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# Micro Gondwana: soil and litter mesofauna in the subalpine and alpine of North-West Nelson, southern New Zealand

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## ABSTRACT

Alpine ecosystems are vulnerable to the warming climate, yet alpine soil mesofauna remains the less studied part of NZ biodiversity. Here we present a survey of soil mesofauna communities of three mountain peaks in the Nelson-Tasman and Marlborough regions of the South Island of New Zealand. We assessed changes in abundance, diversity and trophic composition along the elevational gradient from subalpine forests to alpine herb fields (800–1600 m a.s.l.) and analysed the influence of selected environmental factors on mesofauna. Taxon richness was expected to decrease and the proportion of predators to increase in alpine habitats, as has been observed elsewhere. Sub-alpine beech forests harboured a high diversity of soil mesofauna, many of which are Gondwanan relics. There was a decline in abundance and taxonomic richness of mesofauna with increasing elevation. However, no proportional increase in predators with increasing elevation was seen – alpine mesofauna assemblages had lower predator-to-herbivore ratios than upland forests. Several interesting taxa – harpacticoid copepods, moss bugs (Hemiptera: Peloridiidae), unique-headed bugs (Hemiptera: Enicocephalomorpha), micro-spiders, mite harvestmen, Neelidae springtails and acarifauna are discussed in more detail. Baseline data such as these advance the knowledge of native fauna and provide a baseline for ecological monitoring in the alpine zone.

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## Introduction

Alpine ecosystems are important globally with high levels of endemic and rare species, yet there is still a gap in global data on soil biodiversity in alpine regions (Guerra et al. 2020; Praeg et al. 2025).

In Australasia, alpine environments are found in the small area of Australian Alps in mainland Australia, in central and south-eastern Tasmania, and across extensive areas of New Zealand. Defined by having less than 94 days per year with the mean air temperature above 0.9°C but not exceeding 6.4°C (Paulsen and Körner 2014), these environments are cold, wet, snowy and windy, with a short growing season. The invertebrates which

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inhabit these areas have distinctive morphological and physiological traits – dark colouration, pubescence and freeze-tolerance (Hodkinson 2005; Buckley et al. 2015). The alpine environments and their species are especially vulnerable to the warming climate and may disappear in the long term, as they undergo range contraction and higher-altitude displacement (White and Sedcole 1991; McGlone and Walker 2001; Halloy and Mark 2003; Freeman et al. 2018; Schmeller et al. 2022).

In New Zealand (NZ), the alpine environments and their biota are geologically very young; permanent widespread alpine habitats appeared only <2 mya with the uplift and weathering of the Southern Alps (Winkworth et al. 2005; Heenan and McGlone 2013). Today, NZ has c. 30,000 km<sup>2</sup> area of alpine environment, with extensive areas in the South Island, and some peaks (e.g. Aoraki, Mount Cook, 3764 m a.s.l.) permanently covered with snow. In the North Island, alpine areas are less extensive and more fragmented (Mark and Dickinson 1997). The lower alpine zone is generally covered with tussock (*Chionochloa* spp.), which at higher elevations gives way to small shrubs and herbfields. The alpine plants here are often prostrate or cushion-forming (Mark and Dickinson 1997; Mark 2013).

Much of the knowledge of NZ alpine invertebrates is based on incidental collections – these result in descriptions of new species as well as new records for species localities, but do not give us information about communities. More detailed information exists only for those taxa and regions where experts are (or have been) working (e.g. Salmon 1941; Hammer 1966, 1967, 1968). More recent additions to the NZ alpine invertebrate fauna include three species of alpine terrestrial flatworms (Tricladida: Geoplanoidea) (Johns 1998), eight new species of subalpine and alpine Myriapoda (Scheller and Barratt 2012), more than 40 new species of alpine Oribatida and Prostigmata mites (Acari) (Olszanowski 1998; Colloff 2015; Ermilov et al. 2015, 2016, 2019; Ermilov and Minor 2015a, 2015b, 2015c, 2015d, 2016a, 2016b, 2018a, 2018b, 2019; Khaustov and Minor 2018a, 2018b, 2020, 2025), two new species of alpine springtails (Collembola) (Babenko and Minor 2015; Potapov et al. 2017), a new species and records of alpine Coleoptera (Liebherr et al. 2011; Leschen and Buckley 2015) and new synonymy for alpine grasshoppers (Orthoptera: Acrididae) (Trewick et al. 2023).

The NZ alpine invertebrate fauna is diverse with strong evidence of Gondwanan heritage and, at a species level, regional endemism is very high (Boyer and Giribet 2009). Genetic and distributional data for NZ alpine invertebrates reflects contractions and expansions of alpine habitat during Pleistocene glaciation cycles, but the presence of refugia during glaciation cycles is strongly inferred (Trewick et al. 2001; Hill et al. 2009; O'Neill et al. 2009; Leschen and Buckley 2014; King et al. 2020). The Nelson-Tasman region of the NZ South Island is particularly interesting, because a forested refugium is believed to have existed there during the last glacial maximum (Buckley et al. 2009; Marshall et al. 2009) and today it is a biodiversity hotspot containing a high proportion of endemic plant and animal alpine species (Wardle 1963; Mark 2013; Taylor-Smith et al. 2019). However, the alpine soil fauna of the Nelson-Tasman region has never been studied systematically.

Knowledge of biodiversity is intrinsic to preserving NZ biological heritage yet changes in soil biodiversity due to warming climate are difficult to predict in NZ alpine zone, because the baseline data for monitoring are largely lacking. Soil arthropods remain the less studied part of NZ alpine invertebrate fauna. For example, two thirds of soil

arthropod species collected in alpine Central Otago were new to the NZ fauna and 40% were new to science (Minor et al. 2016). Buckley et al. (2015) summarised the gaps and challenges in our knowledge of NZ alpine biodiversity and highlighted the need to add information on alpine species distributions, especially among hyperdiverse soil communities and in biodiversity hotspots areas such as north-west Nelson.

Here we present data from a survey of communities of soil and leaf-litter dwelling mesofauna on three mountain peaks in the Nelson-Tasman region of the South Island of New Zealand. The term ‘mesofauna’ here is used to include small arthropods with body size ranging 200  $\mu\text{m}$  to 2 mm as well as some myriapods, insect larvae and other arthropods small enough to fit through the  $\sim 2$  mm mesh of the extractors. Our objectives were to assess the changes in abundance and diversity of mesofauna along the elevational gradient from subalpine forests on upland slopes to alpine herb fields (800 m to 1600 m a.s.l.) and to analyse the influence of selected environmental factors (elevation and soil parameters) on mesofauna.

The cold temperatures and short growing season in alpine ecosystems limit primary productivity, and this influences the structure and dynamics of the food webs. Although soil mesofauna communities at all elevations are dominated by detritivores and microbivores, the environmentally constrained energy flows mean that alpine habitats are expected to support smaller and less diverse communities, leading to shorter and therefore proportionally more predator-heavy food chains (Chen and Wise 1999; Post 2002; Doi 2012; Potapov et al. 2022; Steinwandter and Seeber 2023). We hypothesised that the high diversity and the large number of specialised endemic species in upland forests will be replaced in the alpine zone by less abundant and less diverse assemblages of taxa with increased ecological plasticity and with a higher proportion of predators (Makarova 2002; Chernov 2008; Steinwandter and Seeber 2023).

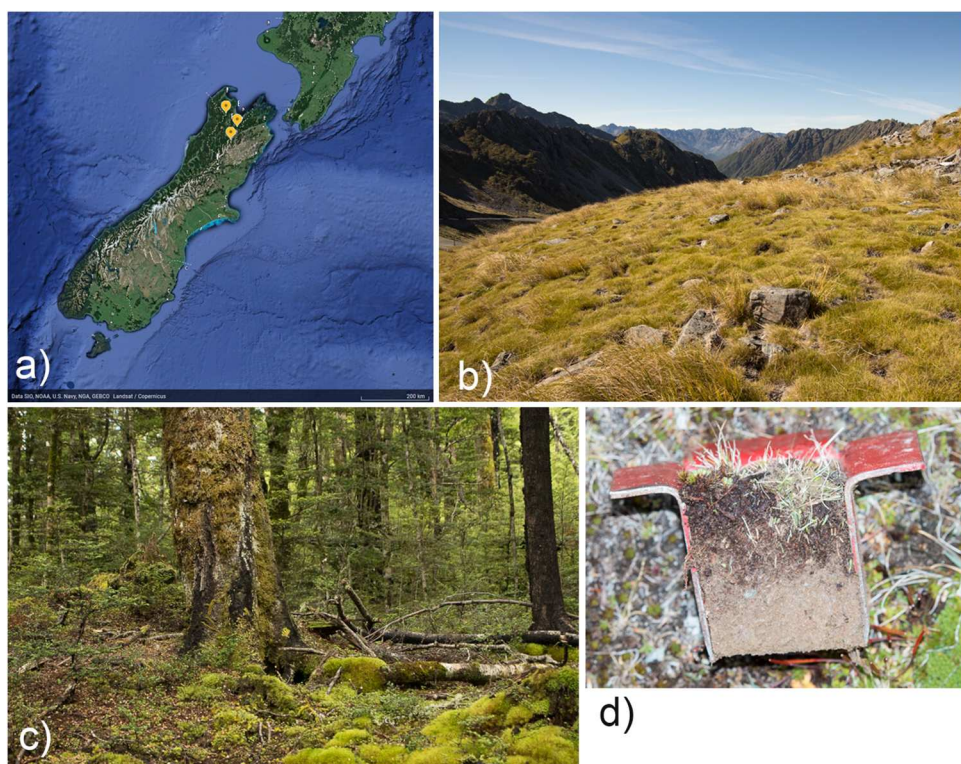
## Methods

### Study sites

The data were collected in sub-alpine forests and alpine zone of three mountain peaks in the Nelson-Tasman and Marlborough regions of the South Island of New Zealand (latitude 41°12'S to 41°53'S) (Figure 1). The areas all have high annual rainfall (over 2000mm), high cloud cover, cool summers and cold winters, and relatively shallow soils.

1. Mount Arthur (1795m, Tuao Wharepapa in Māori), a peak in the Wharepapa/Arthur Range which lies within the Kahurangi National Park, in the north-west Nelson. The underlying bedrock consists largely of hard crystalline marble, with some quartzite and limestone (Johnston 1974; Heron 2018). Samples were collected along the Mt Arthur summit track at 1490–1550 m (alpine zone) and at three elevations between 1000 and 1200 m (sub-alpine forest).

The alpine areas had fragmented vegetation with a mosaic of herbfield and carpet grass *Chionochloa australis* (Buchanan) Zotov among numerous marble outcrops and patches of bare soil. Plants common in the herbfield were (in the order of abundance): *Celmisia spectabilis* Hook.f. ssp *spectabilis*, *Pentachondra pumila* (J.R.Forst. et G.Forst.) R.Br., *Raoulia eximia* Hook.f., *Helichrysum intermedium* Kottaim,



**Figure 1.** **a**, Sampling sites in the Nelson-Tasman region of NZ; **b**, alpine habitat; **c**, subalpine beech forest; **d**, a soil core (5 × 5 × 5 cm) for mesofauna extraction.

*Phyllachne colensoi* (Hook.f.) Berggr., *Celmisia incana* Hook.f., *Astelia petriei* Cockayne, *Lepidothamnus laxifolius* (Hook.f.) Quinn. Less common were *Chionochloa pallens* Zotov ssp *pallens*, *Celmisia sessiliflora* Hook.f., *Dracophyllum marmoricola* S.Venter, *Gaultheria depressa* var. *novae-zealandiae* D.A.Franklin, *Oreobolus pectinatus* Hook.f. and others. Moss *Racomitrium pruinosum* (Hook.f. & Wilson) Müll.Hal. and ground lichens occurred on bare soil.

The sub-alpine forests at this site were relatively open, with silver beech *Lophozonia menziesii* (Hook.f.) Heenan et Smissen, some mountain beech *Fuscospora cliffortioides* (Hook.f.) Heenan et Smissen, and a sparse understorey of broadleaves and small-leaved shrubs. At lower elevations red beech *Fuscospora fusca* (Hook.f.) Heenan et Smissen was present. At higher elevations (c. 1100–1200 m) just below the tree line, the forest transitioned to a cloud forest with *Dracophyllum traversii* Hook.f. and with dwarf silver beech trees covered in abundant epiphytic lichens.

2. Ben Nevis (1619 m), a peak in the Richmond Range within the Mt Richmond Forest Park, on the Tasman side of the Tasman-Marlborough regional boundary. The geology of the region is complex; this area of Richmond Range largely consists of schist and greywacke sandstone (Heron 2018). Samples were collected on descent from the Ben Nevis summit along the Ben Nevis track, at three elevations above 1600 m (alpine zone) and at three elevations between 970 and 1230 m (sub-alpine forest).

The vegetation of the alpine zone included large areas of carpet grass *Chionochloa australis*, patches of herbfield with *Celmisia spectabilis* ssp *spectabilis*, *Pentachondra pumila* and *Dracophyllum pronum* W.R.B.Oliv., also with numerous rock outcrops and areas of bare soil where mosses *Racomitrium pruinosum* and *Racomitrium ptychophyllum* (Mitt.) Hook.f. formed large cushions and ground lichens were present. Less common plants in sampled areas included *Anisotome aromatica* Hook.f., *Coprosma cheesemanii* W.R.B.Oliv., *Gaultheria depressa* var. *novae-zealandiae*, *Luzula* sp.

The sub-alpine forests were relatively open, at higher elevations with mountain beech *Fuscopora cliffortioides* and occasional silver beech *Lophozonia menziesii*, and at lower elevations with red beech *Fuscopora fusca*. The understorey included *Griselinia littoralis* (Raoul) Raoul, *Coprosma* sp. and other shrubs. The moss *Dicranoloma robustum* (Hook.f. & Wilson) Paris was abundant on the ground in some places.

- Rainbow Ski Area (1760m), on the eastern side of the St. Arnaud Range adjacent to the Nelson Lakes National Park, Marlborough region. The underlying bedrock consists of undifferentiated Triassic sandstone and mudstone (Heron 2018). Samples were collected at three elevations on the ridge outside the skiing area and at three elevations along the Rainbow Ski Area access road, above 1500 m (alpine zone) and between 850 and 1300 m (sub-alpine forest).

The alpine zone was largely covered with carpet grass *Chionochloa australis*, interrupted by bare rock and soil, and by areas of herbaceous vegetation with *Celmisia sessiliflora*, *Celmisia spectabilis* ssp *spectabilis* and *Lycopodium fastigiatum* (R.Br.) Holub. Less common plants in sampled areas were *Chionochloa pallens* Zotov ssp *pallens*, *Coprosma perpusilla* Colenso ssp *perpusilla*, *Veronica hectorii* ssp *coarctata* (Cheeseman) Garn.-Jones, *Gentianella* sp.

The sub-alpine forests occurred on steep sloping ground with mountain beech *Fuscopora cliffortioides* at higher elevations and at lower elevations mostly red beech *Fuscopora fusca*; with understorey of broadleaves and abundant ferns, ground mosses and lichens, including *Polystichum vestitum* (G. Forst.) C. Presl, *Blechnum pennamarina* subsp. *alpina* (R.Br.) A.R.Field, *Notogrammitis billardierei* (Willd.) Parris, *Dicranoloma robustum*, *Hypopterygium didictyon* Müll.Hal., *Ptychomnion aciculare* (Brid.) Mitt. and *Pseudocypbellaria foveolata* (Delise) Malme.

## Sampling

The samples (soil cores) for mesofauna extraction were collected in late January 2017 (Southern Hemisphere summer) along 100 m transects at each elevation. In the alpine zone of Mt Arthur our sampling was interrupted by adverse weather and only 15 soil cores were collected there; in the alpine zone of two other mountain peaks 18 soil cores (six cores per transect) were collected. In the sub-alpine forest zone, 18 soil cores were collected on each mountain. GPS readings (coordinates and elevation) were recorded for each individual soil core. Soil temperature and soil moisture at 5 cm depth were measured very near to each sample (within 10 cm<sup>2</sup>) at the time of collection. Soil moisture was measured using a TDR 300 Soil Moisture Probe (Spectrum Technologies Inc., USA). Measurement of soil moisture was repeated three times at each point

and the average of the three readings was then recorded. Soil temperature was measured using a QM7216 Digital Stem Thermometer (Jaycar Co., NZ).

Soil cores were collected using a stainless-steel corer (25 cm<sup>2</sup>); the volume collected included the litter/turf/moss layer, plus 5 cm soil depth (Figure 1). The soil samples were kept chilled until delivered to the laboratory. The mesofauna were extracted in modified Berlese extractors for a week into 75% EtOH. The mesh size in the extractors is about 2 mm. Not all samples could be extracted immediately due to the capacity of extractors and some were kept at 4°C for one to three weeks. Samples for immediate extraction or 4°C storage were allocated randomly. There was some decline in mean extracted abundances (less than 7% per week of storage), but the slope of OLS regressions was not significantly different from zero ( $p = 0.1618$  for alpine samples,  $p = 0.3266$  for beech forest samples). Random allocation of samples to extraction vs. storage was designed to minimise the systematic bias. The mesofauna were identified to the closest taxonomic unit within our expertise, normally to order or family level. There is no single source for identification of NZ soil mesofauna, but the compendium in Chinn (2017) is a good starting point.

Species richness (species per core) was quantified at the level of morphospecies for most mesofauna taxa apart from Acari. The functional composition of mesofauna communities was approximated using trophic categories of soil mesofauna following Potapov et al. (2022). For taxa which may include variable feeding modes at this level of taxonomic resolution (e.g. Coleoptera larvae, other Prostigmata), the feeding mode was entered as 'mixed'. 'Other Prostigmata' included several species from Eupodoidea, Tydeoidea, Tarsonemidae and others, some predatory, scavengers and plant feeders, but the majority probably fungivores (Hessein and Perring 1986; Potapov et al. 2022).

### Statistical analysis

Abundance was expressed as the number of individuals per soil core, richness as the number of taxa per soil core. R v4.2.3 (R Core Team 2021) was used to calculate statistics for abundance and richness and to create graphics. One data point (soil core #8, Mt Arthur, alpine) had a uniquely high density of two species of oribatid mites (Acari: Oribatida): 358 individuals core<sup>-1</sup> of *Hypochothoniella minutissima* (Berlese, 1903) and 989 ind. core<sup>-1</sup> *Totobates cf. minor* Hammer 1967. These species are (*H. minutissima*) or are likely to be (*T. cf. minor*) general detritivores and fungal feeders (Schneider et al. 2004) and such high localised density indicates an unusual concentration of resources. As there was an actively used public walking track nearby and hare faecal pellets were present in the area, this data point was excluded as an outlier for the analysis of total abundances and trophic structure but conservatively kept included for the community analysis.

Correlation analysis was used to check for correlation between environmental factors (elevation, soil moisture and soil temperature). Since both soil moisture and soil temperature were significantly correlated with elevation across all sites, only elevation was used as an environmental factor for further analysis of total mesofauna abundance and taxon richness. Nested generalised linear mixed models (proc glmmix, SAS 9.4) with negative binomial or gamma distribution (chosen based on the AIC fit statistics)

were used to test the effect of elevation on abundance and taxon richness. Site (mountain range) was entered in the model as a random factor.

The distance-based redundancy analysis (dbRDA) using Bray–Curtis distance on square root transformed abundance counts in PRIMER 7 (Clarke et al. 2014) was used to visualise differences in soil mesofauna between sub-alpine beech forests and alpine habitats and to represent the variation in the mesofauna community composition explained by the environmental gradients. Taxa with abundance of less than 10 individuals across all samples were pooled as ‘Others’ in this and the following Permanova analysis. Permanova in PRIMER 7 on square-root transformed abundances with the Bray–Curtis distance as similarity measure was used to test for differences in mesofauna community composition and in community functional composition between habitats (sub-alpine forest vs. alpine); the model had a nested structure with different mountain ranges entered as a random factor. The environmental variables (elevation, temperature, soil moisture) were used as covariates in the model.

Significance level  $\alpha = 0.05$  was used for all statistical tests.

## Results

Alpine and sub-alpine habitats harboured a high diversity of soil mesofauna, many of which are Gondwanan relics (Table 1). Several interesting taxa are discussed below.

### *Harpacticoid copepods*

These tiny crustaceans are rarely mentioned in soil fauna surveys. The majority of the species are aquatic and are often one of the dominant taxa in marine and freshwater sediments. However, a number of species live in thin water films in terrestrial environments. Forty-five species of harpacticoid copepods from 16 genera and 7 families are described from New Zealand from a wide variety of habitats (Wells et al. 1982; Lewis 1984). Surprisingly, harpacticoid copepods are common members of the NZ soil fauna in forests, alpine environments and even in many agricultural soils (authors own observations).

In our samples, harpacticoid copepods were widespread in the subalpine beech forests and also present in the alpine zone, with the highest density in the Rainbow Ski Area (mean 933.3 ind. m<sup>-2</sup> and max 6400 ind. m<sup>-2</sup> in beech forests)

### *Peloriidiidae (Hemiptera)*

Peloriidiidae, or moss bugs, are sap-feeding hemipterans in the primitive suborder Coleorrhyncha. Unusually for sap-feeders, Peloriidiidae feed on mosses and liverworts. The family has a typical Gondwanan distribution, including Chile, Argentina, New Zealand, New Caledonia, eastern Australia and Tasmania, and Lord Howe Island (Larivière et al. 2011). The NZ Peloriidiidae fauna includes 3 genera and 13 species, all endemic to NZ (Larivière et al. 2011).

In our samples, Peloriidiidae were found in Mt Arthur sub-alpine beech forest at mid-elevation (1066–1024 m), where two species were present: *Xenophyes cascus* (Bergroth, 1924), 15 individuals in three samples with the liverwort *Bazzania* sp.; and *Oiophysa*

**Table 1.** Mesofauna (total counts) in litter and soil of subalpine beech forests and alpine environments in the Nelson-Tasman, South Island of New Zealand, summer 2017.

Region Taxa Habitat	Mt Arthur		Ben Nevis		Rainbow Ski	
	beech	alpine	beech	Alpine	Beech	alpine
Coleoptera (Carabidae)	8	1	20	1	9	5
Coleoptera (Staphylinidae)	48	5	38	12	14	8
Coleoptera (Curculionidae)	12	4	31	2	25	1
Coleoptera (Zopheridae)	1	–	5	–	6	–
Coleoptera (Leiodidae)	1	–	7	–	1	–
Coleoptera (Ptiliidae)	–	–	18	1	44	1
Coleoptera (other)	2	–	2	3	2	–
Coleoptera (juv.)	49	11	81	21	91	10
Diptera (adult)	1	3	1	1	2	2
Diptera (juv., mostly Nematocera)	128	7	246	23	147	55
Lepidoptera (juv.)	2	–	50	–	33	–
Hymenoptera (Formicidae)	–	–	1	–	–	–
Hymenoptera (other)	–	–	9	1	–	2
Hemiptera (Coccoomorpha)	15	76	283	216	80	255
Hemiptera (Peloriidiidae)	20	–	–	–	–	–
Hemiptera (Enicocephalomorpha)	24	4	6	3	3	1
Thysanoptera	–	13	2	1	16	1
Chilopoda (Geophilidae)	17	2	5	1	5	4
Chilopoda (Henicopidae)	7	–	36	10	4	2
Symphyla	40	8	181	5	40	11
Diplopoda juliform (juv.)	4	2	11	–	1	–
Diplopoda (Polydesmida) juv.	2	–	6	–	2	8
Diplopoda (Siphonophorida)	–	–	1	–	–	–
Pauropoda	33	10	21	10	67	6
Protura	12	6	91	82	3	2
Araneae	39	1	32	4	13	7
Opiliones (Cyphophthalmi)	–	–	63	20	–	–
Opiliones (Laniatores)	1	1	–	–	–	–
Pseudoscorpionida	3	–	4	–	4	–
Copepoda (Harpacticoida)	33	–	18	2	42	3
Isopoda (Styloniscidae)	18	4	1	1	41	3
Amphipoda (Talitridae) juv.	–	–	4	–	–	1
Oribatida (Enarthronota)	158	434	648	474	506	209
Oribatida (Crotoniidae)	3	–	7	8	2	2
Oribatida (Oppiidae)	1224	293	2103	547	944	265
Oribatida (Ceratozetoidea)	414	85	95	206	6	235
Oribatida (other)	5020	1688	1397	847	521	713
Astigmata	82	50	108	84	33	152
Mesostigmata (Uropodina)	655	21	568	58	159	36
Mesostigmata (Gamasida)	1568	346	1985	604	1524	373
Prostigmata (Labidostommatidae)	–	–	–	–	3	–
Prostigmata (Bdellidae)	12	5	7	–	1	2
Prostigmata (Trombidioidea)	–	11	7	2	7	8
Prostigmata (Nanorchestidae)	197	348	750	205	166	275
Prostigmata (Scutacaridae)	38	85	210	128	76	73
Prostigmata (Pygmephoridae)	31	3	43	40	5	12
Prostigmata (other)	562	846	3392	1251	1167	516
Collembola (Neelidae)	87	4	29	5	17	–
Collembola (Poduromorpha)	804	187	1428	437	362	346
Collembola (Isotomidae)	2305	1010	5290	947	1717	416
Collembola (Entomobryidae)	93	23	67	31	134	24
Collembola (Symphypleona)	15	10	30	6	15	2
<b>Total</b>	<b>13573</b>	<b>5609</b>	<b>20483</b>	<b>6307</b>	<b>8062</b>	<b>4050</b>

Note: Sampling area: 5 × 5 cm; sampling depth: vegetation/litter plus 5 cm soil depth; sample number:  $n = 15$  in Mt Arthur alpine,  $n = 18$  in all other habitats.

*ablusa* Drake and Salmon 1950, five individuals in a sample with the moss *Dicranoloma robustum*.

### **Enicocephalomorpha (Hemiptera)**

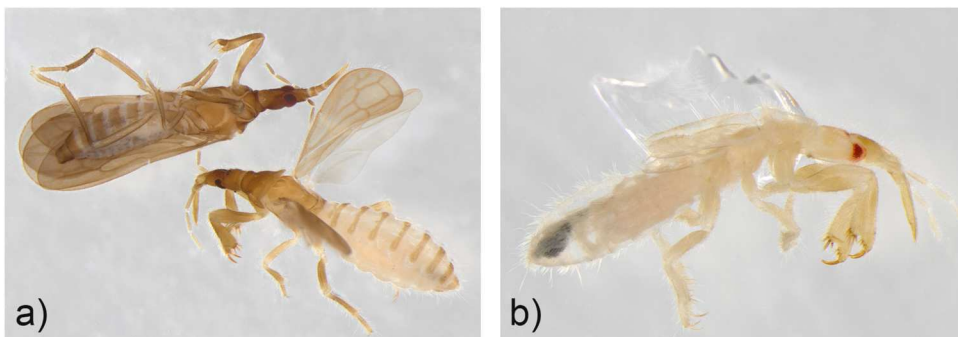
Known as ‘unique-headed bugs’ or ‘gnat bugs’, Enicocephalomorpha include members of two heteropteran families – Enicocephalidae and Aenictopecheidae (Carver et al. 1991). Found throughout the world, these unusual bugs are soil predators, typically 2–4 mm in length, with characteristic raptorial front legs. In New Zealand, the incidence of this group is especially high in the Nelson region (13 records in the NZ Arthropod Collection for Nelson, vs. 25 records for the rest of New Zealand).

Enicocephalomorpha were common in our soil samples (Figure 2) and were present in both sub-alpine beech forests and alpine areas of all three mountains. The species found were *Gourlayocoris mirabilis* (Gourlay, 1952), *Aenictocoris powelli* Woodward, 1956 and *Maoristolus tonnoiri* (Bergroth, 1927).

### **Micro-spiders (Araneae)**

The soil core size and 2 mm mesh of the Berlese extractors meant that most of the large spiders were excluded from our sampling. However, there was an interesting micro-spider fauna represented in the samples. In addition to juveniles of larger species, the samples contained a number of tiny spiders from subfamily Micropholcommatinae (fam. Anapidae), formerly a separate family Micropholcommatidae (micro-Gondwanan spiders). As the name suggests, Micropholcommatinae are extremely small, with body length ranging from 0.5 to 2 mm, and have Gondwanan biogeography. These spiders live in moist environments in mosses and leaf litter (Propistsova et al. 2023). The 34 described species occur in Chile, Australia, Tasmania, New Zealand, Lord Howe Island, New Caledonia and Papua New Guinea (Rix and Harvey 2010).

The species found in our samples was *Rayforstia vulgaris* (Forster and Platnick 1959), which was present in sub-alpine beech forests of Mt Arthur, Ben Nevis and Rainbow Ski Area (800–1200 m). One individual of *R. vulgaris* was also collected in the alpine zone of



**Figure 2.** Predatory soil Enicocephalomorpha (Hemiptera) from samples collected in this study (Nelson/Tasman, NZ): **a**, *Maoristolus tonnoiri* (Bergroth, 1927); **b**, *Aenictocoris powelli* Woodward, 1956 resting on a glass shard.

Rainbow Ski field at 1717m in litter under carpet grass *Chionochloa australis*. *Rayforstia vulgaris* is a common and relatively widespread species in the South Island of New Zealand (Rix and Harvey 2010).

Additionally, a *Duripelta* sp. (Orsolobidae) was collected in beech forests of Mt Arthur and Ben Nevis. The Orsolobidae is a family of six-eyed spiders with about 180 described species in 30 genera (World Spider Catalog 2024). Most genera are endemic to New Zealand and the Australian region, but several genera occur in southern Africa and South America (Forster and Platnick 1985; Platnick and Brescovit 1994). The genus *Duripelta* has 17 species which are all NZ endemics.

Also present were several Hahniidae (dwarf sheet spiders) in beech forests of Mt Arthur, Ben Nevis and Rainbow Ski Area.

### **Mite harvestmen (*Cyphophthalmi*, *Pettalidae*)**

Pettalidae are a monophyletic family of small opilionids with Southern Gondwanan distribution (Australia, Chile, Madagascar, New Zealand, South Africa, Sri Lanka), a pattern which is inferred to be the result of vicariance as their dispersal ability is poor (Boyer and Giribet 2007). The New Zealand mite harvestmen have received substantial attention, covering both evolutionary and taxonomic studies; currently 30 species are described with a few more awaiting description (Boyer and Giribet 2007, 2009; Giribet et al. 2012; Boyer et al. 2022).

The one species present in our samples was *Aoraki denticulata* (Forster, 1948), which was common in samples from Mt Richmond Forest Park (Ben Nevis) and locally found in high abundances (mean density 1400 ind. m<sup>-2</sup>, max 7200 ind. m<sup>-2</sup> in subalpine forests, mean 444 ind. m<sup>-2</sup> and max 4400 ind. m<sup>-2</sup> in alpine environments). *Aoraki denticulata* is endemic to the South Island of New Zealand and is found in leaf litter throughout Nelson and Marlborough, and as far south as Arthur's Pass (Boyer et al. 2022).

### **Collembola**

On a higher taxonomic level, the springtail fauna of alpine Nelson-Tasman showed structural similarities to the trends seen in other alpine and polar assemblages: a decrease in the representation of Entomobryidae and Symphypleona with elevation or latitude and an increase in the more primitive Isotomidae and Poduromorpha (Babenko 2002; Stebaeva 2003; Xie et al. 2022). The springtail assemblages, especially in the alpine, were dominated by Isotomidae (Entomobryomorpha). Isotomidae are characterised by high ecological plasticity and are highly represented in polar and alpine environments (Potapov 2001).

Our samples also contained relatively high numbers of Neelidae, which are tiny (body size around 0.3–0.5 mm) and an often-ignored group of Collembola. Neelidae inhabit soil, litter, epiphytes, mosses, dead wood and sometimes found in caves (Papáč and Kováč 2013; Schneider et al. 2013). All Neelidae in our samples belonged to the genus *Megalothorax*, with 3 or 4 species present in the material. The species from Mt Arthur beech forests was very abundant, exclusive to the Mt Arthur beech forest samples and the only Neelidae species found in the area. This species has now been described as *Megalothorax zealanterolenis* in Schneider et al. (2023). These springtails were widespread in

our samples and locally found in high abundance (mean density 2800 ind. m<sup>-2</sup>, max 10,800 ind. m<sup>-2</sup>). The new species may be geographically restricted, as it was not observed in subalpine beech forests of the two other mountains sampled in the same region. This species has strong similarities to *Megalothorax* species from Patagonia and Tasmania (Schneider et al. 2023). The other *Megalothorax* species in the samples were not as abundant. They may include at least two further new species.

### Mites (Acari)

The acarifauna was dominated by Oribatida, Mesostigmata and Prostigmata. Oribatid mites are characterised by long life cycles, long adult survival, low fecundity and are not tolerant of soil disturbance, although a few cosmopolitan species can tolerate disturbance and reproduce quickly (Maraun and Scheu 2000). These mites are detritivores (feed on leaf litter and decomposing woody material) and microbivores (feed on soil algae and fungi), but some taxa are predators/scavengers (e.g. some Oppiidae) and others graze on mosses, lichen and higher plants (Schneider et al. 2004; Maraun et al. 2023). Currently, 466 species of oribatid mites are known to occur in New Zealand (Subías 2022). Oribatida in our samples had highest abundance and diversity in the subalpine forests (Table 1). The structural trends seen in Oribatida assemblages mirrored those seen in the arctic and alpine regions elsewhere, with Enarthronota and Ceratozetoidea proportionally more highly represented in the alpine zone (Behan-Pelletier 1999; Fischer and Schatz 2013; Minor et al. 2017).

Other abundant mites included predatory Mesostigmata and diverse Prostigmata, which comprise predators (Bdellidae), sucking phytophages, mycophages (Pygmephoridae) and algophages (Nanorchestidae) (Walter 1988). The fauna of soil Prostigmata in NZ is still poorly known, although more work has been done recently (Qin 1998; Fan and Zhang 2005; Fan et al. 2016; Khaustov and Minor 2018a, 2018b, 2020, 2025).



**Figure 3.** Box plots and cloud plots showing per sample **a**, total abundance and **b**, taxon richness of soil mesofauna in sub-alpine beech forests and alpine habitats in Nelson-Tasman region of NZ, 2017. Cloud plot: the height of the cloud indicates the probability density of data points; the length of the cloud indicates the overall variability of data. Box plot: the black line is the median, the white diamond is the mean.

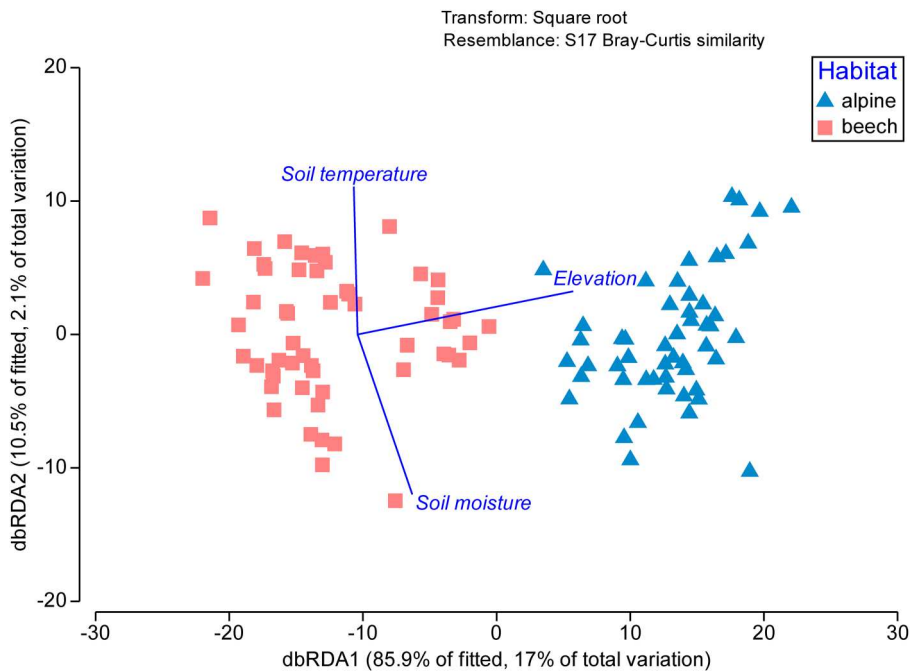
**Table 2.** PERMANOVA results for mesofauna assemblages mesofauna in sub-alpine beech forests and alpine habitats in Nelson-Tasman region of New Zealand.

Source	df	SS	MS	Pseudo-F	<i>P</i> -value
Habitat	1	3451.7	3451.7	2.426	0.009
Site(Habitat)	4	11948.0	2987.0	3.83	0.001
<i>Covariates</i>					
Elevation	1	18195.0	18195.0	5.544	0.001
Soil temp	1	2158.1	2158.1	1.086	0.350
Soil moisture	1	1917.4	1917.4	1.625	0.108
Residuals	96	74870.0	779.9		
Total	104	1.1254E + 05			

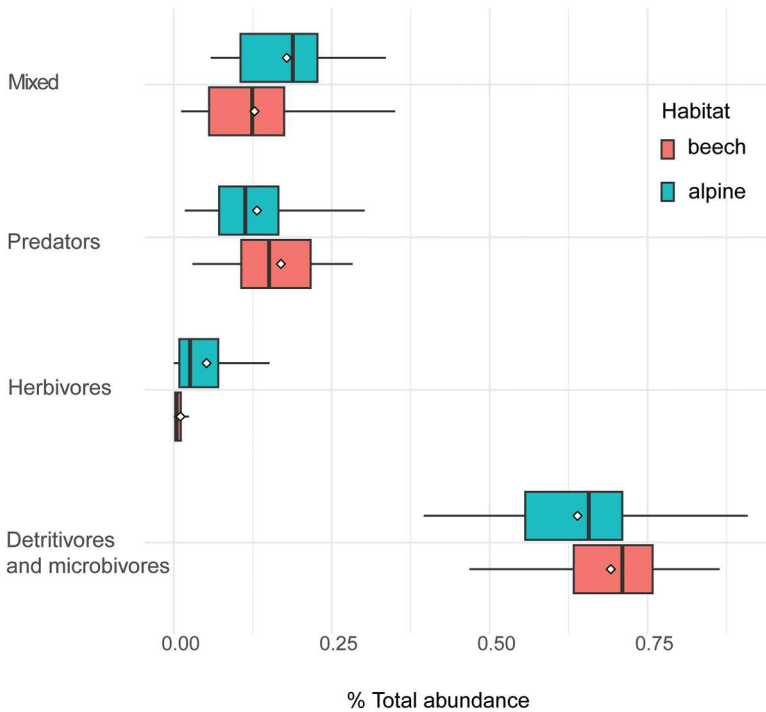
Note: Site (random factor) identifies sampling area (mountain peak). Covariates are continuous variables.

### Abundance, diversity and trophic structure

Mesofauna abundance and taxon richness decreased with increasing elevation (Figure 3; abundance  $F_{1,101} = 70.59$ ,  $P < 0.0001$ , richness  $F_{1,100} = 45.89$ ,  $P < 0.001$ ). The mesofauna community assemblages reflected effects of elevation and habitat (beech vs. alpine); the effects of soil moisture and soil temperature were not significant (Table 2). Elevation (dbRDA axis 1) explained over 80% of variation in the mesofauna community composition due to environmental gradients; but the overall dbRDA explained only 19% of the variation in the community data (Figure 4). At the broad taxonomic level most of the taxa crossed over to the alpine zone but declined in abundance. A few taxa were



**Figure 4.** Distance-based redundancy analysis (dbRDA) for soil mesofauna in sub-alpine beech forests and alpine habitats in Nelson-Tasman region of NZ. The dbRDA axis: fitted variation represents the variation in the mesofauna community composition explained by the three environmental gradients (continuous variables); total variation represents the overall variation in the community data.



**Figure 5.** Trophic composition of mesofauna communities (as % of total abundance) in sub-alpine beech forests and alpine habitats in Nelson-Tasman region of NZ. Detritivores (litter feeders) and microbivores (fungal and bacterial feeders) are pooled. 'Mixed' included those Prostigmata mites (Eupodoidea, Tydeoidea, Tarsonemidae) for which feeding mode is unresolved at this level of identification – most are plant feeders or fungivores. Mean is indicated as a white diamond, median as a black line.

absent in the alpine samples (Pseudoscorpionida, Peloridiidae, Lepidoptera larvae), while other taxa strongly declined (Myriapoda, Aranea, Harpacticoida, Coleoptera larvae).

The trophic composition of mesofauna communities in all cases was dominated by microbivores – Oribatida mites, Astigmata mites, Collembola and some Prostigmata mites (Nanorchestidae, Pygmephoridae, Scutacaridae) and detritivores – Diplopoda, Isopoda and insect larvae (Figure 5). Predators, dominated by predatory beetles, Enicocephalomorpha hemipterans, centipedes, spiders, mite harvestmen, mesostigmatid mites and some prostigmatid mites (Bdellidae, Trombidioidea), decreased in relative abundance with elevation ( $F_{1,101} = 82.28$ ,  $P < 0.0001$ ), while herbivores (dominated by scale insects and thrips) increased in the alpine ( $F_{1,101} = 6.19$ ,  $P = 0.015$ ) (Figure 5). Elevation had a stronger effect on functional composition of mesofauna assemblages than vegetation type (habitat) (Table 3).

## Discussion

Systematic surveys of alpine soil fauna are rare in Australasia, and often are conducted at a higher taxa level, with invertebrates identified to orders or families (Green 1982, 1997, 2002; Doran et al. 2003; Slatyer et al. 2017; but see Greenslade 2002). The mesofauna

**Table 3.** PERMANOVA table of results for community trophic structure in sub-alpine beech forests and alpine habitats in Nelson-Tasman region of New Zealand.

Source	df	SS	MS	Pseudo-F	<i>P</i> -value
Habitat	1	277.36	277.36	1.995	0.208
Site(Habitat)	4	1258.7	314.67	4.709	0.001
<i>Covariates</i>					
Elevation	1	2096.5	2096.5	6.056	0.023
Soil temp	1	236.15	236.15	1.167	0.298
Soil moisture	1	146.8	146.8	1.314	0.231
Residuals	96	6415.2	66.83		
Total	104	10431.0			

Note: Site (random factor) identifies sampling area (mountain peak). Covariates are continuous variables.

assemblages in our sites were dominated by Acari (Prostigmata, Mesostigmata, Oribatida) and Collembola, which are dominant taxa in arctic and arctomontane ecosystems elsewhere (Behan 1978; Addington and Seastedt 1999; Makarova 2015). Numerically, alpine invertebrate communities of Australasia are dominated by Araneae and Coleoptera, and by mesofauna – Acari and especially Collembola (80%) (Green 1997; Grey 2002; Andrew et al. 2003; Minor et al. 2016, 2017; Green and Slatyer 2020).

Our data showed a decline in mesofauna abundance and taxa richness with increased elevation. Elevational gradients in diversity and abundance are well documented (e.g. Rahbek 1995; Hodkinson 2005; Descombes et al. 2017) and consistent trends have been observed in a variety of invertebrate taxa (Olson 1994; Wolf 1994; Lobo and Halffter 2000; Pyrcz et al. 2009; Zhang et al. 2012), plants (Pendry and Proctor 1997; Roos et al. 2019; Coelho et al. 2021) and soil microorganisms (Bryant et al. 2008; Zhang et al. 2015). However, a decline in abundance and/or taxonomic richness with increasing elevation is common but not universal (Rahbek 1995; Andrew et al. 2003). Andrew et al. (2003) observed instances of decreasing invertebrate richness and abundance with elevation in mountains of Tasmania and New Zealand, but the trends were not consistent among regions, among different mountains within a region, or between the invertebrate and bryophyte communities. Species richness in invertebrate communities often declines with elevation or peaks at mid-elevation, but increased abundance of micro-habitats at higher elevations can produce increases in species richness (Olson 1994; Andrew et al. 2003; Hodkinson 2005). Vegetation type (e.g. coniferous vs. broadleaf forest) can also have more significant influence than elevation on the soil C/N ratio and on the distribution of soil bacterial and fungal taxa along an elevational gradient (Yao et al. 2017).

The proportion of predators in soil and litter ecosystems can be influenced by a number of factors, including resource availability, environmental conditions and habitat complexity (Bardgett et al. 1998; Chen and Wise 1999; Hansen 2000; Doblas-Miranda et al. 2009; Kalinkat et al. 2013). Although soil invertebrate communities at all elevations are dominated by detritivores and microbivores (Potapov et al. 2022; Steinwandter and Seeber 2023), we expected that the proportion of predators would increase in high alpine habitats, as has been observed elsewhere: an increase in proportion of omnivores and predators at high elevation was found for soil macro- and mesofauna in Europe (Fischer et al. 2014; Steinwandter et al. 2018; Steinwandter and Seeber 2023; Lux et al. 2024). This can be linked to productivity in alpine environments being limited by colder temperatures and shorter growing seasons, leading to less abundant

and diverse invertebrate communities and shorter food chains (Chen and Wise 1999; Post 2002; Doi 2012). However, no proportional increase in predators was seen in our data. In contrast, alpine environments supported larger herbivore populations and had lower predator-to-herbivore ratios than upland forests. Some predators may have been undercounted due to insufficient taxonomic resolution for some taxa (e.g. Prostigmata), and omnivory is prevalent and difficult to quantify in soil food chains (Thompson et al. 2007; Potapov et al. 2019; Potapov 2024). However, a more possible explanation for these results is that soil food chains in the studied New Zealand alpine are not as short, due to complex habitat structure in alpine herb fields, high biodiversity and high abundance of potential prey. Species diversity in the New Zealand alpine is known to be high comparing to other alpine regions, perhaps due to the lack of complete glaciation and hypothesised refugia (Buckley et al. 2009; King et al. 2020).

An intriguing resource availability hypothesis is that introduced mammalian species in the subalpine and alpine can stimulate soil mesofauna. The density of the introduced herbivore the brown hare (*Lepus europaeus* Pallas 1778) is high in the alpine zone of Nelson-Tasman (Wong and Hickling 1999). Hare dung has a fertilising effect on the plants in their feeding areas (Wong and Hickling 1999). With estimated daily defecation rate of 410 pellets per hare, 0.144 g pellet dry weight and the average pellet decay time of 3 years, it has been estimated that vegetation consumption by hares in some New Zealand grasslands can reach 188 kg ha<sup>-1</sup> year<sup>-1</sup> (Flux 1967; Perry and Robertson 2012). Introduced ungulates may also be present in the areas (Fraser et al. 2000). Low intensity grazing is known to increase the abundance of soil fauna and the structural complexity of soil food webs compared to no or heavy grazing (Schon et al. 2008; Steinwandter et al. 2018; Wan et al. 2021). Elsewhere it has been found that light grazing and dung deposition in alpine environments benefits soil invertebrate communities, allowing some taxa to extend their upper elevational limit (Steinwandter et al. 2018). While predators such as stoats and mice prey on invertebrates in the New Zealand alpine zone (O'Donnell et al. 2017), mammalian predators target larger invertebrates ( $\geq 1$  cm body length) (Bremner et al. 1984; Towns et al. 2009) and are unlikely to directly affect mesofauna with body length under 2 mm. The result would be the channelling of ecosystem energy flows into mesofauna (Gibbs 2009), but this hypothesis needs further investigation.

Changes in mean temperatures and precipitation are predicted to occur over the coming century (IPCC 2013; Schmeller et al. 2022), and ecological zonation is expected to shift along the elevational gradients. Alpine ecosystems are expected to be adversely affected by the future climate change (Halloy and Mark 2003; Gentili et al. 2015; Verrall and Pickering 2020). Data presented here represent only a single snapshot of the soil mesofauna community, and longer sampling might uncover further biodiversity. However, even a single sampling event provides baseline data to help to fill the gaps identified in Buckley et al. (2015), advance the knowledge of the native fauna, and support assessment of environmental management strategies in the alpine. Our knowledge about the feeding preferences and life cycles of small arthropods in New Zealand alpine zone is scarce, and many species are undescribed. Studies of individual species and whole communities using tools such as stable isotope analysis and biological traits analysis will be important to explain observed patterns and to link them to the food-web structuring and ecosystem-level processes in the alpine system, in view of a changing world climate.

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## Data availability statement

The data that supports the findings of this study are available from corresponding author upon request.

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