21***	<i>Dendrolaelaps</i> sp.	1.50	0.03
Cillibidae sp.	0.001	0.22***			
<i>F. marionensis</i>	<0.001	0.31***			
Low					
<i>Nanorchestes</i> sp.	<0.001	0.43***	<i>Nanorchestes</i> sp.	1.86	0.02
<i>A. crozetensis</i>	0.003	0.30***	<i>A. crozetensis</i>	1.69	0.04
<i>E. minutus</i>	0.02	0.21**			
<i>L. australis</i>	<0.001	0.05			
<i>C. antarcticus</i>	0.02	0.10			
Mixed Pickle					
High					
<i>Nanorchestes</i> sp.	0.04	0.09*	<i>C. caecus</i>	1.56	0.05
			<i>C. antarcticus</i>	1.74	0.02
			<i>A. crozetensis</i>	1.76	0.02
Middle					
<i>C. caecus</i>	0.02	0.05**	<i>C. caecus</i>	1.38	0.05
Rhodacaridae sp.	<0.001	0.11***	Rhodacaridae sp.	2.24	<0.001
			<i>C. dubius</i>	1.42	0.04
Low					
<i>F. marionensis</i>	<0.001	0.16***	<i>F. marionensis</i>	1.76	0.002
<i>Dendrolaelaps</i> sp.	0.003	0.13***	<i>Dendrolaelaps</i> sp.	1.70	0.004
<i>C. dubius</i>	0.004	0.11***	<i>C. caecus</i>	1.39	0.04
<i>Nanorchestes</i> sp.	0.001	0.16***	<i>Nanorchestes</i> sp.	1.5	0.02
			<i>E. macquariensis</i>	0.95	0.05

			<i>Megalothorax</i> sp.	1.46	0.02
Swartkops					
High					
<i>C. caecus</i>	<0.001	0.06	<i>C. caecus</i>	1.43	0.04
<i>T. bisetosa</i>	0.02	0.13**	<i>T. bisetosa</i>	1.60	0.01
Middle					
<i>C. dubius</i>	0.02	0.05**	<i>C. dubius</i>	1.43	0.05
<i>C. antarcticus</i>	<0.001	0.11***			
Low					
<i>D. marionensis</i>	0.003	0.08***	<i>D. marionensis</i>	1.64	0.03
<i>M. striata</i>	0.01	0.07**	<i>M. striata</i>	1.88	<0.001
<i>Nanorchestes</i> sp.	0.003	0.08***	Acari sp3	1.73	0.003
			<i>T. bisetosa</i>	1.34	0.05

iii. Spatial non-randomness

Mite and springtail abundances were mostly spatially randomly distributed across all the stands, except springtail abundance in the Stony Ridge middle stand with significant clustering into gaps and patches (Appendix 3). However, several individual species had significant aggregation in various stands (Table 4, Fig. 4). *Cryptopygus caecus* was aggregated in 58 % of stands and *C. dubius* in 33 % of stands, while the other significantly aggregated species had an aggregated pattern in only one or two stands (Table 4). Thus, microarthropods did largely not show spatial non-randomness, except for springtail abundance in one case and for a few individual species in certain stands.

Plant characteristics and microarthropod spatial heterogeneity

Plant characteristics were generally randomly distributed in all stands (I_a values, Appendix 4). Exceptions where variables were significantly non-randomly distributed were for plant size in the Stony Ridge high and low, Mixed Pickle high and Swartkops low stand, percentage dead tissue in the Stony Ridge low, Swartkops high and low stands and percentage grass cover in the Tafelberg low, Mixed Pickle middle and low stands (Appendix 4).

Spatial association identified only four cases in which mite or springtail abundance were significantly associated with plant characteristics (Appendix 5). Mite abundance was associated with plant size in the Stony Ridge high stand and with percentage dead tissue in the Stony Ridge low stand, while springtail abundance was associated with percentage dead tissue in the Stony Ridge high and low stands (Fig. 6) (Appendix 5). For individual species, 11 cases of significant association were

observed. *Cryptopygus caecus* was associated with plant size in the Stony Ridge high and Mixed Pickle high stand and with percentage dead tissue in the Swartkops high stand. *Austroppia crozetensis* was associated with plant size in the Mixed Pickle high and percentage dead tissue in the Stony Ridge low stand. Furthermore, *Ereynetes macquariensis*, *Folsomotoma marionensis* and *Megalothorax* sp. were associated with percentage grass cover in the Mixed Pickle low stand; *Domitorina marionensis* and *Macquarioppia striata* associated with percentage dead tissue and *Tullbergia bisetosa* with plant size in the Swartkops low stand (Appendix 6).

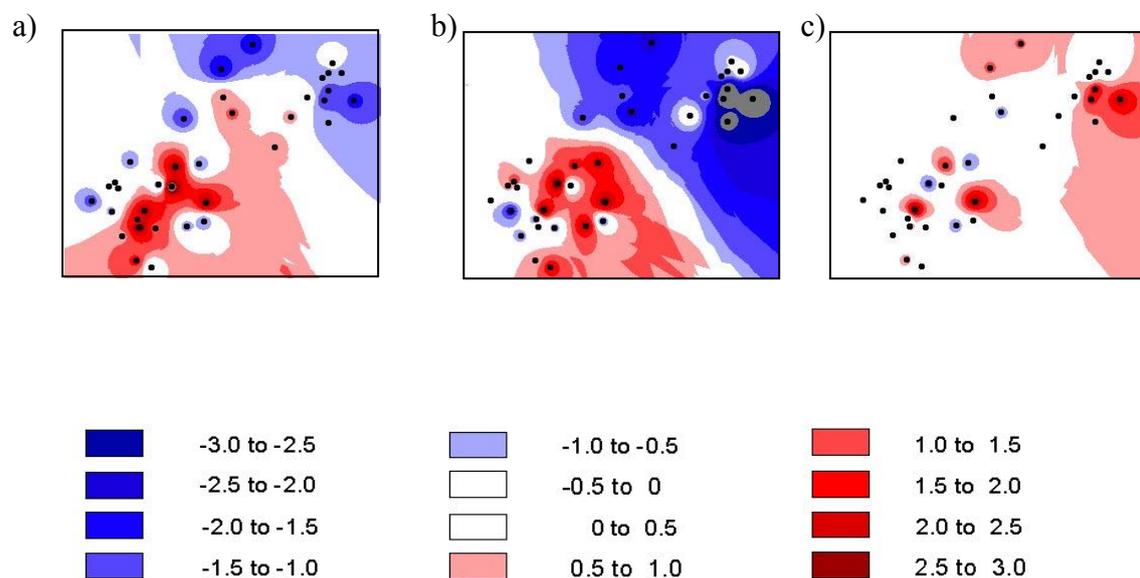


Fig. 6. Interpolated (least distance weighted, Perry et al. 1999) spatial clustering and spatial association of springtail abundance and % dead tissue in plants at Stony Ridge low stand. Spatial clustering of a) springtail abundance (overall index of aggregation $I_a = 1.34$, $P = 0.14$) and b) % dead tissue ($I_a = 1.65$, $P < 0.05$). In a) and b) areas coded > 1.5 denote areas of significant clustering and areas < 1.5 areas of significant negative clustering. Spatial association (c) between springtail abundance and % dead tissue ($X = 0.38$, $P = 0.03$) in the Stony Ridge low stand. (c): Areas coded as > 0.5 are significantly positively associated and those < -0.5 are significantly negatively associated (Winder et al. 2005). This example was deliberately chosen to show significant aggregation of, and association between, variables.

In summary, the spatially implicit methods revealed aggregated, random and regular distributions for microarthropods, whereas the spatially semi-explicit and explicit methods revealed a generally random distribution of microarthropod abundances across stands of *Azorella selago* plants, with only a few apparently incidental cases of significant aggregation (Table 5). Likewise, plant characteristics were randomly distributed in most cases and were associated with mite and springtail abundance and species abundances in only a few stands.

Table 5. Summary of aggregation patterns in mite and springtail abundances (N) and the abundances (N) of sufficiently common species as determined by different statistical approaches, representing an increasing degree of spatial information used in the analyses (down the column). X = absence of aggregated patterns (except 1 case); even = even distribution, ✓ = aggregated patterns; individual species aggregation expressed as the percentage of cases in which aggregated patterns were observed.

Statistical method	Mite N	Springtail N	Individual species N
Statistical heterogeneity (implicit)			
Variance-mean ratio (VMR)	✓	✓	93%
Morisita's index (I_M)	x	x (1)	60%
Taylor's power law (b)	even	x	0 %
Spatial structure (semi-explicit)			
Moran's I (fixed distance class)	x	x (1)	13%
Moran's I (equal point pairs)	x	x (1)	9%
Spatial non-randomness (explicit)			
Index of aggregation (I_a)	x	x (1)	16%

Discussion

The form of spatial heterogeneity in total mite and springtail abundance identified across the three approaches (implicit (only the Morisita's index), semi-explicit and explicit) was generally similar, i.e. demonstrating random distributions in most cases. Furthermore, plant characteristics were also randomly distributed and were generally not associated with microarthropod abundances.

Although the outcomes of the implicit (Morisita's index), semi-explicit and explicit approaches were similar, each method has a different biological

interpretation. Implicit methods reveal heterogeneity in the combined variation of microarthropod abundance data across a stand, i.e. across sampling points (Perry 1998b; Veldtman 2004). The random distribution found by the Morisita's index indicates that the probability that two randomly selected microarthropod individuals in a stand are from the same plant is equal to than it would be if all microarthropod individuals were randomly distributed across the stand (Hurlbert 1990). The semi-explicit approach (spatial structure) reveals the distance between plants in which microarthropod abundances are more similar than expected (Legendre and Legendre 1998; Veldtman 2004). This method did not reveal significant spatial structure in the first distance class, indicating that microarthropod abundances were not more similar in plants within a radius of 3.2 m than expected by chance (3.2 m being the distance of the first distance class in the fixed distance class method). Microarthropod abundances may be more similar in plants further than 3.2 m apart, but since microarthropods most likely disperse to the neighbouring plants, significant and consistent spatial structure at larger distances seemed unlikely. Furthermore, the explicit approach indicated the position in a stand of plants with high or low microarthropod abundance (Perry 1998b; Wiens 2000; Veldtman 2004). The explicit approach revealed random distributions in microarthropod abundances across a stand, indicating that there were not specific areas within a stand with significantly higher or lower abundances of microarthropods. Therefore, using the three different analytical approaches, total microarthropod abundance within a stand of *Azorella selago* plants was not heterogeneous statistically (with the exception of the variance-mean ratio, which was not considered useful because of its dependence on the population density, Hurlbert 1990), spatially structured or spatially non-randomly distributed.

In contrast to the absence of spatial heterogeneity in total microarthropod abundances, individual species abundances varied between random, even and aggregated distributions across the three statistical approaches. In most stands of *Azorella selago*, individual species abundances were aggregated using the variance-mean ratio, but fewer cases of aggregation (still more than half) were observed with the Morisita's index. In contrast, in the majority of stands, individual species abundances were randomly distributed using the semi-explicit (spatial structure) and explicit (spatial non-randomness) approaches. The spatial heterogeneity found in some species abundances emphasized the importance of examining individual species

in addition to total microarthropod abundance to fully understand the spatial heterogeneity in microarthropod assemblages.

The absence of spatial heterogeneity in total microarthropod abundances across stands found here is in contrast to findings from other studies (Ettema and Wardle 2002). For example, mites and springtails were aggregated in stands of Arctic tussocks and Antarctic moss turves (Usher and Booth 1984; Hertzberg et al. 2000; Ims et al. 2004), between samples in soils and caves (Ducarme and Lebrun 2004) and across bags of stored wheat in storerooms (Athanassiou et al. 2003). Three possible reasons for the difference between this study and other studies may be applicable, i.e., the analytical method used, the scale of the study and different underlying mechanisms.

In this study three different approaches were used, i.e. implicit, semi-explicit and explicit methods, to describe the spatial heterogeneity in microarthropod abundance. However, in the majority of other studies involving microarthropods, implicit methods, e.g. variance-mean ratio, were mostly used, which indicated aggregated patterns in microarthropod abundances (Usher 1969; Usher and Booth 1984, 1986; Hertzberg et al. 2000; Athanassiou et al. 2003; Ducarme and Lebrun 2004; Ims et al. 2004). Therefore, the outcome of the variance-mean ratio in this study is in accordance with the outcomes of the other studies. However, in this study the outcomes of the other implicit method (Morisita's index), the semi-explicit and explicit methods revealed random distributions of individuals. In fact, Hurlbert (1990) argued that the variance-mean ratio is not a good measure of aggregation, since an index cannot be used both as a measure of departure from randomness (Poisson distribution) and as an index of aggregation. Pielou (1974) also stated that a pattern could not be concluded to be random only because the variance-mean ratio equals one. The variance-mean ratio also depends on population density (Hurlbert 1990; Taylor 1984). Therefore, Hurlbert (1990) suggested another implicit method, i.e., the Morisita's index, as a superior alternative method, since this index is independent of population density. Indeed, in Hurlbert's (1990) study, the Morisita's index gave more realistic outcomes than the variance-mean ratio on the spatial distribution of montane unicorns, i.e. aggregated patterns using the variance-mean ratio and random patterns using the Morisita's index (Hurlbert 1990), which are similar to results obtained here for mites and springtails. Hurlbert (1990) further suggested (although he did not demonstrate) that an even better method would be one in which all spatial information

is used. Indeed, it has now been shown that semi-explicit and explicit methods have more power to describe spatial distributions (Legendre and Legendre 1998; Perry 1998b; Veldtman and McGeoch 2004; Veldtman 2004). Therefore, the different, and more advanced, analytical methods used in this study appear, at least in part, responsible for the difference in outcomes of microarthropod distribution patterns in comparison with other studies.

Furthermore, as mentioned earlier the scale of observation of a study is likely to influence the outcome of the form of spatial heterogeneity of biota. In this study, Taylor's Power Law indicated a random distribution in microarthropod abundances (except for mite abundance and *Eupodes minutus*, which were evenly distributed). However, the results of Taylor's Power Law in this study were calculated on an island-wide scale (data were combined across all sites for regressions) and not across plants in a stand as used in the other studies. Since Usher and Booth (1984) used Taylor's Power Law to describe distributions for some of the species found in this study, this method was included. However, all the microarthropod species abundances in Antarctic moss-turves in Usher and Booth's (1984) study were aggregated. Their study, however, was at a fine scale, i.e., distribution patterns within plants (Usher and Booth 1984). Although parameter b in Taylor's Power Law is a constant and considered characteristic of a species (Taylor 1961; Park and Cho 2004), the values are greatly influenced by sample scale as well as sample size, total number of individuals sampled, plant species and region (Yamamura 2000; Duncan et al. 2001; Lam et al. 2002; Park and Cho 2004; Burgio et al. 2005; Hui et al. in press). Therefore, the b value was different between our study and that of Usher and Booth (1984), even for the same species, most likely as a consequence of the difference in sampling scale.

Further, since spatial heterogeneity of microarthropod abundance across stands of *Azorella selago* plants was absent, it is likely that spatial heterogeneity may be present at smaller scales. Habitat selection is likely to occur at smaller scales, e.g., within plants, where the risk of desiccation is lower, and microarthropods can search optimally for the best microhabitat (Usher 1969; Baguette and Mannechez 2004; Callaghan et al. 2004; McGeoch and Price 2004). Indeed, spatial heterogeneity of microarthropod abundances has been observed within *A. selago* plants, with higher abundance on the southern, colder sides of plants (coinciding with the side which receives the cold, dry southern winds) (Hugo et al. 2004, Chapter 1). Therefore, it is

important to compare studies, which were conducted on the same scale or on multiple scales, since spatial patterns of microarthropod abundances differ between scales of observation.

Different underlying mechanisms may also result in different spatial patterns in microarthropod abundances across studies. A variety of mechanisms have been proposed for observed microarthropod distributions, i.e., variable resource quality and quantity (Holland et al. 1999; Ims et al. 2004), patchy distribution of food (Ducarme and Lebrun 2004) and favourable microclimate, i.e. temperature and moisture in certain areas (Holland et al. 1999; Athanassiou et al. 2003; Ims et al. 2004). On Marion Island, plant characteristics, i.e. plant size, percentage dead tissue and percentage grass cover were generally randomly distributed across a stand, using the explicit approach. Additionally, only in a few cases were microarthropod abundances associated with plant characteristics. Therefore, the spatial distribution of plants and their characteristics did generally not contribute to explaining the absence of spatial heterogeneity in microarthropod abundance on Marion Island at the within-stand scale.

Although resources have been shown to be important determinants of microarthropod distributions in other systems (Holland et al. 1999; Ducarme and Lebrun 2004; Ims et al. 2004), the spatial distributions of microarthropods may also be determined by the mobility, stress tolerance and reproductive success of individuals (Hertzberg et al. 2000; Ettema and Wardle 2002; Ducarme and Lebrun 2004). On Marion Island, microarthropods do occur in the fellfield soil (Barendse and Chown 2001) and it can thus be assumed that dispersal occurs between *Azorella selago* plants. However, conditions in the fellfield soil are harsh, with low temperatures, moisture and nutrients (Gremmen 1981). Migrating microarthropods (most of which are particularly susceptible to dehydration, Hopkin 1997, Convey et al. 2003) face higher risk of desiccation in the drier fellfield soil (Gremmen 1981; Hertzberg et al. 2000) compared to conditions in *A. selago* plants (Barendse and Chown 2001). Therefore, given the mobility (Marshall and Chown 1995; Deere 2005) and size (Mercer et al. 2001) of the microarthropods, they are unlikely to search for and locate the best suitable habitat, but rather will colonize the first plant they encounter (Chapman 1994; Hertzberg et al. 1994; Athanassiou et al. 2003). An absence of spatial pattern does not imply an absence of dispersal, but rather an absence of selection of the best plant when dispersal occurs, as well as rates of

emigration greater than local birth and survival rates (Spencer et al. 2002). The fact that spatial heterogeneity in microarthropod abundances was found in other studies, e.g. in stands of Arctic tussocks, may be due to an even less favorable environment between plants. A high mortality rate during migration and/or paucity of dispersal of microarthropods between Arctic tussocks is likely to result in gaps (low) and patches (high) of abundance across stands of plants (Hertzberg et al. 2000). A paucity of dispersal could also be a reason for the consistent aggregated patterns observed in certain species in this study. Species, which were commonly aggregated, are generally deeper litter dwelling species (euedaphic) and are likely to disperse infrequently. Therefore, the different dispersal rate of microarthropods between plants in this study and other studies, along with different abiotic conditions and matrix qualities, may also result in different spatial patterns of microarthropod abundances.

Another reason for spatial heterogeneity of microarthropods in other patchy environments may be due to a difference in reproductive rate in certain plants (Hertzberg et al. 1994; 2000; Ettema and Wardle 2002). Microarthropods living in plants with a more favorable microenvironment may have increased fitness and therefore increased reproductive success (Hertzberg et al. 1994; Strathdee and Bale 1998). However, in this study, the moisture content and temperature inside plants at a specific site were found to be broadly similar, regardless of plant size or epiphyte load (Chapter 1; Hugo et al. 2004). Since the microenvironment was similar in all plants, conditions for reproduction is not likely to be more favorable in certain plants, which could have resulted in the observed random distributions of microarthropod abundance seen in this study and not in others.

In conclusion, mite and springtail abundances, as well as individual species abundances, were mostly randomly distributed across stands of *Azorella selago* plants. These results differ from the outcomes of other studies in which microarthropod abundances were mostly aggregated. This study emphasizes the importance of using more than one analytical method as well as incorporating multiple scales of observation in order to capture the full extent of spatial heterogeneity in microarthropod abundance in fellfield environments on Marion Island, as well as on other islands in the sub-Antarctic region.

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Appendix 1. Mean plant density in a radius of the distance in the first distance class of correlograms using a fixed distance (each distance class = 3.2 m) and equal point (plant) pairs (point pairs = 63) in the 12 stands. The size of and plant density (m^2) in each stand are also included.

Stand	Stand size (m^2)	Plant density (m^2)	Equal point pairs (63)		Fixed distance (3.2 m)	
			Distance (m) in 1 st distance class	Mean plant density within a radius of the distance in the 1 st distance class	# point pairs in 1 st distance class	Mean plant density (within a radius of 3.2 m)
Tafelberg						
High	192.47	0.19	1.6	1.53	218	6.08
Middle	148.8	0.24	4.3	13.94	37	7.68
Low	52.35	0.69	1.4	4.25	286	22.08
Stony Ridge						
High	370.06	0.10	2.2	1.52	111	3.20
Middle	135.76	0.27	2.0	3.39	140	8.64
Low	176.11	0.20	2.9	5.28	71	6.40
Mixed Pickle						
High	86.92	0.40	1.6	3.22	184	12.80
Middle	39.7	0.91	1.1	3.46	366	29.12
Low	38.42	0.94	1.5	6.64	224	30.08
Swartkops						
High	42.79	0.84	1.7	7.63	169	26.88
Middle	31.14	1.16	1.1	4.40	352	37.12
Low	35.54	1.01	1.2	4.57	322	32.32

Appendix 2. Spatial autocorrelation of mite and springtail abundances at three altitudes along four transects on Marion Island, using a fixed distance (3.2 m) and equal point pairs (n = 63). Overall correlogram significance (P) as well as the Morans' *I* value for the first and second distance classes are given. Numbers in bold indicate correlogram significance; *, ** and *** denote significance of the Moran's *I* value at P < 0.05, 0.01 and 0.001 level respectively.

	Fixed distance		Equal point pairs	
	Mites N	Springtail N	Mites N	Springtail N
Tafelberg high				
Correlogram P	<0.001	0.59	0.23	0.87
1 st Morans' <i>I</i>	-0.1	-0.08	0.01	-0.01
2 nd Morans' <i>I</i>	0.04*	-0.01	-0.18	-0.08
Middle				
Correlogram P	0.63	1.00	0.23	0.43
1 st Morans' <i>I</i>	0.03	0.08	0.01	-0.03
2 nd Morans' <i>I</i>	-0.04	-0.09	0.03	-0.07
Low				
Correlogram P	0.49	0.12	0.73	0.17
1 st Morans' <i>I</i>	-0.02	-0.10*	0.10	0.12
2 nd Morans' <i>I</i>	-0.05	0.03	0.14	-0.10
Stony Ridge high				
Correlogram P	0.21	0.10	0.25	0.01
1 st Morans' <i>I</i>	0.08	-0.15	0.09	-0.01
2 nd Morans' <i>I</i>	-0.08	0.04	0.03	-0.18
Middle				
Correlogram P	0.52	0.002	1.00	0.004
1 st Morans' <i>I</i>	-0.06	0.21***	-0.05	0.36***
2 nd Morans' <i>I</i>	-0.03	-0.07	-0.18	0.28 **
Low				
Correlogram P	0.06	0.55	0.16	0.38
1 st Morans' <i>I</i>	0.04	0.11	0.14	0.17*
2 nd Morans' <i>I</i>	-0.14	-0.03	-0.04	-0.01
Mixed Pickle high				
Correlogram P	0.65	0.26	0.17	0.96
1 st Morans' <i>I</i>	-0.03	0.01	0.13	0.06
2 nd Morans' <i>I</i>	-0.04	-0.11	0.05	-0.07
Middle				
Correlogram P	0.43	1.00	1.00	0.05
1 st Morans' <i>I</i>	-0.05	-0.03	-0.002	-0.06
2 nd Morans' <i>I</i>	-0.02	-0.02	-0.06	-0.14
Low				
Correlogram P	1.00	0.52	1.00	0.59
1 st Morans' <i>I</i>	-0.04	-0.05	-0.03	0.04
2 nd Morans' <i>I</i>	-0.02	0.01	-0.13	-0.15
Swartkops high				
Correlogram P	0.27	0.50	0.20	0.60
1 st Morans' <i>I</i>	-0.09	-0.04	-0.24*	0.01
2 nd Morans' <i>I</i>	0.003	-0.08	0.12	0.03
Middle				
Correlogram P	0.41	0.11	0.09	0.99
1 st Morans' <i>I</i>	-0.04	0.03*	0.05	0.04
2 nd Morans' <i>I</i>	-0.01	-0.11*	-0.04	0.05
Low				
Correlogram P	0.63	0.64	0.04	0.16
1 st Morans' <i>I</i>	-0.001	-0.06	0.11	0.08
2 nd Morans' <i>I</i>	-0.06	0.002	-0.22*	-0.15

Appendix 3. SADIE spatial aggregation (overall index of spatial aggregation = I_a) of mite and springtail abundance along four transects at three altitudes on Marion Island. Gaps (v_j) and patches (v_i) with P values are also presented. Numbers in bold indicate significant values.

	I_a	P	v_j	P	v_i	P
Tafelberg high						
Springtail	1.04	0.37	-1.05	0.34	1.18	0.16
Mites	1.17	0.17	-1.28	0.10	1.00	0.43
Middle						
Springtail	0.87	0.67	-0.95	0.50	0.70	0.94
Mites	1.29	0.11	-1.07	0.31	1.14	0.24
Low						
Springtail	0.95	0.55	-0.88	0.74	0.89	0.73
Mites	1.10	0.24	-1.12	0.21	1.05	0.32
Stony Ridge high						
Springtail	0.89	0.69	-0.75	0.89	1.00	0.43
Mites	1.13	0.24	-1.40	0.07	0.83	0.75
Middle						
Springtail	1.73	0.01	-1.99	0.002	1.53	0.04
Mites	0.81	0.82	-0.84	0.74	0.95	0.50
Low						
Springtail	1.34	0.14	-1.07	0.33	1.60	0.06
Mites	1.24	0.19	-1.33	0.15	1.05	0.32
Mixed Pickle high						
Springtail	1.03	0.38	-0.79	0.74	1.19	0.22
Mites	1.09	0.31	-0.97	0.46	0.96	0.47
Middle						
Springtail	0.74	0.94	-0.67	0.99	0.89	0.66
Mites	0.88	0.70	-0.89	0.65	0.91	0.61
Low						
Springtail	1.07	0.30	-1.13	0.21	0.99	0.45
Mites	0.94	0.55	-0.94	0.54	0.87	0.71
Swartkops high						
Springtail	1.05	0.35	-1.13	0.25	0.91	0.58
Mites	0.83	0.75	-0.88	0.66	0.83	0.74
Middle						
Springtail	1.12	0.24	-0.98	0.45	1.00	0.41
Mites	0.94	0.55	-0.97	0.48	0.89	0.65
Low						
Springtail	0.86	0.75	-0.82	0.85	1.07	0.29
Mites	1.26	0.10	-1.30	0.08	1.10	0.25

Appendix 4. Spatial non-randomness (index of aggregation, I_a) for plant characteristics (plant size, % dead tissue and % grass (*Agrostis magellanica*) cover) at three altitudes along four transects on Marion Island (*, ** and *** denotes significance at the $P < 0.05$, 0.01 and 0.001 level respectively).

	Plant size	% dead tissue	% grass cover
Tafelberg			
High	1.32	1.18	-
Middle	1.02	1.01	1.08
Low	1.19	0.96	1.34*
Stony Ridge			
High	3.35**	0.94	-
Middle	0.92	0.92	0.86
Low	2.16*	1.65*	0.99
Mixed Pickle			
High	1.94*	0.79	-
Middle	0.99	1.23	1.60*
Low	1.05	0.86	1.52*
Swartkops			
High	0.96	1.77**	-
Middle	0.83	1.16	-
Low	1.36*	1.36*	1.18

Appendix 5. Spatial association (X) between mite and springtail abundance and plant characteristics: plant size, % dead tissue and % grass (*Agrostis magellanica*) cover. Numbers in bold indicate significant values.

Dependant variable	Environmental variable	X	P	Max critical value
Tafelberg high				
Springtails	% dead tissue	-0.140	0.798	0.437
	Size	-0.472	0.994	0.490
Mites	% dead tissue	-0.088	0.693	0.419
	Size	-0.002	0.377	0.372
Middle				
Springtails	% dead tissue	0.312	0.052	0.384
	% grass cover	-0.297	0.929	0.444
	Size	-0.051	0.675	0.465
Mites	% dead tissue	-0.166	0.831	0.540
	% grass cover	-0.250	0.922	0.425
	Size	-0.018	0.520	0.449
Low				
Springtails	% dead tissue	0.157	0.169	0.450
	% grass cover	0.249	0.058	0.542
	Size	0.174	0.143	0.404
Mites	% dead tissue	0.088	0.331	0.373
	% grass cover	0.151	0.195	0.464
	Size	0.179	0.117	0.378
Stony Ridge high				
Springtails	% dead tissue	0.311	0.046	0.378
	Size	-0.103	0.727	0.481
Mites	% dead tissue	-0.336	0.955	0.364
	Size	0.583	0.007	0.495
Middle				
Springtails	% dead tissue	-0.043	0.578	0.515
	% grass cover	0.035	0.390	0.392
	Size	0.097	0.325	0.499
Mites	% dead tissue	0.095	0.299	0.395
	% grass cover	0.155	0.201	0.419
	Size	0.049	0.377	0.389
Low				
Springtails	% dead tissue	0.376	0.033	0.477
	% grass cover	0.190	0.162	0.370
	Size	-0.237	0.909	0.377
Mites	% dead tissue	0.459	0.007	0.401
	% grass cover	0.048	0.390	0.541
	Size	0.106	0.292	0.523
Mixed Pickle high				
Springtails	% dead tissue	0.133	0.201	0.430
	Size	-0.263	0.922	0.386
Mites	% dead tissue	-0.073	0.649	0.513
	Size	-0.210	0.812	0.333
Middle				
Springtails	% dead tissue	0.213	0.182	0.450
	% grass cover	0.011	0.383	0.375
	Size	0.023	0.507	0.411
Mites	% dead tissue	-0.445	0.994	0.420
	% grass cover	0.317	0.390	0.419
	Size	0.156	0.260	0.454

Low				
Springtails	% dead tissue	-0.175	0.831	0.464
	% grass cover	0.203	0.110	0.470
	Size	0.184	0.175	0.423
Mites	% dead tissue	0.005	0.409	0.382
	% grass cover	0.186	0.143	0.405
	Size	0.148	0.188	0.505
Swartkops high				
Springtails	% dead tissue	-0.118	0.838	0.442
	Size	0.153	0.214	0.418
Mites	% dead tissue	0.012	0.526	0.445
	Size	-0.002	0.571	0.473
Middle				
Springtails	% dead tissue	0.026	0.435	0.431
	Size	0.103	0.292	0.414
Mites	% dead tissue	-0.216	0.896	0.392
	Size	0.041	0.351	0.375
Low				
Springtails	% dead tissue	0.124	0.357	0.460
	% grass cover	-0.317	0.935	0.294
	Size	-0.163	0.805	0.423
Mites	% dead tissue	0.063	0.364	0.360
	% grass cover	-0.125	0.740	0.460
	Size	-0.232	0.552	0.418

Appendix 6. Spatial association (X) between individual microarthropod species and plant characteristics: plant size, % dead tissue and % grass (*Agrostis magellanica*) cover. Spatial association analyses were conducted in cases where significant clustering was present in both the species and the plant characteristic. Numbers in bold indicate significant values.

Stand and species	Plant characteristic	X	P	Max critical value
Stony Ridge high				
<i>C. dubius</i>	Plant Size	-0.04	0.58	5.27
<i>C. caecus</i>	Plant Size	0.47	0.01	4.89
Stony Ridge low				
<i>Nanorchestes</i> sp.	Plant size	-0.11	0.75	4.36
	% dead tissue	-0.43	0.99	4.90
<i>A. crozetensis</i>	Plant size	0.03	0.49	4.56
	% dead tissue	0.42	0.02	4.97
Mixed Pickle high				
<i>C. caecus</i>	Plant size	0.28	0.05	4.09
<i>C. antarcticus</i>	Plant size	-0.57	0.99	4.26
<i>A. crozetensis</i>	Plant size	0.52	0.01	4.03
Mixed Pickle mid				
<i>C. dubius</i>	% grass cover	-0.23	0.88	3.97
<i>C. caecus</i>	% grass cover	-0.21	0.81	4.65
Rhodacaridae sp	% grass cover	0.32	0.08	5.00
Mixed Pickle low				
<i>Dendrolaelaps</i> sp	% grass cover	-0.37	0.97	5.22
<i>C. caecus</i>	% grass cover	-0.31	0.94	4.39
<i>E. macquariensis</i>	% grass cover	0.37	0.01	5.18
<i>F. marionensis</i>	% grass cover	0.43	0.01	3.46
<i>Megalothorax</i>	% grass cover	0.28	0.05	5.34
<i>Nanorchestes</i> sp.	% grass cover	0.11	0.23	4.53
Swartkops high				
<i>C. caecus</i>	% dead tissue	0.48	0.01	5.19
<i>T. bisetosa</i>	% dead tissue	-0.29	0.97	4.21
Swartkops low				
<i>D. marionensis</i>	Plant size	-0.07	0.68	3.89
	% dead tissue	0.29	0.03	3.26
<i>M. striata</i>	Plant size	-0.36	0.96	4.24
	% dead tissue	0.36	0.01	3.19
Acari sp3	Plant size	-0.13	0.81	5.03
	% dead tissue	0.09	0.23	4.99
<i>T. bisetosa</i>	Plant size	0.37	0.01	3.86
	% dead tissue	-0.35	0.97	4.05

CHAPTER 3

The effects of aspect and altitude on distribution patterns in a microarthropod community on sub-Antarctic Marion Island: climate change implications.

Introduction

It has now been unequivocally shown that current climate change is altering species distributions (Walther et al. 2002; Parmesan and Yohe 2003; Root et al. 2003). The ranges of several species are shifting poleward (Parmesan et al. 1999; Parmesan and Yohe 2003; Walther et al. 2002) and upward in elevation (Fielding et al. 1999; Parmesan and Yohe 2003). Furthermore, because species tend to respond individualistically to climate change, this is likely to result in the alteration of community structure and the extinction of some species at local scales (Root et al. 2003; Thomas et al. 2004, McGeoch et al. in press). Knowledge of the current regional and local distributions of species (Heaney 2001; Walther et al. 2002; Sanders et al. 2003), as well as continued monitoring of species distributions are therefore critically important if we are to understand and predict the likely impacts of climate change on future distributions, as well as possible species extinctions (Peterson et al. 2002; Thomas et al. 2004).

Several approaches can be used to predict or demonstrate the impacts of climate change on future distribution patterns, each of which has strengths and weaknesses (Callaghan and Jonasson 1995; Parmesan et al. 2005). For example, databases with years of observation and monitoring data, which track distributional changes through time, can point to underlying mechanisms limiting species ranges (Parmesan et al. 2005). If the underlying mechanisms are climate related, species distributions may follow future climate changes similarly to changes in the past. The disadvantages of this method include the scarcity of long term data sets and the difficulty of interpretation and prediction if species distributions have not changed over time (Parmesan et al. 2005). The 'bioclimatic envelope' approach, on the other hand, entails mapping the current distribution of biota, and matches the observed pattern with the distribution of environmental factors. A suitable biological property of the species (i.e. cold tolerance) is then identified to explain the observed coincidence between the species' distribution and the environmental factor (Parmesan et al. 2005). Applying the species-specific property to predicted changes in the

environmental factor enables one to estimate the potential shift in distribution of the species (Davis et al. 1998; Pearson and Dawson 2003; Thomas et al. 2004). However, there is much debate on the reliability of this approach, because distribution patterns and dynamics of species are not only dependent on environmental factors, but also on biotic factors, such as species interactions (Davis et al. 1998; Lawton 2000; Pearson and Dawson 2003; Parmesan et al. 2005). Therefore, the 'bioclimatic envelope' approach is generally applied at large scales, where environmental influences on species distributions are known to generally be more important than biotic interactions (Pearson and Dawson 2003; Parmesan et al. 2005; Thuiller et al. 2005).

A complementary approach to predicting future species distributions at local and broad scales is to examine the spatial distribution of species across an environmental gradient, such as the temperature gradient found across altitude (Parmesan et al. 2005). Gradients can be seen as natural experiments (Smith et al. 2002; Brehm and Fiedler 2003; Parmesan et al. 2005) offering an analogue for future climates (Hodkinson and Bird 1998; Fielding et al. 1999; Hodkinson and Wookey 1999). For example, current distribution patterns of a species at cold, high altitudes may change with increasing temperature and may eventually resemble the species distribution patterns currently observed at warm, low altitudes. Abiotic factors, e.g. temperature and humidity, change rapidly from high to low altitudes, so that species responses to these factors can be assessed across a relatively small geographic area (Peterson et al. 1997). However, altitudinal gradients may not always be direct analogues of changing climates, since the temperature at certain altitudes may be warmer or colder than expected depending on the season. Furthermore, other factors, such as habitat type, local wind patterns and topography may also change, complicating the conclusions drawn from such studies (Parmesan et al. 2005).

Manipulation experiments, in which environmental variables can be controlled to isolate a single or few variables of interest, have thus also been used to understand likely climate change impacts (Callaghan and Jonasson 1995; Hodkinson and Wookey 1999; Dunne et al. 2004; Parmesan et al. 2005). However, biota may have delayed responses or different initial responses in short term manipulations compared with responses observed when the manipulation is sustained over longer periods, so that short-term experiments may not reveal realistic responses (Chapin et al. 1995; Dunne et al. 2004; Epstein et al. 2004). Ultimately, the integration of several approaches (e.g. short-term experiments combined with gradient studies) will overcome the limitations

of single approaches to understanding and predicting the impact of climate change on species distributions (Hodkinson and Wookey 1999; Dunne et al. 2004; Parmesan et al. 2005).

Although Southern Ocean islands are ideal for gradient and experimental studies to examine the likely consequences of climate change on species assemblages (see Vitousek 2002), only one gradient study (Davies and Melbourne 1999) and one experimental study (Le Roux et al. 2005; McGeoch et al. in press) on Macquarie Island and Marion Island, respectively, exist in the literature. Therefore the understanding of climate change impacts on the biota of these islands remains poor. These islands mostly rise from sea level to high altitudes in the span of only a few kilometres (Huntley 1972), presenting temperature and moisture gradients over relatively small distances. Furthermore, ecosystems on sub-Antarctic islands are remote, relatively closed systems with a harsh environment and fairly low species richness (Smith and Steenkamp, 1990). Southern Ocean islands are thus well-suited to gradient approaches to understanding the biotic consequences of climate change (Bergström and Chown 1999). One such island in the sub-Antarctic is Marion Island (Prince Edward Island group) situated 1770 km south of South Africa (Hänel and Chown 1999).

High latitude areas have and are expected to experience substantial climate changes (IPCC 2001) and the climate on Marion Island is no exception. Climate changes have been observed over the past 50 years on Marion Island with an increase in mean annual air temperature of more than 1.2 °C, an increase in sea temperature of 1.4 °C, an approximate 500 mm decrease in mean annual precipitation and an increase of 3.3 sunshine hours per year (Smith 2002; Melice et al. 2003). The number and size of rainfall events also declined with longer periods of dry spells (Le Roux and McGeoch submitted), which can have even higher impacts on organisms than the decline in mean annual rainfall (Weltzin et al. 2003). Indeed, there is already evidence of significant impacts of climate change on the distribution of biota on and around Marion Island. For example, surface nesting seabird abundance is declining because of environmental changes influencing their prey availability in the ocean (Crawford and Cooper 2003; Crawford et al. 2003; Pakhomov et al. 2004). The aerial cover of the sedge, *Uncinia compacta*, has increased on the nearby Prince Edward Island, due to declining moisture content of mires and warmer temperatures during its growing season (Chown and Smith 1993). The absence of this trend on Marion Island is due to

seed predation by the introduced house mouse, *Mus musculus* (Chown and Smith 1993). Indeed, one of the greatest impacts of climate change is likely to be the more favourable conditions it provides for the establishment and spread of alien species (Smith and Steenkamp 1990; Smith et al. 2001; Chown et al. 2002). It is predicted that populations of the house mouse will increase with warming (Smith and Steenkamp 1990). Increased mouse densities will have a negative impact on their prey densities, which consists mostly of soil invertebrates, especially weevils and plant seeds (Chown and Smith 1993; but see Van Aarde et al. 2004). Declining macro-invertebrates densities again affect the lesser sheathbills (*Chionis minor*: Charadriiformes), which depend on macro-invertebrates as a food source. The abundance of these birds has declined compared to the nearby, mouse-free Prince Edward Island (Huysen et al. 2000). Warming is also likely to favour alien microarthropods, as it has been shown that indigenous species prefer cool sites on the island, whereas introduced species are more abundant in warmer areas (Gabriel et al. 2001; Chown et al. 2002). In addition, warmer climates will affect the life cycles of microarthropods and since alien species generally have shorter generation times than indigenous species, warmer climates will favour the reproduction of alien species (Barendse and Chown 2000). Microarthropods (mites and springtails) are, together with other macro-invertebrates, the main detritivores on sub-Antarctic islands and essential for nutrient cycling and primary production in terrestrial ecosystems (Burger 1985; Smith and Steenkamp 1990; Chown et al. 2002). Therefore, a better understanding of current microarthropod spatial patterns and the possible future distributions on the islands as a consequence of climate change is critical.

Recently a climate change experiment was conducted on Marion Island to investigate the effects of reduced rainfall and increased shading on microarthropods that inhabit a keystone plant species on the island, *Azorella selago* (Le Roux et al. 2005; McGeoch et al. in press). Springtail abundance decreased significantly under experimental drying after only a single year (McGeoch et al. in press). Climate change experiments on microarthropods in the Arctic and Antarctic support these results, showing that moisture, at least for some species, is a more important determinant of species distributions in the region than temperature (Strathdee and Bale 1998; Sinclair et al. 2003; Leinaas and Somme 1984; Leinaas and Fjellberg 1985; Convey et al. 2002; Convey et al. 2003). Additionally, the Antarctic experiments revealed a general decrease in microarthropod (especially springtail)

abundance with warming (Convey 2001, Convey et al. 2002; Hayward et al. 2003). A warmer and drier climate is likely to alter microarthropod community structure (Bergström and Chown 1999; McGeoch et al. in press) and information on current distribution patterns of microarthropods at high latitude systems is thus important.

Therefore, in this study we examine the distribution patterns of microarthropods in the cushion plant, *Azorella selago* (Apiaceae), along a temperature gradient, i.e., across altitude, and compare distribution patterns between the drier, eastern and wetter, western sides of Marion Island. We then compare the patterns observed in this study to observations from climate change experiments involving microarthropods to predict the likely impact of climate change on species distributions on Marion Island (Dunne et al. 2004). Based on the outcome of the Marion Island climate change experiment we predicted that springtail abundance would be lowest at high altitudes and on the drier, eastern side of Marion Island (due to moisture sensitivity of springtails, Hopkin 1997), with no significant difference in mite abundance between altitudes and eastern and western sides. Furthermore, since species might not only respond to environmental factors, but also to specific habitat variables, such as plant size, the relationships between species richness, abundance and community structure and plant characteristics were also examined. Questions asked were: Are there relationships between microarthropod species richness, abundance and community structure and 1) altitude and side of the island, 2) plant characteristics, i.e. plant size, plant height, percentage dead tissue and percentage epiphyte cover?, and 3) how do individual species respond to altitude and side of the island?

Material and methods

Study sites and species

Marion Island (46°54'S; 37°45'E) lies about 1770 km south of Africa, with a surface area of 290 km², which rises to an altitude of 1230 m a.s.l. (Hänel and Chown 1999). The climate is oceanic, with a mean annual temperature of 5.7 °C; mean annual rainfall of approximately 1900 mm (as measured at the meteorological station on the north-eastern coast of Marion Island), a high degree of cloudiness and strong westerly winds (Schulze 1971; Hänel and Chown 1999; Smith 2002). Mean air, soil and within-plant temperatures decrease with an increase in altitude (Blake 1996; Boelhouwers 2003; Nyakatya et al. in prep; Table 1). An air temperature lapse rate of

approximately 4.0 °C every 1000 m is proposed for Marion Island (Klok and Chown 2003), which was supported by Nyakatya et al. (unpublished data) with an approximate difference of 2-3 °C in plants between the high and low altitude stands (Table 1). Wind speed is highest at high altitudes and rainfall peaks at mid-altitudes (Blake 1996), which is probably the result of adiabatic cooling processes (Heaney 2001). Freeze-thaw events are more frequent at mid-altitudes, but at high altitudes these events occur for longer periods with deeper soil freezing (Boelhouwers 2003; Le Roux 2004). Additionally, the western side of the island is colder than the eastern side, at least in summer (Table 1), and it receives more rain and stronger, more consistent wind due its exposure to the dominant westerly winds (Schulze 1971; Gremmen 1981; Le Roux 2004).

The cushion plant *Azorella selago* (Apiaceae) occurs from sea level to about 850 m a.s.l. on Marion Island (DW Hedding, personal communication) and varies in shape, size and density (Le Roux 2004; Hugo et al. 2004, Chapter 1). *Azorella selago* plants are thought to present a more favorable habitat in terms of microclimate and nutrients for microarthropods (Acari: mites and Collembola: springtails) than the fellfield soils in which it grows. Microarthropod densities are higher in plants than in the surrounding epilithic biotope (Barendse and Chown 2001). The grass *Agrostis magellanica* (Lam.) Vahl. is the dominant epiphyte on *A. selago* from about 100 to 500 m a.s.l. (Gremmen 1981; Le Roux 2004).

Twelve stands consisting of 36 *Azorella selago* plants (cushions > 0.15 m) each were selected at three altitudes in four different areas of Marion Island. Plants within plots may be considered independent as neither plant or microarthropod community variables were found to be significantly or consistently autocorrelated at this scale (Chapter 2). The low altitude stands were between 150 and 250 m a.s.l, middle altitude stands between 350 and 450 m a.s.l and the high altitude stands between 500 and 600 m a.s.l. For convenience the three stands, high, middle and low altitude, on each area of the island are together referred to as transects. Two transects were on the eastern side (Tafelberg and Stony Ridge) and two were situated on the western side (labelled Mixed Pickle and Swartkops) of Marion Island. These transects were located in typical grey or black lava fellfield (Table 1). Each *A. selago* plant was digitally photographed from above prior to sampling. Image analyses (software: SigmaScan Pro 5.0, Illinois, USA) were conducted to determine cushion size (surface area = m²), percentage dead tissue (brown or black stem or leaf areas on the plant

surface) and percentage of the plant surface covered by the epiphytic grass, *Agrostis magellanica*.

Table 1. Study stands in fellfield habitat along four altitudinal transects on Marion Island (Temperatures were measured using iButton dataloggers (Thermocron DS1921G, Dallas Semi-Conductors, 0.5C resolution). The dataloggers were inserted three cm deep into three plants per stand for a period of 60 days in winter and 61 days in summer (temperature data from Nyakatya et al. in prep).

Stand	Position 46° South	Position 37° East	Altitude (m a.s.l.)	Summer Temperature (°C) ± SE	Winter Temperature (°C) ± SE
Tafelberg					
Low	52° 749''	49° 651''	176	7.07 ± 0.28	2.60 ± 0.24
Middle	53° 276''	48° 125''	375	6.41 ± 0.31	1.82 ± 0.22
High	53° 670''	47° 293''	588	4.98 ± 0.33	0.52 ± 0.15
Stony Ridge					
Low	54° 917''	51° 435''	163	7.25 ± 0.28	2.52 ± 0.24
Middle	54° 608''	49° 062''	380	5.90 ± 0.31	1.50 ± 0.22
High	54° 059''	47° 978''	620	4.72 ± 0.34	1.14 ± 0.18
Mixed Pickle					
Low	52° 574''	38° 539''	222	5.37 ± 0.26	3.13 ± 0.22
Middle	53° 224''	38° 858''	375	5.00 ± 0.23	2.46 ± 0.20
High	53° 839''	39° 268''	600	3.28 ± 0.30	0.84 ± 0.15
Swartkops					
Low	55° 789''	36° 481''	216	6.02 ± 0.23	3.17 ± 0.22
Middle	55° 818''	37° 225''	415	4.72 ± 0.26	1.58 ± 0.23
High	56° 195''	37° 520''	575	3.42 ± 0.27	1.59 ± 0.19

Sampling

Microarthropods were sampled between November 2002 and February 2003, coinciding with peak abundances observed during summer (Barendse and Chown 2001). Sampling was alternated between east and west stands finishing one transect (high, middle, low) at a time (Table 2) (see Chapter 2 for transit times of samples from sampling sites). Sampling was done using an O'Connor split corer (inside diameter of core = 70 mm, height = 70 mm, surface area = 0.0039 m²). Core samples

were taken from all 36 plants in each stand (except in the Mixed Pickle high altitude stand where one plant was too small to sample), thus a total of 431 cores. The microarthropods were extracted from the cores using a MacFadyen high-gradient extraction protocol of two days at 25 °C and two days at 30 °C (Southwood 1978; Barendse and Chown 2001; Barendse et al. 2002; Hugo et al. 2004). Microarthropod specimens were identified to the lowest possible taxonomic level (usually species), counted and stored in 99 % ethanol at the University of Stellenbosch.

Table 2. Microarthropod species richness and abundance, plant size, % dead tissue in the plant and % grass cover along four transects at three altitudes. The month in which the samples were taken is indicated (n = 36, except Mixed Pickle high n = 35).

	Mean species richness \pm SE	Total Species	Mean abundance \pm SE	Total abundance	Plant size (m ²) \pm SE	Median % dead tissue (range)	Median % grass cover (range)	Date sampled
Tafelberg								
Low	13.94 \pm 0.27	23	204.19 \pm 9.45	7351	0.19 \pm 0.02	13.64 (42.94)	11.39 (23.70)	Dec 2005
Middle	12.89 \pm 0.34	22	261.08 \pm 10.45	9399	0.89 \pm 0.15	3.62 (15.47)	7.22 (35.31)	Dec 2005
High	12.89 \pm 0.33	24	224.36 \pm 12.82	8077	0.15 \pm 0.02	2.97 (29.95)	0	Dec 2005
Stony Ridge								
Low	13.75 \pm 0.33	28	275.33 \pm 12.62	9912	0.30 \pm 0.04	3.04 (25.72)	13.63 (55.35)	Jan 2003
Middle	9.67 \pm 0.35	23	172.19 \pm 14.38	6199	0.26 \pm 0.05	3.81 (26.05)	4.89 (13.43)	Jan 2003
High	12.50 \pm 0.44	27	203.39 \pm 11.78	7322	0.24 \pm 0.05	2.43 (27.88)	0	Jan 2003
Mixed Pickle								
Low	16.69 \pm 0.40	29	349.56 \pm 16.43	12584	0.21 \pm 0.27	4.08 (28.82)	7.55 (22.69)	Dec 2002
Middle	18.39 \pm 0.36	30	316.83 \pm 10.87	11406	0.15 \pm 0.02	6.56 (44.63)	0 (11.42)	Nov 2002
High	15.26 \pm 0.32	22	300.17 \pm 13.62	10506	0.16 \pm 0.02	6.00 (24.94)	0 (2.73)	Dec 2002
Swartkops								
Low	16.17 \pm 0.33	27	322.92 \pm 11.09	11625	0.13 \pm 0.01	5.31 (19.12)	6.46 (26.93)	Feb 2003
Middle	15.89 \pm 0.43	27	290.00 \pm 14.70	10440	0.14 \pm 0.02	6.09 (13.50)	0 (0.44)	Jan 2003
High	14.53 \pm 9.00	28	285.86 \pm 15.47	10291	0.13 \pm 0.03	0.88 (14.14)	0 (1.65)	Jan 2003

Analyses

Generalized linear models (McCullagh and Nelder 1989) were used to determine the relationship between microarthropod species richness and abundance (separate models for each of these dependent variables) in the *Azorella selago* plants and explanatory variables. Explanatory variables (factors in some cases) included were side of the island (east, west), altitude (low, middle, high), plant surface area, plant height, and percentage dead tissue. In addition, separate models for species richness and abundance with island side, altitude, surface area, plant height, percentage dead and percentage grass cover were constructed for the middle and low altitude stands because of the scarcity or absence of grass at high altitude stands. A Poisson error distribution was assumed for species richness and abundance, a logarithmic link function was used and deviance used as a measure of goodness of fit (Dobson 2002). 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).

Mite and springtail community structure at high, middle and low altitudes, as well as on the eastern and western side of Marion Island was examined using cluster analysis based on group averaging and Bray-Curtis similarity measures (Primer v5, Clarke and Gorley 2001). Primer constructs a triangular matrix of Bray-Curtis similarity coefficients between every pair of samples and Analysis of similarity (ANOSIM) and non-metric multidimensional scaling (MDS) ordinations are then calculated from this matrix (Clarke and Warwick 1994). Abundance data were fourth root transformed and standardized prior to analysis (to weigh common and rare species equally (Clarke and Warwick 1994). ANOSIM was used to test for significant differences between the communities on different altitudes and sides (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). Means of mite and springtail abundances across a stand i.e., the mean abundance across 36 samples were used in the MDS ordinations for clarity.

Redundancy Analysis was conducted to examine differences in microarthropod community structure between sides of the island and at different altitudes, and the responses of individual species to these environmental gradients

(CANOCO v4.5; Ter Braak and Šmilauer 2002; Lepš and Šmilauer 2003). Redundancy Analysis (RDA) was chosen after examining the gradient lengths of species in the environmental space following Detrended Correspondence Analysis (DCA) (Jongman et al. 1995). RDA analysis was performed separately on log transformed springtail and mite species data (with post-transformation of species scores and species centering) and displayed in ordination biplots. Springtails and mites were examined separately, because of their different responses to environmental variables (McGeoch et al. in press). The species were entered as dependent variables and side of the island and altitude as nominal environmental variables. Monte Carlo permutation tests (499 permutations) were used to evaluate the significance of the first and all axes (Lepš and Šmilauer 2003). Also, the eigenvalues for the first two axes were used to denote how much of the total variance in the species data was explained by the environmental variables (Lepš and Šmilauer 2003). RDA ordinations approximate the relationships between the species and the environmental variables. In the ordinations microarthropod species are displayed as arrows (the direction of the arrow indicates in which direction species abundance increases) and side and altitude (nominal variables: east, west and low, middle and high stands) as centroids (distances between centroids provide an estimate of the dissimilarity of their species composition) (Lepš and Šmilauer 2003). Mite species that had > 5 % of their variation explained by the first ordination axis was included (Lepš and Šmilauer 2003).

Results

A total of 31 (22 mite and 9 springtail) species and 115111 individuals were collected across the 12 sample stands (Appendix, Table 2). Mixed Pickle mid- altitude stand had the most species (30 species) and the low altitude stand along this transect the highest mean abundance per plant (349.56 individuals/plant) (Table 2). The lowest species richness was found at the Tafelberg mid-stand (22 species) and the lowest mean abundance at Stony Ridge mid-stand (172.19 individuals/plant). The mite species *Eupodes minutus* constituted 40 % of all individuals sampled and 76 % of all mite individuals. The most abundant springtail species was *Folsomotoma marionensis*, which constituted 35 % of all springtail individuals.

Island side and altitude contributed significantly to explaining mite and springtail species richness and abundance (Table 3). Plant characteristics contributed to explaining variability in species richness and abundances in only a few cases. Plant

size explained significant variability in mite species richness and abundances, plant height in mite abundance and springtail species richness and percentage grass cover in mite species richness (Table 3).

Table 3. Model fit and contribution of explanatory variables to the generalized linear models for mite and springtail species richness (S) and abundance (N). Letters in bold indicate significant values. (Analyses including % grass cover were only conducted for middle and low altitude plots (8 plots) due to the scarcity or absence of grass at high altitude plots).

Dependent variable	df	Deviance/ df	Explanatory variable	df	χ^2	P	Sign of estimate
Mite S	422	1.00	Cushion area	1	3.94	0.05	-
			Height	1	1.60	0.21	-
			% dead	1	1.78	0.18	+
			Island side	1	205.35	<0.001	-
			Altitude	2	13.88	<0.001	-
			Side*Altitude	2	27.94	<0.001	-
Mite N	422	1.00	Cushion area	1	3.93	0.05	+
			Height	1	5.23	0.02	+
			% dead	1	0.01	0.94	-
			Island Side	1	12.76	<0.001	-
			Altitude	2	3.07	0.21	-
			Side*Altitude	2	0.03	0.99	-
Springtail S	422	1.00	Cushion area	1	0.03	0.87	-
			Height	1	4.79	0.03	+
			% dead	1	1.34	0.25	+
			Island side	1	71.47	<0.001	-
			Altitude	2	27.53	<0.001	-
			Side*Altitude	2	19.20	<0.001	-
Springtail N	422	1.00	Cushion area	1	0.67	0.42	-
			Height	1	0.72	0.40	-
			% dead	1	0.35	0.55	+
			Island Side	1	207.59	<0.001	-
			Altitude	2	12.34	0.002	-
			Side*Altitude	2	0.66	0.72	-
Mite S (8 plots)	280	1.00	Cushion area	1	2.25	0.13	-
			Height	1	1.04	0.31	-
			% dead	1	0.30	0.54	-
			% grass	1	6.07	0.01	-
			Island Side	1	150.99	<0.001	-
			Altitude	1	1.73	0.19	-
Mite N (8 plots)	280	1.00	Side*Altitude	1	23.09	<0.001	-
			Cushion area	1	1.20	0.27	-
			Height	1	3.47	0.06	-
			% dead	1	0.03	0.86	-
			% grass	1	0.36	0.55	+
			Island Side	1	5.51	0.02	+
Springtail S (8 plots)	280	1.00	Altitude	1	0.67	0.41	-
			Side*Altitude	1	<0.001	0.98	-
			Cushion area	1	0.02	0.90	-
			Height	1	4.66	0.03	-
			% dead	1	2.20	0.14	-
			% grass	1	6.89	0.01	+
			Island Side	1	44.55	<0.001	-

Springtail N (8 plots)	280	1.00	Altitude	1	2.27	0.13	
			Side*Altitude	1	17.42	<0.001	
			Cushion area	1	1.05	0.31	
			Height	1	1.43	0.23	
			% dead	1	0.20	0.66	
			% grass	1	0.51	0.47	-
			Island Side	1	104.54	<0.001	
			Altitude	1	4.32	0.04	
			Side*Altitude	1	0.79	0.38	

Mite and springtail species richness, as well as springtail abundances were significantly higher on the western side of the island (Fig. 1). Furthermore, mite and springtail species richness and springtail abundance were also significantly lower at high altitudes (Fig. 1). Microarthropod abundance declined monotonically with altitude, although not significantly (Fig. 1, Table 3). The significant interaction between side and altitude for mite and springtail species richness (Table 3) demonstrates that the effect of altitude on species richness is different between the eastern and western sides of the island (Quinn and Keough 2002). Mite and springtail species richness showed a mid-altitude peak on the western side, in contrast to the eastern side where the mid-altitude stand had the lowest species richness (Fig. 1).

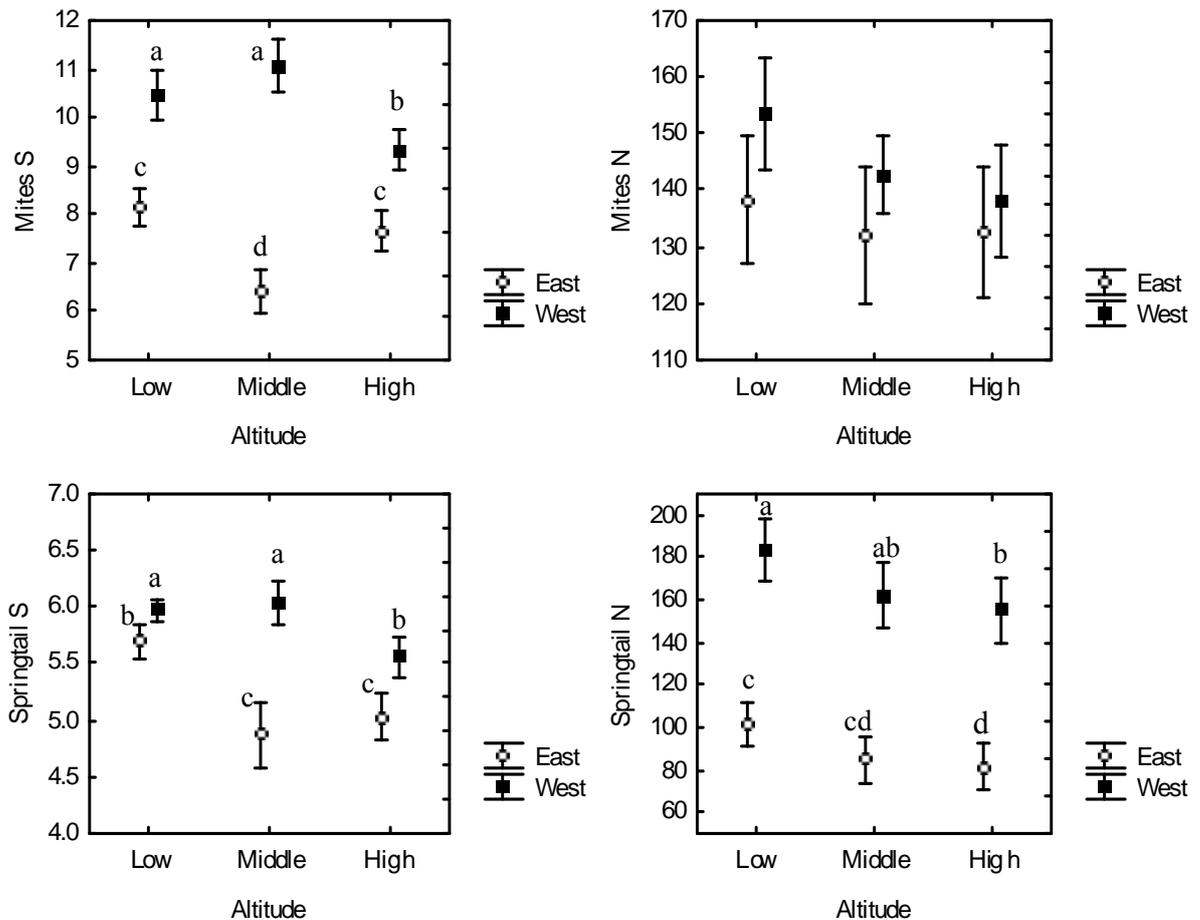


Fig. 1. Interaction plot of mite and springtail species richness (S) and abundance (N) at low, middle and high altitudes on the eastern and western side of Marion Island (weighted means \pm 95% confidence intervals). Different letters (superscript) indicate a significant difference of $P < 0.05$. Model results provided in Table 3.

Springtail communities differed significantly between sides of the island (Global $R = 0.12$, $P = 0.001$) and between altitudes (Global $R = 0.10$, $P = 0.001$) with a lower dissimilarity between the high and low stands (Global $R = 0.16$, $P = 0.001$) than between the high and middle stands (Global $R = 0.08$, $P = 0.001$) or the middle and low stand (Global $R = 0.07$, $P = 0.001$) (Fig. 2a). Similarly, mite community structure also differed significantly between sides of the island (Global $R = 0.35$, $P = 0.001$) and between altitudes (Global $R = 0.12$, $P = 0.001$) with a lower dissimilarity between the high and low stands (Global $R = 0.22$, $P = 0.001$) than between the high and middle stands (Global $R = 0.08$, $P = 0.001$) or the middle and low stand (Global $R = 0.06$, $P = 0.001$) (Fig. 2b).

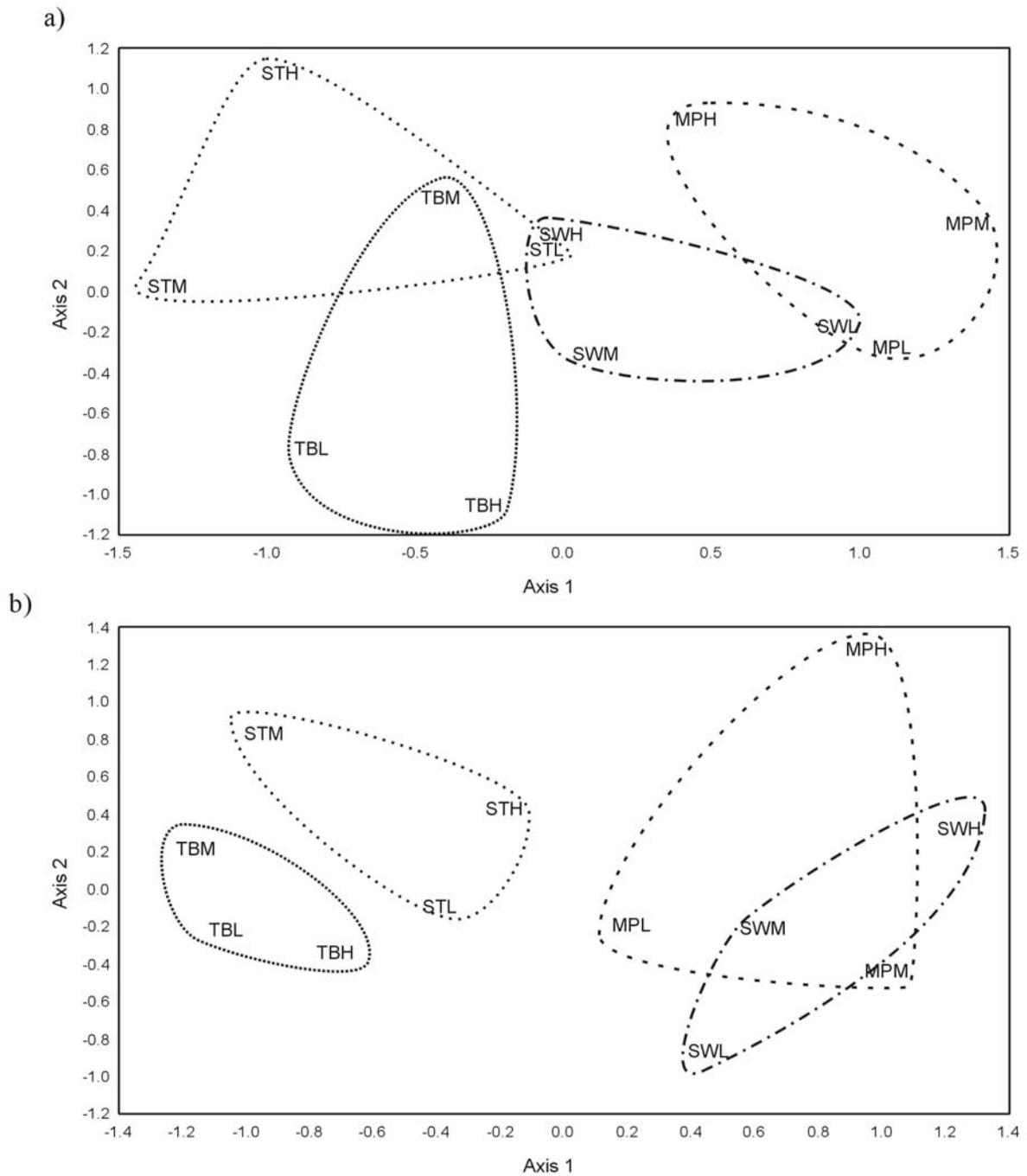


Fig. 2. Non metric multi-dimensional scaling (MDS) ordinations of the assemblage structure of a) springtails and b) mites in *Azorella selago* plants in 12 different sites across Marion Island (Stress: springtails: = 0.13, mites = 0.1) (TB = Tafelberg, ST = Stony Ridge, MP = Mixed Pickle, SW = Swartkops, H = high-, M = middle-, L = low altitude stand).

Redundancy Analysis (RDA) supported these differences (Monte Carlo test results for all canonical axes: springtails: $F = 33.49$, $P < 0.01$; mites: $F = 28.85$, $P < 0.01$). The first axis (vertical axis) in the springtail ordination explained 17 % of the variation in abundance ($F = 86.69$, $P < 0.01$) and separated the western and eastern sides of the island, and the second (horizontal) axis (explaining 5 % of the variation) clearly separated the high stand from the mid and low altitude stands (Fig. 3a). Eight springtail species were more abundant in the western stands and four of these were more abundant at low altitudes (Fig. 3a). For the mite community the first (vertical) ordination axis ($F = 55.85$, $P < 0.01$) explained 12 % of variation in abundance and similarly separated the west from the east, whereas the second (horizontal) axis (7 %) again separated the high stand from the mid and low altitude stands (Fig. 3b). There was much more variability in the responses of mite species to altitude and island side compared to the springtail species. The abundance of twelve mite species was higher at the western side and one of these was more abundant at the high altitude stands, while only two mite species were more abundant in the eastern stands (Fig. 3b).

The alien species, *Isotomurus cf. palustris* (springtail) and Cillibidae sp. (mite) (Appendix), were more abundant on the western, low and middle stands (Fig. 3 a,b), although their abundances remained low throughout. On the western side only 18 individuals of *I. palustris* were collected and none on the east. For the Cillibid mite 673 individuals were collected on the west and only 123 individuals on the eastern side.

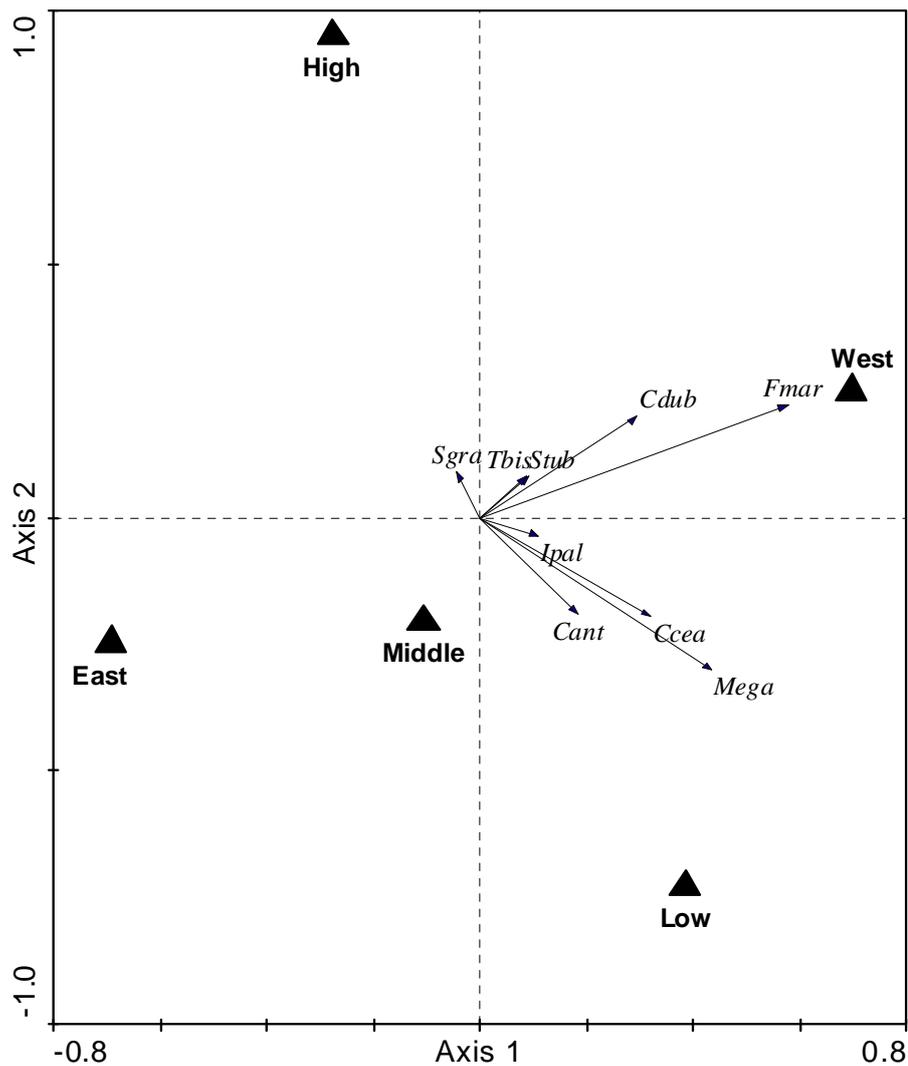


Fig. 3a. Redundancy analysis (RDA) ordination of springtail communities at different altitudes (high, middle, low) and sides of the island (east, west). Altitude and side are presented as centroids and microarthropod species shown as arrows. The RDA1 and RDA2 axis denote how much of the total variance in microarthropod species data is explained by the variables (RDA1 = 17 %, RDA2 = 5 %). The distances between the centroids denote the dissimilarity between the microarthropod communities at different altitudes and sides. The direction of the microarthropod species arrows shows increasing abundance towards that specific variable and the length of the arrow indicates the approximate standard deviation of the species values (Lepš and Šmilauer 2003). Species abbreviations in the Appendix.

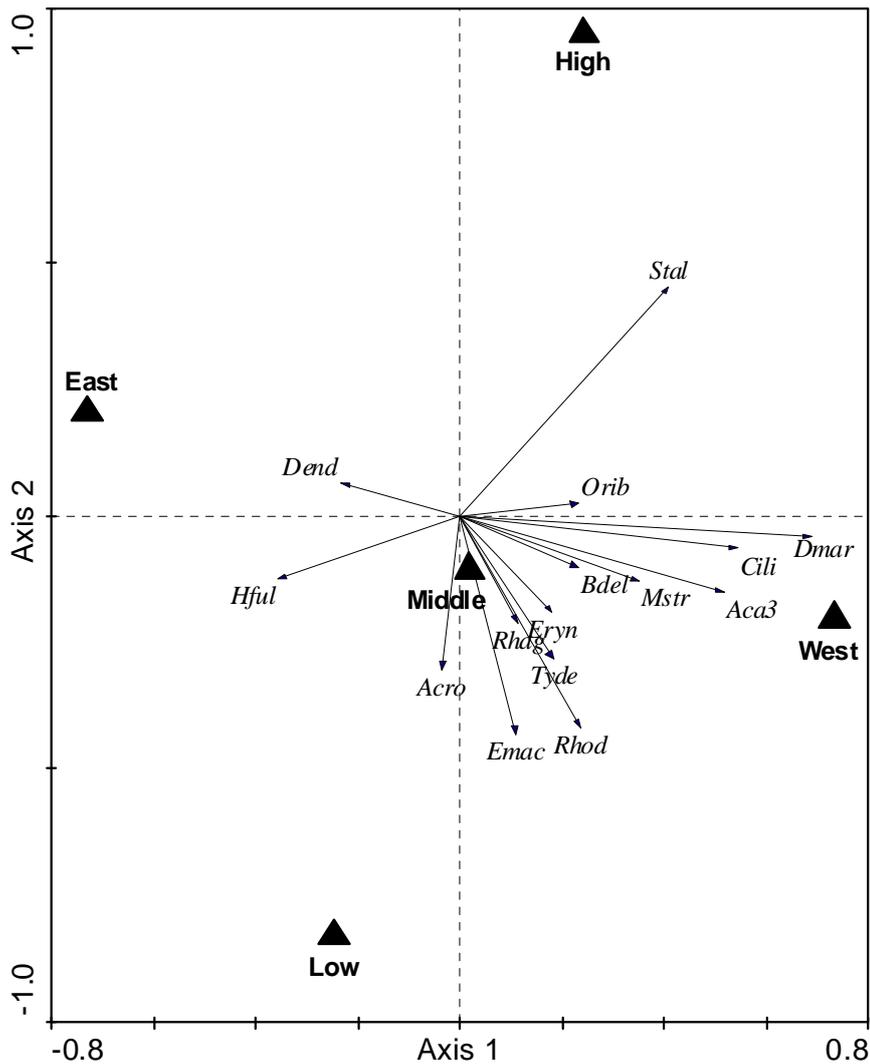


Fig. 3b. Redundancy analysis (RDA) ordination of mite communities at different altitudes (high, middle, low) and sides of the island (east, west). Altitude and side are presented as centroids and microarthropod species shown as arrows. The RDA1 and RDA2 axis denote how much of the total variance in microarthropod species data is explained by the variables (RDA1 = 12 % RDA2 = 7 %). The distances between the centroids denote the dissimilarity between the microarthropod communities at different altitudes and sides. The direction of the microarthropod species arrows shows increasing abundance towards that specific variable and the length of the arrow indicates the approximate standard deviation of the species values (Lepš and Šmilauer 2003). Species abbreviations in the Appendix.

There were also distinct differences in the relative abundances of species between sides of the island (Fig 4a). On the western side the springtail species *Folsomotoma marionensis* and *Megalothorax* sp. were dominant, whereas on the east the dominant species were *Cryptopygus dubius*, *C. antarcticus* and *Tullbergia bisetosa*. The mite species *Eupodes minutus* was by far the most dominant and slightly more so on the eastern side of the island. Other mite species, including *Austroppia crozetensis*, *Nanorchestes* sp., *Halozetes fulvus* and *Dendrolaelaps* were also more dominant on the eastern side. On the western side Rhodacaridae sp., *Ereynetes macquariensis* and *Schwiebea talpa* were the dominant species (Fig. 4a). Changes in dominance of species across altitude were also observed, although these were not as marked as those between sides of the island. Generally, abundance of the springtail *Cryptopygus dubius* was higher at high altitudes, whereas *F. marionensis* was dominant at mid-altitudes (Fig. 4b). For the mites, *E. minutus* was dominant at all altitudes. In addition *A. crozetensis* dominated at lower altitudes, whereas *S. talpa* had higher abundances at high altitudes (Fig. 4b).

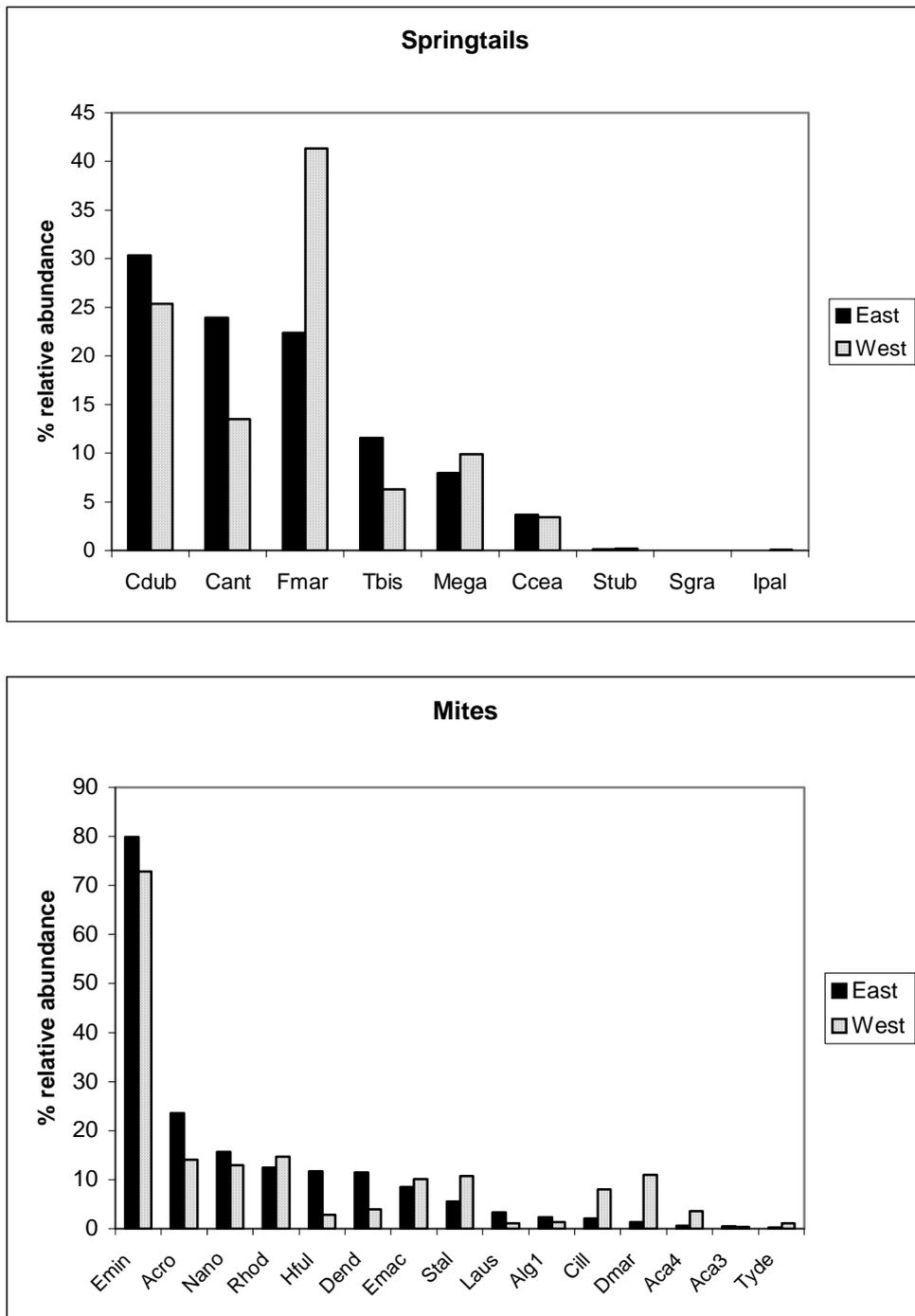


Fig. 4a. Relative abundances of springtail and mite species at the east (black) and west (hatched) side of the island. All mite species other than the dominant *Eupodes minutus* are expressed as a percentage of total individuals excluding *E. minutus*. The seven least abundant mite species are not included. Species abbreviations in the Appendix.

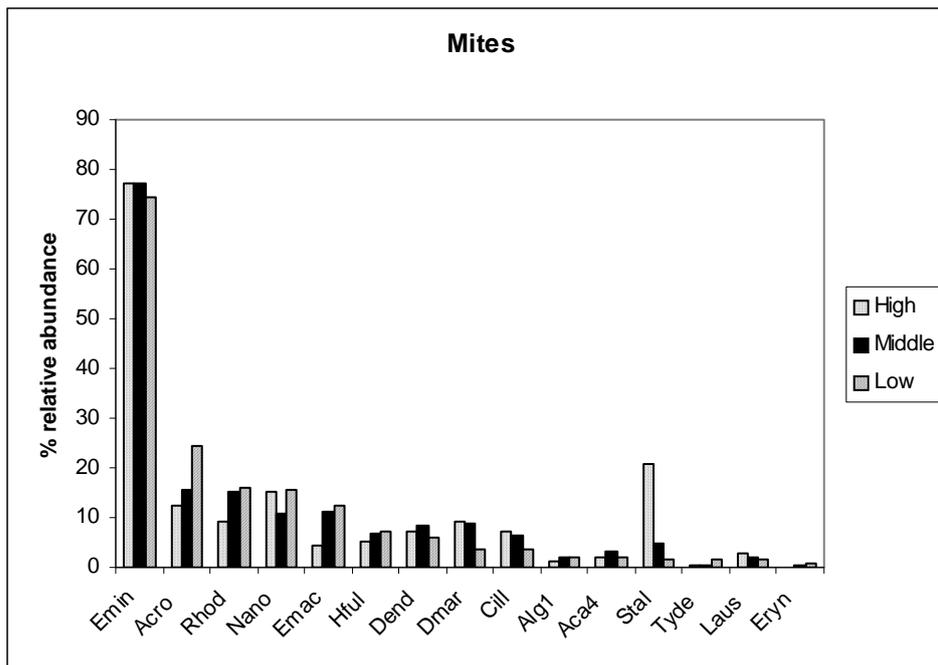
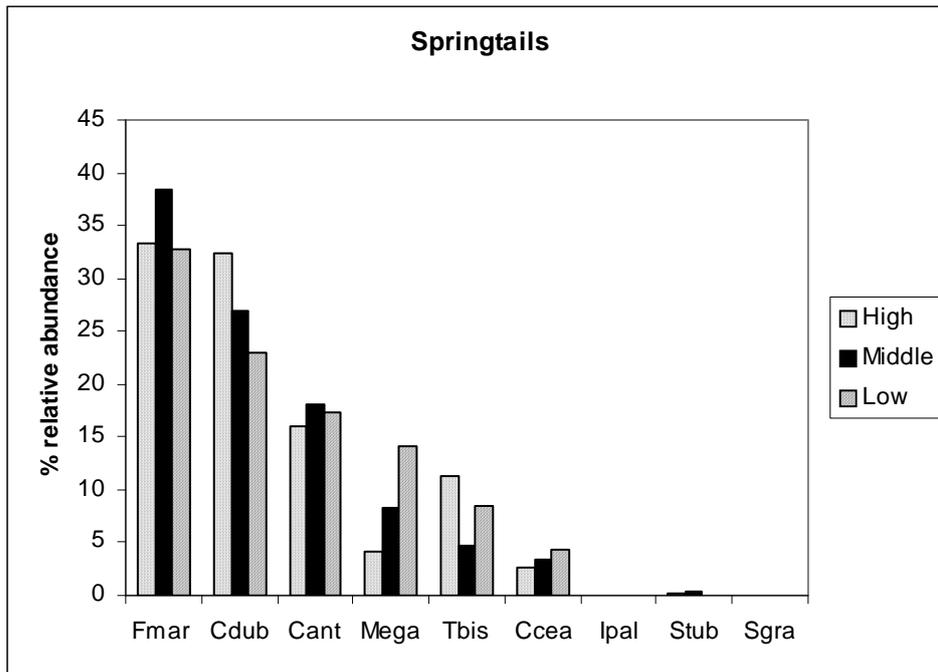


Fig. 4b. Relative abundances of springtail and mite species at high (hashed) middle (black) and low (striped) altitudes. All mite species other than the dominant *Eupodes minutus* are expressed as a percentage of total individuals excluding *E. minutus*. The seven least abundant mite species are not included. Species abbreviations in the Appendix.

Discussion

The strongest pattern in this study was the significant difference in microarthropod species richness, abundance and community structure between the western and eastern sides of Marion Island. Mite and springtail species richness and springtail abundances were significantly higher on the western side, whereas mite abundances were not. The second clear observation was that mite and springtail species richness and springtail abundance were significantly lower at high altitudes, while mite abundances declined, albeit not significantly, with altitude. Furthermore, plant characteristics generally did not contribute to explaining species richness and abundance, and when they did patterns were inconsistent across taxa and sites. Therefore, at the island-wide scale abiotic, rather than biotic, factors appeared to be more important determinants of patterns in microarthropod distribution and community structure (Scheidel et al. 2003).

Island side

Although it has been argued that the direct effects of temperature are more important than other factors in determining invertebrate distributions (Bale et al. 2002), this is not always the case in polar regions. Organisms at high latitudes are limited by temperature, as well as water availability (Kennedy 1993; Convey et al. 2003). Temperature and water are, however, strongly related to each other, especially in polar regions (Hodkinson et al. 1999; Weltzin et al. 2003). For example, wet soils and plants are thermally buffered compared to dry soils and plants (Hodkinson et al. 1999). Since the western side of Marion Island receives more rainfall and has a higher percentage cloud cover than the eastern side (Schulze 1971; Gremmen 1981), a moisture gradient exists across the island. It must be noted that weather conditions might have changed slightly since the report by Schulze (1971), but because more recent weather data on the western side is absent, it is assumed that the difference in climatic conditions with island side has not changed significantly. The moisture gradient across the island presumably results in a higher moisture content in plants on the western side. This difference in moisture, together with the more favourable, buffered temperature inside plants (Nyakatya et al. unpublished), are likely to be important determinants of microarthropod distribution patterns at the island-wide scale. Apart from the direct effects of moisture on microarthropods, moisture also controls rates of organic matter decomposition in fellfield environments (Smith et al.

1993). Therefore, higher decomposition rates may indirectly favour microarthropods in plants on the western side by increasing food resources.

Furthermore, moisture is also likely to be important in determining distributions of desiccation susceptible species (Block and Harrison 1995; Strathdee and Bale 1998; Sinclair et al. 2003; Leinaas and Somme 1984; Leinaas and Fjellberg 1985; Convey et al. 2002; Convey et al. 2003). Most springtail species are not desiccation resistant (Sømme 1995; Hopkin 1997; Hodkinson and Wookey 1999; Convey et al. 2003), and this may explain the fact that springtail abundance was higher on the western side of the island, where there is presumably a more favourable moisture regime. The absence of a strong difference in mite abundance between sides of the island may be due to the higher desiccation tolerance of mites compared to springtails (Hodkinson et al. 1999; Convey et al. 2003). The tolerance of species to desiccation may also result in divergent selection of microhabitats within a plant (Hopkin 1997). For example, deeper litter dwelling species (euedaphic species), which are less desiccation resistant, such as *Cryptopygus caecus* and *Megalothorax* sp. experience more favorable microclimatic conditions inside the plants compared to conditions on the plant surface and are thus to some extent buffered against harsh environmental conditions (McGeoch et al. in press). In contrast, upper, surface dwelling species (hemiedaphic), like *Folsomotoma marionensis*, will be more susceptible to moisture conditions on the plant surface (Hopkin 1997). One would thus expect that the euedaphic and hemiedaphic species would respond differently to different moisture regimes across the island. Indeed, the abundances of the litter dwelling species (*Megalothorax* sp., *C. caecus*) were more similar between the western and eastern sides than the surface dwelling species (*F. marionensis*) (Fig. 4a). These responses of the litter and surface dwelling species are supported by the results of the Marion Island climate change experiment (McGeoch et al. in press). The surface dwelling species revealed lower abundances in the dry-warm treatment than the deeper, litter dwelling species (McGeoch et al. in press). A drier climate is thus likely to have a more severe effect on surface-dwelling species than on the deeper litter dwelling springtail species on Marion Island.

Altitude

This study also found lower species richness and abundance at high altitudes compared to low altitudes. It is generally accepted that species richness and abundance in terrestrial systems decline with altitude (Rahbek 1995; Gaston and Spicer 2004). There are a number of explanations for this decline, which are not always independent of each other e.g., lower plant productivity, less available habitat, and generally lower rainfall at high altitudes (Heaney 2001). The distribution of arthropods across altitudes, as well as responsible mechanisms, has been well documented. For example, soil microarthropod abundances decreased with altitude on Shergyla Mountain in Tibet due to increasing harshness of the environment and less available resources (Jing et al. 2005). Lower arthropod abundance and species richness were also observed at high altitudes in the Venezuelan Andes, because of low plant productivity (Janzen et al. 1976). Arthropod species richness has also been shown to decline with altitude on sub-Antarctic Macquarie Island, as a result of either a decline in temperature or an increase in wind exposure or a combination of the two variables (Davies and Melbourne 1999). Finally, leaf litter invertebrate abundances decreased with altitude in western Panama due to low decomposition rates at high altitudes (Olson 1994). On Marion Island, a mean temperature difference of 2.32 °C in summer was observed between low and high altitude stands (Table 1, Tafelberg transect = 2.09 °C, Stony Ridge transect = 2.53 °C, Mixed Pickle transect = 2.09 °C, Swartkops transect = 2.60 °C). Furthermore, wind speed is known to be highest at high altitudes (Blake 1996) and deep soil freezing occurs for extended periods of time (Boelhouwers 2003). These abiotic factors, i.e. low temperature, low humidity and the generally harsh environment are thus likely to limit microarthropods distributions at high altitudes on Marion Island.

However, most high latitude invertebrates have adapted to withstand cold temperatures (Hodkinson and Wookey 1999; Callaghan et al. 2004; Chown and Nicolson 2004). Therefore, other factors e.g., lower resource and habitat diversity, in combination with declining temperature, may also explain the low abundances of microarthropod distributions at high altitudes (Lawton et al. 1987; Heaney 2001; Jing et al. 2005). On Marion Island the grass, *Agrostis magellanica*, grows epiphytically on *Azorella selago* plants up to approximately 500 m a.s.l. (Gremmen 1981; Le Roux 2004). The roots of *A. magellanica*, which are imbedded in *A. selago* plants, increase nutrients, as well as habitat and nutrient diversity for microarthropods (Seastedt 1984;

Smith and Newton 1986). Indeed, at the within plant scale, more microarthropods were found in areas in *A. selago* plants with more *A. magellanica* (Hugo et al. 2004). However, there was no relationship between *A. magellanica* and microarthropod abundance at this scale, i.e. island wide, supporting the proposition that abiotic factors are more important determinants of microarthropod distributions than biotic factors at the island-wide scale.

Microarthropods as indicators of climate change

The prediction of the effects of climate change on invertebrates with the use of experimental and/or gradient studies depends on whether species adapt to change *in situ* or shift their distributions (Butterfield 1996; Bale et al. 2002). Since the growing-season at high latitudes is short, polar species have fewer generations per year compared to tropical species and therefore have less time to evolve in response to environmental change (Chown and Nicolson 2004). Although polar species may develop faster with warmer temperatures brought about by climate change (Bale et al. 2002), they can only adapt to changes happening within the growing season. Sometimes it is physiologically expensive for insects to adapt to drier or warmer conditions, so that they would rather avoid adverse environmental conditions through behavior and microhabitat selection (Feder et al. 2000; Chown and Nicolson 2004). Microarthropods in polar regions are mostly adapted to withstand cold temperatures, e.g. via supercooling (Hodkinson and Wookey 1999). The temperature that microarthropods experience within *Azorella selago* plants, is well within the range between their upper and lower lethal limits (at least for some species) (Marshall and Chown 1995; Slabber 2005). However, microarthropods, especially springtails, are not resistant to desiccation (Hopkin 1997, Convey et al. 2003) and a combination of low humidity and high temperatures could be lethal. Since it has been found that springtails move to habitats with a more favorable moisture status (Hertzberg et al. 1994; Hayward et al. 2004), it can be assumed that microarthropods are more likely, at least in the short to medium term, to shift their distributions in response to environmental change than adapt physiologically (Callaghan et al. 2004).

Further, if microarthropods shift their distributions, it is important to know if they move in response to biotic, e.g., species interactions, or abiotic factors. Since abiotic factors appear to be more important determinants than biotic factors in determining microarthropod distributions on Marion Island (plant characteristics did

not explain patterns in species richness and abundance), microarthropods have good potential as indicators for monitoring the impact of climate change on biodiversity in the sub-Antarctic (see Convey et al. 2003 for an Antarctic example).

Comparison with experimental evidence

Dunne et al. (2004) argued that a combination of results from gradient and experimental climate change studies is extremely useful to understand and predict the impact of climate change on species distributions (also see Hodkinson and Wookey 1999; Shaver et al. 2000). Therefore, by comparing the results from this study to those from the Marion Island climate manipulation experiment (McGeoch et al. in press), as well as to other field experiments, it is possible to make species-specific predictions for the responses of microarthropods on Marion Island to climate change.

As predicted, in this study, springtail abundance was lower on the drier eastern side, while mite abundance was not significantly different. This supports the results of the Marion Island climate manipulation experiment, where springtail abundance was significantly lower under the dry-warm treatments, while mite abundances did not show a significant response (McGeoch et al. in press) (see Table 4 for a summary). In another field experimental study in Antarctica, water amendment treatments of soil resulted in a significant increase in microarthropod abundances (Convey et al. 2002), highlighting the importance of moisture for microarthropods.

The majority of climate change field experimental studies on microarthropods at high latitudes have investigated the effect of warming on microarthropod distributions. In a three year experiment in the Arctic, springtail abundance declined significantly under warming (increase in 10 % of summer heat budget in warming treatment), while the oribatid (Cryptostigmata) mites were not affected (Coulson et al. 1996; Webb et al. 1998). Similarly, in a four year experiment in Antarctica, springtail abundance declined under warming (2.2 °C - 2.4 °C increase) (Convey et al. 2002). In contrast, Kennedy (1994) found an increase in springtail and mite abundances under warming treatments in an eight year experiment in Antarctica (mean warming 0.44 °C - 0.50 °C). It is thus clear that the responses of microarthropod abundances varied across field experiments, and generalizations regarding the impact of climate change on microarthropods abundances and distributions should be made with caution. Furthermore, in most of these climate change experiments, species showed idiosyncratic responses to the treatments. Similarly, in the Marion Island climate

manipulation experiment only five mite and five springtail species were found to respond significantly to treatments, i.e., mites: *Eupodes minutus*; Rhodacaridae sp., Cillibidae sp., *Macquarioppia striata*, *Halozetes fulvus* and springtails: *Tullbergia bisetosa*, *Folsomotoma marionensis*, *Cryptopygus dubius*, *C. antarcticus travei*, *Sminthurinus tuberculatus*, and the responses were in many instances variable (McGeoch et al. in press). Nonetheless, although the direction of response and species-specific responses vary, the evidence is clear across all these related studies that springtails are highly responsive to changes in climate.

Table 4. Summary of microarthropod abundances and individual species abundances (only those which had a significant response to treatments in the Marion island manipulation experiment) in 1) this study (altitude and side of the island), 2) the Marion Island manipulation experiment (dry-warm and shade treatments and procedural control) and 3) the distribution of the species in vegetation types across the island (from Gabriel et al. 2001 and Barendse et al.2002), as well as 4) the predicted change in abundances with climate change based on current evidence (higher abundance is indicated by ↑, lower abundance by ↓ and cases where prediction regarding climate change cannot be made are indicated by ?).

Species	Gradient	Experiment	Most abundant	Climate change
Springtails	↑ west	↓ dry-warm		↓
Mites	No trend	No trend		?
<i>Eupodes minutus</i>	Slightly ↑ east	↑ dry-warm	<i>Azorella selago</i>	↑
Rhodacaridae sp.	↑ west	↓ dry-warm	Saltspray, manured	↓
Cillibidae sp.	↑ west	↑ shade	Drainage lines, fernbrakes, saltspray, manured	?
<i>Macquarioppia striata</i>	↑ west	↑ shade	Drainage lines, fernbrakes, saltspray, manured	?
<i>Halozetes fulvus</i>	↑ east	↑ proc contr	Saltspray, manured	?
<i>Tullbergia bisetosa</i>	↑ high altitude	↓ dry-warm	<i>Azorella selago</i>	↓
<i>Folsomotoma marionensis</i>	↑ west	↓ dry-warm ↑ shade	Saltspray, manured	↓
<i>Cryptopygus dubius</i>	Slightly ↑ west	↓ dry-warm	<i>Azorella selago</i>	↓
<i>C. antarcticus travei</i>	Slightly ↑ west	↓ dry-warm	<i>Azorella selago</i>	↓
<i>Sminthurinus tuberculatus</i>	No trend	↑ shade	Fernbrake	?

The mite, *Eupodes minutus*, was the most abundant species in the experiment as well as in this study, and although it was significantly more abundant under the dry-warm treatment, its abundance did not differ significantly between island sides or across altitude. However, it was slightly more dominant on the drier eastern side, and therefore, together with the experimental results, it is likely that *E. minutus* prefers drier habitats. Therefore, *E. minutus* abundance might increase, and possibly has already increased, with drying and warming on Marion Island (Table 4). Rhodacaridae sp. abundances were significantly lower under the dry-warm treatment in the experiment and were higher on the wetter, western side of the island. Rhodacaridae sp. thus seems to prefer habitats with higher humidity, which is supported by the high abundance of Rhodacaridae sp. in wet saltspray and manured vegetation on the island (Barendse et al. 2002). Rhodacaridae sp. abundance is thus likely to decline with climate warming on Marion Island. Cillibidae sp. and *Macquarioppia striata* were more abundant in the shade treatment of the experiment (in which the relative humidity around the plant was higher and temperature lower but with narrower temperature ranges, Le Roux et al. 2005) and were also more abundant on the western side of the island. Apart from being wetter, the western side also experiences higher cloud cover, i.e. lower light intensity and lower buffered temperature, at least in summer (Schulze 1971). Furthermore, abundances of these two species are highest in drainage lines, fern brakes, saltspray and manured habitats (Barendse et al. 2002). Cillibidae sp. and *M. striata* therefore seem to prefer moist, shaded and colder habitats. Although cloud cover on Marion Island has decreased over the past 50 years (Smith 2002), *Agrostis magellanica*, and possibly also other plant species, density and altitudinal range are likely to increase, resulting in increased shading of *Azorella selago* plants (Gremmen and Smith 1999; Le Roux et al. 2005). Therefore, if microarthropod species abundances are determined by light intensity, i.e. Cillibidae sp. and *M. striata*, their responses to climate change are difficult to predict. However, if Cillibidae sp. and *M. striata* prefer colder temperature and moisture, their abundances will decrease with climate change. Further, *Halozetes fulvus* showed different responses in the experiment compared with this study. *Halozetes fulvus* abundances were higher under the procedural control than in control plants (more rainfall was received by the plants under the procedural control treatment than the plants under the dry-warm treatment and a slight increase in temperature compared to control plants, see McGeoch et al. in press for details). In this study, *H. fulvus*

abundances were higher on the drier eastern side of the island. *Halozetes fulvus* is most abundant in saltspray and manured areas (Barendse et al. 2002). Therefore, according to the observed occurrence of *H. fulvus* together with the outcomes of the climate change experiment, this species seems to be most abundant in warmer and moist areas. However, this preference was not supported by this study. The response of *H. fulvus* abundances to climate warming and drying is thus difficult to predict and more information about the responses of *H. fulvus* to environmental change is needed before predictions can be made. *Tullbergia bisetosa* was most abundant under the dry-warm treatment. Although *T. bisetosa* abundance was not significantly different between sides of the island, it was significantly higher at high altitudes. This species is also more abundant in *A. selago* plants compared to other plant species on Marion Island (Gabriel et al. 2001). Temperature, rather than moisture, is therefore likely to be the dominant determinant of *Tullbergia bisetosa* distributions and therefore its abundance will decrease under climate warming. *Folsomotoma marionensis* abundance was lower under the dry-warm treatment and higher under the shade treatment. In this study, *F. marionensis* abundance was higher on the wetter and cloudier western side. Furthermore, *F. marionensis* was found to be most abundant in saltspray and manured areas (Gabriel et al. 2001). Therefore, *Folsomotoma marionensis* possibly prefers wet and shaded habitats. *Folsomotoma marionensis* abundances might decrease with the drying climate, but predictions regarding the effect of shading cannot be made. *Cryptopygus dubius* and *C. antarcticus travei* both had lower abundances under the dry-warm treatment, while their abundances were slightly higher on the western side of the island. Both species are more abundant in *A. selago* plants compared to other plant species on Marion Island (Gabriel et al. 2001). Therefore, *C. dubius* and *C. antarcticus travei* seem to prefer habitats with lower temperatures, and may therefore decrease in abundance with warming. *Sminthurinus tuberculatus* abundance was significantly higher under shading, but its abundance was too low in this study to see any trends with altitude or island side (Table 4). Generally, predictions regarding some microarthropod species responses to climate change on Marion Island could be made, because the species showed consistent responses to temperature and moisture in this study as well as in the climate change experimental study.

All the predictions made above are based on the assumption that microarthropods respond to the direct influence of temperature and moisture, i.e.

abiotic factors. However, some species responses are likely to depend on both biotic and abiotic factors and interactions between them, which might be the case in species showing inconsistent patterns (Convey et al. 2002). Nonetheless, some species showed consistent responses in both this gradient study and the climate manipulation experiment. Therefore, assuming direct responses of species to abiotic factors, future warming and drying is likely to have a negative affect on the abundances of *Rhodacaridae* sp., *Tullbergia bisetosa* and *Folsomotoma marionensis*, while *Eupodes minutus* abundances are predicted to increase with ongoing drying of the island. Although predictions regarding climate change cannot be made for all the species, it is clear that species distributions will change, which will result in altered community-assemblage structures of microarthropods on Marion Island.

Alien species

Only two alien species were found in this study, namely the Cillibid mite and the springtail *Isotumurus cf. palustris* (Chown et al. 2002). These species occurred mostly on the western side of the island and also in the lower altitude stands. This supports the findings of Gabriel et al. (2001) that introduced species, especially springtails, prefer warm and wetter sites. Although *I. palustris* was only found on the western side in this study, it was recorded in *A. selago* on the eastern side of the island in previous studies (Barendse and Chown 2001; Gabriel et al. 2001). *I. palustris* abundance was found to be the highest in other plants species, i.e., *Poa cookii*, *Acaena magellanica* and *Blepharidophyllum densifolium*, which occur at low altitudes on Marion Island (Gabriel et al. 2001). The warmer and wetter climate on the western side of the island is likely to permit movement of alien species into *Azorella selago* plants growing at higher altitudes. The distribution of alien microarthropods across the island and especially in the western side stands is of conservation concern, since it is thought that most alien species first arrived on the eastern side of Marion Island (Deharveng 1981; Pugh 1994; Bergström and Chown 1999). If alien species continue to expand their ranges to high altitudes, indigenous species could be displaced. Indeed, Convey et al. (1999) found that the alien springtail, *Hypogastrura purpurescens*, had displaced the indigenous springtail, *Cryptopygus antarcticus antarcticus*, from some habitats on South Georgia. Further climate changes are likely to favor the population growth and consequent range expansion of alien species to higher altitudes, resulting in the alteration of the existing community structure and

possible displacement of indigenous species (Frenot et al. 2005). It must be noted, however, that alien species distribution is not static. Alien species could still spread across the island, even in the absence of climate change by means of continuing dispersal or local adaptation (given their advantage in life history) (Chown et al. 2002; Frenot et al. 2005). Nonetheless, climate change is happening on Marion Island and it will presumably be a major determinant of alien species distribution.

This study has thus shown that there is a clear island side, as well as an altitude effect on the abundance and distribution of the microarthropod community in *Azorella selago*. This is consistent with the presumed difference in moisture on different island sides and the temperature gradient across altitude. However, species respond idiosyncratically to these abiotic factors. Indigenous microarthropods, especially springtails, are likely to be negatively affected by a warmer and drier climate. Although predictions of the indirect effects of climate change on microarthropods, i.e. enhanced epiphyte growth and alien species range expansion are still uncertain, it is still clear from this study that a warmer and drier climate will change the microarthropod community structure within *A. selago* on Marion Island dramatically.

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Appendix. Total and % relative abundance of Acari and Collembola species sampled in four different transects, with abbreviations used in graphs. * = introduced species (Chown et al. 2002).

Species	Abbreviation	Tafelberg	Stony Ridge	Mixed Pickle	Swartkops	% relative abundance
Acari						
Acari sp.1	Aca1	0	1	13	3	0.01
Acari sp.3	Aca3	14	12	13	19	0.05
Acari sp.4	Aca4	16	18	131	170	0.29
Rhodacaridae sp.	Rhod	345	383	491	749	1.71
<i>Dendrolaelaps</i> sp.	Dend	407	266	275	57	0.87
Cillibidae sp. *	Cill	39	84	382	291	0.69
<i>Nanorchestes</i> sp.	Nano	595	319	646	445	1.74
<i>Eupodes minutus</i>	Emin	11310	11848	11177	11489	39.75
<i>Rhagidia</i> sp.	Rhag	4	4	23	9	0.03
<i>Ereynetes macquariensis</i>	Emac	297	198	449	405	1.17
<i>Tydeus</i> sp.	Tyde	8	3	3	96	0.10
<i>Bdellodes</i> sp.	Bdel	0	1	7	25	0.03
<i>Eryngiopus</i> sp.	Eryn	2	5	67	3	0.07
Oribatid sp.1	Orib	0	5	37	11	0.05
<i>Liochthonius australis</i>	Laus	94	104	55	41	0.26
<i>Macquarioppia striata</i>	Mstr	2	9	62	90	0.14
<i>Austroppia crozetensis</i>	Acro	668	710	486	707	2.23
<i>Halozetes fulvus</i>	Hful	326	359	135	106	0.80
<i>Domatorina marionensis</i>	Dmar	41	35	327	605	0.87
<i>Schwiebea talpa</i>	Stal	85	241	423	485	1.07
<i>Algophagus</i> sp.1	Alg1	108	32	100	17	0.22
<i>Algophagus</i> sp.2	Alg2	0	0	0	1	< 0.01
Collembola						
<i>Tullbergia bisetosa</i>	Tbis	1327	897	1381	868	3.88
<i>Folsomotoma marionensis</i>	Fmar	2083	2229	7072	7750	16.60
<i>Cryptopygus dubius</i>	Cdub	3011	2827	5389	3721	12.97
<i>Cryptopygus antarcticus travei</i>	Cant	2552	2058	2249	2597	8.20
<i>Cryptopygus caecus</i>	Ccea	439	273	831	398	1.68
<i>Isotumurus cf palustris</i> *	Ipal	0	0	5	13	0.02
<i>Megalothorax</i> sp.	Mega	1053	481	2383	1158	4.40
<i>Sminthurinus tuberculatus</i>	Stub	1	27	38	26	0.08
<i>Sminthurinus granulosus</i>	Sgra	0	4	3	0	0.01

CHAPTER 4

The microarthropods of sub-Antarctic Prince Edward Island: a quantitative assessment

Introduction

Species geographic ranges are not static. Indeed, they may change over a variety of spatial scales, from the occupancy of patches in metapopulations (Hanski 1999), to large scale shifts in range position owing to changes in climate or habitat suitability (Hill et al. 1999; Root et al. 2003). Presently, the dynamics of species ranges are affected not only by factors that have always influenced them (see Gaston 2003), but also by the local impacts of anthropogenic global climate change (e.g. Parmesan et al. 1999; Walther et al. 2002), and the movement of individuals by humans in an ever-growing wave of biological invasions (Mack et al. 2000; Cassey et al. 2005; Gewin 2005). The latter factors are of considerable importance in the sub-Antarctic, where climate is changing rapidly on many, if not most, islands (Bergström and Chown 1999; Smith 2002). Species from a wide variety of taxa have been introduced to these islands from elsewhere by humans, become established, and spread to become biological invaders with significant impacts (Chapuis et al. 1994; Frenot et al. 2005). In consequence, climate change and biological invasions are viewed as the most significant threats to sub-Antarctic biodiversity (Bergström and Chown 1999; Le Roux et al. 2005; Whinam et al. 2005).

Conserving biodiversity in the face of these threats requires that the biotas of the islands, their local and regional distributions, and the processes underlying these distributions are reasonably well understood. For some taxa and islands this understanding is relatively well developed. In the case of vascular plants and insects, not only are distributions well known (e.g. Gremmen 1981; Vogel 1985; Hughes 1987; Chown 1992; Frenot et al. 2001; Chown and Klok 2001; Turner et al. 2006), but the processes underlying them have been comprehensively investigated at a variety of spatial scales (e.g. Chown et al. 1998, 2002, 2005; Ernsting et al. 1999; Smith et al. 2001; Hugo et al. 2004; Bergström et al. 2005; Greve et al. 2005; Le Roux and McGeoch 2004; Shaw et al. 2005). By contrast, for other groups, such as the bryophytes, lichens, springtails and mites, this understanding lags far behind (but see Bellido and Cancela da Fonseca 1988; Pugh and Barsch 1993; Pugh 1994; Bergström and Selkirk 1997; Convey et al. 1999; Gabriel et al. 2001; McGeoch et al. in press). In

many cases, comprehensive, island-specific inventories remain scarce for these taxa, and in those cases where sampling has been comprehensive (e.g. Marshall and Chown 2002), quantitative assessments of the determinants (or correlates) of distributions remain scarce. Moreover, the dynamics of species ranges, even at the scale of whole-island inventories, are poorly comprehended because regular monitoring is rare at most of the islands (for exceptions see Scott 1990; Ernsting et al. 1999; Gremmen and Smith 1999; Frenot et al. 2001; Slabber and Chown 2002; Bergström et al. 2005). This means that whilst immensely valuable catalogues for many taxa are becoming available (e.g. Pugh 1993, 2004; Pugh et al. 2002; Pugh and Scott 2002), they are static assessments of a dynamic situation. Given the rate and extent of climate change and biological invasions in the sub-Antarctic, conservation managers will consequently find themselves with outdated information on which to base their actions.

Remedying this situation is relatively straightforward for islands that are permanently occupied by scientific personnel. However, this is more difficult for those that are unoccupied, remote, and of special conservation value (owing to the lack of human disturbance) (e.g. Heard Island, I'le des Pingouins) (see e.g. Dreux et al. 1988; Delettre et al. 2003). Nonetheless, periodic, quantitative baseline surveys would go a considerable way to ensuring appropriate conservation measures for them. Here we provide such a survey for the mites and springtails of Prince Edward Island, one of the two islands in the sub-Antarctic Prince Edward group (Smith 1987). This island is considered one of the more pristine in the sub-Antarctic (e.g. Chown et al. 2001), and consequently has been afforded special protection as part of the Prince Edward Islands Special Nature Reserve (Anonymous 1996). Although occasional visits have partly documented the mites and springtails from the island (e.g. Marshall et al. 1999), no studies have comprehensively and quantitatively sampled a variety of habitats on the island.

Materials and methods

Marion Island (46°54'S 37°45'E) and Prince Edward Island (46°38' S 37°57'E) are cool, sub-Antarctic islands that lie to the north of the Antarctic Polar Frontal Zone. They are separated by approximately 19 km and, with exceptions such as extent of Pleistocene glaciations, are thought to have similar climates, and climatic and

geological histories (Smith 1987; Hall 2002). Prince Edward Island (45 km²) is about one sixth the size of Marion Island (290 km²), and rises to only 672 m, by comparison with the latter's 1230 m (Hänel and Chown 1999). The islands share many, but not all of the indigenous species that have so far been found at the archipelago, and Prince Edward Island has far fewer alien and invasive species than Marion Island (e.g. Crafford et al. 1986; Smith 1987; Gremmen and Smith 1999; Chown et al. 2002). For both this reason, and a variety of others, Prince Edward Island has special conservation status within South African law, and visits to the island are constrained both in frequency and duration (Anonymous 1996).

In 2000, the Prince Edward Islands Management Committee granted permission for a short (three days) visit to Prince Edward Island to quantitatively sample mites and springtails especially to assess the extent to which alien and/or invasive species are present at the island. This visit took place in April 2000. Sampling was conducted on the eastern and southern sides of Prince Edward Island in eight habitats (Table 1). Ten samples were taken randomly from each habitat (in an area of approximately 500 m² per habitat) using an O'Connor split corer (inside diameter of core = 70 mm, height = 70 mm; surface area = 0.0039 m²). Microarthropods were extracted from the cores using a MacFadyen high gradient extraction protocol of two days at 25 °C and 2 days at 30 °C (Barendse and Chown 2001). The single exception was fellfield soils from which microarthropods were extracted by flotation in sieved cold water and further by means of differential wetting (Southwood 1980) with kerosene and 70 % ethanol (see Barendse and Chown 2001 for detail). Springtail and mite specimens were identified to the lowest taxonomic level possible (usually species), counted and are in storage in 99 % ethanol at the University of Stellenbosch.

For comparative purposes, the data collected at Prince Edward Island were compared with those collected using identical methods in the same month in 1997 on Marion Island (see Gabriel et al. 2001; Barendse et al. 2002), with the exception of the *Azorella selago* and fellfield soil samples, which were taken in April 1998 as part of the work by Barendse and Chown (2001) and Gabriel et al. (2001) (Table 1). In the latter case, samples at Marion Island were taken by identifying two transects consisting of 4 quadrats each. Five samples were taken from each quadrat giving a total of 40 samples for *A. selago* (using the O'Connor corer), and 40 samples for fellfield (using a 30 cm x 30 cm box sampled to 10 cm depth). For the other habitats,

five quadrats were identified and five samples taken from each quadrat giving a total of 25 samples for each plant species, except for the high altitude mire site where only 4 quadrats were used (20 samples) (Gabriel et al. 2001). As was the case for the Prince Edward Island samples, MacFadyen high gradient extraction was used except for the fellfield samples where flotation and differential wetting were implemented. Extraction efficiency varies with species, life stage and substratum type, and comparisons between similar habitats and species will thus be most reliable.

Table 1. Sampled plant species with notes on the habitat complex, associated plant species, mineral status and characteristics of the soil in which they occur on Marion and Prince Edward Islands (Gremmen 1981; Smith 1987; Smith et al. 1993; Hänel and Chown 1999; Smith et al. 2001; Smith and Steenkamp 2001) (* information extrapolated from Marion Island notes, Gremmen 1981; Smith 1987; Smith et al. 1993; Hänel and Chown 1999; Smith et al. 2001; Smith and Steenkamp 2001) (m a.s.l. = meters above sea level; DR = decomposition rate; soil moisture indicated as % of dry mass; ↑ and ↓ indicate high and low respectively).

Family: Plant species	Habitat complex	Sample sites	m a.s.l.	Soil moist.	Associated plants	Mineral status	Soil characteristics
Marion Island							
Mires							
Bryophytes							
Amblystegiaceae: <i>Sanionia uncinata</i> (Hedw.) Loeske	Mesic mire	Nellie Humps	50	3000	<i>Acaena magellanica</i>	↓ organic C and P ↓ DR	wet, sheltered, organic, ↓ pH
Jungermanniaceae: <i>Jamesoniella colorata</i> (Lehm.) Schiffn.	Dry mire	Nellie Humps	50	1296	<i>Blepharidophyllum densifolium</i>	↓ organic C and P ↓ DR	wet, sheltered, organic, ↓ pH
Scapaniaceae <i>Blepharidophyllum densifolium</i> (Hook.) Ångstr.	Mesic mire	Nellie Humps	50	1296	<i>Jamesoniella colorata</i>	↓ organic C and P ↓ DR	wet, sheltered, organic, ↓ pH
High altitude mire vegetation		Long Ridge South	400			↓ DR	Wet, sheltered, organic, ↓ pH
Middle altitude mire vegetation		Hendrik Fister Kop	250			↓ DR	Wet, sheltered, organic, ↓ pH
Slope							
Vascular plants							
Rosaceae: <i>Acaena magellanica</i> Lam. Vahl	Drainage line	Skua Ridge, Tom, Dick and Harry	100, 75	707	<i>Sanionia uncinata</i>	↑ organic C and P ↑ DR	well drained

Polypodiaceae <i>Blechnum penna-marina</i> (Poir) Kuhn Biotic and salt spray influenced Vascular plants	Closed Fernbrake	Nellie Humps	100	614	<i>Acaena magellanica</i>	↑ organic C, N, P ↑ DR	well drained
Asteraceae: <i>Cotula plumosa</i> Hook. f.	Cotula herbfield	Ship's Cove to Blue Petrel Bay	15-20	658	<i>Poa cookii</i>	↑ Na, Mg, P, N, organic C ↑ DR	Wettish, ↓ pH
Poaceae: <i>Poa cookii</i> Hook. f.	Coastal tussock grassland	Bullard Beach	20	525	<i>Cotula plumosa</i>	↑ organic and inorganic N, C, P ↑ DR	Wettish, ↓ pH
Crassulaceae: <i>Crassula moschata</i> Forst. F.	Coastal saltspray, herbfield	Archway Bay	20	400	<i>Cotula plumosa</i>	↑ Na, Mg, P, Ca, organic C ↑ DR	wettish, ↓ pH
Fellfield							
Vascular plants							
Apiaceae: <i>Azorella selago</i> Hook. f.	Mesic fellfield	Kerguelen Rise	300	329	In fellfield	↑ Ca, Mg, Na, K, N	dry, exposed, mineral basic/saline
Fellfield soil	Mesic fellfield	Kerguelen Rise	300	329	<i>Azorella selago</i> growing in fellfield	↑ Ca, Mg, Na, K, P, N ↓ DR	dry, exposed, mineral basic/saline
Prince Edward Island Mires							
Mire vegetation	Dry mire	Above Cave Bay	50			*↓ DR	*Wet, sheltered, organic, ↓ pH
Slope							
Rosaceae: <i>Acaena magellanica</i> Lam. Vahl	Drainage line	Platkop	150-200	707	* <i>Blechnum penna-marina</i>	*↑ P, organic C and N ↑ DR	*well drained

Polypodiaceae <i>Blechnum pennamarina</i> (Poir) Kuhn Biotic and salt spray influenced	Closed fernbrake	Platkop	150-200	614	* <i>Acaena magellanica</i>	*↑ P, organic C and N ↑ DR	*well drained
Asteraceae: <i>Cotula plumosa</i> Hook. f.	Cotula herbfield	McNish Bay	20	658	* <i>Poa cookii</i>	*↑ Na, Mg, P, organic C and N ↑ DR	*wettish, ↓ pH
Poaceae: <i>Poa cookii</i> Hook. f.	Coastal tussock grassland	Golden Gate	70	525	* <i>Cotula plumosa</i>	*↑ organic and inorganic N, P, C ↑ DR	*wettish, ↓ pH
Crassulaceae: <i>Crassula moschata</i> Forst. F.	Coastal saltspray, herbfield	East Cape	20	400	* <i>Cotula plumosa</i>	*↑ Na, Mg, P, Ca, organic C ↑ DR	*wettish, ↓ pH
Fellfield							
Apiaceae: <i>Azorella selago</i> Hook. f.	Mesic fellfield	Horingberg	550	329	*In fellfield	*↑ Ca, Mg, Na, K, N	*dry, exposed, mineral basic/saline
Fellfield soil	Mesic fellfield	Horingberg	550	329	* <i>Azorella selago</i> growing in fellfield	*↑ Ca, Mg, Na, K, P, N ↓ DR	*dry, exposed, mineral basic/saline

Raw counts of number of individuals per species were converted to densities per square meter for all samples to compare data from different sampling methods. Generalized linear models (McCullagh and Nelder 1998) were used to determine the relationship between species richness and abundance (separate models for each of these dependent variables) and the explanatory variables: island and habitat. A Poisson error distribution was assumed for species richness, whereas a normal error distribution was assumed for density of individuals per square meter, the first being count data and the latter continuous (Quinn and Keough 2002). A logarithmic link function was used in all the models and deviance used as a measure of goodness of fit (Dobson 2002). Models of the same structure were also used excluding exotic species from the data (see Appendix for exotic species).

Differences in microarthropod community structure between islands 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 weigh common and rare species equally) (Clarke and Warwick 1994). Analysis of similarity (ANOSIM) was used to test for significant differences in communities on the two islands (Clarke and Warwick 1994). This is a non-parametric permutation procedure applied to rank similarity matrices underlying sample ordinations that calculated a global R-statistic. The closer a significant global R is to one, the more distinct the difference between those communities (Clarke and Warwick 1994). Non-metric multi-dimensional scaling (MDS) was used to display the relationship between microarthropod communities on the islands in different plant species. These multivariate analyses were also conducted with all exotic microarthropod species removed from the data set to examine the effect of exotic species on community structure within and between Marion Island and Prince Edward Island.

Results and discussion

A total of 37 different microarthropod taxa were sampled from Prince Edward Island (Appendix), eight of which could not be determined to generic level. The Collembola included all Marion Island endemic species, with the exceptions of *Cryptopygus tricuspis* and *Katianna* sp. (Gabriel et al. 2001). Both species are comparatively rare on Marion Island, and tend either not to be found in spatially-limited quantitative

sampling, or to be low in abundance (Gabriel et al. 2001; Hugo et al. 2004). Given the limited sampling at Prince Edward Island, their absence is not unexpected, and it seems likely that further sampling may recover both species from the island and confirmation of their presence must remain a priority. However, it is also possible that the species not found on Prince Edward Island, are truly absent from this island. By contrast, only one invasive alien species, *Ceratophysella denticulata*, was found on Prince Edward Island. This species occurs in large numbers ($> 38\,000$ individuals.m⁻²) on Marion Island, and has been introduced widely across the globe (Christiansen and Bellinger 1995; Greenslade 2002). Although the time of its arrival on Prince Edward Island is uncertain, it seems unlikely that it arrived before annexation of the islands by South Africa, given that so few species were introduced by sealers to Prince Edward Island (Crafford et al. 1986; Cooper and Condy 1988). However, during the 1970s and 1980s regular, reasonably uncontrolled visits were made to Prince Edward Island, and in the latter decade a field hut at Cave Bay was regularly used and resupplied directly from the station at Marion Island. The practice of packing wooden crates on vegetation surrounding the scientific station buildings at Marion Island immediately prior to aircraft and ship operations probably ensured the transfer of this species to Prince Edward Island, given that it is very abundant around the station, and that other species, such as the slug *Deroceras panormitanum*, have been successfully spread around Marion Island in this way (Chown et al. 2002).

Approximately 58 mite species have been recently recorded from Marion Island (excluding species that could not be found in systematic sampling, but which have been reported previously from the island) (Marshall et al. 1999; Chown et al. 2002). Of these, 42 have been regularly recorded in sampling of a variety of habitats, including the shore and intertidal areas on the island (Barendse et al. 2002). A total of 28 species from the quantitative sampling on Prince Edward Island (Appendix) is therefore low, but not unreasonably given the limited sampling which excluded the shoreline (owing to the densities of sub-Antarctic fur seals). That several of the species could not be identified is also a reflection of the absence of formal keys to many of the taxa and the scarcity of suitable taxonomic expertise. Indeed, the state of both mite and springtail systematics in the sub-Antarctic is of considerable concern, given that less than five systematists are concerned with these groups from the region. This means that even for faunas as depauperate as those of the sub-Antarctic, the taxonomic impediment (Samways 1994) remains substantial. Although some

problems exist with DNA barcoding (Will and Rubinoff 2004; Prendini 2005), this does seem to be one way to overcome the current systematic crisis in the region.

Nonetheless, the mite species that were recovered corresponded well with those species regularly found on Marion Island (Marshall et al. 1999), and it is not expected that many new species will be found. Of the 28 species found here, only one is thought to be an alien species: Cilibidae sp. The status of this species is uncertain at the Prince Edward Islands, and it has been classified as alien (Chown et al. 2002) because the family as a whole is absent from all other islands in the sub-Antarctic (Pugh 1993). Until such time as the species is identified its status will remain uncertain, but for precautionary reasons it is considered alien. When and how it might have reached Prince Edward Island is wholly unclear, and its presence may even suggest that it should be considered indigenous to the islands.

In the quantitative analyses, neither mean species richness nor mean abundance differed significantly between the islands (species richness: dev/df = 0.91, $\chi^2 = 1.31$, $P = 0.25$; abundance: dev/df = 1.05, $\chi^2 = 0.74$, $P = 0.39$). However, habitat type contributed significantly to the generalized linear models (species richness: dev/df = 0.91, $\chi^2 = 29.74$, $P < 0.001$; abundance: dev/df = 1.05, $\chi^2 = 68.06$, $P < 0.001$) (Fig. 1 a, c), and a significant interaction between habitat type and island was also identified (species richness $\chi^2 = 57.39$, $P < 0.001$; abundance $\chi^2 = 63.01$, $P < 0.001$). Similar patterns were observed when exotic species were removed from the data set. Again neither mean species richness nor mean abundance differed significantly between islands (species richness: dev/df = 0.95, $\chi^2 = 0.07$, $P = 0.80$; abundance: dev/df = 1.05, $\chi^2 = 0.76$, $P = 0.38$), habitat type was a significant term in the models (species richness: dev/df = 0.95, $\chi^2 = 34.66$, $P < 0.001$; abundance: dev/df = 1.05, $\chi^2 = 63.38$, $P < 0.001$) (Fig. 1 b, d), and the habitat type * island interaction terms were significant (species richness: $\chi^2 = 46.82$, $P < 0.001$; abundance: $\chi^2 = 60.18$, $P < 0.001$).

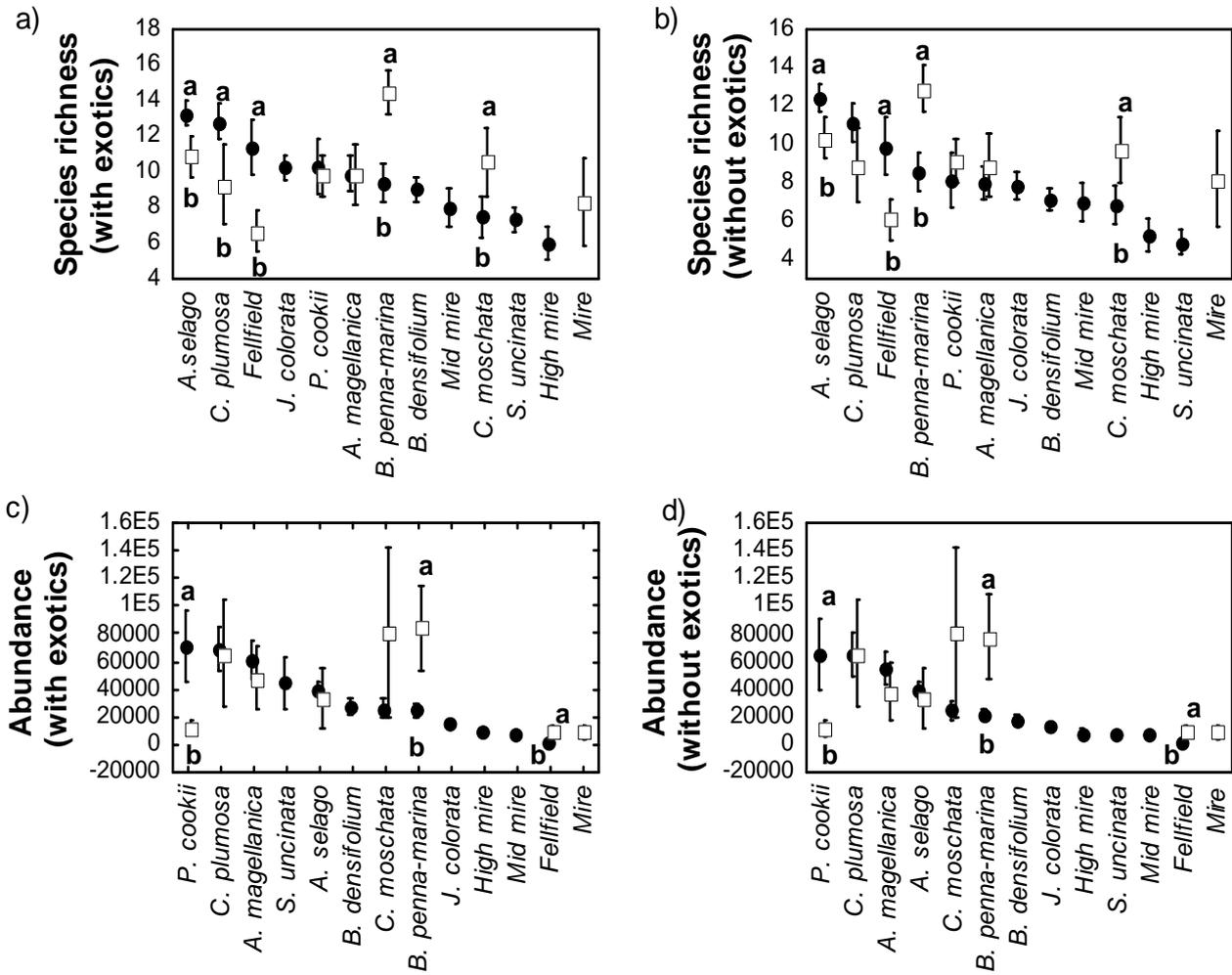
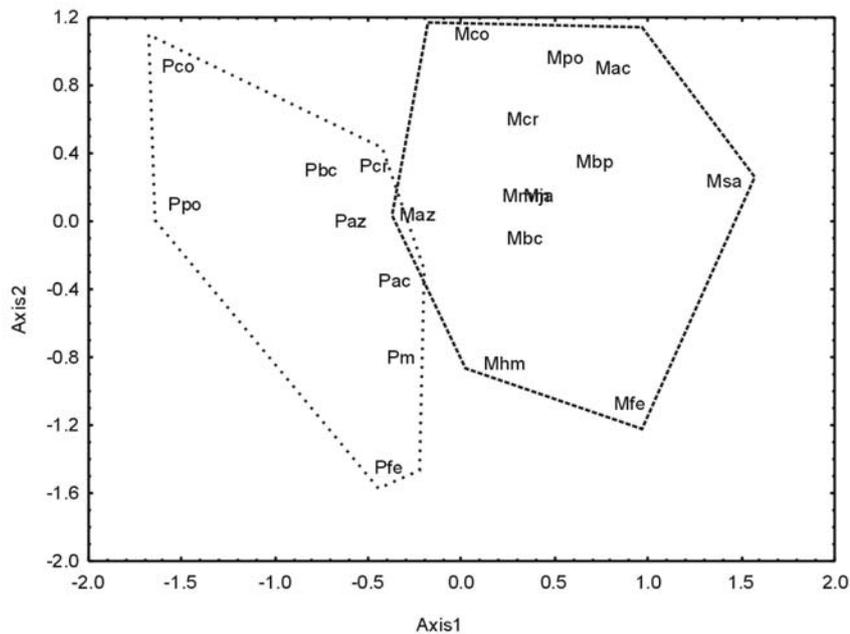


Fig. 1. Species richness (a, b) and abundance (c, d) of microarthropods with and without exotic species in the dataset in different plants species on Marion Island (filled circles) and Prince Edward Island (open squares) (mean ± 95% confidence intervals). Different letters (superscript) indicate a significant difference of $P < 0.05$ between the same plant species on the two islands. (Marion Island: *Acaena magellanica*, *Blechnum penna-marina*, *Cotula plumosa*, *Crassula moschata*, *Poa cookii*; *Jamesoniella colorata*, *Blepharidophyllum densifolium*, *Sanionia uncinata*, Middle altitude mire: $n = 25$, *Azorella selago*, Fellfield: $n = 40$, High altitude mire: $n = 20$; Prince Edward Island: *A. magellanica*, *B. penna-marina*, *C. plumosa*, *P. cookii*, Mire: $n = 10$, *A. selago*, *C. moschata*: $n = 9$, Fellfield: $n = 15$).

To some extent, these results must reflect the difference in sampling intensity between the islands. Greater sampling intensity might have shown up significant differences in abundance owing to the presence of abundant invasive species on Marion Island (Gabriel et al. 2001), especially as higher sampling intensity would have reduced the variance found in the Prince Edward Island samples. It has, however, been suggested that competition from invasive species might reduce the abundances of indigenous ones on sub-Antarctic islands (Convey et al. 1999; Chown et al. 2002), and therefore the direction of any sampling effect cannot be ascertained without further investigation. Nonetheless, these quantitative assessments do demonstrate that habitat type has a significant influence on the abundances of the microarthropods on the islands. Indeed, the influence of habitat type on the abundance of individual species and their contribution to arthropod microarthropod assemblage structure was also clear from the community analyses (Fig. 2a). In this analysis, removal of the alien species also resulted in greater similarity amongst the habitat types on the two islands (Fig. 2b) (in the former case, ANOSIM Global $R = 0.44$, $P = 0.001$; whilst in the latter Global $R = 0.37$, $P = 0.001$). These results are in keeping with other investigations from Marion Island that have demonstrated a significant effect of habitat on invertebrate abundance (Burger 1978; Gabriel et al. 2001; Barendse et al. 2002), and a clear change in assemblage ordination patterns when alien species were removed from the analyses (Gabriel et al. 2001). However, they also highlight significant differences in assemblage composition in similar habitats on the two islands. These differences are not surprising, given that predation by cats radically reduced the spatial distribution of guano input by burrowing seabirds on Marion Island by comparison with Prince Edward Island, and in so doing also likely influenced invertebrate abundance (Crafford and Scholtz 1987). Further investigations are required to substantiate these differences.

a)



b)

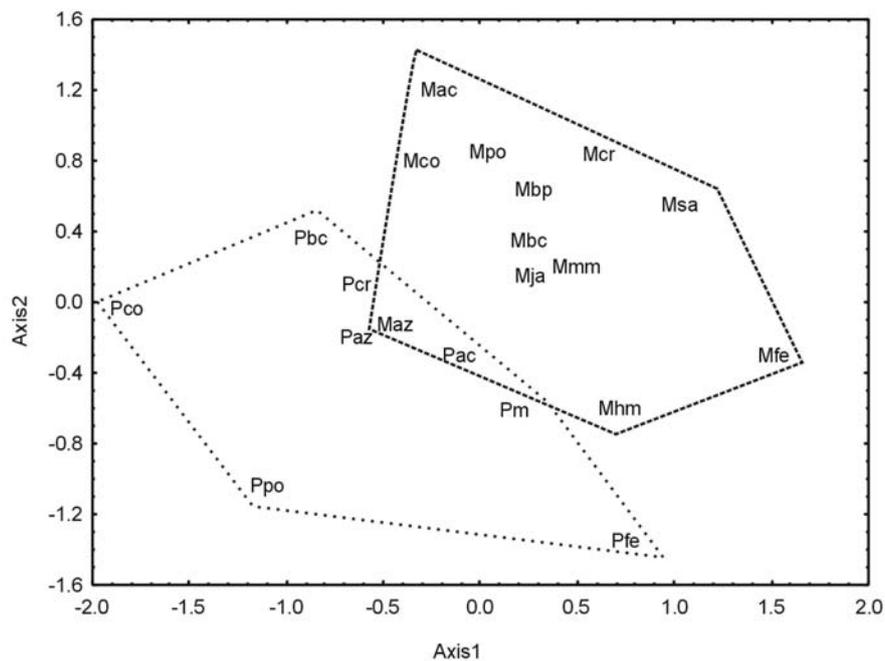


Fig. 2. Non-metric multi-dimensional scaling (MDS) ordination of the abundance of microarthropods on Marion and Prince Edward Islands in different plant species, with exotic species (a) and without exotic species (b). (stress: a = 0.18; b = 0.19). (M = Marion, P = Prince Edward, ac = *Acaena magellanica*, bc = *Blechnum penna-marina*, co = *Cotula plumosa*, cr = *Crassula moschata*, po = *Poa cookii*, az = *Azorella selago*, hm = high mire, mm = mid mire, fe = fellfield, ja = *Jamesoniella colorata*, bp = *Blepharidophyllum densifolium*, sa = *Sanionia uncinata*, m = mire).

In conclusion, this study has provided the first quantitative assessment of the distribution and abundance of microarthropods for Prince Edward Island. Although the sampling was spatially and temporally restricted (owing to management requirements), it revealed patterns similar to that found for other taxa on the nearby Marion Island. That is, habitat type has a profound influence on assemblage patterns, and, more importantly, that Prince Edward Island is not as heavily invaded by microarthropods, as is Marion Island. The latter finding supports the status of the island as one of the more pristine in the sub-Antarctic. Thus, further work to verify the abundances and distributions of the arthropods on the island creates something of a management conundrum, which can only be resolved by the strictest of quarantine measures.

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Appendix. Mean (\pm SE) density of mites (Acari) and springtails (Collembola) in eight plant communities sampled on Prince Edward Island (*Acaena magellanica*, *Blechnum pennamaryna*, *Cotula plumosa*, *Poa cookii*, Mire: n = 10, *Azorella selago*, *Crassula moschata*: n = 9, Fellfield: n = 15) (# introduced species after Chown et al. 2002).

Species	<i>Acaena</i>	<i>Blechnum</i>	<i>Cotula</i>	<i>Crassula</i>
Acari				
Acari sp.1	0	0	0	0
Acari sp.2	25.97 \pm 25.97	0	0	0
Acari sp.3	0	415.58 \pm 182.44	51.95 \pm 51.95	28.86 \pm 28.86
Acari sp.4	0	51.95 \pm 34.63	0	28.86 \pm 28.86
Acari sp.5	0	25.97 \pm 25.97	0	0
Acari sp.7	0	0	25.97 \pm 25.97	0
Acari sp.8	0	0	0	0
Acari sp.9	0	51.95 \pm 34.63	0	0
Rhodacaridae sp.	831.17 \pm 390.67	467.53 \pm 211.37	883.12 \pm 496.16	981.24 \pm 206.61
<i>Dendrolaelaps</i> sp.	51.95 \pm 34.63	51.95 \pm 34.63	14805.19 \pm 2111.56	202.02 \pm 94.62
Cillibidae sp. #	10025.97 \pm 4546.60	6077.92 \pm 954.11	233.77 \pm 157.04	404.04 \pm 156.75
<i>Nanorchestes</i> sp.	25.97 \pm 25.97	51.95 \pm 34.63	0	144.30 \pm 97.87
<i>Eupodes minutus</i>	11896.10 \pm 6174.90	7714.29 \pm 2095.18	6051.95 \pm 2582.95	7445.89 \pm 2576.76
	0	0	0	519.48 \pm 384.77
<i>Tydeus</i> sp.				
<i>Rhagidia</i> sp.	0	51.95 \pm 34.63	0	0
	51.95 \pm 51.95	77.92 \pm 77.92	0	346.32 \pm 188.70
<i>Ereynetes macquariensis</i>				
<i>Bdellodes</i> sp.	259.74 \pm 154.88	103.90 \pm 42.42	0	0
	0	77.92 \pm 39.68	25.97 \pm 25.97	0
<i>Liochthonius australis</i>				
	155.84 \pm 88.30	1194.81 \pm 297.92	0	28.86 \pm 28.86
<i>Macquarioppia striata</i>				
	11220.78 \pm 4063.33	11922.08 \pm 2181.22	883.12 \pm 346.75	3751.80 \pm 2354.48
<i>Austroppia crozetensis</i>				
<i>Halozetes</i> sp.	0	103.90 \pm 57.43	51.95 \pm 34.63	28.86 \pm 28.86
	2779.22 \pm 881.29	649.35 \pm 205.80	1064.94 \pm 293.48	5685.43 \pm 1551.48
<i>Halozetes fulvus</i>				
	0	0	0	0
<i>Podocarus auberti</i>				
	1792.21 \pm 386.13	623.38 \pm 160.58	25.97 \pm 25.97	202.02 \pm 112.70
<i>Domitorina marionensis</i>				
	0	0	0	288.60 \pm 288.60
<i>Schwiebea talpa subantarctica</i>				
	0	155.84 \pm 88.30	9350.65 \pm 7821.40	0
<i>Algophagus</i> sp.				
	0	0	25.97 \pm 25.97	0
<i>Neocalvolia</i> sp.				
Species richness	12	19	13	15
Abundance	39116.88 \pm	29870.13 \pm	33480.52 \pm	20086.58 \pm

	16824.62	6793.48	13999.82	8128.78
Collembola				
	0	233.77 ± 90.39	25.97 ± 25.97	28.86 ± 28.86
<i>Ceratophysella denticulata</i> #				
	1298.70 ± 309.76	857.14 ± 251.08	3272.73 ± 1114.30	490.62 ± 257.73
<i>Tullbergia bisetosa</i>				
	3714.29 ± 1047.62	23324.68 ± 3939.50	181.82 ± 87.02	18903.32 ± 15323.26
<i>Folsomotoma marionensis</i>				
	0	207.79 ± 114.86	22077.92 ± 7101.78	26378.07 ± 4406.69
<i>Cryptopygus dubius</i>				
	129.87 ± 104.26	129.87 ± 58.08	0	1038.96 ± 685.84
<i>Cryptopygus antarcticus</i>				
	0	0	571.43 ± 244.27	606.06 ± 606.06
<i>Cryptopygus caecus</i>				
	3558.44 ± 2018.65	23194.81 ± 7418.46	0	13419.91 ± 8255.92
<i>Megalothorax</i> sp.				
	389.61 ± 96.80	6207.79 ± 869.65	6363.64 ± 2137.06	230.88 ± 152.71
<i>Sminthurinus tuberculatus</i>				
	0	0	0	0
<i>Sminthurinus granulatus</i>				
	5	7	6	8
Species richness				
Abundance	9090.91 ± 3577.09	54155.84 ± 12742.02	32493.51 ± 10710.39	61096.68 ± 29717.07
Total species richness	17	26	19	23
Total abundance	48207.79 ± 20401.71	84025.97 ± 19535.50	65974.03 ± 24710.21	81183.26 ± 37845.85
Species	Poa	Azorella	Mire	Fellfield
Acari				
Acari sp.1	0	28.86 ± 28.86	0	0
Acari sp.2	0	0	0	0
Acari sp.3	77.92 ± 55.44	0	0	17.32 ± 17.32
Acari sp.4	0	0	1038.96 ± 407.94	225.11 ± 79.62
Acari sp.5	0	0	0	0
Acari sp.7	0	0	0	0
Acari sp.8	0	0	0	17.32 ± 17.32
Acari sp.9	0	0	0	0
Rhodacaridae sp.	597.40 ± 145.14	577.20 ± 94.62	77.92 ± 55.44	103.90 ± 61.05
<i>Dendrolaelaps</i> sp.	2311.69 ± 655.33	173.16 ± 86.58	51.95 ± 34.63	103.90 ± 42.42
Cillibidae sp. #	311.69 ± 158.71	404.04 ± 168.28	25.97 ± 25.97	398.27 ± 126.40
<i>Nanorchestes</i> sp.	25.97 ± 25.97	0	25.97 ± 25.97	0
	909.09 ± 482.45	2568.54 ± 1722.62	1350.65 ± 1124.74	138.53 ± 83.56
<i>Eupodes minutus</i>				
	0	0	0	0
<i>Tydeus</i> sp.				
	0	0	0	0
<i>Rhagidia</i> sp.				
	25.97 ± 25.97	317.46 ± 166.42	51.95 ± 34.63	0
<i>Ereynetes macquariensis</i>				
<i>Bdellodes</i> sp.	0	0	51.95 ± 34.63	51.95 ± 27.77

	0	0	77.92 ± 39.68	0
<i>Liochthonius australis</i>				
	0	0	519.48 ± 289.75	17.32 ± 17.32
<i>Macquarioppia striata</i>				
	207.79 ± 75.48	4184.71 ± 1479.76	233.77 ± 105.68	69.26 ± 30.70
<i>Austroppia crozetensis</i>				
<i>Halozetes</i> sp.	623.38 ± 404.62	0	25.97 ± 25.97	0
	1220.78 ± 637.47	57.72 ± 38.18	1454.55 ± 342.40	1679.65 ± 438.94
<i>Halozetes fulvus</i>				
	155.84 ± 88.30	0	0	0
<i>Podocarus auberti</i>				
	25.97 ± 25.97	288.60 ± 109.90	1584.42 ± 508.47	3809.52 ± 892.84
<i>Domitorina marionensis</i>				
	0	57.72 ± 38.18	259.74 ± 122.44	17.32 ± 17.32
<i>Schwiebea talpa subantarctica</i>				
<i>Algophagus</i> sp.	129.87 ± 129.87	0	0	0
	1454.55 ± 1240.97	0	103.90 ± 57.43	0
<i>Neocalvolia</i> sp.				
<i>Hyadesia halophila</i>	233.77 ± 179.33	0	0	0
<i>Hyadesia</i> sp.	181.82 ± 95.24	0	0	0
Species richness	16	10	16	13
Abundance	8493.51 ± 4426.23	8658.00 ± 3933.39	6961.04 ± 3261.77	6649.35 ± 1852.55
Collembola				
	77.92 ± 55.44	0	0	0
<i>Ceratophysella denticulata</i> #				
	961.04 ± 309.88	1616.16 ± 232.23	25.97 ± 25.97	103.90 ± 42.42
<i>Tullbergia bisetosa</i>				
<i>Folsomotoma marionensis</i>	909.09 ± 566.75	7647.91 ± 3257.73	545.46 ± 376.30	0
	259.74 ± 139.61	4098.12 ± 1431.05	0	155.84 ± 61.05
<i>Cryptopygus dubius</i>				
	207.79 ± 93.25	3145.74 ± 1213.24	935.07 ± 506.62	3393.94 ± 592.01
<i>Cryptopygus antarcticus</i>				
<i>Cryptopygus caecus</i>	727.27 ± 402.02	2193.36 ± 592.16	0	0
	0	5281.39 ± 4735.66	545.46 ± 517.24	0
<i>Megalothorax</i> sp.				
<i>Sminthurinus tuberculatus</i>	337.66 ± 225.94	1125.54 ± 1031.72	441.56 ± 177.65	259.74 ± 71.70
<i>Sminthurinus granulatus</i>	415.58 ± 387.59	0	0	0
Species richness	8	7	5	4
Abundance	3896.10 ± 2180.47	25108.23 ± 12493.79	2493.51 ± 1603.78	3913.42 ± 767.17
Total species richness	24	17	21	17
Total abundance	12389.61 ± 6606.70	33766.23 ± 16427.18	9454.55 ± 4865.55	10562.77 ± 2619.72

GENERAL SYNTHESIS

Sub-Antarctic islands are of considerable conservation importance, since they house a large number of indigenous and endemic species (Gressitt 1970; Bergström and Chown 1999; Chown et al. 2001). Indeed, many of the sub-Antarctic islands have received World Heritage status based on an assessment of the indigenous biodiversity, as well as the number of alien species occurring on these islands (Chown et al. 2001). The major threats for the indigenous biota on these islands are climate change, alien species as well as the interaction between climate change and alien species (Chown et al 2002; Frenot et al. 2005). Increasing temperature and decreasing rainfall have been observed on a number of sub-Antarctic islands, e.g., Marion Island, Macquarie Island, Kerguelen Island and Heard Island (Smith and Steenkamp 1990; Bergström and Chown 1999; Smith 2002). Furthermore, a number of alien species has been introduced, and have already established on nearly all sub-Antarctic islands (Chown et al. 2001; Frenot et al. 2005). These species had severe impacts on ecosystems, by outcompeting and displacing indigenous species and altering community composition and structure (Ernsting et al. 1999; Gremmen 1997; Gremmen et al. 1998; Bergström and Chown 1999). More importantly, however, is the enhanced effect of climate change on alien species colonization and invasion ability to sub-Antarctic islands (Bergström and Chown 1999; Frenot et al. 2005). Warming is also likely to favour alien species growth and development since they have shorter generation times, giving them a greater reproductive advantage over the indigenous species (Barendse and Chown 2000). Therefore, alien species already present on islands can change their status from persistent to invasive aliens, and are likely to increase their range of occupancy across an island (Chown 2002; Frenot et al 2005). Together, the impact of climate change and alien species is thus a serious threat to the indigenous species on sub-Antarctic islands.

An important group of organisms on sub-Antarctic islands, which is likely to be threatened by climate change and alien species, are the microarthropods, i.e. mites and springtails (Convey et al. 1999; Gabriel et al. 2001; Greenslade 2002). Microarthropods are important, especially in the sub-Antarctic, for decomposition and mineralization of plant material (Seastedt 1984). Since there are few herbivores on the islands in this region, almost all plant productivity becomes dead organic material and most of the energy and nutrient circulation occurs through the detritus system (Smith

and Steenkamp 1990). Since the microarthropods are detritivores, algivores or fungivores, they form an important part of the detritus system (Hopkin 1997), together with other macro-invertebrates, e.g. *Pringleophaga marioni* (Smith and Steenkamp 1990). The loss of microarthropods from the detritus system has been found to alter the composition of decomposer microflora (Moore et al. 1988) and decrease enzyme activity, decomposition, soil development and respiration processes (Seastadt 1984; Rusek 1998; Teuben and Verhoef 1992). This is also likely to be the case on the Prince Edward Islands (where this study was conducted), where nitrogen availability is low and nutrient turnover and decomposition rates are slow (Smith and Steenkamp 1990; Bergström and Chown 1999). Therefore, since climate change and alien species are likely to alter microarthropod community structure or lead to extinction of some species, information on the current spatial distributions of microarthropods on sub-Antarctic islands is critical to predict the consequences of climate change and alien species on the future survival, distribution and abundance of indigenous biota on these islands (Bergström and Chown 1999).

Furthermore, the impact of climate change and alien species on indigenous biota may differ between scales of observation since spatial patterns and underlying mechanisms differ between scales (Cornell and Lawton 1992; Schneider 2001; Fischer et al. 2004). It is thus important to study microarthropod distribution patterns on more than one scale. This study is the first to quantify spatial patterns in microarthropod abundance, species richness and community structure at multiple scales of observation, i.e., within plant, within a stand of plants, island wide and between islands. Knowledge of spatial patterns and processes in communities at multiple scales has led to improved explanation and prediction in ecology (Levin 1992; Gardner 1998; Benedetti-Cecchi 2001; Harte et al. 2005) and is also important for matters such as species conservation and management (Gardner 1998; Thomas et al. 2001) which is essential for the Prince Edward Islands, as well as other sub-Antarctic islands.

Therefore, I investigated microarthropod distribution patterns in the keystone plant species, *Azorella selago*, in fellfield areas on sub-Antarctic Marion Island on different scales of observation. In the following section a brief summary of observed patterns and processes at the within-plant, within stand, island-wide and between islands scale, will be given. Furthermore, the likely effects of climate change and

alien species on microarthropod communities on Marion Island are discussed and the implications of these effects in the sub-Antarctic region indicated.

Patterns at multiple scales

It has been argued that patterns and processes are dependent on the scale of observation, and therefore it is necessary to investigate communities on more than one scale (Wiens 1989; Hurlbert 1990; Gaston 2000). In this study we included four scales of observation from small to regional scale in order to understand the full extent of spatial heterogeneity in microarthropod distributions in *Azorella selago* plants.

Firstly, microarthropods showed spatial pattern inside *Azorella selago* plants (Chapter 1). Microarthropod abundance was higher in the southeastern and southwestern sides of plants. Temperatures in the southern side of plants were colder compared to the rest of the plant, coinciding with the cold, dry, less frequent wind from the south. Furthermore, since the dominant wind is from the northwest, material and possible additional food resources for microarthropods are deposited on the leeward, i.e. southern side of cushions (Warren Wilson 1959; Chown and Avenant 1992). Microarthropods were also more abundant in areas where *A. selago* plants were covered with the grass, *Agrostis magellanica*, which roots present additional nutrients for microarthropods, because of more mycorrhizae hyphae (Seastedt 1984; Smith and Newton 1986). Therefore, since microarthropods aggregate in favourable microenvironments, i.e. microclimate, resource availability (Usher and Booth 1986), the less harsh microclimatic conditions and additional food resources in the southern half of *A. selago* plants were likely to be responsible for microarthropod distribution patterns within plants.

In contrast to spatial patterns within plants, total microarthropod abundance was not spatially aggregated across stands of *Azorella selago* plants (Chapter 2). Dispersal is likely to occur between plants, since microarthropods do occur in the fellfield soil (Barendse and Chown 2001). However, because of harsh conditions, i.e. low temperatures, moisture and nutrients in fellfield soil (Gremmen 1981), desiccation risk for microarthropods, especially springtails, is high (Hopkin 1997; Convey et al. 2003). Migrating microarthropods are therefore unlikely to search for and locate the best suitable *A. selago* plant, but would rather colonize the first plant they encounter (Chapman 1994; Athanassiou et al. 2003). Furthermore, reproductive rates of microarthropods in plants can be assumed to be similar, since the

microenvironment (temperature and moisture), which is linked to reproductive success, was found to be broadly similar in plants at a specific site (Chapter 1). Fitness of microarthropod populations is thus similar in different plants giving rise to equal reproductive success and eventually random distribution patterns. Therefore equal reproductive success and the random choice of habitat would result in random distributions of microarthropods across a stand of plants.

Further, spatial heterogeneity of microarthropods was observed on an island-wide scale (Chapter 3), with higher springtail abundance and springtail and mite species richness on the western side than on the eastern side of Marion Island. Since the western side of Marion Island receives more rainfall and has a higher percentage cloud cover than the eastern side (Schulze 1971; Gremmen 1981), a moisture gradient exists across the island. The moisture gradient across the island presumably results in a higher moisture content in plants on the western side. This higher moisture status and the more favourable, buffered temperature inside plants (Nyakatia et al. unpublished) on the western side, are likely to be important determinants of microarthropod distribution patterns at the island-wide scale. Mite and springtail species richness and springtail abundance also declined significantly with altitude. This observation might be attributed to harsher environmental conditions, i.e. low temperatures, low rainfall and high wind speed on high altitudes (Heaney 2001; Jing et al. 2005).

The next scale was the between islands scale, i.e. Marion Island and Prince Edward Island (Chapter 4). Microarthropod community structure differed significantly between Marion Island and Prince Edward Island (Chapter 4). More alien species were recorded on Marion Island than on Prince Edward Island. The presence of more alien species on Marion is probably due to the higher human impact on this island, due to the permanently occupied research station on the northeastern side (Chown et al. 1998).

It is thus clear that the distribution of microarthropod abundances is dependent on the scale of observation. Furthermore, the importance of processes also changed from one scale to the next, e.g., temperature is likely to be more important in determining microarthropod distributions within plants than between islands. The different patterns and processes at different scales observed in this study are in accordance with the outcomes of other studies looking at biota distributions on multiple scales (see examples in Krawchuk and Taylor 2003; Fisher et al. 2004;

Johnson et al. 2004; Sunahara and Mogi 2004). Knowledge of the presence or absence of spatial patterns in microarthropods abundances are important, since the presence of spatial pattern could complicate analyses of observational and experimental data, whereas the absence of spatial pattern indicates that the sample scale is too big or too small to capture relevant patterns and processes (Spencer et al. 2002). The scale dependence of observed patterns has implications for field studies in the sub-Antarctic, since studies on distribution patterns in this region have mainly focused on large scale patterns, i.e. between island comparisons (Chown et al. 1998; Davies et al. 1997; Michaux and Leschen 2005). This study is the first to quantify distribution patterns of microarthropods within one plant species on one island and therefore, sets an example for future studies in the sub-Antarctic, with the aim of demonstrating distributions patterns of microarthropods.

Climate change and alien species impacts

The climate on Marion Island has become significantly warmer and drier over the past 50 years (Smith 2002) and is predicted to continue in this manner in the whole sub-Antarctic region (IPCC 2001). A warmer and drier climate may influence the current distribution patterns of microarthropods differently on different scales. Decreasing rainfall is likely to decrease microarthropod, especially springtail, abundances across all scales (Convey 2001; McGeoch et al. in press). Additionally, drying is likely to alter distribution patterns across a stand of plants. Decreasing rainfall, together with warmer temperatures, will result in drier fellfield soil between *Azorella selago* plants (Le Roux and McGeoch submitted). These altered conditions are likely to decrease microarthropod migration rates between plants and birth and death rates within plants may become more important determinants of community structure than migration. Plant specific characteristics may result in divergent growth and development rates within different plants, resulting in aggregated patterns of microarthropods across stands of plants.

Warmer temperatures have been shown to be important for insect distributions (Bale et al. 2002). However, the upper and lower lethal limits of some species on Marion Island (Slabber 2005) are well beyond the range of temperatures that microarthropods experience inside *Azorella selago* plants (Chapter 1). Therefore, warming alone may not have a large influence on microarthropod abundance. However, increasing temperature may have indirect influences on distribution

patterns. For example, the grass, *Agrostis magellanica*, responded positively to warming in a climate change experiment (Le Roux et al. 2005), and therefore may increase in cover on *A. selago* plants as well as expand its altitudinal range. Since microarthropods responded positively to grass, an increase of grass cover may alter their distribution inside *A. selago* plants. Furthermore, an altitudinal range expansion of grass might result in higher microarthropod abundances at higher altitudes and in turn result in a weaker altitudinal trend in microarthropod abundance. Apart from the range expansion of *A. magellanica*, alien plant species, such as *Sagina procumbens*, may be favoured by climate warming resulting in the expansion of its range to higher altitudes (Gremmen and Smith 1999). Its spread into the fellfield soil might provide more surface cover and increased humidity in fellfield resulting in a more favourable surface environment for lateral dispersal for microarthropods (Hertzberg et al. 2000; Coulson et al. 2003).

Furthermore, alien species might alter indigenous species distributions differently at different scales. Since a warmer climate favours alien species, they will be able to expand their altitudinal ranges, with a possible displacement of indigenous species (Convey et al. 1999). However, only a few alien microarthropod species were observed in *Azorella selago* in this study, mostly at low altitudes. Nonetheless, warming may favour the further expansion of alien species to higher altitudes and the consequent colonization of *A. selago* plants at higher altitudes. At the between island scale, more alien species were observed on Marion Island compared to Prince Edward Island. Since alien species are favoured by ameliorated climate, alien species abundances may increase on Marion Island. Furthermore, more alien species may be introduced to Marion Island due to more human traffic to this island. The difference in microarthropod communities between Prince Edward Island and Marion Island will therefore continue to increase. New species might colonize Prince Edward Island from Marion Island via bird-, ocean currents- and wind- transport, but at least human mediated introductions can be prevented.

Climate change, alien species and the interaction between the two are thus a potential serious threat to the indigenous microarthropod species of Marion Island, as well as in the sub-Antarctic. While climate change can only be managed globally and on the long term (Chown et al. 2002), the introduction of alien species to the islands can be prevented. This study highlights the importance of human quarantine measures when visiting the Prince Edward Islands. Human activities must be regulated and quarantine

measures such as washing procedures and inspection of cargo must be applied (Chown et al. 1998; Greenslade 2002; Frenot et al. 2005). The slug, *Deroceras panormitanum*, for example, has been spread across Marion island by means of wooden crates, which was packed on vegetation surrounding the scientific station buildings, from which it was flown to various locations across the island (Chown et al. 2002). Furthermore, the increasing demand for tourism in the sub-Antarctic should also be discouraged or tightly regulated (Frenot et al. 2005). This study therefore contributes to management on the sub-Antarctic islands.

Future research

The impacts of climate change and alien species on indigenous microarthropods outlined above were made from field observations and therefore need to be manipulatively tested with field and laboratory experiments (Grayson and Chapman 2004). Indeed, the Marion Island climate manipulation experiment (McGeoch et al. in press) was a very important contribution to understanding the influence of climate change on microarthropod abundances in the field. However, additional detailed physiological studies are needed on individual species in order to predict individual species responses to altered thermal and precipitation regimes (Convey et al. 2003; Ims et al. 2004; Helmuth et al. 2005). The physiological tolerances of some species have been tested, although most of the tests were done on Arctic microarthropods (Hodkinson et al. 1994, 1996; Hertzberg and Leinaas 1998), Antarctic microarthropods (Convey 1994; Block and Harrisson 1995; Marshall 1996; Sinclair et al. 2003) or sub-Antarctic weevils, flies, moths and spiders (Crafford and Chown 1993; Sinclair and Chown 2002). For microarthropods inhabiting *Azorella selago*, physiological experiments to test temperature or water stress have been done only on *Halozetes fulvus* (Marshall 1996), *Cryptopygus antarcticus*, *Tullbergia bisetosa* and *Isotomurus palustris* (Sinclair and Chown 2002; Slabber 2005). Furthermore, since predictions regarding migration rate of microarthropods through fellfield soil depend on locomotion ability of species, physiological studies on locomotion ability of species might help to this regard. However, until now the locomotion ability of *A. selago* inhabiting species, only include the mite *H. fulvus* (Marshall and Chown 1995; Deere 2005). Although most of the microarthropod species are very small and therefore difficult to experiment with, information about their physiology will be very useful.

Furthermore, ecological studies with the specific aim of quantifying migration of species between plants will improve predictions. Studies using pitfall traps in the Arctic have been conducted and important results regarding migration ability of microarthropods in fellfield environments were obtained (Hertzberg 1997). A similar study could be done in Marion Island fellfield soil with pitfall or sticky traps as an estimate of migration rate of different species between plants.

Seasonal patterns have been found in microarthropod abundance (Barendse and Chown 2001). Since the samples used in this study came from only one sampling period in the summer (coinciding with peak abundance of microarthropods) different spatial patterns may be observed over a broader temporal scale. However, given the destructive nature of the sampling procedure (coring and the resulting mouse burrowing), an assessment of the benefits of additional sampling is needed. This study, together with the climate change experiment (McGeoch et al. in press), give a good idea of patterns of the microarthropod assemblage inhabiting *A. selago* plants at different scales across Marion Island, as well as possible future distributions in response to climate change.

Another important issue needing attention is the absence of recent weather data for the western side of Marion Island, as well as the absence of soil and plant moisture contents data across the island, especially on the western side. Moisture environments across the island need to be explored in detail to confirm the assumptions, i.e., higher rainfall and higher moisture content in plants on the western side, made in this study.

Final conclusion

Springtails and mites inhabiting *Azorella selago* on Marion Island showed spatial patterns at small scale (within the plant), large scales (island wide) and regional scale (between islands), but largely not at a local scale (within stands). The mechanisms possibly responsible for these patterns differ between scales, and range from temperature and nutrient availability at within plant scale, to rainfall at the island-wide scale and alien species at the between-island scale. Environmental changes will alter these patterns and baseline information such as presented here, is essential for predicting the possible impacts of climate change and alien species on microarthropods in fellfield ecosystems on Marion Island as well as on other sub-Antarctic islands.

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