

Habitat Specificity of Mites on Sub-Antarctic Marion Island

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ABSTRACT Studies on sub-Antarctic insects have suggested that species inhabiting the epilithic biotope (cryptogam-dominated habitats) exhibit higher habitat specificity than those species of the vegetated biotope (habitats dominated by vascular plants), and that this is partially the consequence of recolonization of the latter by migration from the former, which acted as glacial refugia during the Neogene. Here, the Acari is used to independently test this idea. To do so, 17 different habitats belonging to both the epilithic and vegetated biotopes were quantitatively sampled on sub-Antarctic Marion Island. These habitats included those on a rocky shore zone, in lowland vegetation, and in a mid-altitude fellfield. Thirty-nine morphospecies/taxa from 27 families were recorded, with a maximum abundance exceeding 300,000 individuals/m⁻². Mite assemblages differed significantly between all habitats, although the most pronounced differences were between the rocky shore, fellfield epilithic, and vegetated biotope habitats. Major differences between the rocky shore and fellfield habitats indicated that a clear distinction must be drawn between these two groups of habitats, although both were previously considered part of the epilithic biotope. It seems likely that the mite fauna of the vegetated biotope was derived mostly from fellfield habitats following deglaciation. Habitat specificity was also more pronounced in the epilithic (rocky shore and fellfield epilithic) species than in those from the vegetated biotope. Thus, the Acari provide support for the hypothesis of reduced habitat specificity in vegetated biotopes, possibly as a consequence of recent recolonization.

KEY WORDS *Azorella selago*, Acari, community structure, habitat specificity, glaciation

BECAUSE OF THEIR location just to the south or north of the Antarctic Polar Frontal Zone, the sub-Antarctic islands of the southern ocean have cold climates that are neither as extreme as those of the Antarctic, nor as mild as those of more temperate regions. In consequence, these islands support a range of vegetation types that vary considerably with altitude. Higher altitude areas tend to be dominated by typically Antarctic fellfield, or wind desert areas, while the lowlands have closed, tundra-like vegetation (Gremmen 1981, Bergstrom and Chown 1999). On the basis of their histories, and lack of vascular vegetation, Chown (1989) grouped these fellfield habitats and the rocky shoreline areas characteristic of most of these islands (e.g., de Villiers 1976, Knox 1994) into a single, 'epilithic' biotope. The habitats constituting this biotope are thought to have been continually present, even during the Neogene glacial maxima, when many of the islands had a substantial ice cover (Hall 1990, Chown 1994, Bergstrom and Chown 1999). However, the extent of these habitats is thought to have varied in concert with climatic fluctuations. However, the hab-

itats characterized by vascular plants (i.e., those of the 'vegetated' biotope, Chown 1989) are thought to have been largely absent at the height of the Neogene glaciations, but more extensive during interglacial periods. In a few instances, vascular species such as those in the genera *Lyallia* and *Azorella* may have been present at the glacial maxima (Schalke and Van Zinderen Bakker 1971, Young and Schofield 1973, Scott 1985).

Investigations of the insect faunas of the sub-Antarctic islands have suggested that differences in habitat specificity and the extent of interspecific interactions in these two major biotopes may be a consequence of the substantial differences in their age, and the fact that the vegetated biotope was colonized from epilithic refugia (Davies 1987, Chown 1994). Thus, insects in the vegetated biotope show little habitat specificity (Chown 1989, Chown and Scholtz 1989, Crafford 1990), although there may be habitat-associated differences in dominance and abundance (Vogel 1985). Likewise, interspecific interactions in this biotope are rare or nonexistent, and this is thought to be largely a consequence of low species richness, low niche occupancy, and abundant resources (Crafford et al. 1986, Crafford 1990). Such a paucity of interspecific interactions is in keeping with what theory would predict for an apparently

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stable, though adverse environment, where abiotic constraints should be more important than biotic interactions (Southwood 1977, Greenslade 1983, Holm 1988).

In contrast, habitat specificity in the epilithic biotope is reasonably common. Coastal habitats such as rocky shores and boulder beaches possess many habitat specific insect species (Crafford et al. 1986, Crafford and Scholtz 1987, Chown 1990), and this appears to be true also of fellfield (Davies 1973; Chown 1989, 1990). In epilithic habitats, biotic interactions are also more common than in the vegetated biotope. For example, parasitism is common on the shore (see Crafford et al. 1986) and interspecific competition is thought to be present both here and in fellfield (e.g., Davies 1972, 1987; Chown 1992). Again, these findings conform with previous findings. For example, Connell (1975, 1980) and Menge and Sutherland (1987) suggested that competition is most likely in moderately harsh physical environments, and Arthur (1987) argued that older communities are more likely to be structured by interspecific interactions than younger ones. Likewise, Holm (1988) suggested that given sufficient time, and hence the accumulation of species, interspecific interactions are likely to develop in stable, adverse environments.

Nonetheless, these generalizations concerning community structure in sub-Antarctic arthropods are not universally supported. For example, Vogel (1985) suggested that the favorable conditions found in lowland vegetated habitats, as opposed to the harsher conditions in the epilithic habitats (e.g., osmotic stress, greater exposure, and more pronounced environmental extremes, for environmental data see de Villiers 1976, Chown and Crafford 1992, Blake 1996), might encourage habitat specificity.

Despite the fact that the arthropod faunas of the sub-Antarctic islands are now relatively well known (Crafford et al. 1986, Greenslade 1990, Pugh 1993, Chown et al. 1998, Marshall et al. 1999), there have been few quantitative studies of micro-arthropod communities (see West 1982, 1984; Bellido and Cancela Da Fonseca 1988 for exceptions). Furthermore, of the studies that have been undertaken, none has set out to provide an independent test of the hypothesis that there are biotope-related differences in arthropod habitat specificity on the sub-Antarctic islands, and that the fellfield areas provided refugia from which lowland vegetation was probably recolonized. Therefore, the aim of this study is to provide just such a test using the Acari, an arthropod subclass that is not only more speciose in the sub-Antarctic than is the Insecta (e.g., compare Crafford et al. 1986 and Marshall et al. 1999), but which has also evolved independently of the insects. This is accomplished by an examination of mite community patterns and habitat specificity across 17 different habitats, belonging to both the epilithic and vegetated biotopes, on sub-Antarctic Marion Island.

Materials and Methods

Study Area. The South African possessions of Marion Island (46° 54' S, 37° 45' E) and Prince Edward Island (see Fig. 1) are typically sub-Antarctic in terms of their location, climate, geology and biology (see Van Zinderen Bakker et al. 1971, Smith 1987, Hänel and Chown 1999 for general information on climate, geology, biota and human presence on the islands). All sampling was undertaken on the eastern side of Marion Island within a radius of 5 km of the research station (Fig. 1).

Eleven habitats from within the vegetated (vascular vegetation) biotope and six habitats within the epilithic biotope were sampled. In the vegetated biotope, and on botanical grounds, Gremmen (1981) identified five community complexes, each characterized by several different plant associations. Within these community complexes, ten representative plant associations (here referred to as habitats), occurring at and below 400 m above sea level (a.s.l.), were sampled. Five of these habitats represent the *Juncus scheuchzerioides*-*Blepharidophyllum densifolium* community-complex and differ only in their dominant bryophyte species (termed the mire group, habitats 1–5 in Table 1). Three of these habitats were chosen at low altitudes (because of the large spatial extent of the mire community complex at low altitudes, Gremmen 1981). Because mires also extend to higher altitudes, a mid-altitude and high-altitude mire were chosen as representative of higher elevation mires, and these are both high altitude variants of *Jamesoniella grandiflora* dominated mires (N.J.M. Gremmen, personal communication). The remaining five vegetated biotope habitats represented the four remaining community complexes (nonmire group, habitats 6–10 in Table 1).

The epilithic biotope comprises rocky shore areas, which were not included in Gremmen's (1981) classification, and the cryptogam-dominated rocky habitat (here termed the fellfield epilithic habitat, habitat 12 in Table 1) in a mid-altitude fellfield community complex. The fellfield community complex (also known as wind-desert or fjaeldmark), which dominates in terms of surface area of the island at and above 300 m a.s.l., except for a small area (≈ 10 km²) of permanent ice-cap (Verwoerd 1971), forms in areas strongly exposed to wind, on a variety of substrates. The dicot, *Azorella selago* Hook f. (Apiaceae) is conspicuously present as discrete cushions in fellfields up to an altitude of 700 m a.s.l., above which cryptogams dominate (Huntley 1972, Gremmen 1981). Therefore, the fellfield community complex cannot strictly be termed a epilithic or vegetated biotope because it contains both components, i.e., the fellfield epilithic (cryptogam-dominated) areas interspersed with *A. selago* cushions. For this study, the *A. selago* cushions within the fellfield habitat (habitat 11 in Table 1) were considered part of the vegetated biotope, while the cryptogam-dominated rocky areas (fellfield epilithic habitat) between the cushions were considered part of the epilithic biotope. This distinction was maintained because

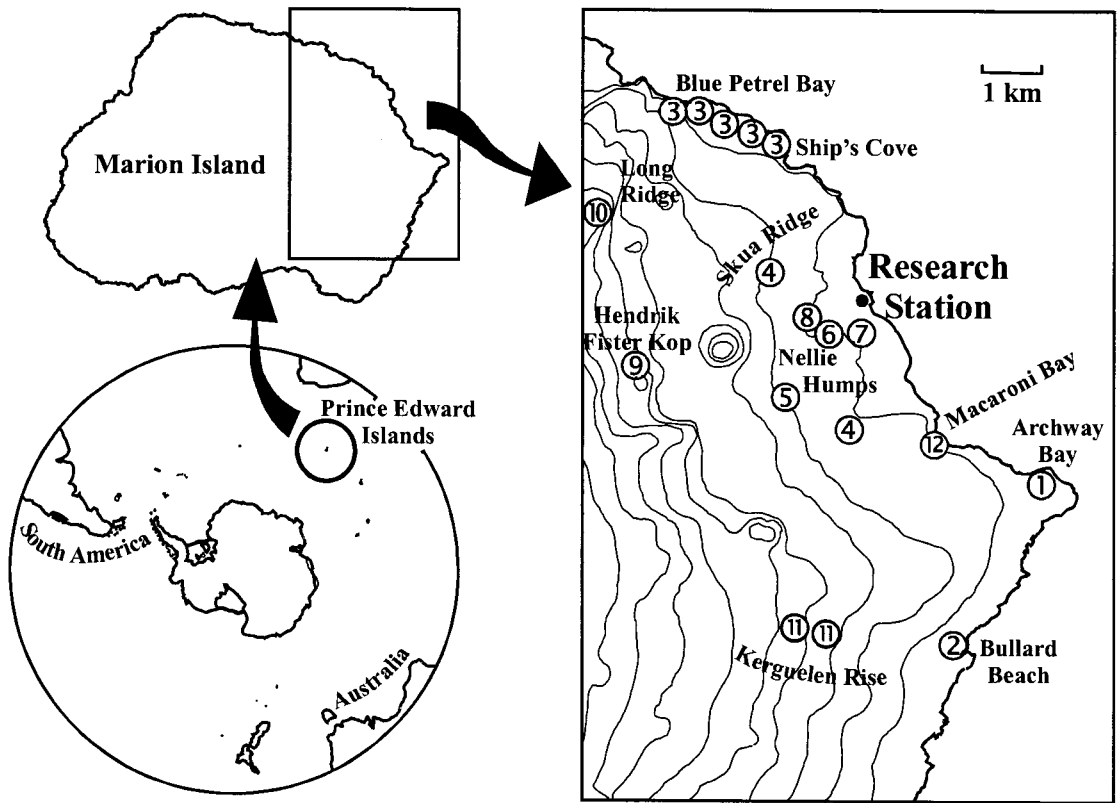


Fig. 1. Locality map showing position of the Prince Edward Islands in the South Polar region, an outline of Marion Island, with the east coast enlarged to indicate the positions of sampling sites. Contours at 50-m intervals. Communities: 1 = *Crassula moschata* herbfield; 2 = *Poa cookii* tussock grassland; 3 = *Cotula plumosa* herbfield; 4 = *Acaena magellanica* drainage line; 5 = *Blechnum penna-marina* lowland slope; 6 = *Blepharidophyllum densifolium* mire; 7 = *Sanionia uncinata* mire; 8 = *Jamesoniella colorata* mire; 9 = mid-altitude mire; 10 = high-altitude mire; 11 = mid-altitude fellfield (which includes both *Azorella selago* cushions and epilithic biotope); 12 = Rocky shore.

Chown (1989) separated these two habitats of the fellfield community complex owing to the wholly different weevil assemblages they support. Furthermore, because Scott (1985) suggested that *A. selago* is the first species to recolonize deglaciated areas, it would seem likely that colonization might proceed via this species. Therefore, to test whether conditions would favor the development of mite assemblages more characteristic of the vegetated biotope, in this epilithic component, we considered the *A. selago* cushions a separate habitat. Throughout the article, the term "fellfield community complex" is reserved for the habitat as a whole, including both the cryptogam-dominated, fellfield epilithic habitat and the vascular *A. selago* habitat (see Table 1).

The other epilithic biotope habitats that were sampled were those found on a gently sloping, unbroken rocky shore. Five distinct shore zones (three littoral and two supralittoral, habitats 13–17 in Table 1) were distinguished, based on distance from the high water mark, and the type of algal or lichen cover present (see de Villiers 1976, Mercer et al. 2000).

Sampling Protocol. The sampling program spanned 2 yr (June 1996 to April 1998). All habitats from the

vegetated biotope, with the exception of *A. selago* cushions, were sampled from 1996 to 1997. Nonmire communities (Table 1) were sampled from June 1996 and every alternative month thereafter until May 1997, and mire communities were similarly sampled from July 1996 to June 1997. The fellfield and rocky shore habitats were sampled from 1997 to 1998. The shore was sampled from June 1997 and every second month until April 1998. Fellfield was sampled every alternative month from July 1997 to April 1998 (the last month sampled for both shore and fellfield was April 1998 owing to logistic constraints).

Vegetated Habitats 1–10. Five 2 by 2-m quadrats (four 1-m² quadrats in the small, high-altitude mires), varying from 20 m to 3.5 km apart, were arbitrarily placed in homogenous patches considered representative of each vegetation type/habitat (Fig. 1). Samples were taken using an O'Connor split-corer (Southwood 1978, Edwards 1991) (i.d. of core = 70 mm and height = 70 mm, surface area ≈ 0.0039 m²). Five cores were collected at randomly determined positions from each quadrat. Thus, 25 cores per sampling month were taken from habitat types with five quadrats (a total of 150 samples for the year, except for *Cotula plumosa*

Table 1. Habitat types sampled on the east coast of Marion Island for this study

Community complex	Habitat	Habitat description	Location and approximate altitude
Oligotrophic (<i>Juncus scheuchzerioides</i> - <i>Blepharidophyllum densifolium</i>) mire complex	1. <i>B. densifolium</i> mire	Areas of peat accumulation with impeded drainage. These three species of bryophytes are important peat-forming plants	All sites in the area between the Scientific Station and Nellie Humps (50 m a.s.l.)
	2. <i>Sanionia uncinata</i> mire		Near Hendrik Fister Kop (250 m a.s.l.)
	3. <i>Jamesoniella colorata</i> mire		Long Ridge South (400 m a.s.l.)
	4. Mid-altitude mire		Coastal cliffs at Archway Bay (20 m a.s.l.)
Salt-spray (<i>Crassula moschata</i>) complex	5. High-altitude mire		
	6. <i>C. moschata</i> halophytic herbfield	Dense mats of the succulent herb, found in shore-zone areas affected by wind-blown sea spray	
Biotically influenced (<i>Callitriche antarctica</i> - <i>Poa cookii</i>) complex	7. <i>P. cookii</i> tussock grassland	Dense stands of tussocks, found in areas influenced by trampling and manuring of animals, in this case penguins	Adjacent to macaroni penguin colony, Bullard Beach North (20m a.s.l.)
	8. <i>Cotula plumosa</i> herbfield	Lush stands of the feathery leafed herb, found in shallow manured soils, also associated with salt-spray	Coastal stretch between Blue Petrel Bay and Ship's Cove (20 m a.s.l.)
Drainage line (<i>Acaena magellanica</i> - <i>Brachythecium</i>) complex	9. <i>A. magellanica</i> drainage line	Tangled mats growing in areas with pronounced subsurface water movement, such as river banks, in springs, flushes, water tracks and drainage lines	Two inland sites, one at Tom, Dick and Harry (75 m a.s.l.), and the other at Skua Ridge (100 m a.s.l.)
Fernbrake (<i>Blechnum penna-marina</i>) complex Fellfield/fjaeldmark	10. <i>B. penna-marina</i> lowland slope	Well-drained, relatively dry lowland slopes, dominated by <i>B. penna-marina</i>	Nellie Humps (100 m a.s.l.)
	11. <i>Azorella selago</i> cushions	Distinct cushions of various shapes and sizes dispersed throughout the fellfield and covering less than 10% of the total surface area. Grasses, club mosses and ferns sometimes grow epiphytically on the cushions.	Kerguelen Rise (250 m a.s.l.)
Littoral	12. Epilithic component	A mixture of boulders, rocks and gravel, which may be sorted by wind or freezing. Numerous encrusting, and cushion- and ball-forming bryophytes. Also contains organic material derived from <i>A. selago</i> and abundant cryptogams.	Kerguelen Rise (250 m a.s.l.)
	13. Red algal zone	Above the upper limit of bull kelp <i>Durvillaea antarctica</i> . Submerged during high tide. Completely covered by filamentous, foliose and encrusting Rhodophyta.	Macaroni Bay (sea level)
	14. <i>Porphyra</i> zone	The mid-littoral zone dominated by the rhodophyte genus <i>Porphyra</i> .	Macaroni Bay (sea level)
Supralittoral	15. <i>Verrucaria</i> zone	First lichen dominated zone which marks the upper littoral. Almost continuously encrusted by the dark grey to black encrusting lichen. Falls in the splash zone.	Macaroni Bay (sea level)
	16. <i>Mastodia</i> zone	Dominated by the dark foliose thalli of the genus <i>Mastodia</i> .	Macaroni Bay (sea level)
	17. <i>Caloplaca</i> zone	The uppermost supralittoral zone covered by a bright yellow encrusting lichen within the genus <i>Caloplaca</i> .	Macaroni Bay (sea level)

Simplified habitat descriptions have been modified from de Villiers (1976), Gremmen (1981), Smith (1987), Hänel (1999), and Mercer et al. (2000).

Table 2. Complete list of Acarine taxa identified in 17 habitats (vegetated and epilithic) on Marion Island, and used in analyses (after Marshall et al. 1999)

Sub-Order	Family	Species
Mesostigmata	Rhodacaridae	Five spp.?
	Digamasellidae	<i>Dendrolaelaps</i> sp.
	Cillibidae	One sp.
Prostigmata	Ologamasidae	One sp.
	Nanorchestidae	Four <i>Nanorchestes</i> spp.?
	Eupodidae	<i>Eupodes minutus</i> (Strandtmann)
	Rhagidiidae	<i>Rhagidia</i> sp.
	Ereynetidae	<i>Ereynetes macquariensis</i> Fain
	Tydeidae	One <i>Tydeus</i> (<i>Pertydeus</i>) sp.
	Unknown prostigmatid sp.	One sp.
	Bdellidae	<i>Bdellodes</i> sp.
	Stigmaeidae	<i>Eryngiopus</i> sp. 1 (fellfield) <i>Eryngiopus</i> sp. 2 (shoreline)
	Erythraeidae	<i>Balaustium</i> sp.
	Tarsonemidae	One sp.
	Pygmephoridae	One sp.
Cryptostigmata	Halacaridae	<i>Halacarellus</i> sp.
	Brachychthonidae	<i>Isobacterus magnus</i> (Lohmann)
		<i>Liochthonius australis</i> Covarrubias
		<i>Macquariopppia striata</i> (Wallwork)
		<i>Austroppia crozetensis</i> (Richters)
		<i>Halozetes fulvus</i> Engelbrecht
		<i>Halozetes belgicæ</i> (Michael)
		<i>H. marinus devilliersi</i> Engelbrecht
		<i>H. marionensis</i> Engelbrecht
		<i>Podacarus auberti</i> Grandjean
		<i>Alaskozetes antarcticus</i> (Michael)
	<i>Domatorina marionensis</i> van Pletzen & Kok	
	Ceratozetidae	<i>Magellozetes antarcticus</i> (Michael)
		<i>Porokalumma rotunda</i> Wallwork
		<i>Schwiebea talpa subantarctica</i> Fain
<i>Algophagus</i> sp. 1 (vegetated biotopes)		
<i>Algophagus</i> sp. 2 (fellfield)		
Astigmata	<i>Algophagus</i> sp. 2 (fellfield)	
	<i>Algophagus</i> sp. 2 (fellfield)	
	<i>Algophagus</i> sp. 2 (fellfield)	
	<i>Algophagus</i> sp. 2 (fellfield)	
	<i>Algophagus</i> sp. 2 (fellfield)	
Winterschmidtidae	<i>Neocalvolia travei</i> Fein	
	<i>Neocalvolia</i> sp. 2	
	<i>Neocalvolia</i> sp. 2	
	<i>Neocalvolia</i> sp. 3 (shoreline)	
	<i>Neocalvolia</i> sp. 3 (shoreline)	
Hyadesiidae	<i>Hyadesia halophila</i> Fain	
	<i>H. kerguelensis</i> Lohmann	

where 25 samples were subsequently lost [i.e., $n = 125$], and 20 per sampling month from the high-altitude mire ($n = 120$). Micro-arthropods were extracted from cores with modified Macfadyen high gradient extraction (2 d at 25°C followed by 2 d at 30°C, Macfadyen 1961). Specimens were retained in 95% ethanol until further examination.

Azorella Selago Habitat 11. In the fellfield habitat the two habitat components (*A. selago* cushions and the epilithic biotope) were considered separately because they required different sampling approaches. Two replicate transects (80 by 40 m) were chosen, each consisting of two adjoining, identical subtransects (80 by 20 m) made up of four 20 by 20-m quadrats. One subtransect was used for sampling of the epilithic component and the other for the *A. selago* cushions. In each quadrat, five core samples were taken, thus 240 *A. selago* cushions were sampled (120 in each of the two replicates). Extraction took place as described previously.

Cryptogam-Dominated Habitat 12. Here, five 30 by 30-cm sampling grids from each of the four quadrats were collected per sampling month (i.e., 20 samples per transect per month and a total of 240 samples for both transects for the year). A sample consisted of the

upper layer of loose rock and plant (i.e., mosses, detritus) material scraped from within a 30 by 30-cm sampling grid down to no deeper than 10 cm. *Azorella selago* cushions and large boulders were purposely avoided. Arthropods were first extracted at the site by means of flotation in sieved (125- μ m mesh size), cold water from a nearby perennial stream. Samples were washed three times each, sieved through 125- μ m mesh, and stored in plastic jars for transport back to the laboratory where further extraction of arthropods from samples was achieved by means of differential wetting (Southwood 1978) with kerosene and 70% ethanol (aqueous phase).

Rocky Shore Habitats 13–17. Six transects perpendicular to the shoreline and stretching from the lower littoral to upper supralittoral were sampled (a different transect was randomly selected for each sampling month). All samples were collected on a single day near the date of spring low tide. Ten samples were randomly selected from a sampling grid (1 by 1 m) consisting of 100 smaller squares (10 by 10 cm) within each of the five zones along the transect; thus, a total of 60 samples per zone for the entire period. Samples were collected by scraping lichen/algae down to the bare rock from within a circular plastic tube into a

Table 3. Mean annual density per m² (±SE) of Acari in 12 terrestrial habitats (fellfield and vegetated) on Marion Island

Order/species	Acacua	Bleeh	Cot	Crass	Poa	Bleph	San	Jam	Hi	Mid	Azorella	Epilith
Mesostigmata (all)	3101 ± 527	1912 ± 226	7683 ± 815	2796 ± 322	2668 ± 276	953 ± 193	1682 ± 360	702 ± 135	323 ± 56	597 ± 125	1657 ± 100	149 ± 11
Rhodacariidae	591 ± 84	338 ± 40	1825 ± 152	1647 ± 122	1266 ± 131	184 ± 32	133 ± 42	71 ± 13	21 ± 7	95 ± 20	723 ± 61	24 ± 4
<i>Dendrolaelaps</i> sp.	62 ± 23	62 ± 28	293 ± 95	102 ± 40	69 ± 16	19 ± 14	10 ± 5	16 ± 5	3 ± 2	5 ± 3	281 ± 23	7 ± 1
Gillibidae	1770 ± 446	1495 ± 197	2330 ± 454	303 ± 53	826 ± 131	726 ± 187	1523 ± 353	612 ± 131	227 ± 45	473 ± 120	652 ± 69	117 ± 10
Ologamasidae	677 ± 125	17 ± 7	3235 ± 394	743 ± 220	506 ± 95	24 ± 9	16 ± 5	3 ± 2	7 ± 3	5 ± 3	—	—
Prostigmata (all)	3558 ± 273	2224 ± 152	3033 ± 479	4424 ± 344	1391 ± 170	1123 ± 145	298 ± 41	1176 ± 144	253 ± 49	407 ± 54	18294 ± 869	43 ± 4
<i>Nanorchestes</i> spp.	10 ± 5	196 ± 40	—	4 ± 4	—	4 ± 2	—	—	—	42 ± 28	662 ± 106	1 ± 0
<i>Eupodes minutus</i>	1046 ± 168	700 ± 103	2039 ± 416	1346 ± 224	542 ± 103	447 ± 131	130 ± 33	400 ± 67	92 ± 36	177 ± 36	15828 ± 790	2 ± 0
<i>Rhagidia</i> sp.	—	—	—	—	—	—	—	—	—	—	23 ± 6	1 ± 0
<i>Ereignetes macquariensis</i>	263 ± 76	30 ± 12	23 ± 11	107 ± 23	85 ± 22	40 ± 11	26 ± 10	29 ± 10	2 ± 2	12 ± 6	1183 ± 80	1 ± 0
Tydeidae	1983 ± 233	1026 ± 127	518 ± 75	2562 ± 260	579 ± 88	579 ± 78	64 ± 12	627 ± 111	104 ± 19	104 ± 19	538 ± 63	16 ± 3
<i>Bdalloides</i> sp.	220 ± 31	64 ± 11	17 ± 8	64 ± 53	49 ± 15	16 ± 6	28 ± 8	80 ± 15	2 ± 2	16 ± 6	28 ± 6	13 ± 1
<i>Eringiopus</i> sp. 1	—	—	—	—	83 ± 39	—	—	—	—	—	—	—
<i>Balaustium</i> sp.	—	—	—	—	17 ± 6	—	—	—	—	—	—	—
Tarsonemidae	10 ± 9	—	17 ± 8	4 ± 2	—	—	—	5 ± 5	—	—	—	—
Pygmephoridae	24 ± 11	2 ± 2	64 ± 29	241 ± 133	14 ± 6	38 ± 17	50 ± 15	35 ± 9	2 ± 2	57 ± 16	31 ± 8	2 ± 1
Unidentified	—	—	—	97 ± 33	23 ± 19	—	—	—	—	—	—	—
prostigmatid	—	—	—	—	—	—	—	—	—	—	—	—
Cryptostigmata (all)	986 ± 177	3,099 ± 322	5,211 ± 462	7,950 ± 680	5,749 ± 419	3,984 ± 408	3,534 ± 333	4,944 ± 442	788 ± 90	2,120 ± 228	5,451 ± 433	1,215 ± 58
<i>Liochthonius australis</i>	2 ± 2	2 ± 2	—	83 ± 57	—	210 ± 113	—	—	2 ± 2	35 ± 28	25 ± 6	11 ± 3
<i>Macquarioroppia striata</i>	12 ± 5	113 ± 20	607 ± 137	930 ± 289	1,632 ± 227	64 ± 20	2 ± 2	326 ± 158	130 ± 44	13 ± 2	258 ± 44	13 ± 2
<i>Magalozetes antarcticus</i>	—	—	—	—	—	—	—	—	—	—	2 ± 2	24 ± 8
<i>Halozetes fulvus</i>	102 ± 21	511 ± 92	1,960 ± 265	4,802 ± 479	2,600 ± 245	929 ± 164	1,479 ± 208	317 ± 51	140 ± 22	442 ± 56	683 ± 70	725 ± 48
<i>Podacarus alberti</i>	61 ± 20	99 ± 43	1,318 ± 160	393 ± 57	1,109 ± 99	258 ± 196	95 ± 17	35 ± 11	33 ± 9	50 ± 12	18 ± 10	—
<i>Domatorina marionensis</i>	269 ± 81	669 ± 81	1,119 ± 37	1,429 ± 182	139 ± 36	2,048 ± 293	1,323 ± 147	3,726 ± 340	300 ± 40	1,221 ± 190	402 ± 52	239 ± 25
<i>Austrotopia crozetensis</i>	540 ± 144	1,713 ± 241	1,208 ± 203	930 ± 289	270 ± 93	476 ± 88	634 ± 157	540 ± 142	31 ± 9	81 ± 36	4063 ± 391	202 ± 25
Astigmata (all)	109 ± 73	31 ± 10	489 ± 96	81 ± 31	73 ± 22	47 ± 12	130 ± 30	29 ± 10	22 ± 7	31 ± 9	41 ± 8	7 ± 2
<i>Schwiebia talpa</i>	94 ± 73	2 ± 2	127 ± 28	5 ± 3	4 ± 2	42 ± 12	111 ± 29	29 ± 10	10 ± 4	26 ± 8	37 ± 7	—
<i>Allogophagus</i> sp. 1	—	14 ± 8	21 ± 13	7 ± 3	21 ± 12	3 ± 2	16 ± 8	—	7 ± 3	3 ± 2	—	—
<i>Allogophagus</i> sp. 2	—	—	—	—	—	—	—	—	—	—	1 ± 1	7 ± 2
<i>Neocalticola travei</i>	5 ± 3	10 ± 5	129 ± 33	43 ± 21	14 ± 6	—	—	—	—	—	—	—
<i>Neocalticola</i> sp. 2	10 ± 6	5 ± 4	212 ± 63	26 ± 11	35 ± 14	2 ± 2	3 ± 2	—	—	2 ± 2	—	—

Acacua = *Acacua magelamica*; Bleeh = *Blechnum penna-marina*; Cot = *Cotula plumosa*; Crass = *Crassula moschata*; Poa = *Poa cookii*; Bleph = *Blepharidophyllum densifolium*; San = *Samonia uncinata*; Jam = *Jamesoniella colorata*; Hi = high-altitude mire; Mid = mid-altitude mire; Azorella = *Azorella selago*; Epilith = epilithic biotope in mid-altitude fellfield. ** Indicates density of less than one specimen per m². n = 150 for all except Hi (n = 120), Cot (n = 125), Azorella and Epilith (n = 240 for both).

Table 4. Mean annual density per m² (±SE) of Acari in the five rocky shore zones (n = 60 for all zones)

Order/species	Red zone	Porphyra zone	Verrucaria zone	Mastodia zone	Caloplaca zone
Mesostigmata (all)	—	—	27 ± 19	456 ± 86	199 ± 52
<i>Dendrolaelaps</i> sp.	—	—	—	42 ± 21	199 ± 52
Rhodacaridae	—	—	27 ± 19	415 ± 80	—
Prostigmata (all)	3,818 ± 794	3,716 ± 975	23,608 ± 5,766	438 ± 100	3,050 ± 433
<i>Eupodes minutus</i>	—	—	—	—	66 ± 34
<i>Halacarellus</i> sp.	12 ± 8	11 ± 11	—	—	—
<i>Isobacterus magnus</i>	3,804 ± 795	3,705 ± 975	23,608 ± 5,766	87 ± 25	—
<i>Eryngiopus</i> sp. 2	—	—	—	351 ± 94	2281 ± 412
Tydeidae	3 ± 3	—	—	—	703 ± 148
Cryptostigmata (all)	620 ± 143	438 ± 87	6,990 ± 1,009	151,042 ± 27,494	3,621 ± 1070
<i>Alaskozetes antarcticus</i>	—	—	—	4,059 ± 1,346	—
<i>Halozetes belgicae</i>	6 ± 4	26 ± 16	265 ± 124	130,380 ± 25,393	1,817 ± 779
<i>H. marinus devilliersi</i>	44 ± 14	8 ± 5	27 ± 27	8 ± 5	0
<i>H. marionensis</i>	570 ± 139	396 ± 84	6,698 ± 1,009	3,841 ± 1,244	0
<i>Podacarus auberti</i>	—	8 ± 5	—	12,748 ± 3,608	27 ± 19
<i>Porokalumma rotunda</i>	—	—	—	8 ± 5	1,777 ± 701
Astigmata (all)	23,001 ± 4,099	36,684 ± 4,138	85,228 ± 10,390	211,954 ± 31,749	4,324 ± 1,431
<i>Algophagus semicollaris</i>	—	—	—	219 ± 81	—
<i>Hyadesia halophila</i>	—	—	—	211,724 ± 31,743	2,984 ± 1,381
<i>H. kerguelenensis</i>	23,001 ± 4,099	36,684 ± 4,138	85,228 ± 10,390	—	—
<i>Neocalvolia</i> sp. 3	—	—	—	11 ± 8	1,340 ± 523

plastic vial, using a scalpel blade. Owing to the variable nature of the lichen and algal cover of the different zones, tubes of two different diameters were used (i.d. of tube = 70 mm for Red, *Porphyra* and *Mastodia* zones and 35 mm for *Verrucaria* and *Caloplaca*). Samples were retained in 70% ethanol.

Arthropods in each sample were separated by hand under a binocular dissecting microscope. Insects and Collembola were considered in separate studies (Gabriel 1999, Hänel 1999, Mercer et al. 2000, Barendse and

Table 5. Mean annual mean mite density ± SE (individuals/m²) and species richness in 17 different habitats

Habitat	Density ± SE (individuals/m ²)	Species richness
Rocky shore		
Red algal zone	27,439 ± 4,510	7
<i>Porphyra</i> algal zone	40,838 ± 4,235	7
<i>Verrucaria</i> lichen zone	115,852 ± 14,975	6
<i>Mastodia</i> lichen zone	363,890 ± 37,200	13
<i>Caloplaca</i> lichen zone	11,194 ± 2,439	9
Non-mires		
<i>Cotula plumosa</i> herbfield	16,416 ± 1,166	19
<i>Crassula moschata</i> herbfield	15,251 ± 953	22
<i>Poa cookii</i> tussock grassland	9,881 ± 610	21
<i>Acaena magellanica</i>	7,754 ± 804	20
<i>Blechnum penna-marina</i>	7,274 ± 536	21
Mires		
<i>Jamesoniella colorata</i> mire	6,851 ± 586	16
<i>Blepharidophyllum densifolium</i> mire	6,106 ± 515	19
<i>Sanionia uncinata</i> mire	5,644 ± 601	17
Mid-altitude mire	3,137 ± 323	19
High-altitude mire	1,112 ± 119	17
Fellfield		
Epilithic biotope in fellfield	1,414 ± 65	21
<i>Azorella selago</i> cushions	25,443 ± 1,131	20

For all terrestrial habitats n = 150 except high-altitude mire (n = 120), *Cotula plumosa* (n = 125), *Azorella selago* and epilithic biotope (n = 240 each). n = 60 for all shore-line zones.

Chown 2001). Mites were sorted into species or morphospecies, identified to the lowest possible taxonomic level and counted (Krantz 1978, Marshall et al. 1999). Because of the large number of new records of undescribed mite species found on Marion Island (Marshall et al. 1999), identification to species level was not always possible. Thus, the family name might well refer to more than a single species. Specifically, Rhodacaridae might refer to up to five different species of which some may be habitat specific (Table 2). Cillibidae refers to a single unknown species, a first record for the sub-Antarctic. Nanorchestidae might include four species, some of which are possibly habitat specific. The family Rhagidiidae includes a single unknown species. Tydeidae includes all tydeid mites, most likely representing a single species of the genus *Tydeus* (*Pertydeus*). The unknown prostigmatid mite found only in *Crassula moschata* and *Poa cookii* is similar to Tydeidae, but was considered sufficiently distinct not to warrant its inclusion in this family. The *Eryngiopus* spp. represent new sub-Antarctic records. The specimens found in the fellfield and on the shore were kept separate (*Eryngiopus* sp.1 and 2). The Algophagidae may be represented by as many as five species. For these analyses, three distinct species were distinguished, one from vegetated biotopes (*Algophagus* sp. 1), one from the fellfield complex (*Algophagus* sp. 2), and another from the shoreline (*Algophagus semicollaris*). The family Winterschmittidae contains three species belonging to the genus *Neocalvolia*, the first two being found in some vegetated habitats and the latter on the shoreline. *Hyadesia kerguelenensis* and *Hyadesia subantarctica* were both present, but were combined under the former species. The specimens referred to as *Isobacterus magnus* might include *Rhombognathus auster*, which was only discovered on the rocky shore elsewhere. Three additional species that were not recorded in Marshall et al. (1999) were also found in the samples. These include a species

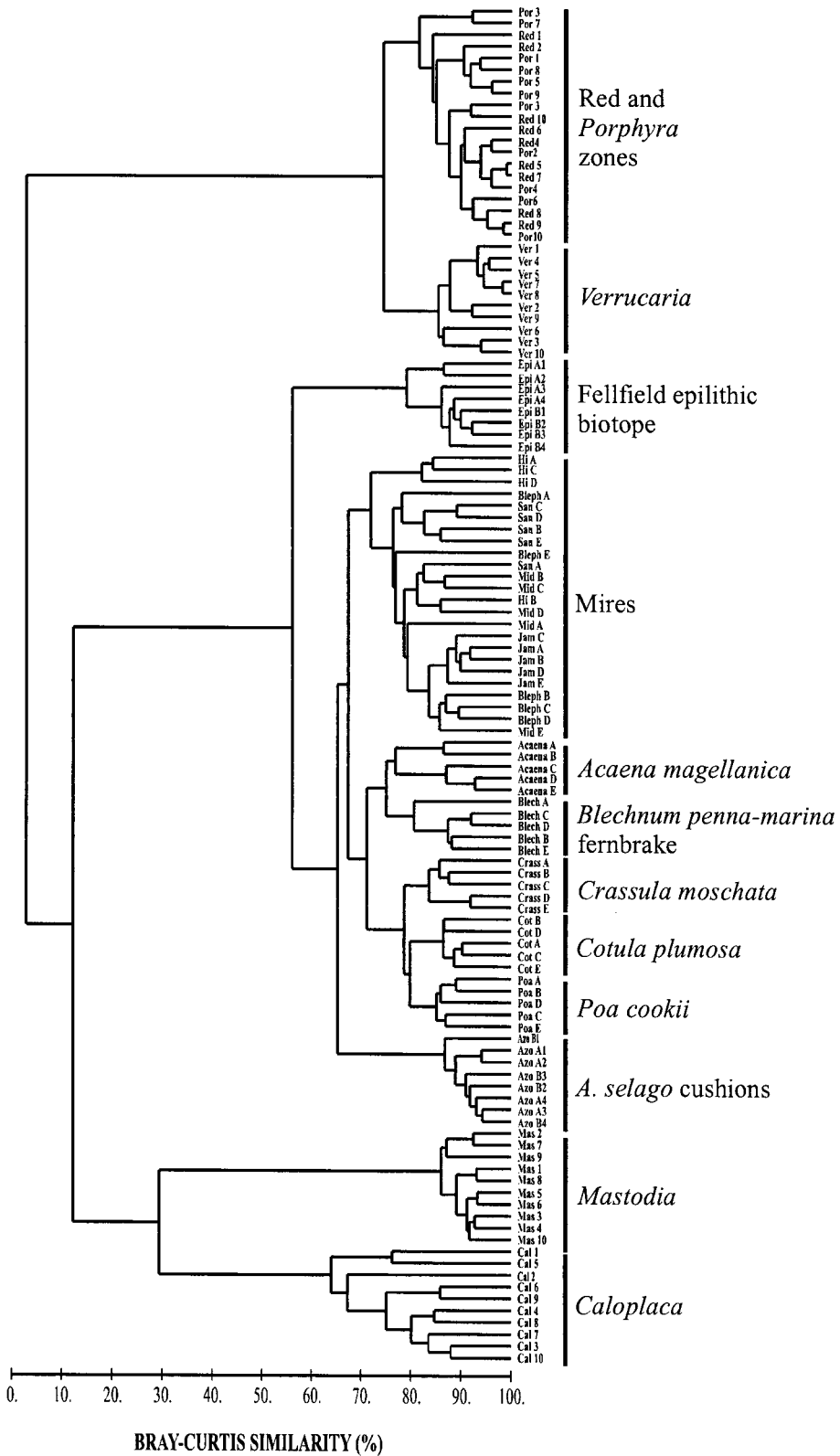


Fig. 2. Dendrogram of cluster analysis of mite abundance in 17 habitats (vegetated and epilithic) on Marion Island.

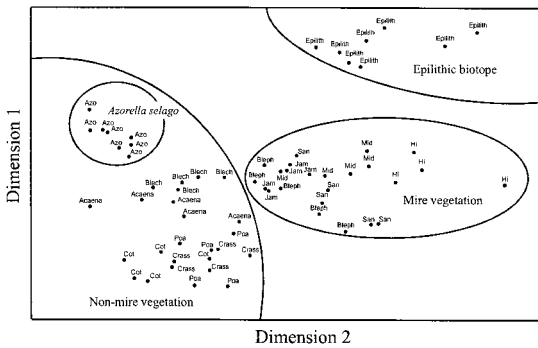


Fig. 3. Nonmetric MDS ordination of abundance of mite species in 12 terrestrial habitats (fellfield and vegetation) (stress = 0.13). *Acaena* = *Acaena magellanica*; *Blech* = *Blechnum penna-marina*; *Cot* = *Cotula plumosa*; *Crass* = *Crassula moschata*; *Poa* = *Poa cookii*; *Bleph* = *Blepharidophyllum densifolium*; *San* = *Sanionia uncinata*; *Jam* = *Jamesoniella colorata*; *Hi* = High-altitude mire; *Mid* = Mid-altitude mire; *Azo* = *Azorella selago*; *Epilith* = epilithic biotope in mid-altitude fellfield.

of Ologamasidae, commonly found in, and apparently restricted to the vegetated biotopes, and two species of prostigmatid mites from the families Tarsonemidae and Pymphoridae. Because of these taxonomic issues we refer to the separate taxonomic units as “species/taxa.”

Counts for all life stages within species were combined. This was relatively straightforward given the low number of species per family, and clear habitat preferences of species in those families containing more than a single species. Samples are housed at the Universities of Durban-Westville and Pretoria, and voucher specimens at the National Collection of Insects, Pretoria.

Data Analyses. Raw counts for species were converted to densities per m^2 for all samples. Mean annual abundance ($\pm SE$) in each habitat was calculated per species, and for all species combined. To examine the extent to which mite assemblage structure differed between habitats, the abundance data were analyzed using procedures within PRIMER version 4.0 (Clarke and Warwick 1994). Densities obtained for replicate samples within each quadrat and across all months were summed to avoid the effects of seasonality and to accommodate a large data set (see Clarke 1993). This resulted in five replicates for each vegetated habitat, except for the high-altitude mire, which had four. The two fellfield habitats, *A. selago* cushions and the epilithic component, had eight replicates each and the rocky shore zones 10 each. A cluster analysis using group-average clustering and based on Bray-Curtis similarity measures was carried out to compare the different habitats. Data were double square-root transformed before analysis to weight common and rare species equally (Clarke and Warwick 1994). Owing to the great dissimilarity between some of the habitats and the associated scale problems, these data were not represented on an ordination plot. Rather,

the shore data were excluded and the remaining sites were examined using a nonmetric multi-dimensional scaling (MDS) ordination. To test for significant differences in mite assemblage structure between the a priori defined habitats, analysis of similarity (ANOSIM) was used (see Clarke 1993). This is a nonparametric permutation procedure applied to the rank similarity matrix underlying sample ordinations that calculates a global R-statistic. If R falls between zero and one it indicates some degree of discrimination between habitat types, the closer to one the higher the significance (Clarke and Warwick 1994).

Using the same species-abundance matrix, the extent of habitat specificity that each mite species or taxon displays was determined using the indicator value (IndVal) method described by Dufrene and Legendre (1997). This procedure expresses the degree of specificity (uniqueness to a habitat) and fidelity (frequency of occurrence throughout a habitat) as a percentage. A high percentage IndVal indicates both high habitat specificity and fidelity for a species and suggests that it is highly representative of the habitat in question. Thus, a species with a high IndVal is not only unique to a habitat but has a high probability of being present in any sample from that habitat (McGeoch and Chown 1998). Species/taxa that reached their maximum and significant ($P < 0.05$) IndVal for a specific habitat were taken to be strong indicator species for that habitat, and for the purposes of this study were considered habitat specific. No level of significance can be calculated for species achieving maximum IndVals at the first level (i.e., for all habitats), because of the random reallocation procedure of habitats among habitat groups used to calculate the IndVals (Dufrene and Legendre 1997). These species represent extreme habitat generalists.

Results

A total of 39 taxa (mostly species) representing 27 families was found (Table 2). Prostigmata was the most speciose group, including 14 species/taxa, followed by Cryptostigmata (12), Astigmata (9), and Mesostigmata (4). In terrestrial habitats (Table 3), Cryptostigmata and Prostigmata were the numerically dominant groups with densities of the latter reaching $> 18,000$ individuals/ m^2 . The Astigmata reached higher densities in the shoreline habitats (Table 4) than in any of the terrestrial habitats, with *Hyadesia halophila* in the *Mastodia* zone reaching the highest density of any species in any habitat ($> 80,000$ individuals/ m^2). Both Cryptostigmata and Prostigmata were also highly abundant in the shoreline habitats. Cryptostigmata generally showed the highest density throughout all habitat types (ranging from ≈ 780 to $\approx 130,000$ individuals/ m^2) followed by the Prostigmata. Mesostigmata were more abundant in terrestrial habitats than on the shoreline.

Mite densities were highest in the shoreline habitats, with the exception of the *Caloplaca* lichen zone (Table 5). Within the vegetated biotope, mite densities were highest in the *Azorella selago* cushions, with

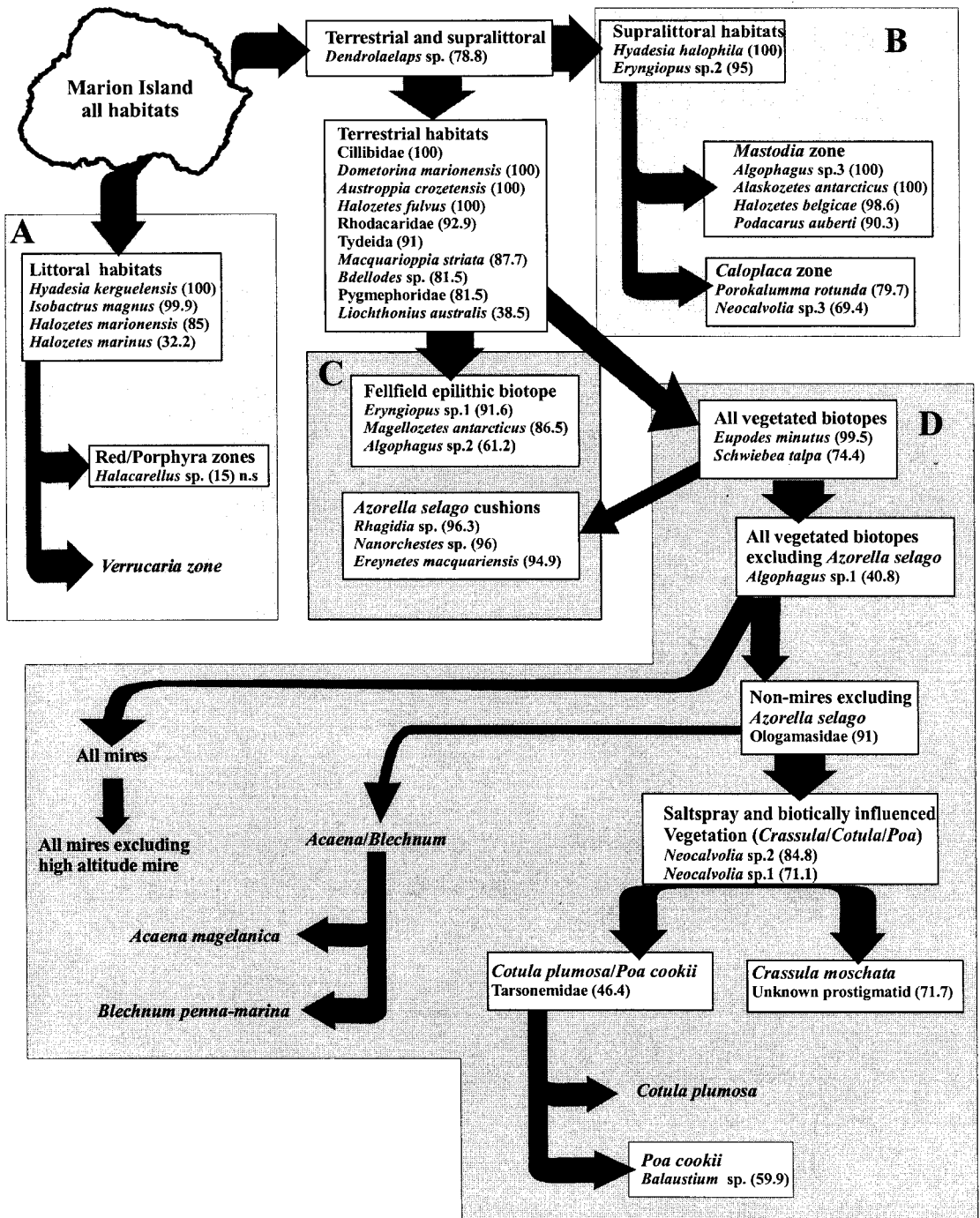


Fig. 4. Flow diagram showing indicator species reaching their maximum indicator values in the habitat groups distinguished by the cluster analysis (Fig. 2) (IndVals in brackets, all significant at $P < 0.05$ except where indicated by n.s.). Boxes: (A) Littoral habitats; (B) Supralittoral habitats; (C) Fellfield habitats; (D) All closed lowland vegetated habitats (excluding *Azorella selago*).

Eupodes minutus (Prostigmata) being the most abundant species. Among terrestrial habitats, total density of mites in the nonmire habitats was consistently

higher than in either the mire habitats or the fellfield epilithic habitat. The shoreline habitats housed fewer species/taxa (ranging between six and 13) than the

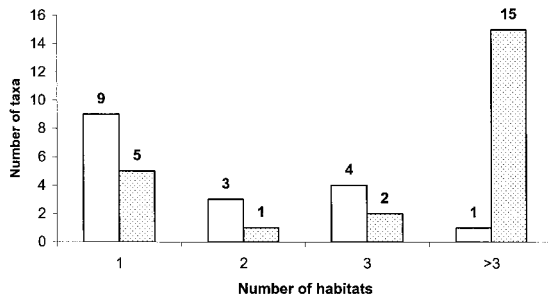


Fig. 5. Number of mite taxa specific to a set number of habitats. Unshaded = epilithic habitats (fellfield and rocky shore). Shaded = vegetated habitats (all vegetation types including *Azorella* cushions).

terrestrial habitats (ranging between 17 and 22) (Table 5).

The cluster analysis (Fig. 2) clearly shows a separation between the mite assemblages of the littoral and other habitats, and between those of the supralittoral and strictly terrestrial habitats (at *c.* 10% similarity). Furthermore, the mite assemblages of the various shore zones are rather different, except for the lowermost Red and *Porphyra* zones, which are indistinguishable. The epilithic component of the fellfield also has a mite assemblage rather different to that from the vegetated biotope. The nonmetric MDS ordination for terrestrial habitats (Fig. 3) shows this clear separation between the epilithic and vegetated biotope, and a further separation between mire and nonmire vegetation types. ANOSIM indicated significant differences (global $R = 0.941$; $P < 0.01$) between all a priori defined habitat types. For all pairwise comparisons of habitats $P < 0.024$.

No taxa reached their maximum indicator values at the first level of all habitats (Fig. 4). At the second level, the three littoral habitats (Fig. 4A), as a group, had four characteristic species that can be considered generalists within these zones, while *Halacarellus* sp. was found to be characteristic (though its IndVal was nonsignificant) of the Red/*Porphyra* zone. Two species were characteristic of the two supralittoral habitats as a group (Fig. 4B), whereas the *Mastodia* and *Caloplaca* zones had four and two characteristic species, respectively. Ten species/taxa reach their maximum IndVals at the level of all terrestrial habitats and are thus generalists in these habitats. Three species were found to be specific to each of the two fellfield habitat components, i.e., *Azorella selago* cushions and the epilithic, cryptogam-dominated component (Fig. 4C). As a group, the remaining vegetated habitats included two characteristic species, whereas of the individual habitats within this biotope only the salt-spray and biotically influenced habitats contained species that reached their maximum IndVals in a single habitat (Fig. 4D). No species were characteristic of individual mire habitats, nor to mires as a group. In general, the epilithic taxa exhibited greater habitat specificity than those taxa found in the vegetated habitats (Fig. 5).

Discussion

The mite densities recorded here are similar to those found on other islands in the sub-Antarctic, and in the Antarctic in general. For example, the exceptionally high densities found in the littoral zones are comparable to those found on Kerguelen Island (Bellido 1981), whereas the densities characteristic of the *Azorella selago* cushions and halophytic herbfields are similar to those found in South Georgian grasslands and mossbanks (West 1984). The higher densities found in the habitats dominated by vascular vegetation compared with those in the bryophyte-dominated mires is also in keeping with the patterns displayed by indigenous Collembola (Gabriel et al. 2001) and insects (Hänel 1999) on Marion Island, and is probably a consequence of differences in plant standing crop between these habitats (Gabriel et al. 2001; see also Smith 1976, 1988).

Although no formal analysis has been undertaken here, it seems reasonable to presume that habitat characteristics have a significant influence on the mite assemblages on the island, as is the case with other components of the fauna (see Gabriel et al. 2001). Although most of the mite species were widespread in the vegetated habitats, there were significant differences between the mite assemblages in all of these habitat types. In addition, the nonmetric MDS ordination illustrates clearly that those vegetation types regarded as most similar on floristic grounds (see Gremmen 1981) have largely similar mite assemblages. For example, the salt spray and biotic community complexes are floristically similar (Gremmen 1981, Smith and Steenkamp 2001), and so too are their mite assemblages. Likewise, assemblages from mire habitats, which are very close floristically (Gremmen 1981), were more similar to each other than they were to those from the other vegetated biotope habitats.

There were, however, major discontinuities between the assemblages in the major biotopes. In the first instance, the cluster analysis indicated that the rocky shore habitats have assemblages very different to those of the terrestrial habitats. Although the supralittoral does share a few species with the some of the coastal, vegetated habitats, these species are generally tourists that are not true resident members of the rocky shore assemblage (see Mercer et al. 2000 for further discussion). There is also a pronounced difference between the assemblage in the fellfield epilithic habitat and those of the vegetated biotope. Although these habitats have several species in common, the former habitat also includes several species that are habitat specific. Furthermore, the coastal and fellfield habitats share no species and therefore have very distinct mite assemblages. These major differences between the assemblages have important implications for the idea that the rocky shore habitats and epilithic fellfield habitat should be included in a single epilithic biotope.

Although there are clearly grounds for separating the rocky shore, vegetated biotope, and fellfield epilithic habitat, the rationale for the inclusion of the

rocky shore habitats and the fellfield epilithic habitat into a single large "epilithic biotope" as was done by Chown (1989) (see introduction) is less apparent. Although such a classification undoubtedly reflects the historical persistence of these habitats (Chown 1989, 1994), the present results suggest that this classification does not reflect similar histories of the mite assemblages in each of these groups of habitats. In the case of the insects, Chown (1989, 1990) suggested that during the height of the Neogene glaciations, arthropods retreated to unglaciated epilithic havens (including both rocky shores and fellfield) from where they subsequently recolonized newly established vegetated habitats, especially at the end of the last glaciation. The distinctness of the shoreline mite fauna and the few species shared with terrestrial habitats suggest that the coastal habitats played a limited role as glacial retreats for more terrestrial species. Almost all species in the rocky shore habitats are restricted to these areas (Fig. 4 A and B), whereas the terrestrial habitats share most species and many habitat generalists occur there. Only a few species, such as *Halozetes fulvus* and *Neocalvolia* spp. (this genus seems restricted to the shore and adjacent salt-spray vegetation) seem likely colonists from the shoreline into the vegetation (see Mercer et al. 2000). These terrestrial species are closely related to mite taxa that show their greatest diversity on the island along the rocky shore. Thus, the coastal arthropod assemblages are likely to have had a history quite distinct from those that have developed in the terrestrial habitats, and this is reflected in current assemblage composition. A closer inspection of insect assemblage structure across all habitats on the sub-Antarctic islands, might indeed show that this is the case elsewhere (see also Wallwork 1972, 1973, and in a broader context Bücking et al. 1998).

Based on the numbers of shared species and preponderance of generalists in the vegetated habitats, it seems that recolonization of the vegetated habitats from the fellfield, and especially via the *Azorella selago* component, is more plausible. The *A. selago* cushions share several species with the fellfield epilithic habitat and these habitats in turn have many species in common with the vegetated areas (even though densities differ between the habitats). In addition, the two fellfield habitat types each have a number of habitat specific species, which show strong biogeographical affinities to the harsher maritime and continental Antarctic habitats. *Magellozetes antarcticus* prefers rocky, unvegetated habitats elsewhere in the Antarctic (Tilbrook 1967, Pugh 1993, Convey 1994) and *Rhagidia* sp., *Nanorchestes* spp. and *Ereynetes macquariensis* (all indicator species for *A. selago* cushions) are common inhabitants of maritime Antarctic moss turves, which seem to share many structural similarities with these cushions (Goddard 1979, West 1982, Usher and Booth 1986). Thus, it seems most likely that the fellfield habitats, with their combination of Antarctic and sub-Antarctic species, acted as refugia during the glacial maxima, and that species recolonized the newly formed vegetated habitats (see Scott 1985) from there. It seems plausible that many species survived in

the cryptogam-dominated epilithic habitat in the fellfield and first colonized newly established *A. selago* cushions, and thereafter the other vegetated habitats. This would be in keeping with the role played by *A. selago* in vegetation succession on the Prince Edward islands (see Scott 1985, Gremmen 1981, and also Frenot et al. 1998). However, because *A. selago* was probably present during the last glacial maximum on several sub-Antarctic islands (Schalke and Van Zinderen Bakker 1971, Young and Schofield 1973, Scott 1985), and tends to have a favorable microclimate (Huntley 1971, 1972; Crafford 1990), it may well have acted as a refugium in its own right (see also Chown 1994). This might also explain the similarity of the mite communities of this species to those of the other vegetated habitats. Whatever the actual route of colonization, it seems likely that the fellfield was a major refugium for mites during the last glacial maximum. Further tests of the applicability of this hypothesis, both to all arthropod species on Marion Island, and to the sub-Antarctic islands in general, now require more sophisticated phylogeographic methods.

With regard to the original hypothesis that habitat specificity is more pronounced in the epilithic biotope species, it is clear that this idea is supported by the data presented here. Mites in both the shoreline and fellfield habitats are more habitat specific than those found in the vegetated biotope, which tend to occur in most habitats (Fig. 5). The few specialists that do occur in the vegetated biotope are mostly restricted to the *Azorella selago* habitat, in keeping with what would be expected for an older habitat type (Arthur 1987, Chown 1992).

In summary, the data presented here support the idea, developed by Chown (1990, 1992, 1994) that habitat specificity is likely to be more pronounced in older, fellfield habitats, than in younger vegetated ones, with *Azorella selago* providing an exception that continues to support the hypothesis (it is an old, vascular habitat). Although Chown (1992) also suggested that interspecific interactions, especially competition, should be more prevalent in the epilithic biotope than in the vegetated habitats, the present data do not allow this hypothesis to be tested at present. Nonetheless, the outcome of the analyses indicates that if such a test is undertaken, a clear distinction must be drawn between the shoreline and inland (fellfield) epilithic biotope assemblages.

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