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Soil resources vs. physicochemical soil properties as drivers of abundance and diversity of low Arctic soil mesofauna communities

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Abstract

Soil mesofauna play pertinent roles in soil processes. For example, microarthropods strongly influence rates of microbial decomposition. The relationship between mesofauna and their environment are understudied in low Arctic ecosystems compared to other regions. A more detailed grasp of these soil assemblages is necessary for understanding the current functioning of these ecosystems. We characterized the soil mesofauna community across different low Arctic habitats to determine which soil properties commonly correlated with soil fauna would best explain their distribution, abundance, and diversity. Samples were taken near five different lakes in northern Finland, in both alpine meadows and sub-alpine birch forests, across a span of available soil habitats (measured by pH, salinity, organic and nitrogen content, soil moisture). Total abundance of the mesofauna community was influenced by a combination of soil factors, but most individual taxa, as well as measures of diversity were best explained by models of one or two influential soil parameters. Poduromorpha springtails and Oribatid mites were best modeled by measures of resource availability, although only Oribatids were significantly, positively related to these resources. All mites and Entomobryomorphid springtails were positively influenced by physicochemical soil moisture and/or salinity. Salinity, in particular, had a strong influence on overall mesofauna community composition. Our results provide further insight into soil fauna assemblages in Northern Finland and further, more extensive research would contribute to a more comprehensive foundation. This will allow for better monitoring of community changes and responses in the face of climate change in the low Arctic.

Keywords Arctic Finland · Soil biota · Collembola · Acari · Soil microarthropods · Fennoscandia

Introduction

Soil biota, most especially soil microbes, are responsible for much of the nutrient cycling of terrestrial ecosystems. As plant tissues senesce, these organisms begin to decompose the plant litter, thus freeing up a multitude of nutrients that foster soil health, which in turn supports plant health and subsequently ecosystem health. The immobilization of soil organic matter, or SOM, is directly controlled by the microbial communities in response to their abiotic environment

Luxton 1982; Seastedt 1984; Coleman et al. 2017). Despite being grazers of microbial communities, we see increased rates of decomposition when they are present, as they disseminate and alter the microbial community, stimulate their activity, mechanically break down litter material, and directly consume litter as detritivores (e.g., Hättenschwiler and Gasser 2005; Kampichler and Bruckner 2009; Peguero et al. 2019; McCary and Schmitz 2021). As such, their fecal matter is an essential and foundational component of soil aggregates and humus (Culliney 2013). Also, it is known that soil mesofauna can often be used as indicator species (Linden et al. 1994; Coleman et al. 2017; Menta and Remelli 2020). For example, oribatid mite community size is positively correlated with the availability of nutrients, and their relative absence or reduced population size can be reflec-

tions of changes in environmental conditions, such as soil

conditions, vegetation types and availability, and permafrost

(Bradford et al. 2017). However, arthropods play a pertinent role in the decomposition process (sensu Petersen and



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dynamics (Nielsen et al. 2012; Markkula et al. 2018). To gain better insights into the aboveground patterns seen in an ecosystem, it is extremely pertinent to have thorough understandings of soil biota communities present.

However, Arctic ecosystems remain relatively understudied regarding the relationships between arthropods and their environment (sensu Ruess et al. 1999; Wirta et al. 2016). Such soils are considered pivotal for climate change research, given their susceptibility to rapid change with small fluctuations in climate (Parker et al. 2022). This is due in part to the large carbon pools found in these soils, caused by the slowed decomposition of SOM (Robinson et al. 1995; Aerts 2006; Klimek et al. 2020), which as established, is controlled by the soil biota communities. Research in nearby subarctic ecosystems show that simulated climate change can influence springtail (Krab et al. 2015), mite (Alatalo et al. 2017), and overall microarthropod (Hågvar and Klanderud 2009) community composition, although this is not always the case (Krab et al. 2014). Such studies show that altered moisture and temperature could influence the mesofauna community directly or indirectly through alterations to the soil habitat. Characteristics of the soil, like salinity, pH, soil water content (SWC), and nutrient content, generally play a role in community composition belowground (e.g., Danks 1992; van Straalen and Verhoef 1997; Chikoski et al. 2006; Pan et al. 2018). Both Arctic and subarctic mesofauna communities also differ among vegetation communities, largely through the vegetative influence on soil organic matter and nutrients (Coulson et al. 2003; Bokhorst et al. 2014, 2017, 2018; Hansen et al. 2016; Parker et al. 2022). A detailed grasp of the relationships between soil properties and the mesofauna community can be beneficial for monitoring changes to the functioning of Arctic, including low Arctic ecosystems, especially with the few indicator species available in this region (Markkula et al. 2018) and the potential lack of functional species redundancy in polar regions (Wall and Virginia 1999; Høye and Sikes 2013). In this project, we aim to describe the community composition of soil mesofauna and their relationships with soil physiochemical properties, which are present in a low Arctic area of northern Finland.

Soil assemblages in low Arctic regions are dominated by nematodes and arthropods, particularly Acari (mites), Collembola (springtails), and insects (Danks 1992; Heggen 2010; Wirta et al. 2016; Gillespie et al. 2020). A keystone mesofauna species is enchytraeid worms which are responsible for the tunneling and subsequent formation of soil aggregates (Aerts 2006; Kaukonen et al. 2013; Briones et al. 2014; Patrício Silva et al. 2014). In Scandinavia, most studies of the soil mesofauna focus on regions in subarctic, northern Sweden, or boreal Norway, where springtail communities in particular correspond to measures of soil resource availability (N

and P) (Krab et al. 2010, 2013a; Bokhorst et al. 2017, 2018), and microclimate influences both springtail and mite communities (Huhta and Hänninen 2001; Krab et al. 2010; Makkonen et al. 2011; Alatalo et al. 2017). In more northern low Arctic regions of Finland, however, prior soil arthropod assemblage research was concentrated in central and southern regions during the 1960s-1980s with limited continued research until recently (Huhta et al. 2010). Therefore, relatively less is known about the soil mesofauna community in more northerly, colder low Arctic areas of the Scandinavian Mountains in NW Finland compared to studies on vegetation and microbial communities (Virtanen et al. 1997; Männistö et al. 2009; Mikola et al. 2014; Boulanger-Lapointe et al. 2017; Viitamäki et al. 2022). It is important that we study this unique region since it is under-surveyed both historically and currently. This low Arctic region houses differing ecosystem types, including sub-alpine forests to high- and low-alpine meadows. The few studies of soil mesofauna in this area show that in the alpine meadows, microarthropod communities differ across sites and are influenced by grazing activity, disturbance, nutrient availability, and SWC (Virtanen et al. 2008; Francini et al. 2014; Mikola et al. 2014). Prostigmatid mite communities also differ across habitat types from the high and low-alpine meadows to sub-alpine forests (Zacharda and Kučera 2010). Beyond these studies focusing on individual taxa or habitat types, it is unclear how the entire mesofauna community differs in relation to soil properties across multiple low Arctic habitat types, both alpine meadows and sub-alpine birch forests, in this region of NW Lapland.

In order to establish the relationships between arthropods and their surrounding environments in Kilpisjärvi, Finland, we analyzed how soil physiochemical properties relate to soil mesofauna (I) abundance, (II) diversity, and (III) community composition, as is described in numerous other ecosystems (e.g., Nielsen et al. 2012; Pan et al. 2018; Menta and Remelli 2020). We focused measurements on the soil properties that are known to influence the soil community across ecosystems, specifically SWC, nitrogen (N) content, pH, salinity, and SOM (following e.g., Booth and Usher 1984; Xu et al. 2012; Ball et al. 2022; Robinson et al. 2022), as they vary naturally in the landscape through heterogeneity created by, for example, different vegetation communities and physical gradients. Our goal was to work across a heterogeneity of these soil properties to determine which of these commonly related edaphic factors would most strongly relate to the soil community in this understudied region of low Arctic Scandinavia. Simply, we hypothesized that the colder annual temperatures and shorter growing season in this northern area of the Scandinavian Mountains would make the soil mesofauna community particularly sensitive



to resource availability, such as SOM, soil N, and SWC, rather than chemical characteristics, such as pH and salinity.

Methods

Site description

This study was conducted in the Kilpisjärvi region of northern Finland (69.0443° N, 20.8033° E) near the border with Norway and Sweden in the Käsivarsi Wilderness Area (Fig. 1). Kilpisjärvi is categorized as a low Arctic ecosystem, characterized by an average temperature of – 2.6 °C and 422 mm of precipitation annually (Mikola et al. 2014). This region experiences a unique combination of climate conditions, being 400 m above sea level yet only 50 km from the coast, leading to the convergence of the Foehn wind from the Scandinavian Alps, continental pressure systems, and the North Atlantic Current. This gives Kilpisjärvi one of the lowest average temperatures in Europe, but with a low degree of continentality (Kauhanen 2013; Lépy and Pasanen

Fig. 1 Map showing the locations of the soils sampled in the Kilpisjärvi region of the 3-country border of Finland, Norway, and Sweden

2017). It has a growing period of only approximately 100 days, shorter than other northern Scandinavian ecosystems, yet supports a high species richness and abundance of vegetation, including shrubs and sedges like *Bistorta vivipara*, *Vaccinium myrtillus*, and *Trollius europaeus*, and wildlife (sensu Olofsson and Oksanen 2005; Männistö et al. 2009; Mikola et al. 2014; Boulanger-Lapointe et al. 2017). The lower elevation areas are dominated by birch forest, with dwarf birch and sedge-dominated communities at higher elevations (sensu Virtanen et al. 1997; Mikola et al. 2014).

Data collection

Samples were taken along transects of increasing distance away from five different bodies of water around the Kilpis-järvi region: Kilpisjärvi, Tsahkaljärvi, Saanajärvi, Kuohkimajärvi, and Leenanlampi. These lake sites cover varying elevations in both the sub-alpine birch forests into the higher elevation alpine meadows, thus representing different vegetative communities that could potentially develop different soil habitats (Table 1). Increasing distance from the lake



Table 1 Description of each of the lake sites from which soil samples were taken, including elevation, pH, electrical conductivity (EC), loss on ignition (LOI), nitrogen content (N), and soil water content (SWC)

| | Kilpisjärvi | Saanajärvi | Leenanlampi | Kuohkimajärvi | Tsahkaljärvi |
|---------------------------------|----------------------|-----------------------|-----------------------|----------------------|-----------------------|
| Elevation (m) | 485.5 | 697.0 | 648.8 | 488.6 | 559.7 |
| pН | 5.3 ± 0.1^{a} | 3.8 ± 0.2^{b} | 4.4 ± 0.3^{ab} | 4.1 ± 0.2^{b} | 4.2 ± 0.5^{b} |
| EC (μ S cm ⁻¹) | 680.1 ± 188.5 | 214.6 ± 44.9 | 179.6 ± 59.5 | 162.7 ± 41.0 | 581.0 ± 364.0 |
| LOI (%) | 75.0 ± 13.5 | 62.0 ± 18.7 | 31.0 ± 15.3 | 36.0 ± 15.3 | 85.7 ± 1.5 |
| Nitrogen (%) | 1.9 ± 0.4^{ab} | 1.8 ± 0.4^{ab} | 0.5 ± 0.21^{a} | 0.6 ± 0.2^{a} | 2.0 ± 0.1^{b} |
| SWC (% g g ⁻¹) | 403.6 ± 71.0^{a} | 213.8 ± 76.6^{ab} | 134.4 ± 71.6^{ab} | 100.9 ± 37.1^{b} | 180.7 ± 62.7^{ab} |

Values are means ± standard error. For soil parameters that significantly differed among lake sites, letters depict the results of a post hoc Tukey HSD test, where lakes with the same letter do not significantly differ from each other



allowed for exploration of differing soil habitats that would arise from the gradient of moisture regimes and vegetation communities within these ecosystem types. Increasing distances from standing water encompasses differing diel/seasonal cycles in soil saturation and therefore soil temperature and plant communities. This also results in a heterogeneity of SOM, pH, and nutrient content correlated to those. Thus, distance from lake edge provides a framework to capture within-site heterogeneity in instantaneous soil moisture, SOM, pH, salinity, and nutrient content that would shift beneath the changing vegetation and moisture regime. The length of the transects varied at each lake to capture the visible gradient in soil saturation and vegetation, ranging from 30 to 200 m, with samples taken at 3 or 4 intervals (depending on length). One transect was conducted per lake, with each lake serving as a replicate site. These samples were taken in June 2019 using a plastic trowel to remove soil beneath the vegetation and litter to approximately 10 cm of depth and placed into a sterile Whirlpak bag. The use of surface soils therefore incorporated largely the organic soil horizons high in organic content, with limited incorporation of deeper, mineral soil layers (Table 1). Samples were then brought back to the lab at the Kilpisjärvi Biological Station.

Approximately 50 g of fresh soil were weighed and placed on modified Tullgren funnels for heat extraction of mesofauna. The modified funnels were made from the sides of aluminum beverage cans fitted with a piece of nylon 1.5-mm mesh screen between the can and an underlying funnel (Ball et al. 2022). A 20-mL plastic vial containing 70% ethanol was snapped onto the funnel stem and placed in a rack. Incandescent C7 clear holiday lights were strung across the top, with one bulb per aluminum can, on a dimmer switch that was gradually increased to full intensity to gradually increase the heat gradient. After 5 d, the vials containing the extracted mesofauna in ethanol were capped. The dry mass of the soil was recorded after drying for 5 d under the funnels and used to calculate gravimetric SWC.

Soil and preserved mesofauna samples were then shipped to Arizona State University. Mesofauna were identified and enumerated using a dissecting microscope at 45× magnification, and expressed as abundance per gram of dry soil. Identification was done to the lowest possible taxonomic order, which was to the order level for most taxa with the exception of Acari (suborder). Richness was measured as the number of taxa in each sample. Shannon diversity and evenness were calculated for each sample.

We also measured electrical conductivity (hereafter EC), a proxy for salinity, using a diluted solution of deionized water to soil (5:1 ratio) on an Orion 4-star pH/EC meter. To find pH, we created a solution of deionized water and soil (2:1 ratio) which steeped for 3 h. A 0.5-g subsample was placed in a muffle furnace set to 550 °C for 3 h, then reweighed to determine the mass loss on ignition (hereafter

LOI), a proxy for SOM. To measure %N, dried subsamples of soil were ground using a Spex ball mill in order to make a homogeneous powder and measured with in a Perkin-Elmer Elemental Analyzer (Ball et al. 2022).

Data analysis

All statistical analyses were conducted using R (version 4.0.2, The R Foundation). First, we tested whether lake sites or distance from the lake edge categorically influence mesofauna communities or soil properties (which would suggest the different lake sites or distance from lake edge represent distinctly different soil habitats rather than comprising a heterogeneity of soil properties). We performed a two-way Analysis of Covariance (ANCOVA) to test for the influence of site (discrete variable) and the distance to the lake edge (continuous covariate), as well as their interaction, on soil community (diversity and abundance, including individual taxa) and physicochemical properties. Total abundance was log transformed to meet the assumptions of normality and heteroscedasticity. Where there was a significant difference among lake sites, a post hoc Tukey HSD test was conducted using package agricolae.

To determine which soil habitat parameters best explained the soil mesofauna community, we then used linear effects mixed models to test for the influence of soil physicochemical parameters on the measures of soil community, while accounting for lake site as a random effect (package *lmerTest*). Given the very different magnitudes of scale upon which these soil parameters are measured, they were first scaled using the "transform" function's "scale" argument. The initial model tested for an additive effect of SWC+LOI+EC+pH+%N. Model selection was performed using AIC backward elimination using the "step" function to identify which soil parameters were included in the best-fit model to describe each of the individual measures of soil community abundance and diversity.

Finally, a canonical correspondence analysis (CCA; function "cca" in package *vegan*) was run to explore the role of soil physicochemical properties in structuring arthropod community composition across the samples.

Results

ANCOVAs revealed no significant influence of lake site or distance from the lake on soil arthropod abundance, richness, Shannon diversity, or evenness, barring one exception: Mesostigmata mites were more abundant at Kilpisjärvi than Leenanlampi (P = 0.026; Table 2). Soil habitat characteristics did vary across the lake sites, although not in a uniform manner (Table 1), representing the span of soil habitats captured in the study. Across the sites, SWC, %N, and



Table 2 Average abundance and diversity of soil microarthropods, as well as the abundance of dominant taxa, across the five lake sites

| | Kilpisjärvi | Saanajärvi | Leenanlampi | Kuohkimajärvi | Tsahkaljärvi |
|-------------------|---------------------|----------------------|---------------------|----------------------|----------------------|
| Total abundance | 12.55 ± 3.73 | 10.76±7.25 | 5.27 ± 2.63 | 4.87 ± 2.54 | 8.87 ± 2.69 |
| Richness | 5.50 ± 0.65 | 3.67 ± 0.88 | 5.75 ± 0.75 | 5.33 ± 0.34 | 6.00 ± 0.00 |
| Shannon diversity | 1.21 ± 0.07 | 0.61 ± 0.19 | 1.24 ± 0.11 | 1.03 ± 0.16 | 1.21 ± 0.15 |
| Evenness | 0.73 ± 0.08 | 0.48 ± 0.08 | 0.72 ± 0.04 | 0.62 ± 0.08 | 0.67 ± 0.08 |
| Oribatida | 7.64 ± 3.11 | 7.27 ± 4.43 | 2.74 ± 1.30 | 3.49 ± 2.02 | 3.06 ± 1.25 |
| Prostigmata | 0.65 ± 0.18 | 0.55 ± 0.30 | 0.24 ± 0.13 | 0.10 ± 0.06 | 0.21 ± 0.02 |
| Mesostigmata | 1.93 ± 0.34^{a} | 0.40 ± 0.23^{ab} | 0.30 ± 0.11^{b} | 0.66 ± 0.36^{ab} | 0.82 ± 0.59^{ab} |
| Poduromorpha | 1.23 ± 0.21 | 2.52 ± 2.40 | 0.84 ± 0.53 | 0.32 ± 0.19 | 3.49 ± 0.90 |
| Entomobryomorpha | 0.83 ± 0.3 | 0.00 ± 0.00 | 0.55 ± 0.54 | 0.27 ± 0.15 | 1.11 ± 0.90 |

Abundances are given in # of individuals per g dry soil. Values are means±standard error. Only Mesostigmatid mites significantly differed among lake sites, and letters depict the results of a post hoc Tukey HSD test where lakes with the same letter do not differ from each other

Table 3 $\,P$ values from the linear mixed-effects models exploring which soil parameters are most influential for soil communities, with Lake as a random effect

| | SWC | LOI | EC | pН | %N |
|-------------------|---------|-------|---------|-------|-------|
| Total abundance | 0.882 | 0.012 | 0.008 | 0.326 | 0.007 |
| Richness | _ | 0.008 | _ | _ | 0.017 |
| Shannon diversity | _ | _ | _ | 0.335 | _ |
| Evenness | _ | _ | _ | _ | 0.301 |
| Oribatida | 0.669 | 0.009 | 0.009 | 0.154 | 0.007 |
| Prostigmata | < 0.001 | _ | _ | _ | _ |
| Mesostigmata | _ | _ | < 0.001 | _ | _ |
| Poduromorpha | _ | 0.127 | _ | _ | 0.558 |
| Entomobryomorpha | _ | _ | < 0.001 | _ | _ |
| | | | | | |

AIC backward model selection was used to determine the model that best fits each metric of soil mesofauna abundance and diversity, from the initial additive effect of each of the measured soil parameters. *P* values are shown only for the factors that were included in the best-fit model. Full statistical results of the AIC and best-fit models can be found in Online Resources 1 & 2

LOI were all positively correlated with each other. EC also increased with % LOI and %N in the soils (P < 0.05 for all three correlations).

Across the sites, the total abundance of all mesofauna was best explained by a combination of all of the measured soil parameters, of which LOI, %N, and EC had a significantly positive effect (Table 3; Fig. 2). Oribatid mites responded the same as total mesofauna abundance, as they tended to be the most dominant taxa present. The other dominant taxa abundant across all samples tended to be best modeled by individual parameters rather than a combination. Prostigmatid mites were best modeled by, and significantly increased by SWC, while both Mesostigmatid mites and Entomobryomorphid springtails were best modeled by a significantly positive relationship with EC. Poduromorphid springtails were best modeled by a combination of LOI and

%N, although neither of them had a significant influence on their abundance.

Shannon diversity and evenness were not strongly related to soil chemistry and are both best modeled by single soil parameters (pH and %N, respectively) that did not have a significant linear relationship (Table 3). The only measure of diversity to be strongly influenced by soil habitat characteristics was richness, which was best modeled by a significant influence of LOI and %N, although the strength of those statistically significant relationships are weak.

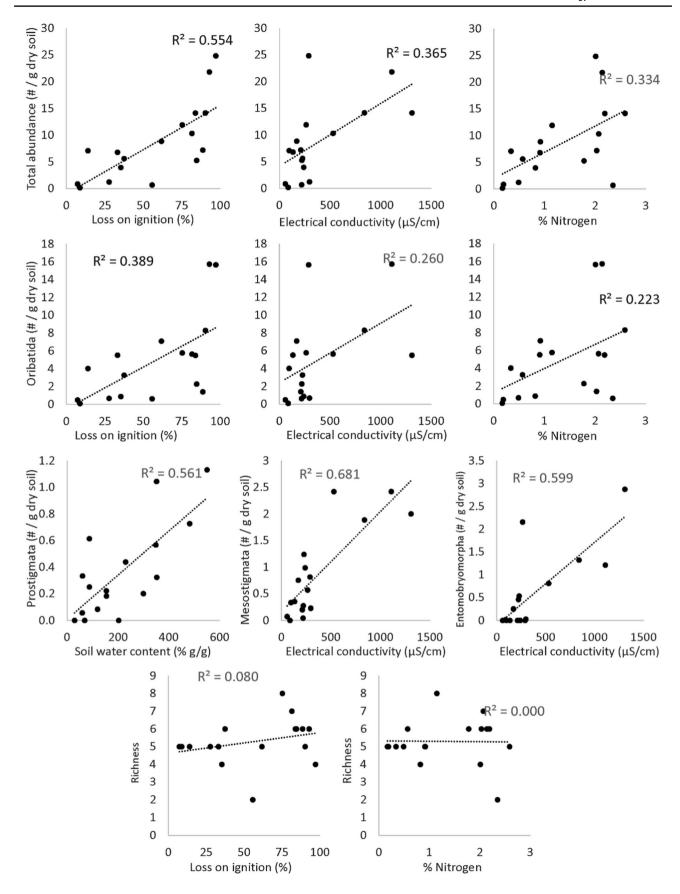
A CCA showed that LOI, pH, %N, and SWC only had a weak effect on the mesofauna community composition (Fig. 3). However, EC had a stronger influence associated with higher abundance of Entomobryomorpha. Similarly, a few taxa were associated with unique arthropod communities. The samples containing Coleoptera larvae clustered to the right of the CCA. Enchytraeids and Diptera also were associated with unique communities, but these taxa were not strongly associated with the soil properties we measured. Notably, samples did not cluster according to site or distance from the lake edge.

Discussion

We sought to determine which of the commonly associated soil parameters best accounted for mesofauna abundance, diversity, and community composition in a low Arctic region of northwestern Finland. Because distance to lake shore and lake site did not have a strong influence on the soil mesofauna community, at least at the Order level, differences among the soil samples are apparently not the result of distinctly different soil habitats at each lake site, allowing us to interpret our results in terms of heterogeneity of soil habitats available across these low Arctic sites (Hansen et al. 2016).



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√Fig. 2 Linear regressions for each of the soil parameters determined to have a statistically significant influence for each measure of mesofauna community abundance and diversity. Only the soil parameters determined to be included in the best-fit model that yielded a significant P value (<0.05; Table 3) are included</p>

Oribatid mite and total mesofauna abundance were best explained by a model including all of the soil parameters measured, but significantly influenced in particular by LOI, EC, and %N. Therefore, the mesofauna community is influenced by substrate availability, but also substrate quality and mineral nutrient availability (both encompassed in total soil %N). This supports our hypothesis that resource availability would be most influential on the soil community. However, other taxa, as well as the diversity and evenness of these communities, were more simply explained by one or two soil parameters rather than a combination. It has been found that soil mites, in addition to other soil invertebrates in Arctic regions, tend to be more affected by variables pertaining to water availability (Hodkinson et al. 1998; Hansen et al. 2016), and in general, soil mites have been found to be more sensitive to changes in SWC than collembola (Lindberg et al. 2002; Tsiafouli et al. 2005). This was true for one suborder of mites in our study, the Prostigmatids, and to an extent also the Oribatids, but not Mesostigmatid mites. Instead, EC was most influential for Mesostigmatid mites, as well as Entomobryomorpha springtails. This suggests that these taxa prefer slightly saltier soils, perhaps reflecting either a greater concentration of nutrient ions or a relative lack of liquid water concentrating those ions, while the other taxa were resilient to relatively narrow changes in EC. Indeed, the soils highest in EC also had among the highest %N content of which much could be present as ions.

Poduromorpha springtail abundance was best accounted for by a model of LOI and %N, reflecting an importance of substrate and nutrient availability rather than the physical environment. Other northern Scandinavian studies also showed a particular sensitivity of Collembola to basal resources (Krab et al. 2014; Bokhorst et al. 2017, 2018), though interestingly neither LOI nor %N had a directly significant relationship with Poduromorpha, despite being the best-fit model, or Entomobryomorpha abundance. Instead, Oribatid mites were more directly influenced by resources than the Collembola. The importance of LOI to some taxa is supported by other studies (Bokhorst et al. 2014; Robinson et al. 2022) that found SOM was responsible for the spatial heterogeneity of key soil properties and therefore the soil biota communities. Therefore, while our study reflects an importance of resources on the total mesofauna community, it also demonstrates that the soil chemical environment is more influential for predatory mites and some springtails, counter to our hypothesis. For predatory taxa, such as Mesostigmatid and Prostigmatid mites, a direct relationship with basal soil resources (LOI, %N) may not be apparent because it would only be indirectly relevant through its influence on prey abundance, resulting in less distinct associations with soil properties (Čoja and Bruckner 2003; Nielsen et al. 2010; Mitchell et al. 2016). No organism had a significant relationship to pH, which may infer that pH does not dictate the presence of the organisms in focus, although further experimentation should be done to corroborate these findings.

Like total abundance, order-level richness was significantly related to LOI and %N, again reflecting this importance of resources. However, Shannon diversity and evenness did not share any statistically significant relationships with the measured soil parameters, signaling that these soil properties did not have a direct effect on the evenness or diversity of the mesofauna community at large. The models that best explained these diversity metrics were individually either pH or %N (respectively), although they did not have a significant linear relationship to diversity. There are several possible explanations for these findings. For one, these communities are well adapted to the adverse conditions associated with these ecosystems (Hodkinson 2005; Alatalo et al. 2017) and, while resource availability might influence their abundance, diversity can be maintained because they may not experience the impacts of these soil variables that are generally seen to influence soil biota communities in other regions. Though SWC only significantly influenced one taxon (Prostigmatid mites), had it been coupled with temperature, a stronger relationship may have been forged with other taxa. As Hodkinson et al. (1998) noted in a different Arctic ecosystem, changes in temperature on its own did not explain the changes in soil mesofauna composition and should be considered alongside SWC.

The range of soil properties measured across our samples was within the range expected for low Arctic soils that are mildly acidic (pH~4-5), low to moderate salinity (160-680 μ S/cm), organic (30–85% LOI), and wet (100–680% g/g; Table 1). Thus, while our data demonstrate how the in situ community responds to soil heterogeneity within this low Arctic region, it represents only a subset of the global range of these soil properties. Some studies that have been conducted over larger gradients of soil properties discovered stronger correlations between soil properties and mesofauna communities than we detected (e.g., Cole et al. 2005; Pan et al. 2018; Ball et al. 2022). It is possible that we would have found more significant correlations if, for example, we were sampling soils across alkaline-to-acidic pH or dryto-wet soils. However, other studies have detected strong relationships using similar magnitudes of soil heterogeneity to our study (e.g., Mitchell et al. 2016; Sterzyńska et al. 2020). Therefore, the limited correlations we found may not necessarily be the result of an ability to detect them over a



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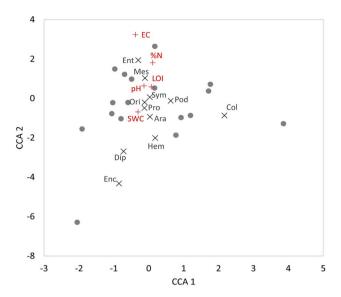
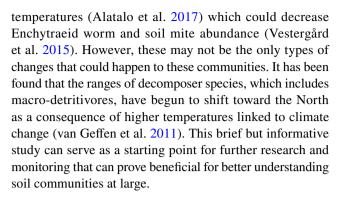


Fig. 3 Canonical correspondence analysis showing how soil samples differ in their mesofauna community in relation to soil physicochemical parameters. Circular dots represent soil samples. The ×'s represent the organisms present, abbreviated by the first three letters of the taxa name: <u>Enc</u>hytraeid, <u>Ent</u>omobryomorpha, <u>Symphypleona</u>, <u>Poduromorpha</u>, <u>Oribatida</u>, <u>Prostigmata</u>, <u>Mesostigmata</u>, <u>Araneae</u>, <u>Coleoptera</u>, <u>Hemiptera</u>, and <u>Diptera</u>. The +'s represented the soil variables of pH, electrical conductivity (EC), loss on ignition (LOI), nitrogen content (N), and soil water content (SWC)

narrow range of soil properties, especially given that our soils represent three–fourfold differences in N, SWC, EC, and LOI. Alternatively, the limited correlations could be due to the fact that some taxa are not strongly linked to resources and the chemical habitat (e.g., Mesostigmatid mites; Čoja and Bruckner 2003; Nielsen et al. 2010). For example, we measured only soil properties representing bottom-up resources, and there may be unmeasured influence of top-down predation, particularly on the smaller, unsclerotized members of the community (Wardle 2006; Schneider and Maraun 2009; Thakur and Eisenhauer 2015).

Since this was a short-term study, we can only discuss the current state of these soil communities. From here, further work should be done to monitor if and how the communities are changing. As established, these soil communities can be sensitive to changes in their local climates (Huhta and Hänninen 2001; Lindberg et al. 2002; Krab et al. 2013b), which can be altered both by climate change and direct human activity. Based on our findings, it is reasonable to predict, in low Arctic ecosystems, that LOI and %N levels may increase (Robinson et al. 1995; Hartley et al. 1999; Nielsen and Wall 2013; Rousk et al. 2016), which could increase populations of microbivorous organisms in response to an abundance of microbes (Schmidt et al. 2000), initiating a bottom-up effect on larger organisms. Further, SWC may decrease due to drought induced by warmer



Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s00300-024-03254-9.

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Author contributions BB designed the study and conducted the field work. RK and BB analyzed the samples and data. RK led the writing of the manuscript with input from BB.

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Data availability The datasets generated and analyzed during the current study are available from the corresponding author on reasonable request.

Declarations

Competing interests The authors declare no competing interests.

Ethical approval Ethics approval was not required for this study.

Informed consent Both authors agreed to participate.

Consent for publications Both authors have given consent for publication.

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