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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 con-

ditions, 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; Rus-

sell 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 condi-

tions (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 $\sim 2^{\circ}\text{C}$) 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 20–35 cm 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 $\sim 150^{\circ}\text{C}$ in the furnace, then cooled further in a desiccator and



A.



B.

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, *Tectocephus 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 Gaussi-

an, 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 *Dracophyllum* 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 *Diacophyllum muscoides* cushions; "R" = under *Raoulia* sp. cushions; "Furrow" = soil in furrows outside of cushion plants. Values are means \pm standard error.

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

*Soil core area: 25 cm², depth: vegetation plus top 5 cm of the soil layer.

**Includes Astigmata (Acaridae, Glyciphagidae) and Endeostigmata (Nanorchestridae, 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 *Dracoph-*

yllum 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
	<i>0.113</i>	<i>0.337</i>	0.002	<i>0.344</i>	0.001	<i>0.064</i>
Oribatida	1.714	2.201	5.545	1.400	5.189	5.039
	<i>0.185</i>	<i>0.161</i>	0.005	<i>0.328</i>	0.003	0.019
Mesostigmata	2.069	1.346	2.236	2.433	1.874	0.831
	<i>0.155</i>	<i>0.316</i>	<i>0.158</i>	<i>0.187</i>	<i>0.215</i>	<i>0.524</i>
Other Acari*	1.500	0.884	4.376	1.583	22.159	2.133
	<i>0.279</i>	<i>0.518</i>	0.026	<i>0.269</i>	0.001	<i>0.144</i>
Collembola	1.659	0.810	2.130	0.828	7.989	0.727
	<i>0.220</i>	<i>0.542</i>	<i>0.121</i>	<i>0.553</i>	0.009	<i>0.597</i>

*Families of Prostigmata, Endeostigmata, and Astigmata.

TABLE 3

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

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

TABLE 3

Continued

Group	Taxon	Indicator value	p-value	Habitat association
	<i>Folsomia</i> sp.	53.1	0.6409	
<i>The Remarkables</i>				
Oribatida	<i>Oxyoppia suramericana</i> (Hammer, 1958)	90.0	0.0396	<i>Dracophyllum</i>
	Brachychthoniidae	80.2	0.0244	Cushions
	<i>Notophthiracarus otagoensis</i> Niedbala, 2016	82.6	0.0938	Cushions
Mesostigmata	Rhodacaridae gen. sp. 2	72.8	0.0350	Cushions
	<i>Gamasellus</i> sp.	32.0	0.7550	
	<i>Acugamasus</i> sp. gr. <i>punctatus</i> Lee, 1970	72.5	0.1558	
	<i>Onchogamasus</i> sp. aff. <i>quasicurtipilus</i> Lee, 1970	70.2	0.0310	<i>Dracophyllum</i>
	<i>Pilellus</i> sp. aff. <i>rugipellis</i> 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	<i>Tullbergia</i> sp. 1	73.6	0.2164	
	<i>Folsomia</i> sp.	62.8	0.0364	Furrows
	<i>Mucromia caeca</i> (Wahlgren, 1906)	71.8	0.0672	<i>Raoulia</i>
	<i>Hemisotoma</i> sp. gr. <i>thermophila</i> (Axelson, 1900)	16.7	1.000	
	<i>Friezea</i> 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 $R^2 = 0.12$, $p(\%OM) = 0.007$, $p(\%H_2O) = 0.065$; Oribatida $R^2 = 0.18$, $p(OM\%) = 0.010$; The Remarkables: all mites $R^2 = 0.15$, $p(\%OM) = 0.008$, $p(\%H_2O) = 0.028$; Collembola $R^2 = 0.09$, $p(H_2O\%) = 0.021$; 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 $R^2 = 0.48$, $p(\text{small}) = 0.001$, $p(\text{asexual})$

$= 0.001$). 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–

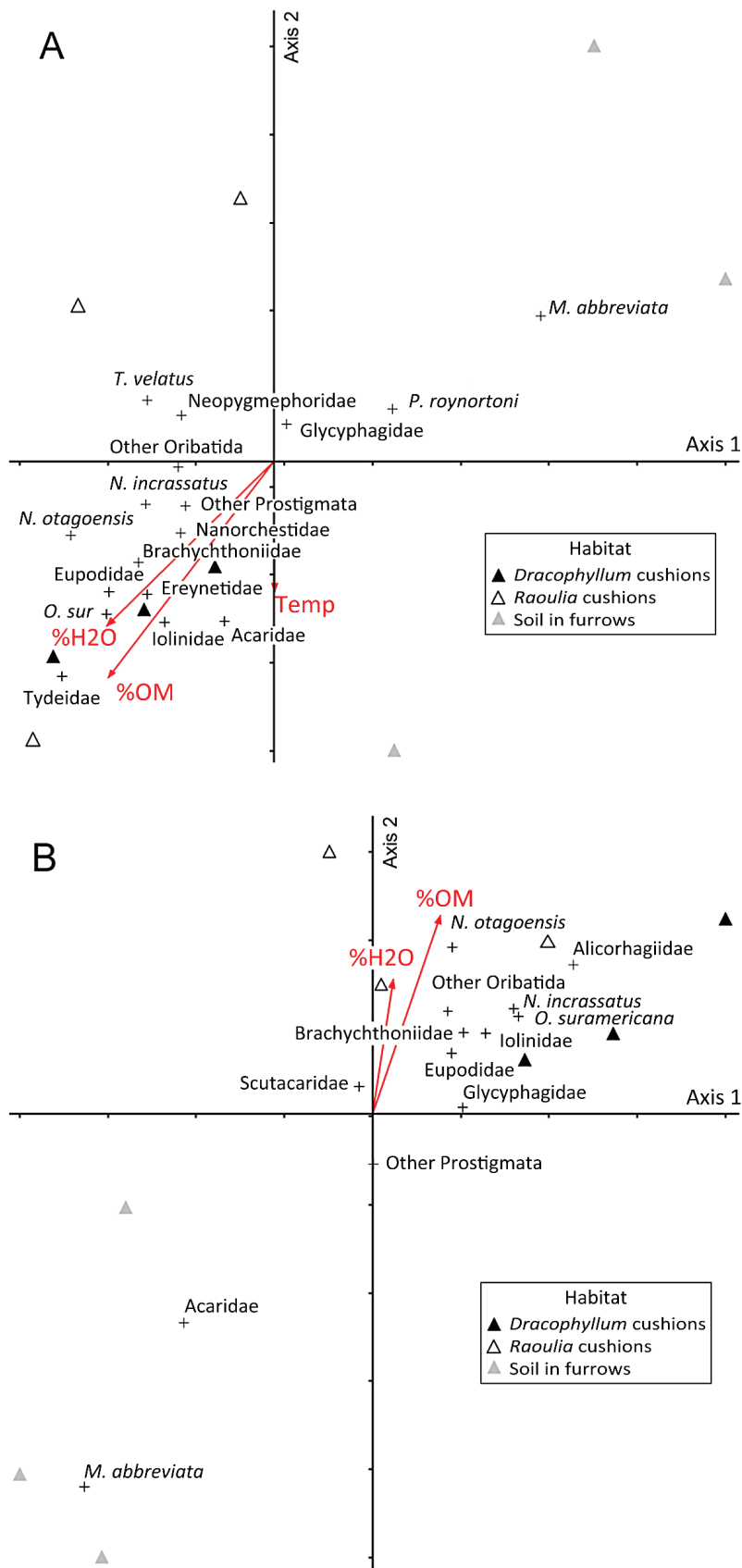


FIGURE 2. Nonmetric multidimensional scaling (NMS) ordinations for mites (Oribatida, Prostigmata, and Astigmata), and soil variables in the high alpine cushion fields, New Zealand, central Otago, summer 2014. %H₂O = soil moisture content (gravimetric); %OM = soil organic matter content; Temp = soil temperature; O.sur = *O. suramericana*. (A) Pisa Range. DistLM best predictors of community composition: $R^2 = 0.12$, $p(\%OM) = 0.007$, $p(\%H_2O) = 0.065$. (B) The Remarkables. DistLM best: $R^2 = 0.15$, $p(\%OM) = 0.008$, $p(\%H_2O) = 0.028$. 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; Bølter et al., 1997; Sørensen et al., 2006). Soil moisture (Booth and Usher, 1986; Hodkinson et al., 1994), cryogenic activity

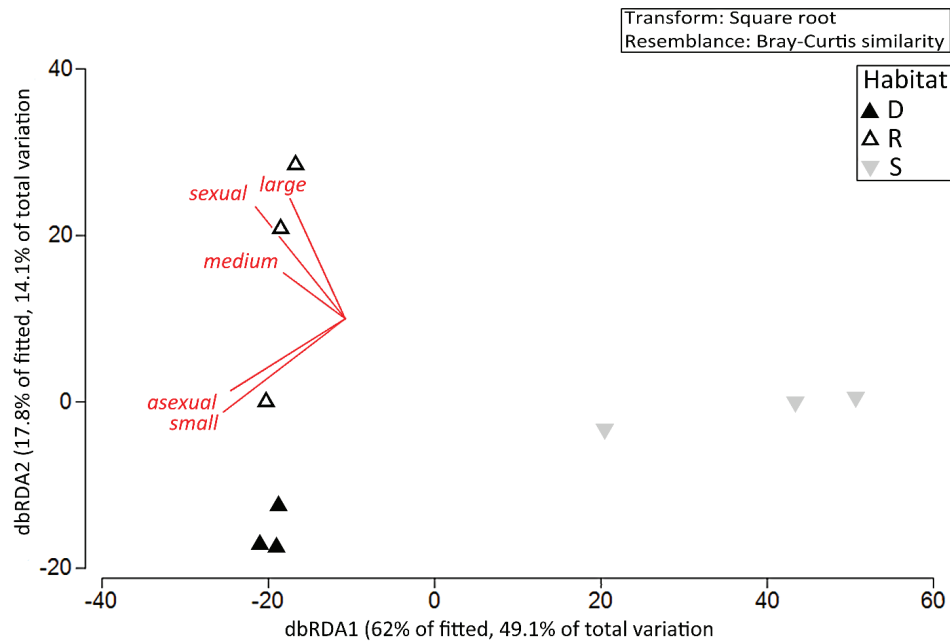


FIGURE 3. Distance-based redundancy analysis (dbRDA) on plot means for Oribatida communities and their ecological traits (body size and reproductive type) in the alpine cushion fields in the Remarkables. Habitats: D = *Dracophyllum* cushions, R = *Raoulia* cushions, S = soil in the open ground. DistLM 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 (Licznier 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 else-

where (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; Sjørnsen 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 Wootey, 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 Wootey, 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 impor-

tance 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; Bølter, 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).

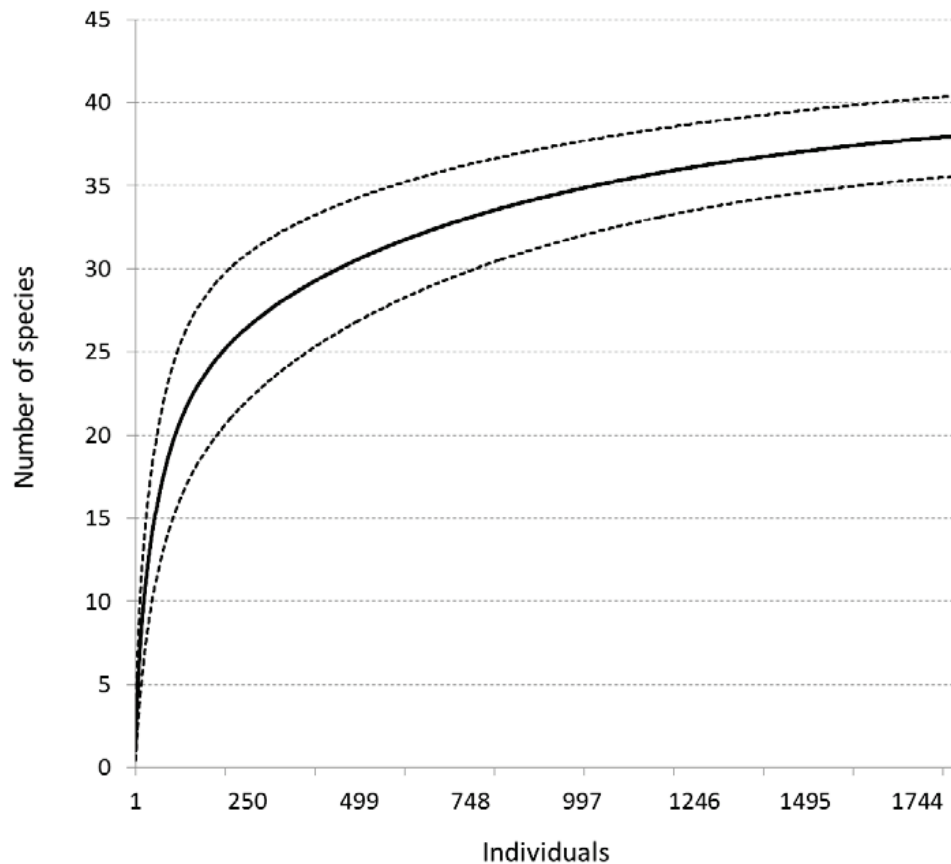


FIGURE 4. Individual-based rarefaction curve for Oribatida in the Old Man's Range. The dashed lines represent 95% confidence intervals.

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 occurred 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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REFERENCES CITED

- Adams, E. C. G., 1971: Ecological studies of microarthropods in a New Zealand pasture soil with special reference to the Collembola (I.). *Pedobiologia*, 11: 321–337.
- Almeida, I. C. C., Schaefer, C. E. G. R., Fernandes, R. B. A., Pereira, T. T. C., Nieuwendamd, A., and Pereira, A. B., 2014: Active layer thermal regime at different vegetation covers at Lions Rump, King George Island, Maritime Antarctica. *Geomorphology*, 225: 36–46.
- Badano, E. I., Jones, C. G., Cavieres, L. A., and Wright, J. P., 2006: Assessing impacts of ecosystem engineers on community organization: a general approach illustrated by effects of a high-Andean cushion plant. *Oikos*, 115: 369–385.
- Badano, E. I., Marquet, P. A., and Cavieres, L. A., 2010: Predicting effects of ecosystem engineering on species richness along primary productivity gradients. *Acta Oecologica*, 36: 46–54.
- Barratt, B. I. P., Tozer, P. A., Wiedemer, R. L., Ferguson, C. M., and Johnston, P. D., 2006: Effect of fire on microarthropods in New Zealand indigenous grassland. *Rangeland Ecology and Management*, 59: 383–391.
- Behan, V. M., and Hill, S. B., 1978: Feeding-habits and spore dispersal of oribatid mites in the North-American Arctic. *Revue d'Ecologie et de Biologie du Sol*, 15: 497–516.
- Behan-Pelletier, V. M., 1999: Oribatid mite fauna of northern ecosystems: a product of evolutionary adaptations or physiological constraints? In Mitchell, R., Horn, D. J., Needham, G. R., and Welbourn, C. W. (eds.), *Acarology IX, Proceedings*. Columbus: Ohio Biological Survey, 87–105.
- Bertness, M. D., and Callaway, R., 1994: Positive interactions in communities. *Trends in Ecology and Evolution*, 9: 191–193.
- Birkemoe, T., and Leinaas, H. P., 2000: Effects of temperature on the development of an Arctic Collembola (*Hypogastrura tullbergi*). *Functional Ecology*, 14: 693–700.
- Bliss, L. C., 1960: Transpiration rates of Arctic and alpine shrubs. *Ecology*, 41: 386–389.
- Bliss, L. C., and Mark, A. F., 1974: High alpine environment and primary production on the Rock and Pillar Range, Central Otago, New Zealand. *New Zealand Journal of Botany*, 12: 445–484.
- Bokhorst, S., Ronfort, C., Huiskes, A., Convey, P., and Aerts, R., 2007: Food choice of Antarctic soil arthropods clarified by stable isotope signatures. *Polar Biology*, 30: 983–990.
- Bölter, M., 2001: Preliminary results about contributions of soil algae and cyanobacteria in microbial communities of Arctic soils—a microscopic approach. *Nova Hedwigia*, 123: 307–315.
- Bölter, M., Blume, H.-P., Schneider, D., and Beyer, L., 1997: Soil properties and distributions of invertebrates and bacteria from King George Island (Arctowski Station), maritime Antarctic. *Polar Biology*, 18: 295–304.
- Booth, R. G., and Usher, M. B., 1986: Arthropod community in a maritime Antarctic moss-turf habitat: life history strategies of the prostigmatid mites. *Pedobiologia*, 29: 209–218.
- Bruno, J. F., Stachowicz, J. J., and Bertness, M. D., 2003: Inclusion of facilitation into ecological theory. *Trends in Ecology and Evolution*, 18: 119–125.
- Bunnell, F. L., MacLean, S. F., Jr, and Brown, J., 1975: *Barrow, Alaska, U.S.A.* Oak Ridge, Tennessee: U.S. Tundra Biome.
- Cannon, R. J. C., and Block, W., 1988: Cold tolerance of microarthropods. *Biological Reviews*, 63: 23–77.
- Cavieres, L. A., Badano, E. I., Sierra-Almeida, A., and Molina-Montenegro, M. A., 2007: Microclimatic modifications of cushion plants and their consequences for seedling survival of native and non-native herbaceous species in the high Andes of central Chile. *Arctic, Antarctic, and Alpine Research*, 39: 229–236.
- Clarke, K. R., Gorley, R. N., Somerfield, P. J. and Warwick, R. M., 2014: *Change in Marine Communities: an Approach to Statistical Analysis and Interpretation*. Third edition. Plymouth: PRIMER-E.
- Coulson, S. J., Hodkinson, I. D., Wooley, C., Webb, N. R., Block, W., Worland, M. R., Bale, J. S., and Strathdee, A. T., 1996: Effects of experimental temperature elevation on High-Arctic soil microarthropod populations. *Polar Biology*, 16: 147–153.
- Coulson, S. J., Hodkinson, I. D., and Webb, N. R., 2003: Microscale distribution patterns in High Arctic soil microarthropod communities: the influence of plant species within the vegetation mosaic. *Ecography*, 26: 801–809.
- Diaz-Aguilar, I., and Quideau, S. A., 2013: Trophic ecology of mesostigmatan and oribatid mites in harvested and control coniferous and deciduous stands of the boreal mixedwood forest determined using N-15 stable isotopes. *Soil Biology and Biochemistry*, 67: 147–154.
- Dufrène, M., and Legendre, P., 1997: Species assemblages and indicator species: the need for a flexible asymmetrical approach. *Ecological Monographs*, 67: 345–366.

- Frost, G. V., Epstein, H. E., Walker, D. A., Matyshak, G., and Ermokhina, K., 2013: Patterned-ground facilitates shrub expansion in Low Arctic tundra. *Environmental Research Letters*, 8: doi <http://dx.doi.org/10.1088/1748-9326/8/1/015035>.
- Grab, S., 2005: Aspects of the geomorphology, genesis and environmental significance of earth hummocks (thufur, pounus): miniature cryogenic mounds. *Progress in Physical Geography*, 29: 139–155.
- Greenslade, P., Boyer, S., and Wratten, S., 2013: New records of springtails in New Zealand pasture: How well are our pastoral invertebrates known? *New Zealand Journal of Agricultural Research*, 56: 93–101.
- Hagvar, S., and Klanderud, K., 2009: Effect of simulated environmental change on alpine soil arthropods. *Global Change Biology*, 15: 2972–2980.
- Hanski, I., and Gilpin, M., 1991: Metapopulation dynamics—brief history and conceptual domain. *Biological Journal of the Linnean Society*, 42: 3–16.
- He, Q., and Bertness, M. D., 2014: Extreme stresses, niches and positive species interactions along stress gradients. *Ecology*, 95: 1437–1443.
- Hertzberg, K., 1997: Migration of Collembola in a patchy environment. *Pedobiologia*, 41: 494–505.
- Hodkinson, I. D., and Wookey, P. A., 1999: Functional ecology of soil organisms in tundra ecosystems: towards the future. *Applied Soil Ecology*, 11: 111–126.
- Hodkinson, I. D., Coulson, S., Webb, N. R., Block, W., Strathdee, A. T., and Bale, J. S., 1994: Feeding studies on *Onychiurus arcticus* (Tullberg) (Collembola, Onychiuridae) on West Spitsbergen. *Polar Biology*, 14: 17–19.
- Hodkinson, I. D., Coulson, S. J., Webb, N. R., and Block, W., 1996: Can Arctic soil microarthropods survive elevated summer temperatures? *Functional Ecology*, 10: 314–321.
- Hodkinson, I. D., Babenko, A., Behan-Pelletier, V., Bocher, J., Boxshall, G., Brodo, F., Coulson, S. J., De Smet, W., Dozsa-Farkas, K., Elias, S., Fjellberg, A., Fochetti, R., Footitt, R., Hessen, D., Hobaek, A., Holmstrup, M., Koponen, S., Liston, A., Makarova, O., Marusik, Y. M., Michelsen, V., Mikkola, K., Mustonen, T., Pont, A., Renaud, A., Rueda, L. M., Savage, J., Smith, H., Samchyshyna, L., Velle, G., Viehberg, F., Vikberg, V., Wall, D. H., Weider, L. J., Wetterich, S., Yu, Q., and Zinovjev, A., 2013: Terrestrial and freshwater invertebrates. In Meltøfte, H. (ed.), *Arctic Biodiversity Assessment: Status and Trends in Arctic Biodiversity*. Akureyri, Iceland: Conservation of Arctic Flora and Fauna, 196–223.
- Ims, R. A., Leinaas, H. P., and Coulson, S., 2004: Spatial and temporal variation in patch occupancy and population density in a model system of an arctic Collembola species assemblage. *Oikos*, 105: 89–100.
- Klaus, M., Becher, M., and Klaminder, J., 2013: Cryogenic soil activity along bioclimatic gradients in Northern Sweden: insights from eight different proxies. *Permafrost and Periglacial Processes*, 24: 210–223.
- Kleier, C., and Rundel, P., 2009: Energy balance and temperature relations of *Azorella compacta*, a high-elevation cushion plant of the central Andes. *Plant Biology*, 11: 351–358.
- Konestabo, H. S., Michelsen, A., and Holmstrup, M., 2007: Responses of springtail and mite populations to prolonged periods of soil freeze-thaw cycles in a sub-arctic ecosystem. *Applied Soil Ecology*, 36: 136–146.
- Körner, C., 2003: *Alpine Plant Life—Functional Plant Ecology of High Mountain Ecosystems*. Heidelberg: Springer.
- Krantz, G. W., and Walter, D. E., 2009: *A Manual of Acarology*. Lubbock: Texas Tech University Press.
- Liczner, A. R., and Lortie, C. J., 2014: A global meta-analytic contrast of cushion-plant effects on plants and on arthropods. *PeerJ*, 2: doi <http://dx.doi.org/10.7717/peerj.265>.
- Lindo, Z., and Visser, S., 2003: Microbial biomass, nitrogen and phosphorus mineralization, and mesofauna in boreal conifer and deciduous forest floors following partial and clear-cut harvesting. *Canadian Journal of Forest Research*, 33: 1610–1620.
- Lindo, Z., and Winchester, N. N., 2007: Oribatid mite communities and foliar litter decomposition in canopy suspended soils and forest floor habitats of western red cedar forests, Vancouver Island, Canada. *Soil Biology and Biochemistry*, 39: 2957–2966.
- Luxton, M., 1982: Studies on the invertebrate fauna of New Zealand peat soils. 2. Restiad peats. *Revue d'Ecologie et de Biologie du Sol*, 19: 553–578.
- Luxton, M., 1983a: Studies on the invertebrate fauna of New-Zealand peat soils. 5. Pasture soils on Kaipaki peat. *Pedobiologia*, 25: 135–148.
- Luxton, M., 1983b: Studies on the invertebrate fauna of New-Zealand peat soils. 3. Fern peats. *Revue d'Ecologie et de Biologie du Sol*, 20: 87–109.
- Makarova, O. L., 2002a: Acarocenoses (Acariformes, Parasitiformes) in polar deserts: 1. Mite assemblages of the Severnaya Zemlya Archipelago: structure of fauna and abundance. *Entomological Review*, 82: 839–856.
- Makarova, O. L., 2002b: Acarocenoses (Acariformes, Parasitiformes) in polar deserts. 2. Cenotic relations, structure of communities, and proportion of suborders. *Entomological Review*, 82: 857–875.
- Makarova, O. L., 2015: The fauna of free-living mites (Acari) of Greenland. *Entomological Review*, 95: 108–125.
- Maraun, M., and Scheu, S., 2000: The structure of oribatid mite communities (Acari, Oribatida): patterns, mechanisms and implications for future research. *Ecography*, 23: 374–383.
- Mark, A. F., 1994: Patterned ground activity in a southern New Zealand high-alpine cushionfield. *Arctic and Alpine Research*, 26: 270–280.
- Mark, A. F., and Bliss, L. C., 1970: The high alpine vegetation of Central Otago, New Zealand. *New Zealand Journal of Botany*, 8: 381–451.
- Markkula, I., 2014: Permafrost dynamics structure species compositions of oribatid mite (Acari: Oribatida) communities in sub-Arctic palsas. *Polar Research*, 33: doi <http://dx.doi.org/10.3402/polar.v33.22926>.
- McMillan, J. H., 1969: The ecology of the acarine and collembolan fauna of two New Zealand pastures. *Pedobiologia*, 9: 372–404.
- Meurk, C. D., 1978: Alpine phytomass and primary productivity in Central Otago, New Zealand. *New Zealand Journal of Ecology*, 1: 27–50.

- Minor, M. A., 2011: Spatial patterns and local diversity in soil oribatid mites (Acari: Oribatida) in three pine plantation forests. *European Journal of Soil Biology*, 47: 122–128.
- Molenda, O., Reid, A., and Lortie, C. J., 2012: The alpine cushion plant *Silene acaulis* as foundation species: a bug's-eye view to facilitation and microclimate. *PLoS ONE* 7: doi <http://dx.doi.org/10.1371/journal.pone.0037223>.
- Molina-Montenegro, M., Badano, E. I., and Cavieres, L., 2006: Cushion plants as microclimatic shelters for two ladybird beetle species in alpine zone of central Chile. *Arctic, Antarctic, and Alpine Research*, 38: 224–227.
- Norton, R. A., 1994: Evolutionary aspects of oribatid mite life histories and consequences for the origin of the Astigmata. In Houck, M. A. (ed.), *Mites: Ecological and Evolutionary Analyses of Life-History Patterns*, 99–135.
- Norton, R. A., and Ermilov, S. G., 2014: Catalogue and historical overview of juvenile instars of oribatid mites (Acari: Oribatida). *Zootaxa*, 3833: 1–132.
- O'Lear, H. A., and Seastedt, T. R., 1994: Landscape patterns of litter decomposition in alpine tundras. *Oecologia*, 99: 95–101.
- Petersen, H., and Luxton, M., 1982: A comparative analysis of soil fauna populations and their role in decomposition processes. *Oikos*, 39: 288–388.
- Peterson, R. A., 2011: Assessing the role of differential frost heave in the origin of non-sorted circles. *Quaternary Research*, 75: 325–333.
- Phillips, N., and Reid, D., 2012: *Biological Traits: Application to the Auckland Council River Ecology Monitoring Programme*. Hamilton, New Zealand: National Institute of Water and Atmospheric Research, Auckland Council Technical Report 2012/001.
- Reid, A. M., and Lortie, C. J., 2012: Cushion plants are foundation species with positive effects extending to higher trophic levels. *Ecosphere*, 3: 1–18.
- Roy, J., Albert, C. H., Ibanez, S., Saccone, P., Zinger, L., Choler, P., Clément, J.-C., Lavergne, S., and Geremia, R. A., 2013: Microbes on the cliff: alpine cushion plants structure bacterial and fungal communities. *Frontiers in Microbiology*, 4: doi <http://dx.doi.org/10.3389/fmicb.2013.00064>.
- Russell, D. J., Hohberg, K., Potapov, M., Bruckner, A., Otte, V., and Christian, A., 2014: Native terrestrial invertebrate fauna from the northern Antarctic Peninsula: new records, state of current knowledge and ecological preferences—summary of a German federal study. *Soil Organisms*, 86: 1–58.
- Schneider, K., Migge, S., Norton, R. A., Scheu, S., Langel, R., Reineking, A., and Maraun, M., 2004: Trophic niche differentiation in soil microarthropods (Oribatida, Acari): evidence from stable isotope ratios (N-15/N-14). *Soil Biology and Biochemistry*, 36: 1769–1774.
- Schon, N. L., Mackay, A. D., Minor, M. A., Yeates, G. W., and Hedley, M. J., 2008: Soil fauna in grazed New Zealand hill country pastures at two management intensities. *Applied Soil Ecology*, 40: 218–228.
- Schon, N. L., Mackay, A. D., and Minor, M. A., 2012: Vulnerability of soil invertebrate communities to the influences of livestock in three grasslands. *Applied Soil Ecology*, 53: 98–107.
- Scott, M. B., Dickinson, K. J. M., Barratt, B. I. P., and Sinclair, B. J., 2008: Temperature and moisture trends in non-sorted earth hummocks and stripes on the Old Man Range, New Zealand: implications for mechanisms of maintenance. *Permafrost and Periglacial Processes*, 19: 305–314.
- Sjursen, H., and Sinclair, B. J., 2002: On the cold hardiness of *Stereotydeus mollis* (Acari: Prostigmata) from Ross Island, Antarctica. *Pedobiologia*, 46: 188–195.
- Sørensen, L. I., Holmstrup, M., Maraldo, K., Christensen, S., and Christensen, B., 2006: Soil fauna communities and microbial respiration in High Arctic tundra soils at Zackenberg, Northeast Greenland. *Polar Biology*, 29: 189–195.
- Sulkava, P., and Huhta, V., 2003: Effects of hard frost and freeze-thaw cycles on decomposer communities and N mineralisation in boreal forest soil. *Applied Soil Ecology*, 22: 225–239.
- Toda, M. J., and Tanno, K., 1983: The convergence of habitat structure in tundra collembolan communities (Insecta: Order Collembola). *The Canadian Entomologist*, 115: 1129–1145.
- Upton, P., Craw, D., and Walcott, R., 2014: Far-field deformation resulting from rheologic differences interacting with tectonic stresses: an example from the Pacific/Australian plate boundary in Southern New Zealand. *Geosciences*, 4: 93–113.
- Walker, D. A., Romanovsky, V. E., Ping, C. L., Michaelson, G. J., Daanen, R. P., Shur, Y., Peterson, R. A., Krantz, W. B., Reynolds, M. K., Gould, W., Gonzalez, G., Nicolsky, D. J., Vonlanthen, C. M., Kade, A. N., Kuss, P., Kelley, A. M., Munger, C. A., Tarnocai, C. T., Matveyeva, N. V., and Daniels, F. J. A., 2008: Arctic patterned-ground ecosystems: a synthesis of field studies and models along a North American Arctic transect. *Journal of Geophysical Research*, 113: 1–17, doi <http://dx.doi.org/10.1029/2007JG000504>.
- Walker, D. A., Kuss, H. P., Epstein, H. E., Kade, A. N., Vonlanthen, C., Reynolds, M. K., and Daniels, F. J. A., 2011: Vegetation of zonal patterned-ground ecosystems along the North American Arctic Transect. *Applied Vegetation Science*, 14: 440–463.
- Webb, N. R., Coulson, S. J., Hodkinson, I. D., Block, W., Bale, J. S., and Strathdee, A. T., 1998: The effects of experimental temperature elevation on populations of cryptostigmatic mites in High Arctic soils. *Pedobiologia*, 42: 298–308.
- Wharton, D. A., 2011: Cold tolerance of New Zealand alpine insects. *Journal of Insect Physiology*, 57: 1090–1095.
- Zettel, J., 2000: Alpine Collembola—adaptations and strategies for survival in harsh environments. *Zoology*, 102: 73–89.

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