

Effects of multi-level warming on soil nematodes and microarthropods in tundra heath mesocosms

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ARTICLE INFO

Keywords:

Nematode
Collembola
Acari
Nitrogen
Warming
Tipping point
Climate chamber

ABSTRACT

Soil fauna, including nematodes and microarthropods (mites and springtails), regulate nutrient cycling and decomposition, yet their responses to warming remain unclear in temperature-sensitive tundra ecosystems. We experimentally warmed intact tundra heath monoliths from northern Sweden under five temperature treatments (ambient to +9 °C) for 20 weeks. Monoliths were dominated by either *Betula nana* or *Empetrum nigrum* subsp. *hermaphroditum*. After incubation, we quantified nematode and microarthropod densities and community composition. Warming altered both nematode and microarthropod communities, with responses mediated by vegetation type, trophic group, and taxon. Microarthropods densities were generally more sensitive to warming, especially under the dominance of *E. nigrum*, whereas nematode communities showed stronger compositional shifts. Overall nematode densities were stable across warming levels, except for fungivorous nematodes, which decreased linearly with warming. In contrast, total and carnivorous microarthropod densities increased linearly with warming, while springtails and fungivorous microarthropods displayed non-linear, U-shaped responses. Together, these results demonstrate that soil fauna responses to warming range from negligible to linear and non-linear, underscoring the importance of experimental designs that span multiple warming levels. The strong dependence of these responses on vegetation context and trophic identity emphasizes the need to account for local environmental heterogeneity when predicting tundra ecosystem responses to climate change.

1. Introduction

Soil fauna, including nematodes and microarthropods, play fundamental roles in ecosystem processes including organic matter decomposition, nutrient mineralization, and biogeochemical cycling (Coleman et al., 2024). The resistance and resilience of these functionally diverse groups to environmental perturbations is essential for sustaining ecosystem functioning. Understanding their responses is especially relevant to tundra ecosystems, which store large amounts of global soil carbon (C) as soil organic matter (SOM), and may be highly sensitive to global change (Clemmensen et al., 2021). Warming may accelerate SOM decomposition and trigger the release of large amounts of C into the

atmosphere (Alatalo et al., 2017; Bardgett and van der Putten, 2014; Mack et al., 2004), with soil nematodes and microarthropods potentially playing important roles in mediating the magnitude of these C losses. However, empirical evidence for the responses of these groups of soil fauna to warming in tundra ecosystems remain mixed. Ruess et al. (1999) demonstrated that higher temperatures increased nematode densities only when combined with fertilization. Further, Stark et al. (2023) found no overall warming effect on total nematode density, although densities of fungivorous nematodes increased depending on reindeer migration and grazing intensity. Responses of microarthropods to warming in tundra ecosystems have also often been weak or non-significant (Alatalo et al., 2015; Alatalo et al., 2017; Coulson et al.,

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1996; Sjörsen et al., 2005; Krab et al., 2019), although shifts in microarthropod abundances and community composition along a tundra elevational gradient has been reported (Bokhorst et al., 2018).

Most studies examining effects of warming on soil fauna rely on single-level temperature manipulations (typically +0.4–2 °C), potentially overlooking non-linear or threshold responses (Kardol et al., 2012). In contrast, multi-level warming experiments conducted in sub-tropical forests, alpine meadows, and subarctic grasslands have revealed non-linear shifts in soil fauna densities (Cui et al., 2023; Li et al., 2025; Thakur et al., 2023). To our knowledge, however, comparable data are lacking for tundra ecosystems. Non-linear warming responses in organisms may include unimodal (hump-shaped) patterns, reflecting the existence of optimal temperatures for traits related to population density (Pawar et al., 2024). Furthermore, ecological communities may undergo abrupt, non-linear changes when environmental drivers such as temperature surpass ecological thresholds, resulting in regime shifts toward alternative stable states (Munson et al., 2018). Ecosystems experiencing high abiotic stress, particularly those dominated by foundation species that strongly modify local environmental conditions, are especially prone to such threshold dynamics (Osland et al., 2025), and tundra ecosystems meet these criteria well.

Environmental heterogeneity may further obscure warming effects when covarying environmental factors with strong influences on the focal organisms are not accounted for (Catford et al., 2022). Heath tundra patches differ in dominant vegetation (namely dwarf shrubs), and such differences in vegetation composition could modulate the responses of soil fauna to warming. For example, shrub removal can alter the effects of warming on nematodes in boreal forests and alpine grasslands (De Long et al., 2016; Yang et al., 2025). Similarly, the availability of soil nitrogen (N) strongly influences soil faunal communities. For example, N fertilization can increase the abundance of omnivorous nematodes and microarthropods (Betancur-Corredor et al., 2023; Stark et al., 2023) and mediate the warming responses of fungal-feeding nematodes (Ruess et al., 1999), suggesting that variation in N availability can modulate warming effects in N-limited tundra soils. Consequently, the spatial heterogeneity in soil N availability may shape nematode and microarthropod densities along with the effects of warming and vegetation type. To capture relevant aspects of belowground N availability for soil fauna, we focused on total soil N, root N, and microbial biomass N (MBN). Soil N and MBN serve as indicators of detrital and microbial resource availability, whereas root N represents the resource base for plant-feeding soil fauna. Including both vegetation type and N pools in our analyses allows us to assess how these variables mediate the responses of soil fauna to warming.

In this study, we used a mesocosm experiment to test how soil nematodes and microarthropods (mites and springtails) respond to a gradient of warming intensities (ambient up to +9 °C), applied to intact tundra heath monoliths in climate-controlled chambers. We compared responses between soils dominated by two dominant dwarf shrubs: *Betula nana*, an ectomycorrhizal (ECM) deciduous species, and *Empetrum nigrum* subsp. *hermaphroditum*, an ericoid mycorrhizal (ERM) evergreen species. Both ECM and ERM fungi promote organic matter decomposition and plant nutrient acquisition (Read and Perez-Moreno, 2003). However, ERM plants can suppress the germination and growth of ECM plants through the accumulation of low-quality, polyphenolic-rich litter (Mallik, 2003). This litter-driven nutrient limitation and associated allelopathic effects can also constrain microbial and soil fauna activity (Wardle et al., 1998; Ruess et al., 1998), potentially reducing the capacity of soil fauna to acclimate to warming in ERM-dominated soils. Additionally, we accounted for variation in belowground N variables. By examining changes in soil fauna density under multiple levels of warming while accounting for variation in dominant shrub species and key belowground N variables, we aimed to better understand the shape of warming responses in soil nematodes and microarthropods and to identify underlying mechanisms. We also examined changes in community composition to detect warming responses not captured by

density alone. We tested two hypotheses: 1) Soil nematode and microarthropod densities will increase linearly with warming, or show unimodal (hump-shaped) responses; 2) Warming effects will be weaker in *E. nigrum* mesocosms than in *B. nana* mesocosms, reflecting the reduced acclimation capacity of soil fauna in ERM-dominated soils.

2. Materials and methods

2.1. Study site and sampling design

Sampling was conducted in August 2023 within a 20-ha area located on the slope of Mount Suorooaivi, near Abisko, in northern Sweden (68°21'N, 18°49'E). The elevation was 600–700 m, above the local tree line (approx. 500 m), relatively flat, and dominated by heath vegetation. There were two dominant species with contrasting fungal symbionts: the ectomycorrhizal (ECM) *Betula nana*, and the ericoid mycorrhizal (ERM) *Empetrum nigrum* subsp. *hermaphroditum*. For each species, 20 intact monoliths of tundra vegetation (24 cm × 30 cm wide) were excavated. Other plant species that were present in these monoliths included *Vaccinium vitis-idaea*, *Vaccinium uliginosum*, *Arctostaphylos alpina*, and an unidentified species of *Festuca*. Surfaces were also covered with mosses and lichen, which were included in the aboveground biomass. The monoliths were placed in plastic containers perforated at the bottom for drainage and treated as ‘mesocosms’ with two contrasting dominant shrub species. Only the soil organic horizon was sampled, resulting in the soil depths of the mesocosms ranging from 5.1 to 11.9 cm (mean = 8.3 cm, SD = 1.6 cm).

2.2. Experimental setup

We first put the mesocosms through artificial winter to reset their phenology to the beginning of their growing seasons, following Junttila, Hänninen (2012) and Pop et al. (2000). This was done by gradually lowering the temperature, day length and photosynthetic photon flux density (PPFD) of photosynthetically active radiation (PAR) inside the climate chambers (for incubation conditions, see Appendix A).

The mesocosms were then incubated in five climate-controlled growth chambers (Conviron GEN2000) for 20 weeks (eight per chamber, four per shrub species, $n = 4$), simulating the growing season in Abisko, from snowmelt to complete leaf senescence (May–October). Each chamber represented a different warming treatment: ambient, + 2.3°C, + 4.6°C, + 6.9°C, and + 9.0°C, in line with the design of the ‘Spruce and Peatland Responses Under Climatic and Environmental change’ (SPRUCE) experiment (Hanson et al., 2017). The ambient temperature regime that we used was derived from hourly air temperature measurements (15 cm above the soil surface) recorded during the 2021–2022 growing seasons by nine loggers distributed across heath tundra at Mount Suorooaivi (elevation 365–950 m). Averaging data across multiple years and logger positions minimized the influence of local microclimatic variation and sampling year on the ambient temperature profile. The selected loggers were chosen so that their average elevation matched the elevation at which the tundra monoliths were collected. Each temperature treatment consisted of 20 weeks of hourly temperature changes, with each week representing a week during the growing season in the field, thereby capturing realistic patterns of diurnal and seasonal dynamics (see Supplementary Material 1 for the full description of treatments).

Soil moisture was maintained at field capacity by watering mesocosms twice a week, based on pre-calculated target weights. Moisture-weight calibration was conducted at the beginning of the experiment and adjusted twice during the incubation period to account for plant growth. For these adjustments, soil moisture was measured non-destructively using a ML3 ThetaProbe Soil Moisture Sensor and a HH2 Moisture Meter (Delta-T Devices, Cambridge, UK). Light levels in all chambers followed natural above-canopy PAR fluctuation data (hourly, with weekly updates) sourced from the Abisko-Stordalen Palsa Bog

meteorological station for the years 2020–2022 (Sweden et al., 2021; Sweden et al., 2022).

Mesocosms were rotated weekly within chambers and biweekly between chambers to minimize potential confounding effects of mesocosm positioning within and between chambers. The mesocosms were grouped into four blocks of ten mesocosms, each containing all combinations of mesocosms from each of the warming treatments and dominant shrub species. After 20 weeks, all mesocosms were destructively harvested block by block and in randomized order within the blocks.

2.3. Microarthropod extraction and classification

A 10 cm diameter soil core that extends down to the bottom of the mesocosm was extracted near the center of each mesocosm, and microarthropods were extracted using Tullgren funnels for up to two weeks until the cores were completely dry (van Straalen and Rijninks, 1982). Specimens were preserved in 70 % ethanol. Mites were identified to the order level and classified into four feeding groups: microbivorous detritivores (Oribatida), fungivores (family Tydeidae of the Prostigmata), omnivores (Astigmata and most Prostigmata), and carnivores (Mesostigmata including those from the infraorder Uropodina) (Coleman et al., 2018; Potapov et al., 2022). Springtails were also identified to the order level. All springtail groups were treated as fungivores, except for the carnivorous sub-family Frieseinae of the Poduromorpha (Berg et al., 2001; Brussaard et al., 1990). The remaining soil core was oven-dried at 100°C for four days, passed through a 1 mm sieve, and weighed to gain the dry soil weight. Microarthropod density was then expressed as abundance per g dry soil. For data on the numbers and community compositions of extracted microarthropods, see Appendix B.

2.4. Nematode extraction and classification

From each mesocosm, ten 1.7 cm-diameter cylindrical soil cores that extend down to the bottom of the mesocosms were randomly collected using an apple corer. Root debris were removed from the soil samples and approximately 70 ml of soils per mesocosm were collected for analysis. The soils were weighed, and the weight of their dry mass was later calculated based on the dry matter content (DMC) estimated from their subsamples. The dry soil mass was then used to express nematode density as abundance per 100 g dry soil. Nematodes were extracted using a rapid centrifugal-flotation method (Jenkins, 1964) and then fixed in a saturated solution of dimethyl sulphoxide, disodium ethylenediaminetetraacetic acid, and saturated NaCl (DESS) following Yoder et al. (2006). All nematodes in each sample were counted, and 150 individuals per sample were identified to family level (or super-family level for Dorylaimoidea) and assigned to one of five feeding groups: plant feeders, bacterial feeders, fungal feeders, omnivores, and carnivores, following Yeates et al. (1993). Omnivorous and carnivorous nematodes were combined into a single omni-carnivore group. For data on the numbers and family compositions of extracted nematodes, see Appendix B.

2.5. Soil sampling and physiochemical analyses

From each mesocosm, aboveground plant biomass was harvested prior to microarthropod and nematode extractions, dried at 60 °C for four days and weighed. Three soil samples (10 cm × 10 cm, full depth of the mesocosm) were collected, passed through a 4 mm sieve, and homogenized for subsequent soil analyses. These three samples were combined to obtain a representative sample of the mesocosm and to ensure sufficient soil for analyses after removing the roots. A subsample of this homogenized soil was used for pH analysis by mixing the soil with distilled water in a 1:2.5 w/w ratio and measuring the pH of the mixture with a SevenCompact pH meter S210 (Mettler Toledo, Ohio, USA). Another subsample was refrigerated at 5°C for the estimation of soil

microbial biomass nitrogen (MBN) by chloroform fumigation extraction following Brookes et al. (1985a) and using the correction factor $K_{EN} = 0.54$ (Brookes et al., 1985b) as recommended by Halbritter et al. (2020). Additional subsamples were frozen at −20°C until analyses for dry matter content, soil organic matter (SOM) content, and total nitrogen (N) content. The DMC was determined by oven-drying approx. 5 g of soil at 100°C overnight. The SOM was measured via loss-on-ignition at 550°C for six hours (Walkley and Black, 1934; Schulte and Hoskins, 2011). Total N content was measured by drying the subsampled soils at 60 °C, finely grinding them by bead-beating, and drying them again at 60 °C for four days, before analyzing them with a Flash EA 2000 elemental analyzer (Thermo Fisher Scientific, Bremen, Germany). Root N content was measured following the same methodology as soil N, on roots smaller than 2 mm diameter that were sieved out of the soil samples, homogenized, washed, and subsampled. For data on differences of belowground N variables between *B. nana* and *E. nigrum* mesocosms, see Appendix C.

2.6. Data analyses

2.6.1. Soil nematode and microarthropod densities

We first tested the effects of warming, dominant shrub species, and belowground N variables on soil fauna densities by linear modeling. Models were constructed for both the combined dataset (including both *B. nana* and *E. nigrum* mesocosms, $n = 40$) and individual datasets for each dominant shrub species ($n = 20$ each). This approach allowed us to identify both general trends across shrub species and shrub species-specific responses of soil nematodes and microarthropods. The full models included the following explanatory variables: warming (both linear and squared terms to test for quadratic responses), soil N content, MBN concentration, root N concentration, and dominant shrub species (included only in models for combined datasets, coded as dummy variables: *B. nana* = 0, *E. nigrum* = 1). To further test potential non-quadratic, non-linear warming responses, we also fitted generalized additive models (GAMs). In the models, warming was modeled as a smooth (non-linear) term, while the belowground N variables and dominant shrub species were included as linear predictors. We compared the performance of linear models and GAMs using Akaike Information Criteria to determine whether non-linear models provided a better fit. We also constructed linear models and GAMs including interaction effects between warming and dominant shrub species, but no significant interaction effects were detected, and the linear models and GAMs with no interaction performed similarly well or better than the interaction models, so the results of these models are not shown.

All soil fauna densities were log-transformed to meet normality assumptions, which were verified using the Shapiro-Wilk test. We removed one zero value from the omnivorous microarthropod dataset, as it could not be log-transformed. All continuous explanatory variables were standardized using z-transformation to assess their relative effects. Multicollinearity among predictors was assessed by calculating variance inflation factors and tolerance values. Multicollinearity between the variables included in the models and other potential environmental covariables (soil pH, DMC, SOM content, aboveground biomass, and mesocosm soil depth) were also assessed, but no collinearity was found, which excludes the possibility of confounding effects of these variables.

2.6.2. Community composition

For analyzing the community composition of soil nematodes and microarthropods, we used stepwise canonical correspondence analyses (CCA) to test the explanatory power of warming, dominant shrub species, and N resource variables. We then evaluated the statistical significance of the effects of these variables using Permutational Multivariate Analysis of Variance (PERMANOVA). To visualize differences in nematode and microarthropod community composition, we used non-metric multidimensional scaling (NMDS) with explanatory variables overlaid. For nematodes, stepwise CCA was chosen over stepwise

redundancy analysis (RDA) based on detrended correspondence analysis (DCA), where the longest gradient length exceeded four standard deviation units, indicating a unimodal species response and thus justifying the use of CCA (Šmilauer and Lepš, 2014). For microarthropods, the longest DCA gradient fell between two and four standard deviation units, making both CCA and RDA suitable. However, since both methods produced comparable results, only the stepwise CCA results are presented. As with the statistical modeling of density data, stepwise CCAs and PERMANOVAs were first conducted on the combined dataset (including both *B. nana* and *E. nigrum* mesocosms), followed by analyses of the datasets for each of the two plant species separately. PERMANOVA was performed using 999 permutations.

All statistical analyses were conducted in R v4.3.1 (R Core Team, 2023). GAMs were implemented using the *mgcv* package (Wood, 2017). DCA, stepwise CCA, stepwise RDA, PERMANOVA, NMDS, and explanatory variable overlay on NMDS plots were conducted using the *vegan* package (Oksanen et al., 2022), and all data visualizations were created using *ggplot2* (Wickham, 2016).

3. Results

3.1. Nematode densities

No nematode groups responded to warming, other than fungal-feeders. The density of fungal-feeders decreased linearly with warming levels for the combined data and for *Empetrum nigrum* subsp. *hermaphroditum* mesocosms, but not for the *Betula nana* mesocosm data (Fig. 1).

No significant interaction effects were detected between warming levels and dominant shrub species, and linear models and Generalized additive models (GAMs) without interaction terms included always performed similarly or better. In these linear models and GAMs, nematode densities were not influenced significantly by dominant shrub species, although nematode densities varied significantly between dominant shrub species when tested separately (Appendix D).

The influence of belowground nitrogen (N) variables on nematode

densities varied between feeding groups and dominant shrub species, but were all positive when statistically significant (Table 1, Appendix E). Correlation with soil N was only observed for fungal feeders in *B. nana* mesocosms. Microbial biomass N (MBN) was correlated with total nematode densities and densities of nematodes from all feeding groups except omni-carnivores for the combined data. Correlations were also observed for some nematodes in *B. nana* mesocosms, but for none of the nematode feeding groups in *E. nigrum* mesocosms. Correlation with root N was limited to the density of omni-carnivores in *E. nigrum* mesocosms.

3.2. Soil nematode community compositions

Nematode community composition was best explained by warming levels and dominant shrub species when data from *B. nana* and *E. nigrum* mesocosms were analyzed together (constrained proportion=0.171) (Fig. 2a). The Permutational Multivariate Analysis of Variance (PERMANOVA) result showed that both warming levels and dominant shrub species significantly influenced community composition. Stepwise canonical correspondence analysis (CCA) and PERMANOVA results were similar for both *B. nana* (constrained proportion = 0.140) and *E. nigrum* (constrained proportion = 0.121) mesocosms, with warming levels having a statistically significant influence on nematode community composition. No significant effects of belowground N variables were detected.

3.3. Microarthropod density

Both linear and non-linear warming responses were observed for microarthropods (Table 2, Fig. 3). Total microarthropod density increased linearly with warming levels but only for *E. nigrum* mesocosms. Springtail density was positively quadratically correlated with warming levels for combined data, while GAM performed better than linear models for *E. nigrum* mesocosms, indicating a non-quadratic non-linear correlation where springtail density decreased non-linearly with warming up to +4.6 °C and then increased with further warming,

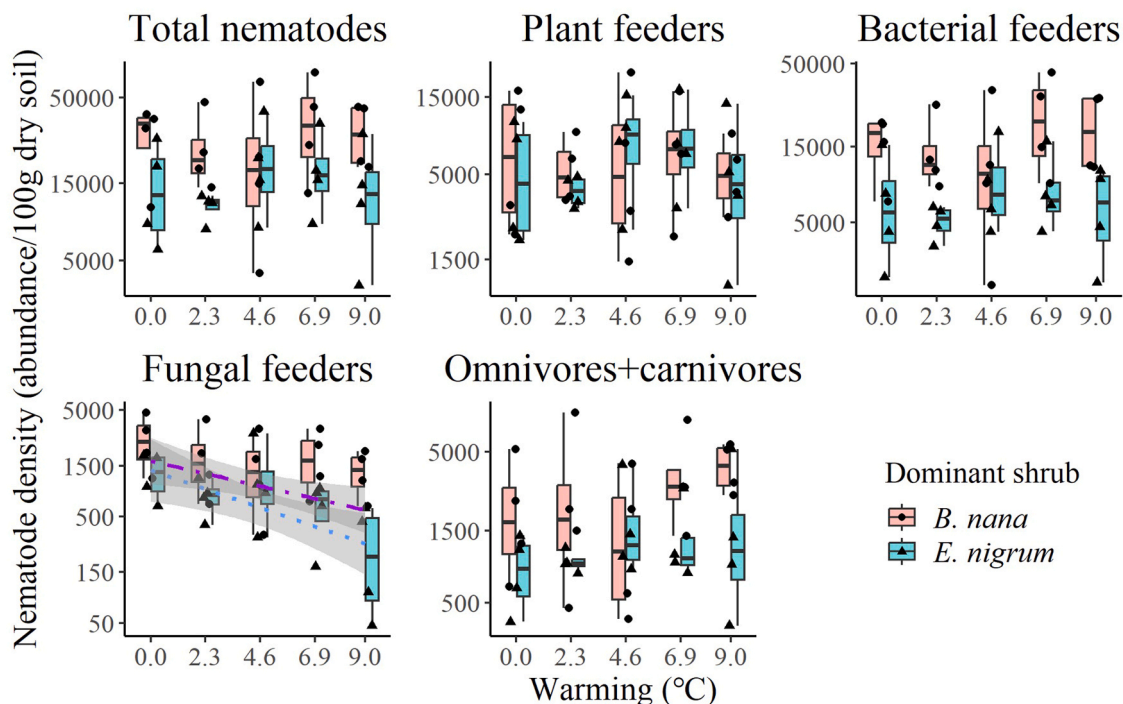


Fig. 1. Warming responses of nematode densities in *Betula nana* mesocosms (pink boxes, circles) and *Empetrum nigrum* subsp. *hermaphroditum* mesocosms (blue boxes, triangles). Vertical axes are on a logarithmic scale. Boxes show the 25–75 % quantiles and whiskers show the 95 % quantiles. Lines show smoothed curves of statistically significant warming responses. Blue dotted and purple dot-dashed lines indicate warming responses of nematodes in *E. nigrum* mesocosms, and combined data, respectively. Shaded areas denote 95 % confidence intervals.

Table 1

Results of linear models or Generalized Additive Models (GAMs) for nematode densities in the combined dataset, *Betula nana* mesocosms, and *Empetrum nigrum* subsp. *hermaphroditum* mesocosms. Reported values represent coefficients for quadratic terms of warming (warming²), linear warming, soil N, microbial biomass N (MBN), root N, and dominant shrub species (coded as *B. nana* = 0 and *E. nigrum* = 1). All predictor variables were standardized by z-transformation to allow comparison of coefficient magnitudes. Statistically significant coefficient are shown in bold, with significance levels denoted as $P < 0.05$ (*), $P > 0.01$ (**), and $P > 0.001$ (***). When a GAM provided the better fit, "GAM" is shown in place of coefficient values for warming, and the significance of the smooth term is indicated using bold text and asterisks following the same notation.

Data	Variable	Total nematodes	Plant feeders	Bacterial feeders	Fungal feeders	Omnivores and carnivores
Combined	Warming ²	0.056	GAM	0.088	-0.040	0.087
	Warming	0.040	GAM	0.066	-0.391**	0.230
	Soil N	-0.008	-0.080	-0.018	0.000	0.106
	MBN	0.357**	0.377*	0.386***	0.355*	0.255
	Root N	0.272	0.348	0.279	0.260	0.248
	Dominant shrub species	0.063	0.675	-0.139	-0.299	-0.070
<i>B. nana</i>	Warming ²	0.204	0.059	0.217	0.209	0.343
	Warming	-0.026	-0.122	0.004	-0.242	0.290
	Soil N	0.156	0.137	0.087	0.335*	0.357
	MBN	0.328*	0.277	0.409*	0.162	0.055
	Root N	0.165	0.245	0.175	0.125	0.108
	Dominant shrub species	0.0251	-0.006	0.027	-0.069	-0.060
<i>E. nigrum</i>	Warming ²	0.146	0.194	0.141	-0.475*	0.287
	Warming	-0.224	-0.370	-0.163	-0.330	0.019
	Soil N	-0.224	-0.370	-0.163	-0.330	0.019
	MBN	0.298	0.319	0.279	0.269	0.280
	Root N	0.136	0.080	0.136	0.186	0.302*
	Dominant shrub species					

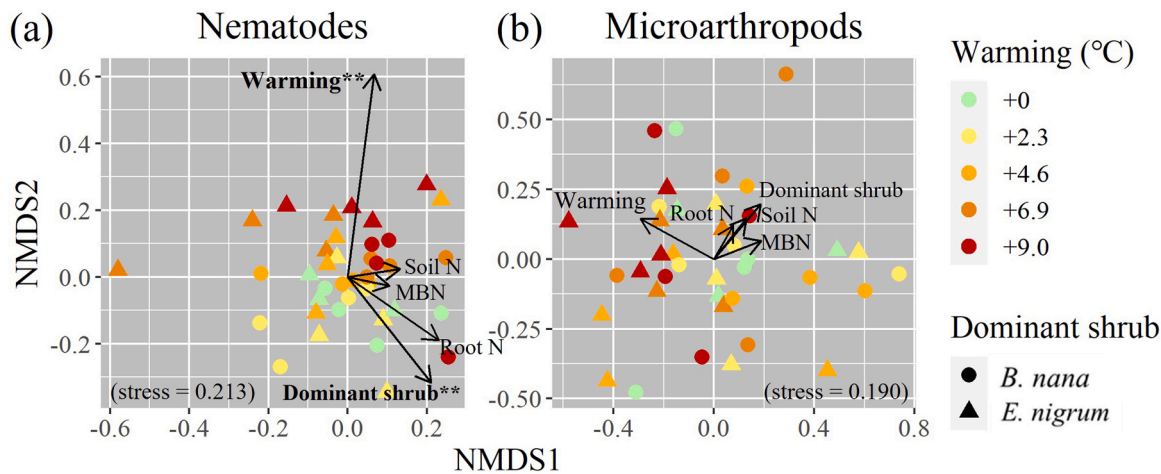


Fig. 2. Effects of warming on community composition of (a) nematodes at the family level and (b) microarthropods at the order level, in *Betula nana* (circle) and *Empetrum nigrum* subsp. *hermaphroditum* (triangle) mesocosms. Visualization was done by non-metric multidimensional scaling (NMDS). Arrows with text indicate overlaid explanatory variables: warming, dominant shrub species, soil nitrogen (N) content, microbial biomass N (MBN) content, and root N content. Bold text signifies explanatory variables selected by stepwise canonical correspondence analysis, and their significance levels based on permutational multivariate analysis of variance are denoted as $P < 0.05$ (*), $P < 0.01$ (**), and $P < 0.001$ (***). Stress values of each NMDS are shown in parentheses on the bottom of the plots.

resulting in a U-shaped curve similar to the combined data. Fungivorous microarthropod density also showed similar positive quadratic correlations with warming levels for combined and *E. nigrum* mesocosm data. Carnivorous microarthropod density increased linearly with warming levels but only for *E. nigrum* mesocosms. Mite densities, microbiodetritivorous microarthropod densities, and omnivorous microarthropod densities did not respond significantly to warming.

There were no significant interaction effects of warming levels and dominant shrub species on microarthropod densities, and linear models and GAMs without interactions always performed similarly or better than when they were included. In the linear models and GAMs, the influence of dominant shrub species on microarthropod densities was also not statistically significant (Table 2). These results were similar to when the effect of dominant shrub species were tested separately (Appendix D).

The influences of belowground N variables varied between microarthropod groups and dominant shrub species (Table 2, Appendix F). Soil N did not correlate with microarthropod densities for the combined

data. Correlations with soil N were positive and limited to springtails and fungivorous microarthropods for the *B. nana* mesocosms data, but negative and limited to total microarthropods, mites, and microbiodetritivorous microarthropods for the *E. nigrum* mesocosm data. Correlations of microarthropod groups with MBN were negative for total microarthropods, springtails, and fungivores in *B. nana* mesocosms. Root N was only correlated with total microarthropod density for the combined dataset.

3.4. Microarthropod community composition

Stepwise CCA selected none of the warming, dominant shrub species or belowground N variables for explaining the community composition of microarthropods in the combined data and *B. nana* mesocosms (Fig. 2b). However, for the *E. nigrum* mesocosms, the community composition of microarthropods was influenced by soil N, and this effect was found to be statistically significant by PERMANOVA.

Table 2
Results of linear models or Generalized Additive Models (GAMs) for microarthropod densities in the combined dataset, *Betula nana* mesocosms, and *Empetrum nigrum* subsp. *hermaphroditum* mesocosms. Reported values represent coefficients for quadratic terms of warming (Warming²), linear warming, soil N, microbial biomass N (MBN), root N, and dominant shrub species (coded as *B. nana* = 0 and *E. nigrum* = 1). All predictor variables were standardized by z-transformation to allow comparison of coefficient magnitudes. Statistically significant coefficients are shown in bold, with significance levels denoted as P < 0.05 (*), P > 0.01 (**), and P > 0.001 (***). When a GAM provided the better fit, “GAM” is shown in place of coefficient values for warming, and the significance of the smooth term is indicated using bold text and asterisks following the same notation.

Data	Variable	Total micro-arthropods	Springtails	Mites	Microbi-detritivores	Fungivores	Omnivores	Carnivores
Combined	Warming ²	0.161	0.464*	0.060	-0.025	0.476*	-0.023	0.286
	Warming	0.284	0.324	0.219	0.224	0.248	-0.034	0.316
	Soil N	0.031	0.242	-0.004	0.028	0.305	0.288	0.034
	MBN	-0.267	-0.310	-0.302	-0.328	-0.353	-0.382	-0.282
	Root N	0.565*	0.301	0.651	0.692	0.250	0.457	0.693
	Dominant shrub species	0.334	-0.229	0.521	0.727	-0.278	-0.721	0.094
<i>B. nana</i>	Warming ²	0.378	0.526	0.308	0.200	GAM	0.259	0.547
	Warming	0.343	0.431	0.257	0.282	GAM	0.446	0.334
	Soil N	0.460	0.731*	0.425	0.480	0.756*	0.866	0.515
	MBN	-0.712*	-0.893*	-0.716	-0.759	-0.889*	-0.952	-0.808
	Root N	0.529	0.324	0.594	0.647	0.241	0.253	0.581
	Warming ²	0.272	GAM*	0.131	0.087	0.794*	-0.011	0.396
<i>E. nigrum</i>	Warming	0.445*	GAM*	0.386	0.372	0.410	-0.297	0.579*
	Soil N	-0.441*	-0.223	-0.492*	-0.524*	-0.237	-0.073	-0.393
	MBN	0.090	0.281	0.025	0.012	0.157	-0.197	0.173
	Root N	0.030	-0.059	0.046	0.012	-0.063	0.398	0.231

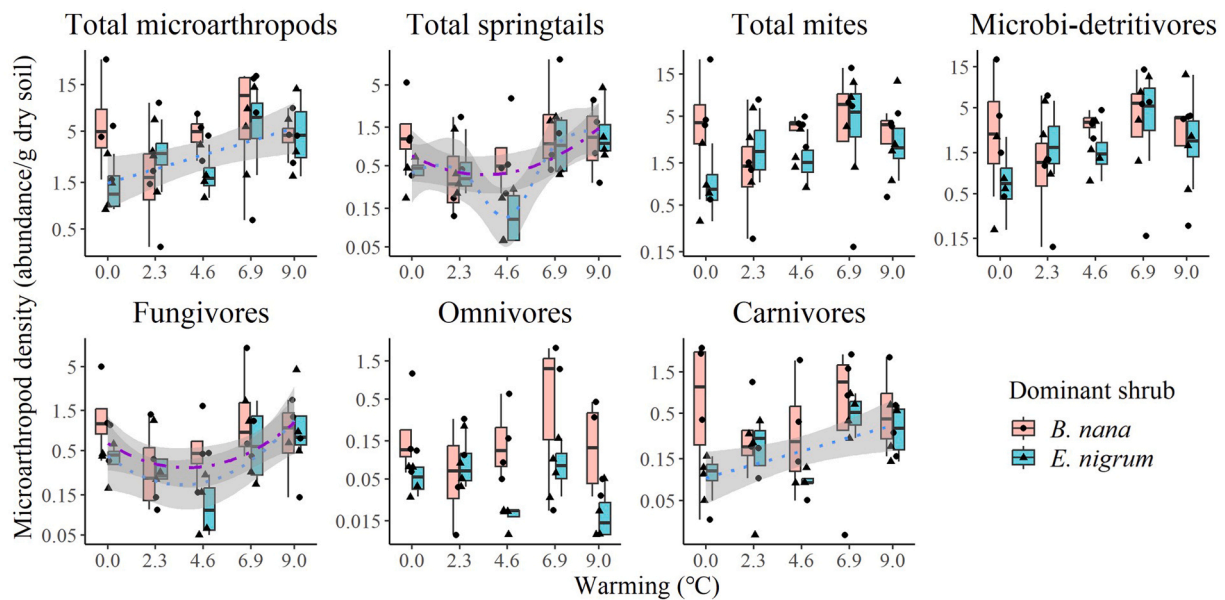


Fig. 3. Warming responses of microarthropods (mites, springtails) in *Betula nana* mesocosms (pink boxes, circles) and *Empetrum nigrum* subsp. *hermaphroditum* mesocosms (blue boxes, triangles), shown for total densities and individual trophic groups. Vertical axes are on a logarithmic scale. Boxes represent the 25–75 % quantiles and whiskers show the 95 % quantiles. Lines show smoothed curves of statistically significant warming trends. Blue dotted, and purple dot-dashed lines indicate warming responses of nematodes in the *E. nigrum* mesocosm data and the combined data, respectively. Shaded areas denote 95 % confidence intervals.

4. Discussion

Soil nematode and microarthropod groups exhibited a wide range of responses to warming that depended on taxonomic identity, feeding groups, and dominant vegetation type. The multi-level warming design allowed us to test for the presence of threshold responses in soil nematode and microarthropod densities. Although no clear thresholds were detected, the results demonstrate that the absence of thresholds does not necessarily mean that responses were linear, as U-shaped non-linear warming responses were observed. The effects of belowground nitrogen (N) variables on soil nematode and microarthropod densities also varied across feeding groups and dominant shrub species. Furthermore, community compositional responses to warming were more pronounced for nematodes, whereas density responses were stronger for microarthropods, indicating contrasting acclimation strategies between these

soil faunal groups.

4.1. Hypothesis 1: Effects of warming on soil nematodes and microarthropods

Our first hypothesis was only partially supported. Only two faunal groups increased in density with warming, and we found no hump-shaped warming responses. Instead, most nematodes and microarthropod groups showed non-significant, negative, or U-shaped responses across the warming gradient. The generally weak nematode responses align with previous open-top chamber studies (De Long et al., 2016; Kardol et al., 2010; Ruess et al., 1999), suggesting that tundra soil nematodes are not strongly temperature-limited. Our results further indicate that the absence of warming effects in earlier studies is unlikely to reflect insufficient warming magnitude. However, because our

experiment imposed short-term, abrupt warming, it primarily captures immediate responses. Longer-term warming may elicit different outcomes. For example, multi-year warming in alpine meadows reduced nematode abundance, an effect attributed jointly to warming and substantial soil drying (Han et al., 2024).

Fungivorous nematodes and microarthropods (primarily springtails) both responded to warming, but in contrasting ways. Warming can favor saprotrophic and arbuscular mycorrhizal fungi over root-associated endophytes, potentially increasing decomposition of soil organic matter while reducing total fungal biomass (Moravcová et al., 2023). In our system, such shifts likely involved saprotrophic fungi to a greater extent, given the dominance of non-arbuscular shrubs. A resulting decline in fungal resources may explain the linear decrease in fungivorous nematodes with warming, although fungal responses to temperature are known to be highly context-dependent. Indeed, other studies have reported stable (D'Alò et al., 2024) or even increasing (Clemmensen et al., 2006) fungal biomass under warming in alpine systems and tundra-boreal forest ecotones. This suggests that the response of fungivorous nematodes observed here is likely linked to fungal dynamics specific to our study system rather than representing a universal warming effect. In contrast, the U-shaped springtail response may reflect vertical redistribution within the soil profile. For example, short-term warming in a subarctic bog reduced springtail densities in surface litter, while populations in deeper layers remained stable (Krab et al., 2013). In our experiment, warming-induced drying may have reduced surface populations, resulting in the initial decline, whereas higher warming levels may have increased springtail abundance in deeper, moister soil layers; the combined response across soil layers may explain the observed U-shaped pattern at the mesocosm level. Notably, such non-linear responses would be obscured in single-level warming experiments, potentially explaining previously reported non-significant springtail responses in tundra warming studies (Alatalo et al., 2017; Sjörsen et al., 2005).

In *Empetrum nigrum* subsp. *hermaphroditum* mesocosms, total and carnivorous microarthropods increased with warming, suggesting that low temperatures constrained these groups and that warming up to +9 °C alleviated those constraints. In contrast, mites and mite-dominated feeding groups (microbi-detritivores and omnivores) showed no significant responses, consistent with long-term tundra warming studies (Alatalo et al., 2017; Sjörsen et al., 2005). Carnivorous microarthropods were the only feeding group to increase consistently with warming, supporting evidence that higher trophic levels may be especially sensitive to climate change due to greater metabolic demands, smaller populations, or strong bottom-up control (Voigt et al., 2003; Gilman et al., 2010).

Total microarthropod density responded to warming, whereas nematode density did not. This divergence may partly reflect trophic position, as carnivorous and omnivorous microarthropods occupy higher trophic levels and commonly prey on nematodes (de Ruiter et al., 1995; Heidemann et al., 2014). Differences in habitat use may also contribute. Microarthropods are concentrated near the soil surface (Faber and Joosse, 1993; Luxton, 1981; Setälä and Aarnio, 2002), where warming-induced increases in energy availability are greatest, whereas nematodes often extend deeper into the soil profile (Coleman et al., 2024). Although this vertical buffering is less relevant in our mesocosms which are warmed from all sides, nematodes may nonetheless be more vulnerable to warming-induced drying. Because nematodes depend on water films for movement (Bardgett, 2005) as opposed to microarthropods which live in air-filled pores (Coleman et al., 2024), even short drying events—despite frequent watering—may have offset potential thermal benefits, resulting in weaker responses relative to microarthropods.

Although we did not detect any short-term responses of mite densities, longer exposure under more extreme warming could alter mite densities through cumulative changes in plant and microbial communities (Björk et al., 2007). Moreover, our experiment isolated

temperature effects by maintaining relatively constant soil moisture. In natural systems, warming-induced drying (Barreto et al., 2021; Kardol et al., 2010; Thakur et al., 2018) and altered winter conditions, including freeze-thaw dynamics (Koltz et al., 2018) may amplify or fundamentally alter soil fauna responses.

4.2. Hypothesis 2: Effects of dominant shrub species on warming responses

We found no significant interactive effects of warming and dominant shrub species on nematodes or microarthropod densities, refuting our second hypothesis. However, comparisons between *Betula nana* and *E. nigrum* mesocosms provide partial and unexpected evidence for shrub-specific modulation of warming responses. Significant warming effects were detected in the combined dataset and in *E. nigrum* mesocosms, but not in *B. nana* mesocosms, indicating weaker warming responses under *B. nana*. This result runs counter to our expectation and suggests that soil fauna associated with *E. nigrum* are more sensitive to warming. One possible explanation is that the secondary metabolites and nutrient-poor litter of *E. nigrum* (González et al., 2015; Wardle et al., 1998; Ruess et al., 1998) exacerbate, rather than buffer, soil faunal sensitivity to climate warming.

4.3. Influence of belowground N availability

We expected indicators of belowground N availability to correlate positively with soil nematode and microarthropod densities and to influence community composition. In the combined dataset, dominant shrub species had no significant effects. Instead, nematode densities were positively related to microbial biomass N (MBN), while microarthropod densities were positively related to root N. These results suggest that MBN and root N capture vegetation effects as continuous predictors rather than categorical shrub-type effects.

When analyzed separately, however, soil faunal responses diverged between shrub species (Fig. 4). In *B. nana* soils, higher total soil N was positively associated with fungivorous soil fauna, supporting the role of soil N as an indirect resource mediated through microbial biomass. In contrast, in *E. nigrum* soils were negatively correlated with soil N. *E. nigrum* soils are relatively N-poor (see Appendix C), and this pattern may reflect enhanced N mineralization and plant uptake under higher densities of microarthropods such as microbi-detritivorous mites. In *B. nana* mesocosms, MBN promoted bacterial-feeding nematodes but reduced fungivorous microarthropods and springtails, consistent with resource partitioning driven by shifts in the fungal:bacterial biomass ratio. Root N was positively correlated with omni-carnivorous nematodes in *E. nigrum* soils, suggesting sensitivity to plant-derived nutrient inputs to the belowground compartment.

4.4. Soil nematode and microarthropod community composition

Community composition responded differently than density. Nematode community composition was significantly affected by warming across all datasets, whereas microarthropod community composition showed no detectable warming response. This contrast suggests distinct acclimation strategies: nematodes responded to warming primarily through compositional shifts, whereas microarthropods responded mainly through changes in abundance. Dominant shrubs likewise influenced nematode, but not microarthropod composition, indicating greater sensitivity of nematode assemblages to vegetation context. Given the lack of strong warming effects on nematode feeding-group densities, compositional shifts were likely not driven solely by changes in trophic structure, although declines in fungivorous nematodes may have contributed. Instead, warming may have altered community-level properties such as diversity, energy flux, or network structure, with potential cascading effects on decomposer-driven processes including litter decomposition and nutrient mineralization (Du et al., 2022; Wan

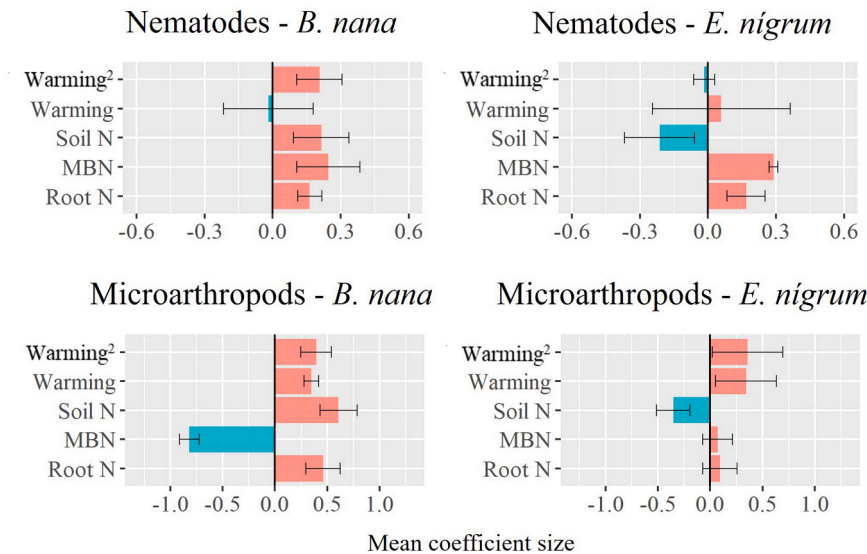


Fig. 4. Horizontal bar plots showing mean liner model coefficient sizes of quadratic terms of warming (Warming²), warming, soil nitrogen (N) content, microbial biomass N (MBN) content, and root N content. Coefficients are averaged across each taxonomic group (nematodes and microarthropods) and dominant shrub species in the mesocosms (*Betula nana* and *Empetrum nigrum* subsp. *hermaphroditum*). Error bars represent standard deviations. Coefficient values from models where generalized additive models (GAMs) performed better than linear models were substituted with linear model results, since coefficient values for warming and the quadratic term of warming were unavailable for GAMs.

et al., 2022; Zhang et al., 2025).

Soil N influenced community composition only for microarthropods in *E. nigrum* mesocosms, suggesting tighter coupling to locally available N in these nutrient-poorer soils. This stronger warming sensitivity of soil fauna in *E. nigrum* mesocosms likely reflects combined effects of allelopathic compounds and nutrient limitation associated with *E. nigrum* litter (González et al., 2015; Wardle et al., 1998; Ruess et al., 1998). However, limited taxonomic resolution may have obscured subtler compositional shifts in microarthropods. In addition, multivariate

analyses could not detect non-linear responses, and our focus on abundance rather than biomass may have missed warming-induced shifts documented for mites (Thakur et al., 2023) and springtails (Holmstrup et al., 2018).

4.5. Conclusions

Our results demonstrate that soil mesofauna responses to warming are diverse and context dependent, varying in both direction (positive

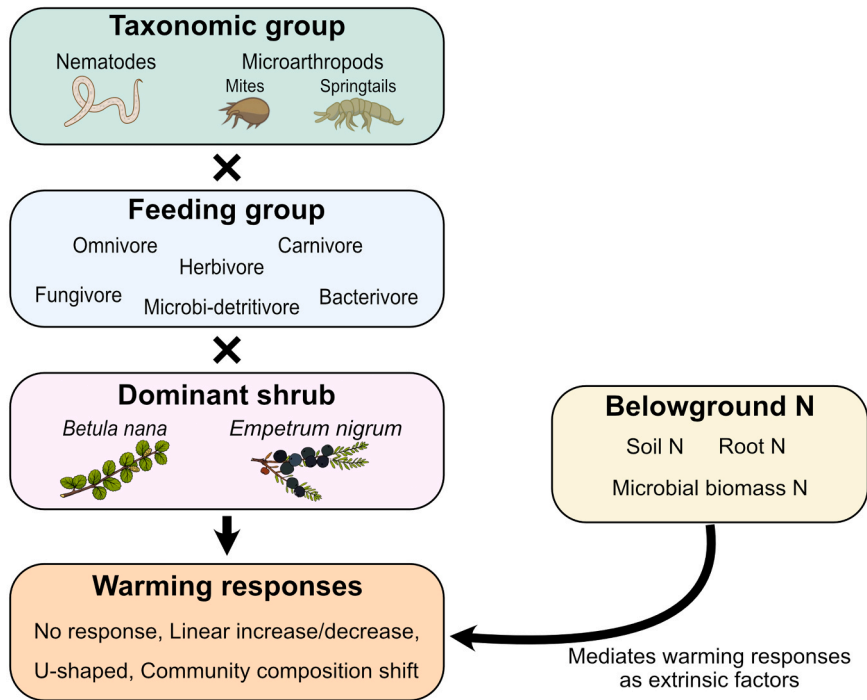


Fig. 5. Conceptual diagram showing how the types of responses of soil fauna to warming in our experiment are determined by their taxonomic group, feeding group, dominant shrub species (*Betula nana* and *Empetrum nigrum* subsp. *hermaphroditum*), and their interactions, as well as the role of belowground nitrogen (N) in soils, roots and the microbial biomass as factors that mediate the nature of the response.

versus negative) and shape (linear versus non-linear) across taxonomic and feeding groups (Fig. 5). Nematodes and microarthropods utilized contrasting acclimation strategies: nematodes primarily adjusted through shifts in community composition, whereas microarthropods responded via changes in density. Warming sensitivity was greater in *E. nigrum* mesocosms, and both density and composition were further modulated by belowground N availability in ways that depended on shrub species and feeding group. The detection of non-linear responses underscores the importance of using multiple warming levels when assessing tundra ecosystem responses. No single response curve or warming threshold characterized soil nematodes and microarthropods indicating that warming effects must be evaluated at functionally and ecologically coherent groupings rather than aggregated taxonomic units.

Scaling from plot-level responses to ecosystem-scale predictions requires explicit consideration of local environmental heterogeneity. Our findings show that ignoring such variation risks masking real, context-dependent responses. While this study focused on vegetation type and N availability, additional sources heterogeneity including soil moisture, winter processes, herbivory, and topographic variation, are likely to further mediate warming responses. Moreover, soil fauna in other tundra vegetation types, such as herb-dominated meadows or *Salix*-dominated wetlands, may respond differently. Future studies will benefit from incorporating multiple warming levels, functional group-based approaches, and explicit tests of how local environmental context constrains soil faunal responses to climate warming and the ecosystem processes they regulate.

CRediT authorship contribution statement

Paul Kardol: Writing – review & editing, Validation, Supervision, Resources, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization. **David A. Wardle:** Writing – review & editing, Supervision, Methodology, Conceptualization. **Aimée T. Classen:** Writing – review & editing, Supervision, Methodology, Conceptualization. **Sandra Jämtgård:** Writing – review & editing, Supervision, Resources, Methodology, Conceptualization. **Floretta Setia Pradana:** Writing – review & editing, Writing – original draft, Visualization, Software, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Mika Lemoine:** Writing – review & editing, Writing – original draft, Visualization, Software, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Kohsuke Tanigawa:** Writing – review & editing, Writing – original draft, Visualization, Supervision, Software, Project administration, Methodology, Investigation, Formal analysis, Data curation, Conceptualization.

Funding

European Research Council (ERC) under the European Union's Horizon 2020 research and innovation program (grant agreement no. 864287—THRESHOLD—ERC-2019-COG)

Declaration of Generative AI and AI-assisted technologies in the writing process

During the preparation of this work, the author used ChatGPT to assist with writing. The authors reviewed and edited all text produced by the tool, and take full responsibility for the final content of the manuscript.

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.

Acknowledgements

We thank Catherine Priemer, Hassan Ridha, and Ilse van Duuren for their help with mesocosm harvesting and processing. We are also grateful to Anders Jonsson at the Biogeochemical Analytical Facility, Umeå University, and Jenny Ekman and Meredith Blackburn at the Biogeochemical Analyses Laboratory, Swedish University of Agricultural Sciences, for conducting soil and plant chemical analyses. We thank ICOS Sweden, Eric Lundin, and Janne Rinne for providing the dataset “Ecosystem meteo time series (ICOS Sweden) from Abisko-Stordalen Palsa Bog,” and the staff of Abisko Scientific Research Station for their logistical support.

Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.pedobi.2026.151122.

Data availability

All data and R codes will be made publicly available on OSF from the following link upon acceptance of the manuscript for publication <https://osf.io/gk2r4/overview>.

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