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Effects of cushion plants on high-altitude soil microarthropod communities: cushions increase abundance and diversity of mites (Acari), but not springtails (Collembola)

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ABSTRACT

Cushion plants in alpine ecosystems act as nurse species, which modify and alleviate environmental conditions and positively influence the diversity and abundance of other organisms. Soil fauna in alpine environments should benefit from nurse plant facilitation, but this has not been investigated. We compared diversity, abundance, and community structure of soil microarthropods (Collembola, Oribatida, Mesostigmata, Prostigmata, Endeostigmata, and Astigmata) under cushion plants and in adjacent open microsites in high altitude patterned ground landscapes in New Zealand. We investigated how cushion plants influence environmental factors, and how environmental factors and species traits contribute to microarthropod community structure. The results show that cushion plants are a key in maintaining the biodiversity of soil microarthropods in the high alpine. Cushion plants maintain higher moisture and organic matter content in the soil, provide productive and structurally complex habitat, and mitigate disturbance. Abundance and species richness of Oribatida, Mesostigmata, and Prostigmata were higher under cushion plants. In contrast, abundance of Collembola was higher in open microsites, while their species richness similar in and out of cushions. Oribatida assemblages were dominated by small asexual species, indicating a disturbed environment. Oribatida community structure was significantly related to the microhabitat in two out of three mountain ranges. Collembola assemblages were similar in and out of cushions. Higher soil moisture and organic matter content under cushion plants were significant in explaining patterns in microarthropod assemblages, although high percentage of variability was not explained by environmental variables. There was no effect of cushions on soil temperatures. Species identity of the cushion plant did not influence abundance, species richness, or community assemblages of mites and springtails; however, some species were associated with either *Dracophyllum* or *Raoulia* cushions.

INTRODUCTION

It is recognized that facilitation, that is, non-trophic positive interactions among species, is one of the key factors among the processes structuring ecological communities, and that prevalence and significance of facilitation are especially great in high-stress environments (Bertness and Callaway, 1994; Bruno et al., 2003; He and Bertness, 2014). In alpine ecosystems, cushion plants act as foundation and nurse species, providing structurally unique microhabitats with more stable environmental conditions, and positively influencing the diversity and abundance of other organisms (Badano et al., 2006, 2010; Cavieres et al., 2007; Molenda et al., 2012, and many others; see also review by Liczner and Lortie, 2014). The importance of cushion plants as foundation species for alpine invertebrates is especially pronounced (Liczner and Lortie, 2014), but comparatively poorly studied (Molina-Montenegro et al., 2006; Badano et al., 2010; Molenda et al., 2012; Reid and Lortie, 2012).

In New Zealand, one of the harshest environments for plants and animals is that of the patterned ground landforms (alpine cushion fields), which occupy extensive areas in the high alpine zone (above 1500 m a.s.l.) of the fault-block mountains in the South Island (Mark and Bliss, 1970; Bliss and Mark, 1974; Mark, 1994). The cushion field microtopography comprises repeated small earth hummocks 15–30 cm in height and 0.7–1.5 m in diameter (Mark, 1994). The crests of hummocks and stripes are occupied by ultradwarf cushion shrubs; the furrows between hummocks contain some herb and lichen species, as well as bare soil (Mark and Bliss, 1970). This topography is hypothesized to be an active periglacial landform maintained by seasonal differential freezing (Mark, 1994; Scott et al., 2008). The patterned ground landforms are not unique to New Zealand, and similar microtopographic structures are found in polar or high-altitude periglacial environments in North America, Africa, Greenland, Iceland, and Fennoscandia (Grab, 2005; Walker et al., 2008). These landforms are easily damaged, very slow to recover, and potentially susceptible to impact by climate change, so understanding factors that maintain biodiversity in these communities is critical.

The alpine cushion fields are subjected to extreme and fluctuating temperatures, strong winds, and short growing season (Mark, 1994; Scott et al., 2008). We hypothesized that cushion plants in the high alpine patterned ground landscapes have a critical role in creating favorable environmental conditions and facilitating biodiversity of common invertebrate inhabitants of alpine soils—microarthropods. Microarthropods—mites (Acari) and springtails (Collembola)—are abundant and ubiquitous in the High Arctic, Antarctic, and high alpine environments (O'Lear and Seastedt, 1994; Hagvar and Klanderud, 2009; Hodkinson et al., 2013; Russell et al., 2014) and correlate significantly to soil moisture gradients and vegetation cover in tundra-like ecosystems (Coulson et al., 2003; Russell et al., 2014). In New Zealand almost no quantitative data on communities of Collembola and mites are available outside of agricultural areas (McMillan, 1969; Adams, 1971; Luxton, 1982, 1983a, 1983b; Barratt et al., 2006; Schon et al., 2008, 2012; Minor, 2011; Greenslade et al., 2013). Nothing is known about microarthropod communities in the alpine cushion fields in New Zealand, or about microarthropod diversity patterns in relation to microtopography and vegetation in these ecosystems, although the importance of plants as foundation species for microarthropods has been demonstrated in the High Arctic (Coulson et al., 2003).

In this study, we explored (1) diversity and abundance of soil microarthropods under cushion plants and in adjacent open microsites in patterned ground alpine cushion fields, (2) whether (and how) cushion plants influence community assemblages of microarthropods, (3) how cushion plants influence environmental factors, and (4) how environmental factors and species traits contribute to microarthropod community structure.

Methods

Study Sites

The data were collected on 17–19 February 2014 in the high alpine zone (1600–1900 m a.s.l.) of three mountain ranges (the Pisa Range, the Old Man's Range, and the Remarkables) in the Central Otago region of the South Island of New Zealand (44°40′–45°40′S).

The Central Otago ranges are relatively recent mountains that began forming 2–5 m.y. ago on an ancient schist peneplain due to accelerated folding and uplift along a series of faults in the underlying crust. Prior to the mountain-building, this area is thought to have been low-lying without an alpine zone (Upton et al., 2014). During the Pleistocene, the ranges were subject to repeated glaciation events and considerable erosion, which produced schist rock outcrops (tors) characteristic of the alpine landscape in the area.

The alpine cushion fields are characterized by tundra-like vegetation and harsh weather conditions (Mark and Bliss, 1970). There is a complex ground pattern of earth hummocks 15–30 cm in height, with furrows in between (Fig. 1). The crests of hummocks are dominated by cushion-forming ultradwarf shrubs *Dracophyllum muscoides* Hook. f. (Ericaceae) and *Raoulia* sp. (Asteraceae, most likely *Raoulia hectori* Hook.f.); in furrows, there is largely bare soil with sparse lichens and herbs. The soil in alpine cushion fields is a fine-textured loess 2–30 cm deep, underlain by schist fragments (Mark, 1994). The climate of the high-alpine zone is cold all year round with a relatively small annual temperature range (mean annual air temperature ~2 °C) and frequent freeze-thaw cycles. Snow falls during almost every month of the year and forms a near-continuous cover for 4 to 6 months (Mark and Bliss, 1970). Soils at 10 cm depth remain unfrozen during the four warmest months (Mark and Bliss, 1970; Scott et al., 2008). On average, freezing occurs in every month of the year and only 20% of days are frost-free (Mark and Bliss, 1970; Scott et al., 2008).

Sampling

Nine alpine cushion fields were sampled (three on each mountain range) in February 2014. Cushion fields varied in size from 0.1 ha to over 2 ha; the distances between individual fields varied from 0.5–2.1 km in Old Man's Range and Pisa range, to 0.13–0.25 km in the Remarkables. In each cushion field (plot), 8–10 paired samples were collected from within cushion plants and from the furrow next to each cushion (4–5 cushion-furrow pairs). In each plot, both *Dracophyllum* and *Raoulia* cushions were sampled (2–3 of each plant species). Cushions were 20–35cm across (often irregular in shape), and 2–4 cm deep. The stem densities are very high (12.3–18.9 stems cm^{-2} for *D. muscoides*, 15.5–18.3 stems cm^{-2} for *R. hectori*) (Bliss and Mark, 1974). Soil cores for microarthropod extraction were collected using a stainless steel corer (125 cm^2); the volume collected included the entire vegetation layer (if within cushions), plus the soil 5 cm in depth. Soil samples for moisture and carbon analysis were collected simultaneously. Temperature readings were collected at the depth of 5 cm. Soil cores were kept chilled and delivered to the lab the next day; microarthropod samples were either extracted immediately in modified Berlese extractors for a week into 75% ECOH, or if not extracted immediately (due to capacity of extractors), were kept at 4 °C. Samples for immediate extraction or 4 °C storage were allocated randomly.

Soil moisture (%) was measured as a gravimetric loss. Soil was sieved through a 2 mm sieve, weighed, oven-dried at 60 °C for 48 hours, cooled in a desiccator for 15 min, and weighed again. Soil organic matter (%) was measured as a carbon loss on ignition. The sieved oven-dried soil from moisture analysis was reduced to 5 g subsamples, weighed, and placed into a 400 °C furnace for at least 16 hours. Soil was allowed to cool to ~150 °C in the furnace, then cooled further in a desiccator and

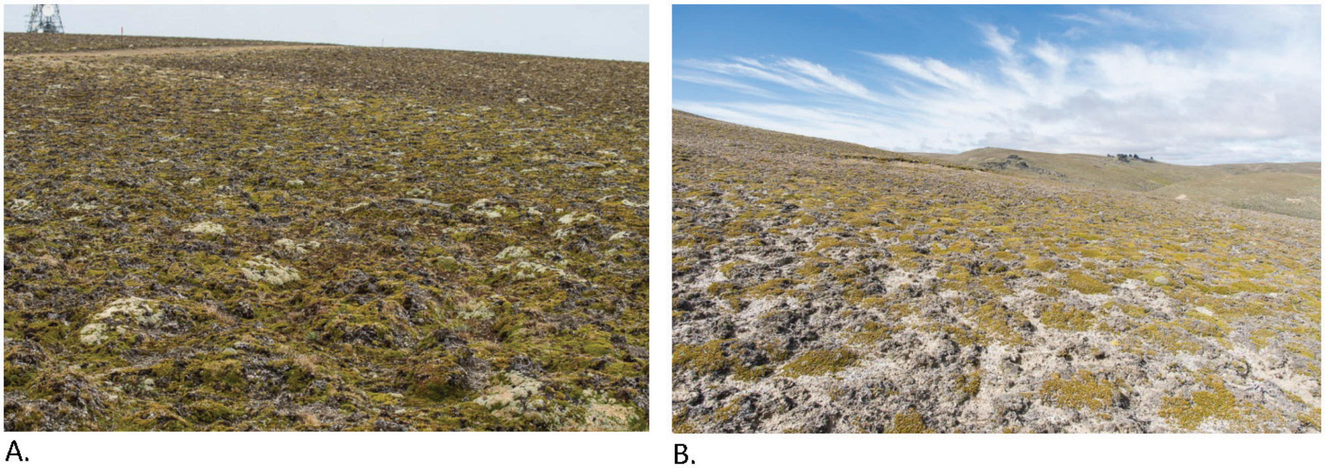

FIGURE 1. Study sites: patterned ground landscapes with dwarf shrub cushion vegetation in the high alpine zone, New Zealand, central Otago, summer 2014. (A) Old Man's Range; (B) Pisa Range.

weighed. Preweighed, washed and oven-dried porcelain jars were used for soil analysis.

Identification and Ecological Traits

Collembola, Oribatida, and Mesostigmata were identified to a species/morphospecies level, except Brachychthoniidae, which were pooled in the analysis. Unidentifiable nymphs were included in overall abundance counts but excluded from community analysis. Other Acari (Prostigmata, Endeostigmata, and Astigmata) were identified to a family level. Keys from Krantz and Walter (2009) and primary species descriptions were used for identification. For Oribatida mites, we recorded ecological traits of species—their body size and reproductive mode. Body size was assigned as "small" (<350 μm), "large" (>540 μm), or "medium" (all others). Reproductive mode was assigned as "asexual" from literature (e.g., Brachychthoniidae, *Tectocepheus velatus*) or if no males were observed in our samples of an abundant species (e.g., *Pterochthonius roynortoni*, *Oxyoppia suramericana*); reproductive mode was assigned as "sexual" if both males and females were present in our samples in approximately equal numbers (most other species). For each site, species abundance data were converted to trait abundances following Philips and Reid (2012).

Statistical Analysis

We used a generalised linear mixed model (SAS PROC GLIMMIX) to test the effect of cushion plant (under cushion vs. soil in furrow), as well as the effect of cushion plant species (*Dracophyllum* vs. *Raoulia*) on soil properties (soil temperature, moisture, and organic matter content) and on abundance and species richness of Collembola, Oribatida, Mesostigmata, Prostigmata, and other Acari (Endeostigmata and Astigmata), with the mountain range and plot as random factors and cushion-furrow pairs as a repeated measure. Soil temperatures in each mountain range were stratified by the cushion field, because the three cushion fields within the same mountain were visited at different hours of the day, which affected the overall air temperature. Abundance was expressed as the number of individuals per soil core; richness, as the number of taxa (species or families) per soil core. The Gaussian, Poisson, and the negative binomial distributions (chosen based on the fit statistics) were used for different variables. SAS 9.3 (SAS Institute) was used to perform analysis.

PERMANOVA in PRIMER 7 (Clarke et al., 1994) on sqrt-transformed abundances with the Bray-Curtis distance as similarity measure was used to test for differences in community composition between habitats (under cushions vs. soil in furrows), and between *Dracophillum* and *Raoulia* cushion species; plot effect (different cushion fields) was entered into the model as a random factor. Each mountain range was analyzed separately, because microarthropod assemblages differed significantly. Taxa with low abundance (fewer than 10 individuals) were excluded from this analysis. The distance-based linear modeling (DistLM procedure) with stepwise variable selection using AICc criterion was used to test which environmental variables or ecological traits best explain patterns of community similarity. The nonmetric multidimensional scaling (NMS) ordination was used to display the significant results. Indicator Species Analysis in PC-Ord for Windows, version 5, MjM Software (Dufrêne and Legendre, 1997) was used to quantify the associations between individual taxa and habitats. Significance level $\alpha = 0.05$ was used for all statistical tests.

Results

Microarthropod Abundance and Diversity

Overall, 9065 Oribatida, 2027 Mesostigmata, 3951 Collembola, 9518 Prostigmata, 873 Endeostigmata, and 392 Astigmata specimens were collected, which belonged to 158 taxa. Although the abundance and richness of all taxa were site-dependent, the trends were similar across all three mountain ranges (Table 1). Abundance and species richness of Oribatida, Mesostigmata, and Prostigmata mites were higher under cushions comparing with the soil in furrows (Oribatida: abundance $F_{1,36} = 28.50$, $P = 0.001$, richness $F_{1,36} = 46.53$, $P = 0.001$; Mesostigmata: abundance $F_{1,36} = 6.29$, $P = 0.017$, species richness $F_{1,36} = 9.05$, $P = 0.005$; Prostigmata: abundance $F_{1,36} = 12.67$, $P = 0.001$, richness $F_{1,36} = 13.60$, $P = 0.001$). Other Acari were also more abundant under cushions ($F_{1,36} = 8.72$,

TABLE 1

Soil properties, microarthropod abundance (individuals per soil core*), and microarthropod species richness (species/other taxa per soil core) in alpine cushion fields, central Otago, New Zealand, February 2014. "D" = under *Dracophyllum muscoides* cushions; "R" = under *Raoulia* sp. cushions; "Furrow" = soil in furrows outside of cushion plants. Values are means ± standard error.

	Old Man's Range			Pisa Range			The Remarkables		
	D	R	Furrow	D	R	Furrow	D	R	Furrow
Soil properties									
Water content (%)	32.14 ± 3.65	30.81 ± 2.54	28.03 ± 1.96	21.19 ± 0.84	20.38 ± 0.74	19.46 ± 0.78	21.12 ± 1.01	24.17 ± 2.07	20.24 ± 1.22
Organic matter (%)	14.97 ± 3.49	12.69 ± 2.32	10.91 ± 1.60	9.88 ± 1.05	7.05 ± 0.91	6.39 ± 0.66	9.47 ± 1.256	11.71 ± 2.77	7.36 ± 0.98
Temperature (°C)	8.88 ± 0.11	8.67 ± 0.15	8.63 ± 0.10	10.24 ± 0.24	10.28 ± 0.31	10.56 ± 0.29	12.92 ± 0.326	13.36 ± 0.32	13.46 ± 0.37
Abundance									
Oribatida	96.67 ± 18.83	100.6 ± 15.64	73.83 ± 14.73	92.14 ± 21.96	63.71 ± 10.90	48.64 ± 9.56	162.94 ± 54.65	124.36 ± 37.46	41.6 ± 23.31
Mesostigmata	43.33 ± 7.23	59.3 ± 14.05	45.08 ± 12.22	16.86 ± 2.18	17.0 ± 2.47	14.43 ± 2.48	14.19 ± 2.69	15.21 ± 2.42	10.67 ± 2.57
Prostigmata	122.92 ± 38.01	100.83 ± 36.98	122.16 ± 38.97	92.86 ± 39.0	100.64 ± 28.83	34.86 ± 14.5	173.63 ± 69.76	95.86 ± 20.75	45.67 ± 9.82
Other Acari**	25.83 ± 8.71	12.75 ± 3.06	29.08 ± 8.21	12.5 ± 2.68	13.21 ± 2.63	13.79 ± 2.86	17.63 ± 7.64	11.14 ± 6.23	10.73 ± 3.59
Collembola	60.17 ± 13.65	52.4 ± 8.35	63.08 ± 11.09	49.14 ± 10.45	53.93 ± 14.43	42.79 ± 8.13	43.31 ± 13.73	40.64 ± 10.16	51.73 ± 10.33
Richness									
Oribatida	8.67 ± 1.35	6.5 ± 1.35	7.25 ± 1.19	7.21 ± 1.04	6.29 ± 0.79	4.43 ± 0.56	6.5 ± 1.24	6.0 ± 0.99	3.6 ± 0.92
Mesostigmata	6.5 ± 0.69	6.4 ± 0.92	5.417 ± 0.72	4.21 ± 0.46	4.21 ± 0.52	3.64 ± 0.49	2.87 ± 0.32	3.78 ± 0.32	2.8 ± 0.30
Prostigmata	7.75 ± 0.82	4.5 ± 0.87	6.5 ± 0.63	6.57 ± 1.12	6.57 ± 0.81	4.5 ± 0.73	6.38 ± 0.60	5.5 ± 0.67	5.2 ± 0.38
Collembola	7.25 ± 0.61	6.4 ± 0.78	6.25 ± 0.72	4.93 ± 0.80	6.36 ± 0.64	5.36 ± 0.56	4.56 ± 0.52	4.5 ± 0.44	4.87 ± 0.47

*Soil core area: 25 cm^2, depth: vegetation plus top 5 cm of the soil layer.

**Includes Astigmata (Acaridae, Glyciphagidae) and Endeostigmata (Nanorchestidae, Alicorhagiidae).

P = 0.006). In contrast, abundance of Collembola was higher in furrows ($F_{1,36}$ = 7.73, P = 0.009); species richness of Collembola was similar under the cushion plants and in furrows ($F_{1,36}$ = 0.49, P = 0.4893). The species identity of cushion plant had no effect on abundance or species richness of mites and springtails.

Communities of Oribatida and "other" mites (Prostigmata + Endeostigmata + Astigmata) were significantly related to the habitat type in two out of three mountain ranges (Table 2). Collembola assemblages were similar between cushions and open ground in the Old Man's Range and Pisa Range, but more strongly associated with the habitat in the Remarkables (Table 2). Community assemblages of Mesostigmata were similar under cushion plants and in the open ground in furrows (Table 2). Species identity of cushion plants largely did not influence microarthropod community composition (Table 2), except for Oribatida in the Remarkables, where the effect of plant species was significant; the Indicator Analysis (Table 3) also suggested that some of the species were associated with either *Dracophyllum* or *Raoulia* cushions. Habitat preferences of individual taxa were somewhat inconsistent across the three sampled mountain ranges (Table 3). For example, *Oxyoppia suramericana*, one of the most abundant oribatid mites in all three areas, was associated with cushion plants in the Pisa Range and in the Remarkables, but was equally abundant under cushions and in the surrounding open ground in the Old Man's Range (Table 3).

Environmental Factors, Species Traits, and Microarthropod Community Structure

Across the three mountain ranges, soil water content was higher under cushion plants compared with the soil in furrows (Table 1) ($F_{1,40}$ = 17.65, P = 0.001), and was not dependent on the species of cushion plant ($F_{1,40}$ = 0.13, P = 0.722). Similarly, soil organic matter content was higher under cushions ($F_{1,40}$ =54.75, P = 0.001) and not dependent on the species identity of the cushion plant. There was no difference in soil temperature between

TABLE 2

PERMANOVA results (pseudo-F, Monte-Carlo *p-values*) for testing the hypotheses of no difference in microarthropod community assemblages under alpine cushion plants vs. in the surrounding soil, central Otago, New Zealand, February 2014; mixed model with cushion field (*n* = 3 in each mountain range) as a random effect. Values significant at *p* < 0.05 are in bold.

	Old Man's Range		Pisa Range		The Remarkables	
	In/Out cushions	Plant species	In/Out cushions	Plant species	In/Out cushions	Plant species
All taxa	1.944	1.301	**5.383**	1.238	**9.988**	2.631
	0.113	*0.337*	***0.002***	*0.344*	***0.001***	*0.064*
Oribatida	1.714	2.201	**5.545**	1.400	**5.189**	**5.039**
	0.185	*0.161*	***0.005***	*0.328*	***0.003***	***0.019***
Mesostigmata	2.069	1.346	2.236	2.433	1.874	0.831
	0.155	*0.316*	*0.158*	*0.187*	*0.215*	*0.524*
Other Acari*	1.500	0.884	**4.376**	1.583	**22.159**	2.133
	0.279	*0.518*	***0.026***	*0.269*	***0.001***	*0.144*
Collembola	1.659	0.810	2.130	0.828	**7.989**	0.727
	0.220	*0.542*	*0.121*	*0.553*	***0.009***	*0.597*

*Families of Prostigmata, Endeostigmata, and Astigmata.

TABLE 3

Taxa with relative abundance >5% within their group, and their habitat associations, with indicator values (Dufrêne and Legendre, 1997) and *p*-values for the Monte Carlo test. Values significant at $p < 0.1$ are in bold.

Group	Taxon	Indicator value	*p*-value	Habitat association
	Old Man's Range			
Oribatida	*Notophthiracarus otagoensis* Niedbała, 2016	**60.2**	**0.0480**	*Raoulia*
	Oxyoppia suramericana (Hammer, 1958)	41.4	0.4281	
	Brachychthoniidae	48.9	0.8270	
	Tumerozetes circularis Hammer 1966	36.7	0.8612	
Mesostigmata	Uropodina non det. 1	54.1	0.2132	
	Uropodina non det. 2	34.4	0.9594	
	Metagynella sp.	51.1	0.4573	
	Rhodacaridae gen. sp. 1	37.1	0.8832	
	Rhodacaridae gen. sp. 2	40.8	0.6605	
Other Acari	Iolinidae (Tydaeolinae)	49.8	0.6073	
	Eupodidae	**77.0**	**0.0366**	Cushions
	Nanorchestidae	70.7	0.2539	
	Scutacaridae	**80.2**	**0.0730**	Furrows
Collembola	*Mucromia caeca* (Wahlgren, 1906)	55.6	0.2214	
	Tullbergia sp. 2	73.6	0.2362	
	Cryptopygus sp. gr. *antarcticus* Willem, 1902	59.2	0.8958	
	Cryptopygus dubius Deharveng, 1981	33.3	1.000	
	Parisotoma cf. *raffi* (Womersley, 1934)	**100.0**	**0.0112**	Cushions
	Entomobrya sp.	**82.8**	**0.0810**	Furrows
	Azoritoma sp.	35.1	0.7510	
	Friesea sp. 1	41.3	0.6461	
	Pisa Range			
Oribatida	*Oxyoppia suramericana* (Hammer, 1958)	**94.6**	**0.0634**	Cushions
	Macrogena abbreviata Ermilov & Minor 2015	**94.8**	**0.0344**	Furrows
	Tectocepheus velatus (Michael, 1880)	32.7	0.8348	
	Notophthiracarus otagoensis Niedbała, 2016	35.6	0.7149	
	Brachychthoniidae	**89.8**	**0.0364**	Cushions
	Neophysobates incrassatus Ermilov & Minor 2015	44.4	0.4229	
	Pterochthonius roynortoni Ermilov & Minor, 2015	38.9	0.6909	
Mesostigmata	*Acugamasus* sp. gr. *punctatus* Lee, 1970	**61.5**	**0.0224**	Cushions
	Hydrogamasellus cf. *antarcticus* (Trägårdh, 1907)	26.8	0.8992	
	Rhodacaridae gen.sp.2	13.6	1.000	
	Phytoseiidae gen.sp.1	61.8	0.1856	
Other Acari	Eupodidae	**90.4**	**0.0126**	Cushions
	Iolinidae (Tydaeolinae)	54.6	0.1054	
	Ereynetidae	54.9	0.5009	
	Nanorchestidae	**73.4**	**0.0348**	Cushions
Collembola	*Tullbergia* sp. 1	26.3	0.9382	
	Parisotoma sp.	51.2	0.1084	
	Mucromia caeca (Wahlgren, 1906)	**62.4**	**0.0660**	*Raoulia*
	Cryptopygus sp. gr. *antarcticus* Willem, 1902	40.4	0.6361	

TABLE 3

Continued

Group	Taxon	Indicator value	*p*-value	Habitat association
	Folsomia sp.	53.1	0.6409	
	The Remarkables			
Oribatida	*Oxyoppia suramericana* (Hammer, 1958)	**90.0**	**0.0396**	*Dracophyllum*
	Brachychthoniidae	**80.2**	**0.0244**	Cushions
	Notophthiracarus otagoensis Niedbała, 2016	**82.6**	**0.0938**	Cushions
Mesostigmata	Rhodacaridae gen. sp. 2	**72.8**	**0.0350**	Cushions
	Gamasellus sp.	32.0	0.7550	
	Acugamasus sp. gr. *punctatus* Lee, 1970	72.5	0.1558	
	Onchogamasus sp. aff. *quasicurtipilus* Lee, 1970	**70.2**	**0.0310**	*Dracophyllum*
	Pilellus sp. aff. *rugipellis* Lee & Hunter, 1974	29.6	1.000	
Other Acari	Acaridae	**91.4**	**0.0146**	Furrows
	Iolinidae (Tydaeolinae)	**89.9**	**0.0120**	Cushions
	Eupodidae	**83.5**	**0.0120**	Cushions
Collembola	*Tullbergia* sp. 1	73.6	0.2164	
	Folsomia sp.	**62.8**	**0.0364**	Furrows
	Mucromia caeca (Wahlgren, 1906)	71.8	0.0672	*Raoulia*
	Hemisotoma sp. gr. *thermophila* (Axelson, 1900)	16.7	1.000	
	Friesea sp. 2	49.8	0.8114	

cushions and the soil in furrows, and no effect of cushion plant species.

Among measured environmental variables, differences in soil organic matter and water content best explained patterns observed in microarthropod community assemblages (Fig. 2). The DistLM results indicated significance of the environmental predictors, but also high variability in community similarity patterns not explained by measured environmental variables (DistML Pisa: all mites R^2 = 0.12, p(%OM) = 0.007, p(%H2O) = 0.065; Oribatida R^2 = 0.18, p(OM%) = 0.010; The Remarkables: all mites R^2 = 0.15, p(%OM) = 0.008, p(%H2O) = 0.028; Collembola R^2 = 0.09, p(H2O%) = 0.021; Oribatida R^2 = 0.09, p(OM%) = 0.005).

For Oribatida mites, the functional community composition (based on body size and reproductive mode) was not significantly different inside and outside of cushion plants in Old Man's Range and Pisa Range sites, but was significantly linked to the habitat in the Remarkables (PERMANOVA pseudo-$F_{1,8}$ = 12.406, p = 0.002), where presence of small and asexual species best explained variability in community composition (DistML R^2 = 0.48, p(small) = 0.001, p(asexual) = 0.001). This result reflects the overall numerical dominance of small asexual Oribatida under cushion plants; two of them, Brachychthoniidae and *O. suramericana*, together comprised 66% of total Oribatida community. None of the recorded ecological traits was associated with the open ground habitat (Fig. 3).

DISCUSSION

Our results show that cushion plants provide a favorable microhabitat and support higher abundance and species richness of soil mites (but not Collembola) than the intervening open ground. Similar effect on arthropods was found for alpine cushion plants elsewhere and for vegetated patches in polar environments (Coulson et al., 2003; Molina-Montenegro et al., 2006; Molenda et al., 2012; Russell et al., 2014). The microarthropod assemblages in our sites were dominated by Prostigmata and Oribatida, which, together with Collembola, are often most abundant arthropods in arcto-montane ecosystems (Behan and Hill, 1978; Makarova, 2002a, 2002b, 2015). The observed abundances (17,000–65,000 ind. m^{-2} for Oribatida, 16,500–

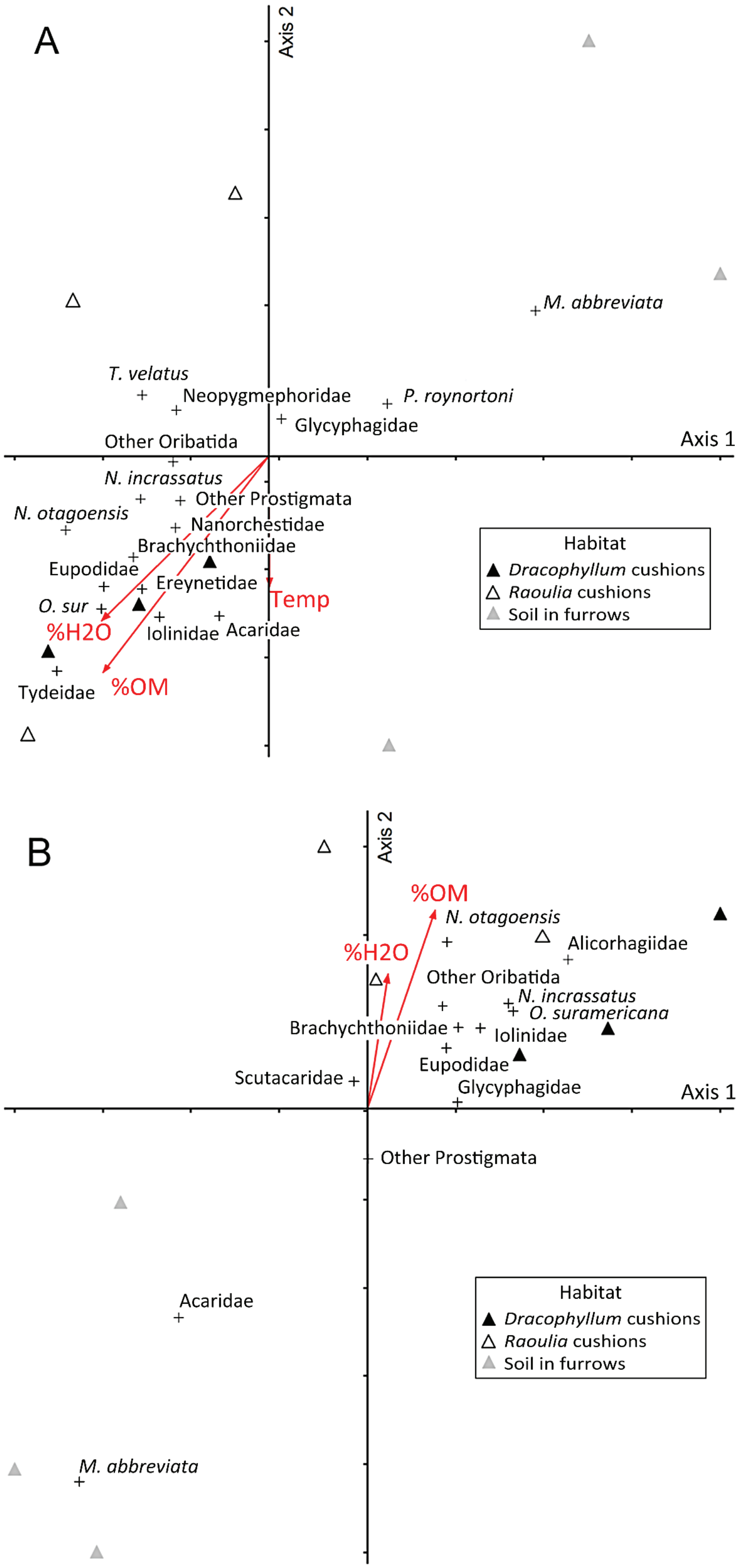

FIGURE 2. Nonmetric multidimensional scaling (NMS) ordinations for mites (Oribatida, Prostigmata, and Astigmata), and soil variables in the high alpine cushion fields, New Zealand, central Otago, summer 2014. %H2O = soil moisture content (gravimetric); %OM = soil organic matter content; Temp = soil temperature; O.sur = *O. suramericana*. (A) Pisa Range. DistLM best predictors of community composition: $R^2 = 0.12$, $p(\%OM) = 0.007$, $p(\%H2O) = 0.065$. (B) The Remarkables. DistLM best: $R^2 = 0.15$, $p(\%OM) = 0.008$, $p(\%H2O) = 0.028$. See Table 3 for Oribatida species.

75,000 for Prostigmata, 16,000–25,000 ind. m^{-2} for Collembola) are comparable to what is found across tundra-like ecosystems (Coulson et al., 1996; Petersen and Luxton, 1982; Bölter et al., 1997; Sørensen et al., 2006). Soil moisture (Booth and Usher, 1986; Hodkinson et al., 1994), cryogenic activity

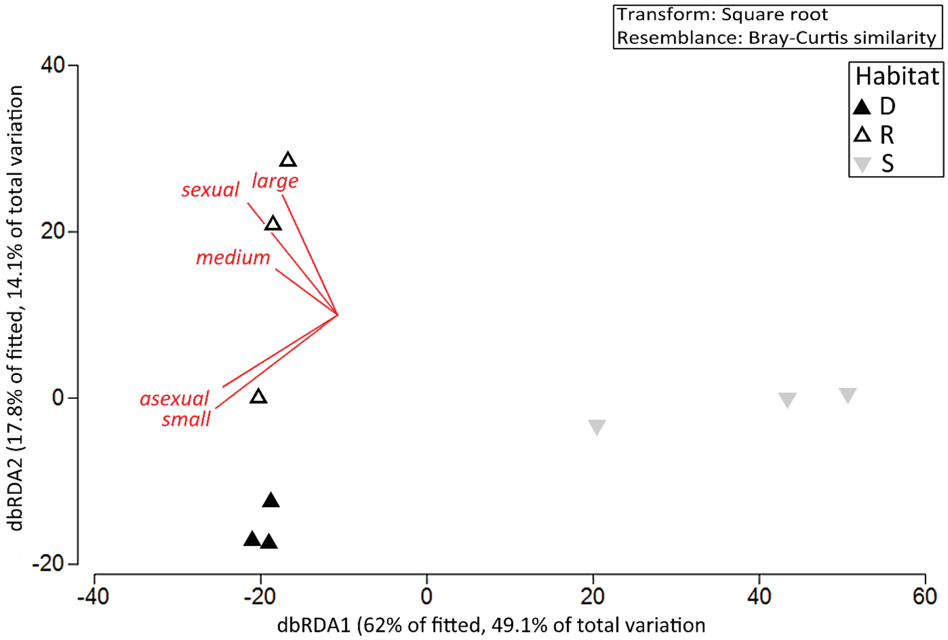

FIGURE 3. **Distance-based redundancy analysis (dbRDA) on plot means for Oribatida communities and their ecological traits (body size and reproductive type) in the alpine cushion fields in the Remarkables. Habitats: D = *Dracophyllum* cushions, R = *Raoulia* cushions, S = soil in the open ground. DistLM best predictors of community composition: $R^2 = 0.48$, $p(\text{small}) = 0.001$, $p(\text{asexual}) = 0.001$.**

(Markkula, 2014), and food availability (Webb et al., 1998) are the important factors structuring microarthropod communities in high alpine and tundra environments. Below we discuss the role of cushion plants in creating favorable microclimate, provision of resources, and alleviation of substrate instability.

Amelioration of Abiotic Environment

Mitigation of stressful environmental conditions is one of the main aspects of facilitation of arthropod diversity by alpine cushion plants (Liczner and Lortie, 2014). Generally, cushion plants maintain higher and more stable relative humidity than the surrounding open ground, and mediate dramatic changes in soil moisture during the growing season (Molina-Montenegro et al., 2006; Badano et al., 2010; Molenda et al., 2012). Similarly, in alpine Central Otago, soil moisture was higher under cushion plants in summer and autumn (Mark, 1994; Scott et al., 2008; our data). Moisture gradients are critically important to soil fauna and may limit distribution of microarthropod species to certain suitable microsites, despite the abundance of potential food resources elsewhere (Toda and Tanno, 1983; Booth and Usher, 1986; Hodkinson et al., 1994). In our study sites, moisture gradient was clearly apparent but less important for microarthropod community structuring (Fig. 2), probably because soil moisture is not limiting; the mean annual precipitation in these cushion fields is ~1600 mm (rain and snow), and soil moisture remains close to field capacity throughout the growing season (December to March) (Mark and Bliss, 1970).

Temperature moderation by cushion plants is an important part of facilitation by abiotic stress reduction (Molina-Montenegro et al., 2006; Almeida et al., 2014). Cushion plants buffer daily temperature extremes common in high alpine environments and have less pronounced diurnal patterns than the surrounding open ground (Kleier and Rundel, 2009; Badano et al., 2010; Molenda et al., 2012; Reid and Lortie, 2012). However, we saw no effect of temperature on microarthropod communities, and studies in Central Otago cushion fields found no significant difference in summer soil temperatures under cushion plants and in the open ground (Mark, 1994; Scott et al., 2008; our data). In addition, the temperature moderation by cushion plants in our study ecosystem is overridden by the effect of the snow cover during the winter. Central Otago cushion fields occupy exposed areas, and continuous severe winds remove the insulating snow cover from crests of hummocks and deposit it in the furrows; as a result, crests (and thus cushion plants) freeze earlier and faster than furrows, and remain frozen for longer; for about five months of the year the crests with cushion plants remain continuously frozen from the surface to at least 20 cm depth (Mark, 1994; Scott et al., 2008). In snow-covered furrows the daily minimum temperatures are higher and the soil remains unfrozen at 20 cm depth and only intermittently frozen at 5 cm depth. In spring, crests are exposed earlier than furrows and are subject to temperature fluctuations, while the furrows stay under the snow for longer and are decoupled from daily temperature extremes (Scott et al., 2008).

In general, cold-tolerance, rather than cold-avoidance, is a strategy utilized by arthropods in New Zealand alpine environments, due to frequent and unpredictable temperature fluctuations (Wharton, 2011). Mites and Collembola resist freezing using supercooling, with a number of antifreeze compounds known (Cannon and Block, 1988; Zettel, 2000; Sjursen and Sinclair, 2002). Daily temperature fluctuations and freeze-thaw cycles during the growing season are believed to pose few survival problems for mites and collembolans, provided that soil moisture is not limiting (Hodkinson et al., 1996; Hodkinson and Wookey, 1999). Experimentally increased number of freeze-thaw cycles did not increase the mortality of microarthropods and even stimulated soil microbial biomass and microarthropod populations (Sulkava and Huhta, 2003; Konestabo et al., 2007). Some microarthropods of cold environments use behavioral adaptations to deal with the cold: Collembola, for example, are highly mobile and practice sun-basking to boost metabolism (Birkemoe and Leinaas, 2000; Zettel, 1999/2000). At the same time, Behan-Pelletier (1999) concluded that there is no evidence that oribatid mites in cold environments passively thermoregulate by seeking warmer microhabitats. Overall, there is no indication that soil microarthropods actively use cushion plants as thermal refuges.

Resource Provision

Resource availability is an important factor affecting abundance and community composition of microarthropods in high alpine and tundra environments (Webb et al., 1998). Microarthropods in polar and high alpine environments tend to evolve broader niches, particularly with respect to food availability (Hodkinson and Wookey, 1999). Most of Collembola are not specialized feeders, consuming unicellular algae, fungal mycelium, plant litter, living plants, and lichens (Hodkinson et al., 1994; Bokhorst et al., 2007). Oribatida feed on litter, soil fungi and algae, and woody material (Phthyracaridae), or they are omnivorous (some Oppiidae) (Schneider et al., 2004; Diaz-Aguilar and Quideau, 2013). Prostigmata and Endeostigmata include predators (Rhagidiidae), phytophages (Tetranychidae, Tarsonemidae), mycophages (Eupodidae, Pygmephoridae), and algophages (*Nanorchestes*, *Penthalodes*) (Makarova, 2015).

The distribution patterns we observed indicate strong effect of cushion plants as resource providers and suggest some degree of habitat or food resource preference in individual microarthropod taxa. For example, high abundance of *Notophthiracarus otagoensis* in cushions reflects the availability of woody material (shrub branches), as immatures in this group are endophagous in wood (Norton and Ermilov, 2014). Cushion plants are relatively productive above- and belowground (Bliss and Mark, 1974; Meurk, 1978); *Dracophyllum muscoides* and *Raoulia hectori* cushions in Central Otago grow very slowly (shoots elongate by 3–8 mm during the growing season), but the total productivity is high due to very high stem densities (Bliss and Mark, 1974); the standing biomass is 2–4 kg m^{-2} (Meurk, 1978). Belowground biomass is also considerable; annual root production in the cushion community dominated by *D. muscoides* was estimated at 200–240 g m^{-2} (Bliss and Mark, 1974).

Abundance and species richness of microarthropods often correlate with soil organic matter content (Bölter et al., 1997; Russell et al., 2014). Cushion plants support the accumulation of organic matter in the soil (Mark, 1994; Cavieres et al., 2007; Scott et al., 2008; our data), and affect soil fungal and bacterial communities

(Roy et al., 2013). The roots and root exudates associated with plants can also influence soil microarthropod communities (Lindo and Visser, 2003). The preference for a particular species of cushion plant seen in some microarthropod taxa in our study is interesting. As a food resource, the two plant species differ in caloric values and total lipid content (Bliss and Mark, 1974), and may affect soil microbial communities in different ways. Although our data did not show any differences, the intensity of microclimate and soil modification may be different for the two cushion plant species, as these are a function of their physical structure, transpiration rate, pigments, and effects on albedo (Bliss, 1960; Körner, 2003; Molina-Montenegro et al., 2006; Almeida et al., 2014).

Disturbance Mitigation

Biological processes in tundra-like periglacial ecosystems operate in an unstable physical environment, as these systems are subjected to repeated natural disturbances, for example, cryoturbation (Hodkinson and Wookey, 1999). Cryoturbation has been identified as an important factor in creating and maintaining patterned ground landscapes (Mark, 1994; Walker et al., 2008). It is also an important factor structuring microarthropod communities in periglacial environments (Markkula, 2014). In alpine cushion fields, cryoturbation is associated with differential freezing and frost-heave during frequent freeze-thaw cycles throughout the growing season (Mark, 1994; Frost et al., 2013), resulting in vertical and lateral soil movement and substrate instability (Klaus et al., 2013; Peterson, 2011). The distribution of basic ecological traits (body size and reproductive mode) of Oribatida in our alpine cushion fields revealed patterns typical for environments with high levels of disturbance—the dominance of small asexual species, also seen in the High Arctic (Norton, 1994; Behan-Pelletier, 1999).

In patterned-ground alpine landscape, cushion plants attenuate frost heave and reduce soil movement (Walker et al., 2008, 2011). Our results show that cushions act as habitat patches that support abundant and species-rich communities; the effect is especially pronounced for Oribatida. The importance of disturbance as a structuring force for microarthropod communities, especially for Oribatida, has been stressed frequently (Behan-Pelletier, 1999; Maraun and Scheu, 2000; Lindo and Winchester, 2007). Compared with other microarthropods, oribatid mites are characterized by long life cycles, high adult survival, and low fecundity (Norton, 1994). Stability and structural complexity of the habitat are the major determinants of Oribatida species richness (Lindo and Winchester, 2007). While most studies on facilitation of arthropods by cushion plants focus on favorably modified microclimate (see review in Liczner and Lortie, 2014), we suggest that in a patterned ground landscape cushion plants play a critically important role in providing physically stable habitat in a highly disturbed environment.

Between cushions, repeated soil disturbances create mineral-rich open microsites exposed to the sun (Frost et al., 2013), which we hypothesize play a key role in the small-scale habitat diversity by providing sites of soil micro-autotroph production. In tundra environments, algae and cyanobacteria occur in the surface 0–2 cm layer of the soil, and in favorable conditions can reach high densities (Bunnell et al., 1975; Bölter, 2001). Microarthropods, which are algae and cyanobacteria feeders and which are mobile, quick to reproduce, or tolerant of disturbance, would be favored in such an environment. Species found in high abundance in furrows between cushions, such as Collembola and the small oribatid mite *Macrogena abbreviata* Ermilov et Minor 2015, are probably generalist colonizers and are able to exploit disturbed habitat.

CONCLUSIONS

The patterned-ground cushion fields in New Zealand alpine zone are a unique environment, with differentiated microclimatic conditions and regular disturbance. Cushion plants in these environments act as foundation species, which provide productive and structurally complex habitat, maintain higher moisture and organic matter content in the soil, and mitigate disturbance, which results in increased diversity and abundance of many soil microarthropod taxa. Our results support the view that cushion plants are a key in maintaining the biodiversity of arthropods in the high alpine (Molenda et al., 2012).

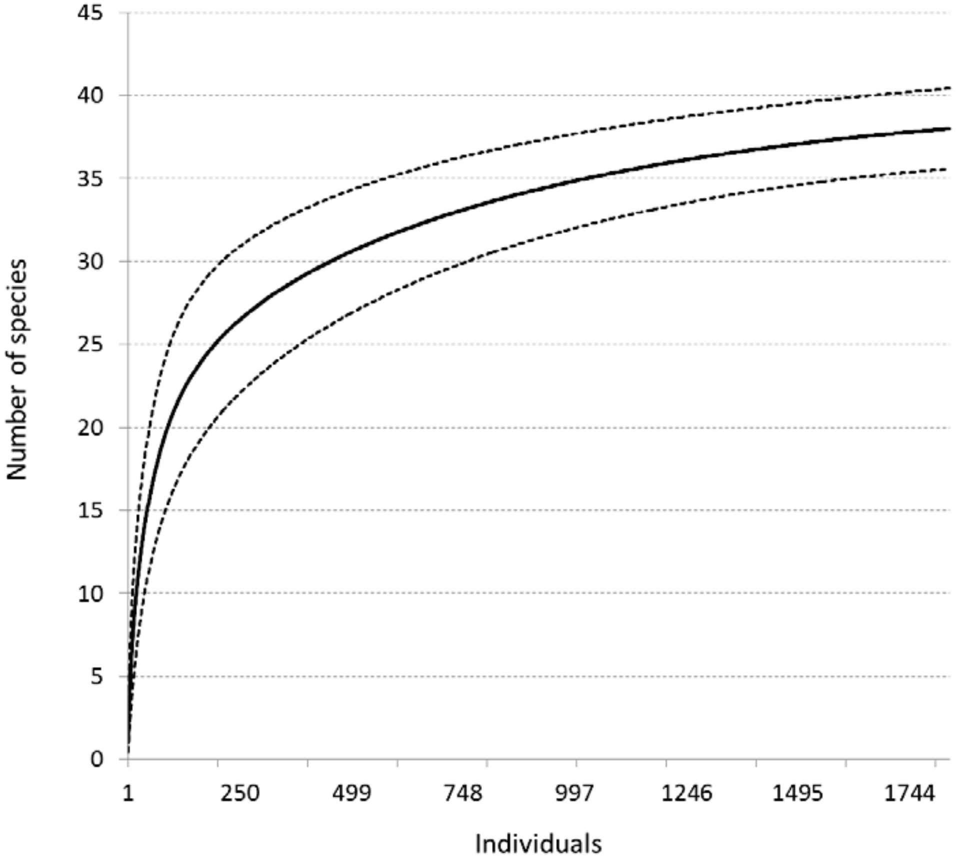

FIGURE 4. Individual-based rarefaction curve for Oribatida in the Old Man's Range. The dashed lines represent 95% confidence intervals.

Distribution of soil microfauna in tundra-like soils reflects their response to changes in physical environments and in the availability of food resources (Hodkinson and Wookey, 1999). Although it is possible that cushion plants in the New Zealand alpine mitigate temperature fluctuations, there is no evidence that soil microarthropods actively use cushions as thermal refuges; instead, it is likely that many species-habitat associations reflect disturbance or availability of resources, as taxa sensitive to disturbance (Oribatida) and specialist plant-feeders occured in higher numbers under cushion plants. On the other hand, Collembola, many of which are mobile, generalist feeders and able to colonize disturbed patches (Hodkinson et al., 1994; Hertzberg, 1997), were more abundant in open microsites between cushions.

We hypothesize that cushion plants facilitate microarthropods in the high alpine by acting as "biodiversity islands" and providing source-sink system for species that colonize open ground. Within a heterogeneous environment, dispersion from favorable refuges permits continuous recolonization of habitats (Hanski and Gilpin, 1991). The distribution patterns we observed in Old Man's Range Oribatida, with higher abundance and species richness under cushions but community composition similar throughout the site, suggest such a source-sink "diffusion" relationship. In these cases, the greater species richness seen under cushions is probably a manifestation of the individual-based rarefaction curve (Fig. 4).

Microarthropods show species-specific responses to habitat patchiness, and extinction-colonization dynamics differ between species (Hertzberg, 1997; Ims et al., 2004). The data presented here highlight a major research need: studies of life history traits of individual species, such as feeding, demography, and dispersal, are crucial for explaining the significance of observed community patterns in relation to species traits and environmental variables across alpine habitats, and for linking these patterns to potential mechanisms of community assembly and species coexistence. We join Molenda et al. (2012) in advocating that cushion plant communities in the high-altitude patterned ground landscapes in New Zealand should be treated as an umbrella for biodiversity conservation and as a promising subject for future research in view of a changing world climate.

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