



## Original article

# Characterizing snow relict assemblages of soil arthropods at risk of disappearing due to climate change

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## ABSTRACT

Climate change is reducing snow cover and duration in montane regions, threatening snow-dependent ecosystems, yet how soil arthropods respond to altered snow regimes in montane regions remains unclear. This study investigates soil arthropod and vegetation assemblages in late-lying snowbed habitats and adjacent alpine heath at ~950 m elevation in the Cairngorms National Park, Scotland. Using paired transects, we compared plant and soil arthropod communities as well as functional adaptations of specimens across habitats. As expected snowbeds exhibited higher soil moisture, fewer freeze-thaw cycles, and distinct graminoid-dominated vegetation compared to closely located hillslope. While overall arthropod community composition did not differ significantly between habitats, abundance of Acari and Collembola and some functional groups were greater in the adjacent hillslope, whilst Acari mites were negatively associated with soil moisture. These findings suggest that environmental filtering shapes arthropod communities at fine ecological scales. As snowbed habitats decline under climate change, trait-based monitoring may be critical for detecting subtle shifts in soil biodiversity and ecosystem function.

## 1. Introduction

Climate change is likely to have many impacts on natural systems, but particularly so to snow cover and duration in temperate and mountain ecosystems. In recent years snow cover and duration has broadly decreased in montane regions [1,2], resulting in direct pressures on sensitive upland species and ecosystems reliant on winter snow cover. Understanding the likely impacts of decreased snow cover on key fauna is therefore crucial in understanding how these ecosystems may change in the future.

In mountainous regions, snow patches form during the melting season primarily due to interactions between terrain and wind during the winter months [3,4]. In Scotland, instances of semi-permanent patches fully melting have increased in recent years [5,6], with no snow surviving anywhere for each of the past four years (2022 - 2025). Prior to 2022, there were only six previous instances of complete national snowmelt in the previous 180 years. Snow cover and duration in the Cairngorm mountains of Scotland was also found to have decreased between 1969 and 2005 [7]. Such events are only likely to increase under future climate change scenarios [7,8], with snow at mid to upper

altitudes (600 – 900 m) in Scotland at significant risk [9], although sporadic and localised variations are likely within this environment [10, 11].

Mountainous habitats have relatively high biodiversity due to fine-scale habitat heterogeneity [12,13], resulting from steep topography and fine-scale variation in abiotic conditions [14]. Late laying snow plays a critical role in above and below-ground ecological processes that define these habitats. For plants, it creates a shorter growing season which favours specialist alpine species at the expense of generalists [15–17] whilst during the winter it provides an insulating layer from freezing air [18], protecting both the under-laying plants [19,20] and resulting in a warmer soil microclimate [21,22]. Below-ground, snow cover protects from freeze-thaw cycles that can stress microbial communities and lead to significant changes in soil nutrient dynamics [23–25], whilst snow cover duration has strong implications for the timing and rate of plant litter decomposition [26].

Soil arthropods play central roles in decomposition [27,28], nutrient mineralisation [29,30], and microbial regulation [27,30], thereby underpinning ecosystem functioning in alpine systems where primary productivity is low and nutrient cycling tightly constrained. Because

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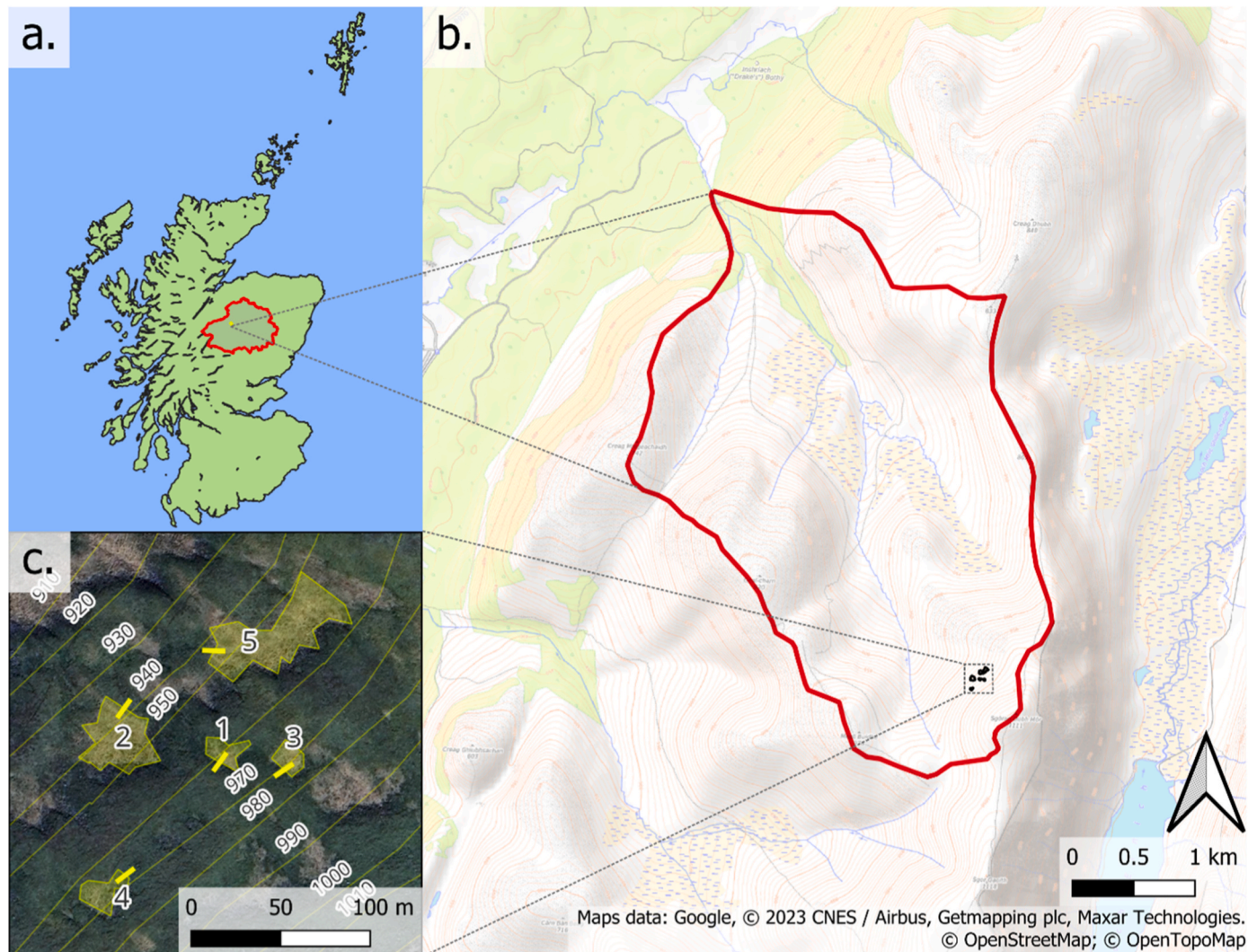
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they are highly responsive to microclimatic conditions [13,31–35] and soil moisture [36], and exhibit distinct morphological and ecological adaptations to edaphic life [37], their community structure is strongly shaped by environmental filtering. In particular, functional traits associated with vertical habitat use, desiccation tolerance, and degree of soil specialisation may respond predictably to changes in snow cover duration and associated shifts in soil temperature and moisture regimes. As a result, trait-based frameworks offer a mechanistic lens through which environmentally driven restructuring of soil communities can be assessed, particularly where microclimatic shifts alter edaphic conditions.

Only a few studies have looked at the response of above and below ground arthropod communities to reduced snow cover and duration in alpine environments. Hiramatsu & Usio [31] suggest that some alpine carabids have adapted versatile activity patterns in response to the changeable microclimatic conditions found in alpine environments. Spider [13,32] and Collembola [35] communities have been shown to be at least partially responsive to snow cover and melt, whilst a study in the European Alps [34] found no correlation between snow melt and the density of soil micro- (collembolans, oribatid mites) and macro- (spiders, beetles) arthropods, instead they suggested micro-arthropod communities were principally driven by soil porosity and soil organic matter

content. Snow manipulation experiments in alpine environments found idiosyncratic responses to earlier snow melt depending on species [33], whilst Leingärtner et al. [32] found earlier snowmelt increased the abundance of predatory and parasitic species more than herbivorous ones. In arctic environments, arthropods have been shown to be sensitive to snow cover and duration [38,39], with snow depth and winter air temperatures acting to regulate soil arthropod communities [40]. However many species and groups have evolved extreme cold tolerance (e.g. in the arctic [41]), which may be different for oceanic alpine species. Collectively, these studies suggest that responses to altered snow regimes may be highly context-dependent, varying across taxa and functional groups. This variability highlights the need for integrative approaches that link community composition to ecologically meaningful trait variation.

In this paper we explore above- and below-ground arthropod assemblages within and adjacent to late-lying snowbed habitats at ~950 m a.s.l. in the Cairngorm Mountains, Scotland, UK. Despite long-term monitoring of snow cover at this site, little is known about how associated soil faunal communities respond to variation in snow duration. Using both new and historical data from a long-term ecological monitoring site, we test the hypothesis that extended snow cover alters habitat conditions in ways that structure both plant and soil arthropod



**Fig. 1.** Maps of study area showing a) the location within the Cairngorms National Park, Scotland (yellow dot); b) the location of plots on the northwest slopes of Sgoran Dubh Mor in the Allt a'Mharcaidh catchment (Cairngorms LTER, outlined in red); and c) the five 10 m research transects centred on the boundary of snowbeds (highlighted in yellow) and adjacent hillslope habitats. Contour heights are in meters above sea level. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

assemblages. Specifically, we hypothesise (H1) that extended snow cover structures plant communities by favouring snowbed specialists, resulting in compositional differences between snowbeds and adjacent alpine heath. Because vegetation influences litter inputs, soil organic matter, and soil microclimate, we further hypothesise (H2) that associated differences will be reflected in soil arthropod abundance, diversity, and functional composition between habitats. Together, these hypotheses imply that reductions in snow cover duration may weaken habitat-specific environmental filtering, with consequences for soil biodiversity and ecosystem functioning under future climate scenarios.

## 2. Methods

### 2.1. Location

The research was undertaken at the UK Environmental Change Network (ECN) long-term ecological & environmental research site (Cairngorms LTER) in the Allt a' Mharcaidh catchment, Cairngorms National Park, Scotland, UK (Fig. 1; <https://deims.org/5a04fee1-42aa-47e9-abfc-043a3eda12ac>). The site ranges from 325 to 1111 m above sea level, encompassing a range of habitats from mature woodland, through wet and dry heaths to bryophyte dominated alpine heaths at the upper elevations. While Scotland as a whole has a temperate maritime climate, the high plateau of the Cairngorms experiences harsher, arctic-alpine (sub-arctic) conditions that are unique in the UK. The mean July (summer) temperature at the study site is 9.4 °C, whilst mean January temperature (winter) is -1.4 °C. Annual precipitation is greater than 943 mm. Soils are alpine podzols formed on granite parent material, with acidic, nutrient-poor, organic-rich surface horizons.

Snow on the North-West facing slope of Sgoran Dubh Mor (57.083, -3.813) has been monitored using fixed-point repeat photography for 21 winter seasons between 2002 and 2023. Over this period, winter snow duration was variable [2], but snow generally persisted from mid-November (mean day  $317 \pm 17.38$  SD) to late-April (mean day  $148 \pm 17.14$  SD). Late-laying snow patches occupy hollows in the hillslope formed beneath boulder solifluction lobes. These hollows allow for a greater accumulation of winter snow than surrounding slopes, whilst also protecting from wind-scouring.

### 2.2. Sampling methods

An area containing spatially and floristically distinct snowbeds on the NW facing slope of Sgoran Dubh Mor was selected for the study at an elevation of between 940 and 970 m (Fig. 1c). Five paired snowbed and adjacent hillslope habitat plots were selected in an area where aspect, slope, elevation and winter snow cover duration were all broadly similar. The paired plots reflect as far as possible the same environment. All snowbeds were within 75 m of a central point, and although varying in size, each was physically distinct from its neighbours. A 10 m transect was established on the boundary of each snowbed, extending 5 m into the snowbed and adjacent hillslope habitats, the ends of which were the designated sampling points. Soil sampling was conducted in August 2023, approximately 10 weeks after complete snowmelt, when soils were fully thawed and accessible.

During an earlier sampling campaign vegetation was recorded at each sampling point using a 1 m<sup>2</sup> quadrat (subdivided into 100, 10 × 10 cm cells), with the presence of all vascular species recorded for each cell, and percentage surface cover of each species recorded at the 1 m<sup>2</sup> level. Re-inspection of the plots in 2023 suggested little, if any, change had occurred in vegetation assemblage, and plots were not re-surveyed on this occasion.

At each sampling point, two 150 mm long soil cores (separated by 2 m) were collected (n = 20) using a 50 mm diameter corer, containing a section of removable pipe. Extracted cores were capped for transport, then separated into two depth profiles (0-75 mm and 75 – 150 mm) on the same day, before being stored overnight in sealed plastic bags at

5 °C. Soil moisture readings were taken using a handheld theta probe inserted into the sidewall of the hole immediately after excavation of the soil core.

Arthropods from the 40 soil samples were extracted using Berlese-Tullgren funnels for seven days, with specimens collected directly into 70% ethanol. All taxa were identified to order level, except for Acari, which were identified to sub-class. Eco-morphological index (EMI) values were assigned following the QBS-ar protocol of Parisi [37]. For each higher taxonomic group, we identified the morphotype showing the highest degree of morphological adaptation to soil life and attributed an EMI score accordingly. In the QBS-ar system, euedaphic forms (EMI = 20) represent the most strongly soil-adapted morphotypes and are characterised by absence of pigmentation, absence of furca, and short or strongly reduced appendages. Hemiedaphic forms show partial adaptation, while epedaphic morphotypes retain pigmentation and well-developed appendages and therefore receive low EMI values.

Because Collembola encompass morphotypes spanning several levels of soil adaptation, we distinguished fully euedaphic from slightly euedaphic forms using the trait-based criteria defined in the QBS-ar EMI scoring scheme. According to the index, slightly euedaphic Collembola (EMI = 10) are very small, lack pigmentation, and retain a reduced (small) furca, whereas fully euedaphic Collembola (EMI = 20) exhibit complete absence of pigmentation, absence of the furca, and short/reduced appendages. For each soil sample we calculated: abundance of each arthropod group, total abundance of all arthropods, diversity (number of functional groups present in a sample) and soil quality.

Soil temperature was monitored at 10 cm soil depth using Geo-Precision M-log 5W loggers set to record hourly. Loggers were installed in 2014 and subsequently downloaded using 433 MHz radio to prevent further physical disturbance to the soil.

### 2.3. Analytical methods

All statistical analyses were carried out in R [42]. Soil arthropod counts were analyzed using a negative binomial GLM to account for overdispersion in the count data, with ecomorphological group (EMI), habitat, and soil depth as fixed effects. Initially interaction terms were tested (likelihood ratio  $\chi^2$  and Wald tests) but as some interaction estimates were undefined due to sparse data in certain combinations, were not significant ( $p > 0.10$ ), and did not improve model fit ( $\Delta AIC \approx 2$ ), we retained the simpler additive model for improved interpretation. Type II Wald  $\chi^2$  tests were used to assess significance of model terms (r package: car, v3.1-3), and estimated marginal means with Tukey-adjusted pairwise contrasts (r package: emmeans, v1.11.2) were calculated to compare abundances among EMI categories within each habitat. For taxa-EMI functional groups, only groups where at least 1 specimen was collected from both habitats were included.

Summary analyses were undertaken to understand the soil microarthropd community structure, including taxa abundance, evenness and diversity (Shannon H), utilising the community ecology package 'vegan' (v2.6-6). Prior to community analysis, soil moisture was included alongside habitat to assess independent explanatory power of co-variables, and was found to be strongly structured by habitat ( $F(1,18) = 24.22$ ,  $p < 0.001$ ) in a one-way ANOVA. Habitat explained 57.4% of the variance in soil moisture ( $\eta^2 = 0.574$ ; r package: DescTools, v0.99.60), indicating a strong effect of habitat type on soil moisture conditions. To avoid issues of multicollinearity, habitat alone was therefore retained as the sole co-variate.

Abundance matrix for vegetation and soil arthropod communities were firstly normalized using Hellinger transformation to reduce the influence of very abundant species while preserving the structure of the data. To establish whether the vegetation and arthropod assemblages were unique between habitats, a Permutational Multivariate Analysis of Variance (PERMANOVA) using a Bray-Curtis dissimilarity matrix was used with multivariate homogeneity of group dispersions checked using betadisper and permutation tests. Dissimilarity between plots was then

examined using hierarchical clustering and NMDS bi-plots. To identify individual contributions of vegetation taxa to community dissimilarity between the snowbed and adjacent hillslope habitats, a similarity percentage (SIMPER) analysis was undertaken. Additionally indicator species were identified using the multipatt function in the indicpecies package (v1.8.0) [43], based on the IndVal.g statistic (group-based indicator value statistic) with 999 permutations.

### 3. Results

#### 3.1. Characteristics of the snowbed environment

Visually, snowbed habitats were clearly distinct from the adjacent hillslope. Twelve vascular plant species were recorded in total, along with bryophytes, lichens (including aggregates), and areas of exposed rock and bare ground (Supplementary Table 1). Snowbeds supported a richer plant community, with higher species richness compared to the adjacent hillslope (Table 1), although overall diversity was similar.

Soils in snowbeds were notably wetter than the adjacent hillslope, with consistently higher moisture levels. Soil temperature regimes also differed between habitats (Table 1). Snowbed soils were protected from the coldest winter temperatures due to the buffering effect of laying snow, resulting in 80 % fewer freeze-thaw cycles annually than the adjacent hillslope, whose soils suffered from colder minimum temperatures and more frequent freezing events. Despite snowbed soils exhibiting marginally warmer maximum temperatures during the summer months, overall the mean annual temperature and thermal sums (degree days) were similar between habitats.

Non-metric multidimensional scaling (NMDS) revealed distinct clustering of plant communities based on habitat type (stress = 0.0678, Fig. 2a). This was confirmed by PERMANOVA of the vegetation community revealing that habitat significantly influences vegetation composition ( $F(1,8) = 7.928, p = 0.007$ ), accounting for 49.8 % of the variation in plant community composition. A multivariate dispersion test (PERMDISP) was not statistically significant ( $F(1,8) = 3.614, p = 0.081$ ), indicating that differences between habitats reflect actual differences in community composition and validating the PERMANOVA findings.

Hierarchical clustering using Bray–Curtis dissimilarity and complete linkage grouped the vegetation plots into two distinct clusters, corresponding exactly to snowbed and adjacent hillslope habitats (Fig. 2b). Within-habitat dissimilarities ranged from 0.10 to 0.41, while the major split between snowbed and adjacent hillslope communities occurred at a Bray–Curtis distance of 0.64, indicating greater similarity within than between habitats.

SIMPER analysis identified the key species differentiating snowbeds and adjacent hillslopes. *Cladonia* lichens were the most influential,

**Table 1**

Characterisation of two montane habitats (snowbed and adjacent hillslope) in the Cairngorms National Park, Scotland. Soil temperature (10 cm), degree days (base = 0 °C) and freeze-thaw cycles are the annual means over a complete 8 year period (2014–2021) with SD is shown in brackets ( $n = 1$  per habitat). Vegetation variables are mean values ( $n = 5$  per habitat), whilst soil moisture was duplicated at each site ( $n = 10$  per habitat). Statistics include anova F and P (significance <0.05)).

	Snowbed	Adj. hillslope	F	P
Mean Soil T °C	3.98 (0.45)	3.69 (0.27)	2.511	0.135
Min Soil T °C	0.015 (0.04)	-0.476 (0.32)	18.65	<0.001
Max Soil T °C	17.13 (1.53)	15.79 (1.08)	4.142	0.061
Degree Days (sum)	1416.42 (120.61)	1348.93 (98.73)	1.501	0.241
Freeze-thaw	1.62 (3.11)	8.5 (5.61)	9.195	0.09
Soil moisture $m^3 \cdot m^{-3}$	0.79 (0.24)	0.39 (0.08)	24.22	<0.001
Veg Richness	12.2 (2.59)	8.6 (1.52)	7.2	0.023
Veg Shannon	2.01 (0.23)	1.85 (0.2)	1.443	0.264

contributing 7.5 % to the Bray-Curtis dissimilarity and being significantly more abundant in the adjacent hillslope ( $p < 0.001$ ), as was the bryophyte *Racomitrium lanuginosum* (3.8 % contribution;  $p = 0.018$ ). Conversely, graminoid species such as *Nardus stricta* (6.3 %;  $p < 0.001$ ) and *Trichophorum caespitosum* (5.4 %;  $p < 0.001$ ), were exclusive to the snowbed habitat and strongly contributed to the dissimilarity. Indicator species analysis further identified that *Cladonia* lichens (IndVal = 0.977,  $p = 0.01$ ) and *Racomitrium lanuginosum* (IndVal = 0.827,  $p = 0.05$ ) were significant indicators species of the adjacent hillslope, whilst *Nardus stricta* (IndVal = 0.894,  $p = 0.04$ ) was an indicator of snowbed habitats.

#### 3.2. Soil arthropod communities

In total 363 individual arthropods belonging to 8 taxa (Acari, Collembola, Coleoptera, Diptera, Psocoptera, Thysanoptera, Araneae, Hemiptera) were collected from the 40 soil core profiles (Supplementary Table 2). Arthropod community metrics varied strongly with soil depth, while habitat exerted comparatively minor effects. Abundance was significantly higher in soils from the adjacent hillslope compared to the snowbed ( $F(1,36) = 9.23, p = 0.004$ ), with 68.3 % of all individual specimens collected from adjacent hillslope soils. Soil depth exerted an even stronger influence on abundance, with shallow soils (89 % of all specimens collected) supporting greater abundance than deep soils ( $F(1,36) = 70.73, p < 0.001$ ). Taxa richness ( $F(1,36) = 0.02, p = 0.883$ ; Fig. 3c), Shannon diversity ( $F(1,36) = 0.06, p = 0.810$ ) and evenness ( $F(1,36) = 0.14, p = 0.709$ ) showed no habitat effect, whilst richness ( $F(1,36) = 36.99, p < 0.001$ ) and diversity ( $F(1,36) = 25.59, p < 0.0001$ ) were significantly higher in shallow soils. Evenness was also depth-dependent ( $F(1,21) = 10.29, p = 0.0042$ ), with deep soils showing greater evenness than shallow soils. Although this is somewhat counterintuitive, the increased community evenness with depth is likely an artifact of the very low abundances in the deeper soil.

Mites (Acari) were the most abundant taxa in both habitats (Fig. 3b) followed by springtails (Collembola), with mites accounting for 49% of specimens collected in snowbed habitats, and 60% on the adjacent hillslope. Collembola accounted for 40% and 37% respectively. Coleoptera, Psocoptera and Diptera were found in both habitats at low numbers, whilst Thysanoptera, Hemiptera and Araneae were present in samples from the snowbed habitat but absent from the adjacent hillslope (Fig. 3b).

#### 3.3. Functional variability of taxa between habitats

Taxa were classified by ecomorphological index (EMI) to reflect soil-adaptive traits. Euedaphic forms dominated (90.9%), while hemiedaphic (5.8%) and epedaphic (3.3%) taxa were rare. Abundance differed strongly among EMI groups ( $\chi^2 = 25.76, p < 0.001$ ) and soil depth ( $\chi^2 = 6.45, p = 0.011$ ), with a marginal habitat effect ( $\chi^2 = 3.74, p = 0.053$ ) (Fig. 4). EMI was the best predictor, with euedaphic taxa consistently dominant, ranging from 5.9 individuals in deep snowbed soils to 44.8 in shallow soils from the adjacent hillslope. Epedaphic and hemiedaphic taxa remained scarce (<8 individuals) and did not significantly differ from each other ( $p > 0.6$ ), whilst increasing soil depth reduced arthropod counts by 60–70%. Arthropod communities are therefore overwhelmingly euedaphic, with dominance amplified in shallow soils and adjacent hillslope habitats.

Significant habitat-related differences in abundance were detected for three taxa specific functional groups. Highly euedaphic (EMI 20) Acari (estimate = -0.972, SE = 0.451,  $z = -2.16, p = 0.031$ ), slightly euedaphic (EMI 10) Collembola (estimate = -1.187, SE = 0.501,  $z = -2.37, p = 0.018$ ) and hemidaphic (EMI 8) Collembola (estimate = -2.773, SE = 1.110,  $z = -2.49, p = 0.0128$ ) were all significantly more abundant in the adjacent hillslope compared to the snowbed habitats (Fig. 5).

Only three taxa functional groups had enough data to analyse for an association with moisture (Fig. 6). The abundance of soil dwelling Acari

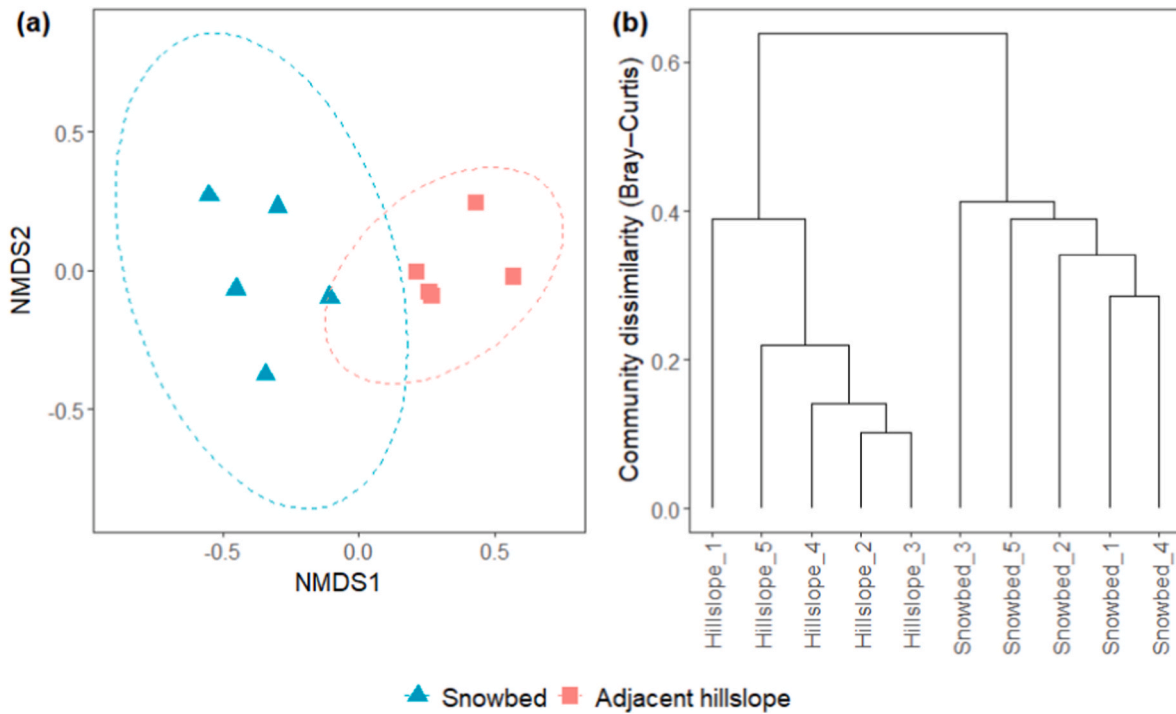


Fig. 2. a) NMDS ordination of the vegetation community surveyed from snowbed and adjacent hillslope habitats in the Cairngorms National Park, Scotland. b) Hierarchical clustering dendrogram based on Bray-Curtis dissimilarity, grouping plots according to similarity in vegetation composition.

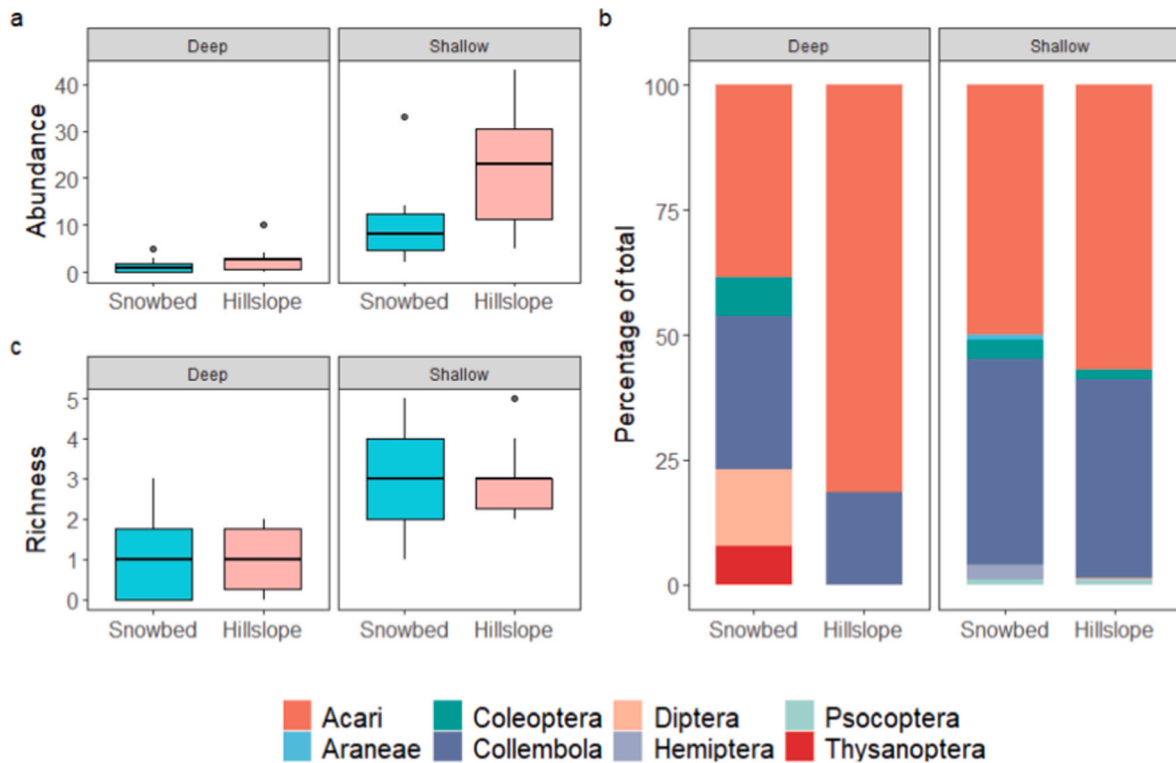
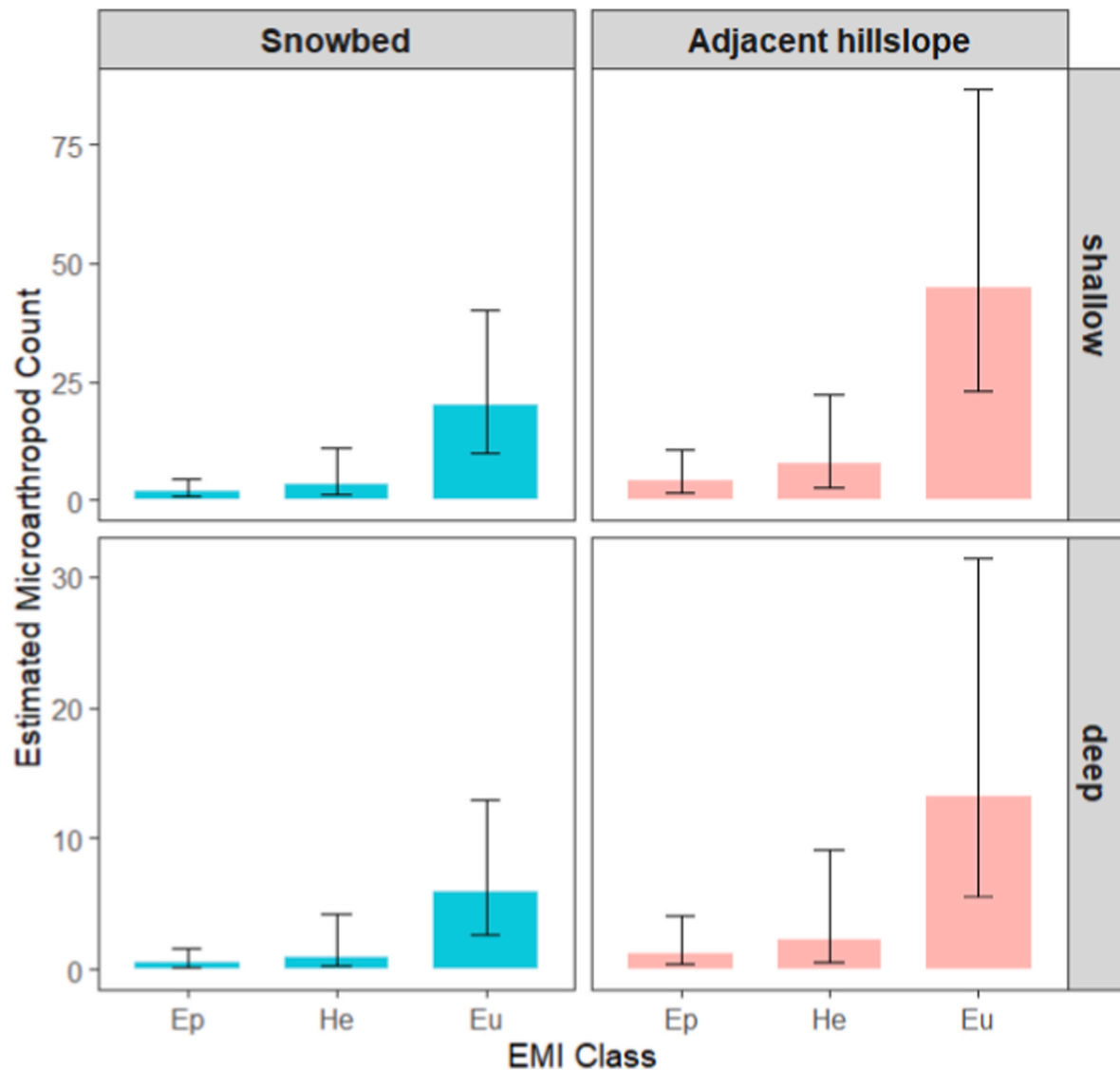


Fig. 3. Summary plots for soil arthropods collected from two contrasting montane habitats (late snowbed and adjacent arctic-alpine heath) and two soil depths (shallow: 0-75 mm; deep: 75-150 mm) located in the Cairngorms National Park, Scotland, UK. (a) total abundance of arthropods; (b) total abundance of taxa as a percentage of all specimens collected in each habitat and depth); and (c) richness of different arthropod taxa.

was negatively associated with soil moisture, with higher moisture levels corresponding to lower abundance ( $F(1,18) = 6.04, p = 0.024$ ). In contrast, neither group of soil adapted Collembola (EMI 20:  $F(1,18) = 0.19, p = 0.665$ ; EMI 10:  $F(1,18) = 0.30, p = 0.590$ ) showed significant

relationships with moisture.

Non-metric multidimensional scaling (NMDS) revealed little separation in arthropod community composition between snowbed and adjacent hillslope habitats (stress = 0.1717), with substantial overlap in



**Fig. 4.** Model-estimated soil arthropod abundance ( $\pm 95\%$  CI) for three Ecomorphological Index (EMI) classes (Epedaphic (Ep), Hemiedaphic (He), and Euedaphic (Eu)) collected from two contrasting montane habitats (late snowbed and adjacent arctic-alpine heath) and two soil depths (shallow: 0–75 mm; deep: 75–150 mm) located in the Cairngorms National Park, Scotland. Estimates are derived from a negative binomial GLM and adjusted for all factors.

ordination space (Fig. 7a). PERMANOVA indicated no significant difference in community structure between habitats ( $F(1,18) = 0.465$ ,  $p = 0.803$ ), which was confirmed by hierarchical clustering (Fig. 7b) which showed no distinct clusters according to habitat type. Furthermore, a test for homogeneity of multivariate dispersions (PERMDISP) showed no significant difference in within-group variability ( $F(1,18) = 1.284$ ,  $p = 0.269$ ). SIMPER analysis identified several taxa contributing to dissimilarity, particularly highly euedaphic Acari and slightly euedaphic Collembola, but none showed statistically significant contributions. Indicator species analysis also failed to detect any taxa significantly associated with either habitat.

#### 4. Discussion

Given that soil arthropods develop complex relationships with specific plant species [34,44,45], ground cover thickness [46], temperature [46], soil moisture [47–49] and nitrogen deposition [46], it seems likely that communities associated with snowbeds may be at particular risk to climate change, where increased temperature [50,51], nitrogen [52], coupled with reduced snow cover and associated soil moisture are likely to have severe impacts on the plant assemblage. To understand the likely

risk that environmental change poses to snowbed soil arthropod communities, it is first important to understand how these habitats and associated arthropod communities differ.

In support of H1, snowbeds in our study supported unique floral assemblages dominated by graminoids typical of nutrient-poor, wet acidic soils, such as *Trichophorum caespitosum* and *Nardus stricta*. These habitats were buffered from extremes of temperature and freeze–thaw cycles by winter snow and exhibited higher soil moisture compared to adjacent hillslopes. Despite these differences, and contrary to H2, overall arthropod community composition did not differ significantly between habitats, as confirmed by NMDS and PERMANOVA. This suggests strong functional convergence and high mobility among soil fauna, consistent with Seeber et al. [34], who reported similar patterns across snowbed gradients in the European Alps. However, functional group-level responses revealed important ecological distinctions, underscoring the value of trait-based approaches in detecting subtle habitat-driven patterns that whole-community analyses may overlook [53]. Differences in vegetation structure and soil moisture regimes between habitats likely mediate the observed functional responses. Snowbeds were characterised by persistently high soil moisture under graminoid-dominated vegetation, whereas adjacent hillslopes supported

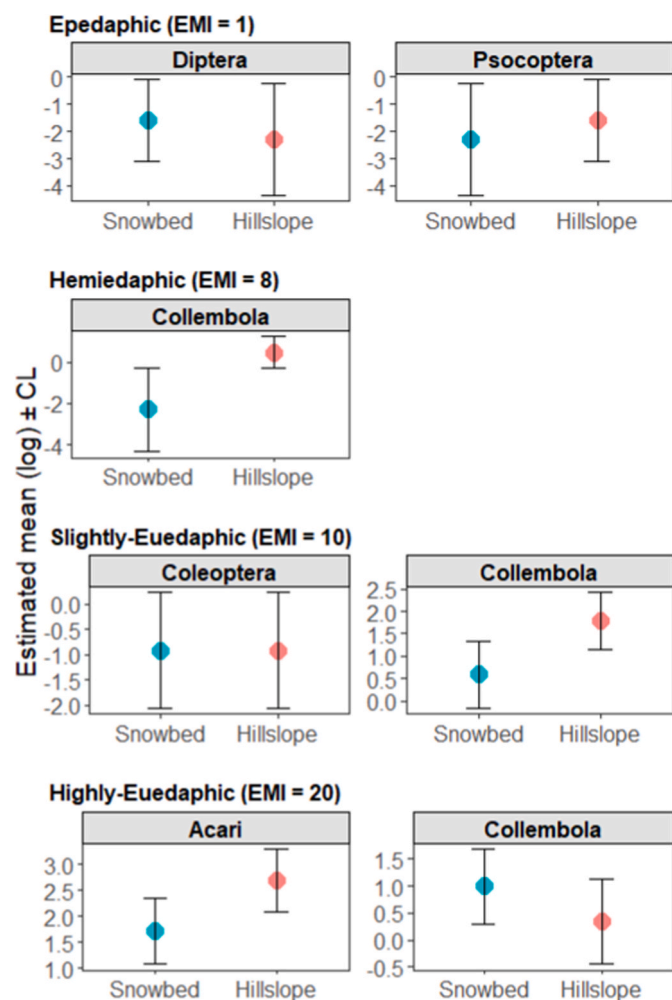


Fig. 5. Estimated marginal means (EMMs) for abundance of 7 arthropod functional groups collected from two contrasting montane habitats (late snowbed and adjacent arctic-alpine heath hillslope) in the Cairngorms National Park, Scotland. EMMs were derived from a negative binomial generalized linear model. Points represent log-scale EMMs for each taxon, with vertical bars indicating 95% confidence limits. Plots arranged by eco-morphological index (EMI) value, with each descending row representing increasing adaptations to living in soil.

structurally complex bryophyte mats over comparatively drier soils. Bryophytes modify near-surface microclimatic conditions and contribute slowly decomposing litter that influences organic matter accumulation and microbial processing [54–56]. In contrast, high and sustained soil saturation in snowbeds may constrain oxygen availability and alter decomposition dynamics. Such differences in substrate structure, aeration, and resource quality provide plausible mechanisms by which habitat-specific vegetation and moisture regimes filter arthropod functional groups.

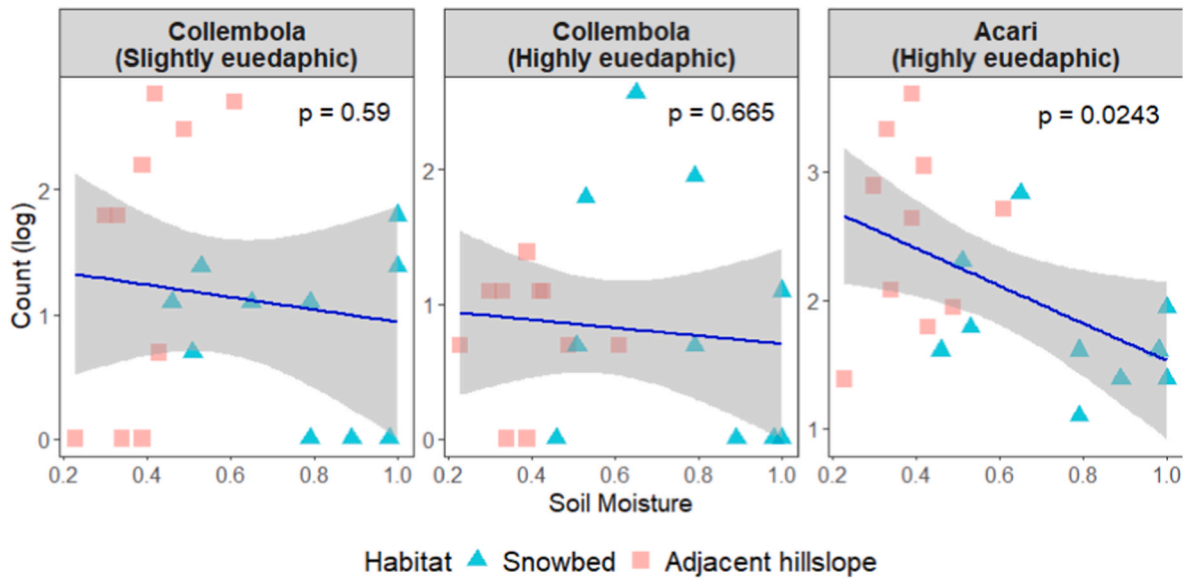
Euedaphic forms (organisms adapted to live entirely within the soil) — particularly Acari and Collembola — dominated both habitats, accounting for 89% of snowbed and 97% of hillslope specimens, consistent with patterns in other soil-dwelling communities [57]. The top four taxa (Acari, Collembola, Coleoptera, Diptera) mirrored observations from Australian alpine snowbeds [58]. Notably, highly euedaphic Acari, slightly euedaphic Collembola, and hemiedaphic Collembola (adapted to live in the lower litter and upper soil layers) were significantly more abundant in adjacent hillslope soils than snowbeds. These patterns likely reflect environmental filtering, where habitat conditions selectively favour taxa with specific traits, specifically in relation to microclimatic and edaphic conditions, such as lower soil moisture [48,59] and specific vegetation assemblages. Acari abundance declined with increasing soil

moisture, consistent with González-Macé & Scheu [60] who showed that excessive saturation can cause oxygen deprivation and physical stress. While mites generally prefer moist soils, waterlogged conditions may be detrimental. Furthermore species of Collembola and Oribatid mites (a major order of the Acari) are known to have specialist habitat, plant or soil moisture specific needs [34,45,61]. For *Racomitrium* moss-sedge heaths, broadly similar to our adjacent hillslope, Mitchell et al. [62] found clear relationships between Oribatid mites and Collembola and plant community composition, which may in part explain our greater abundances of ‘moss-mites’ [44,45] and less-highly adapted Collembola on the adjacent hillslope in similar plant communities. Additionally, Seeber et al. [34] found soil porosity and soil organic matter mostly drove arthropod community composition in alpine snowbeds, but concluded overall that invertebrate assemblages are similar across a range of snowbed habitats, and that mobility of arthropods provided challenges for interpretation.

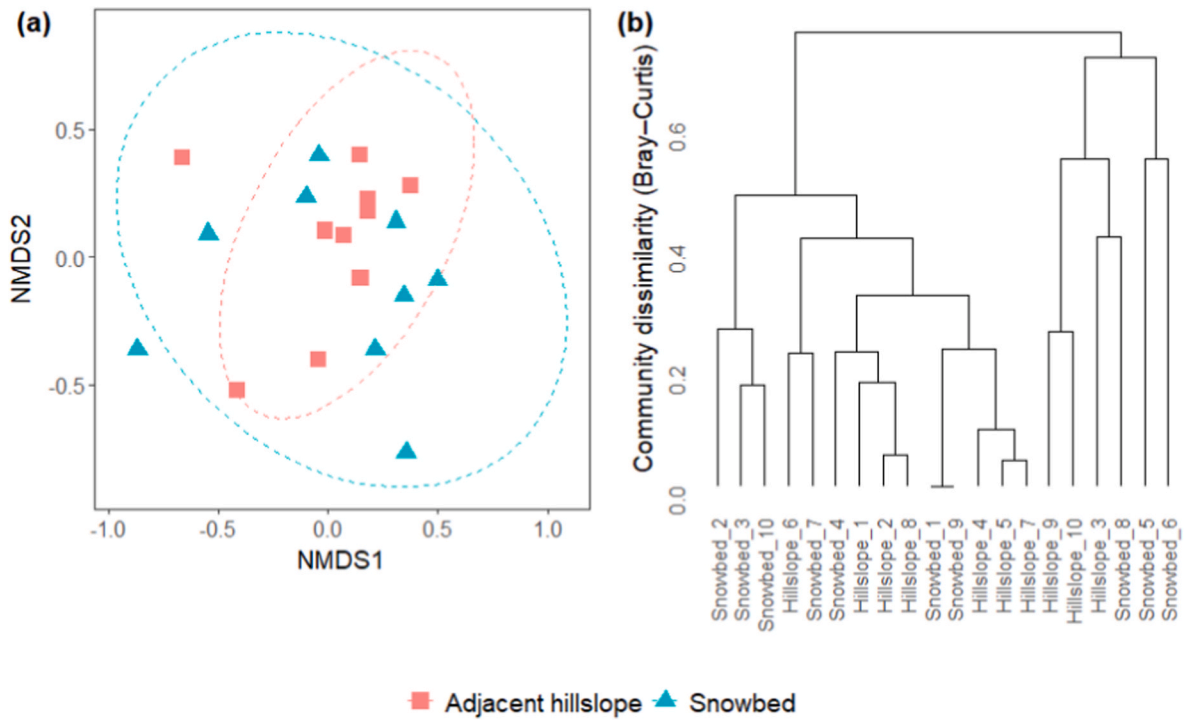
Soil depth, reflecting accumulated organic matter at the surface layer [63], exerted the strongest influence on arthropod assemblages, with shallow layers (0–75 mm) supporting nearly 90% of individuals and significantly higher richness and diversity compared to deeper soils. These patterns align with expectations that organic matter, aeration, and root interactions are concentrated near the surface, creating favourable conditions for soil fauna [27,64,65]. Depth-related filtering likely interacts with habitat conditions: shallow hillslope soils combined lower moisture with higher plant-derived inputs from the relatively thick bryophyte litter layer, thus amplifying abundance differences relative to snowbeds. This vertical stratification emphasizes that arthropod responses to climate change will depend not only on horizontal habitat shifts but also on changes in soil profile characteristics [66,67].

While the morpho-functional approach adopted here allowed us to detect ecologically meaningful trait variation, it does not provide species-level resolution of potential cryophilic or relict taxa that may be restricted to long-lasting snowbeds. Consequently, we cannot determine whether specialist cold-adapted species persist within these micro-refugia or whether generalist taxa are increasingly colonising as snow duration declines. Detecting such fine-scale compositional turnover would require detailed taxonomic or molecular analyses and represents an important direction for future research. Soil moisture was prioritised as a focal variable because it is directly mediated by snow duration and represents a key physiological constraint on soil arthropods. Although soil organic matter and nutrient content may also differ between habitats, these were not directly quantified in this study and represent important avenues for future research.

In conclusion, H1 was clearly supported, with distinct plant community differences emerging between snowbeds and adjacent hillslopes. In contrast, H2 was only partially supported: while whole-community arthropod composition did not differ significantly between habitats, functional group patterns and trait-specific responses revealed meaningful ecological divergence. These findings indicate that although broad community identity is conserved, environmental filtering and habitat-specific traits structure arthropod assemblages at finer scales. Recognising these functional distinctions is essential when considering how soil communities may respond to future reductions in snow cover, because shifts in functional traits may precede detectable species turnover and directly influence ecosystem processes such as decomposition and nutrient cycling. Trait-based approaches provide a process-oriented framework for long-term monitoring because functional traits are directly linked to soil processes such as decomposition, nutrient mineralisation and microhabitat use. Although species-level identification can reveal patterns of specialist persistence or turnover, trait-based metrics may respond more directly to environmental filtering and ecosystem functioning. In systems where subtle microclimatic change is expected to alter edaphic conditions gradually, shifts in functional composition may therefore provide early and ecologically meaningful indicators of change.



**Fig. 6.** Relationship of soil arthropod abundance (log +1) and soil moisture for three functional taxa groups (highly euedaphic (Ecomorphological Index (EMI) = 20) Acari and Collembola (EMI = 20), and slightly euedaphic Collembola (EMI = 10)) collected from two montane habitats (snowbed, adjacent hillslope) in the Cairngorms National Park, Scotland.



**Fig. 7.** a) NMDS ordination of soil arthropod functional community, collected from two contrasting montane habitats (late snowbed and adjacent arctic-alpine heath) in the Cairngorms National Park, Scotland. b) Hierarchical clustering dendrogram based on Bray-Curtis dissimilarity, grouping plots according to similarity in arthropod composition.

**CRedit authorship contribution statement**

**Christopher Andrews:** Writing – review & editing, Writing – original draft, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Elli Groner:** Writing – review & editing, Investigation, Conceptualization. **Sofia Galeano:** Investigation. **Maor Tikochinsky:** Investigation. **Jan Dick:** Writing – review & editing, Supervision, Investigation.

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## Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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## Appendix A. Supplementary data

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