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Research Article

Contrasting effects of temperature across trophic levels in geothermally warmed soil food webs

Estela Folch Chaos¹✉, Charlotte Alster², Louis Schipper¹ and Andrew D. Barnes¹

¹Te Aka Mātuatua – School of Science, University of Waikato, Hamilton, New Zealand

²Department of Soil and Physical Sciences, Faculty of Agricultural and Life Sciences, Lincoln University, Lincoln, New Zealand

Correspondence: Estela Folch Chaos (estelafc1994@gmail.com)

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Global warming is altering the structure and dynamics of ecological communities, with significant consequences for soil food webs. Rising temperatures are expected to accelerate metabolic rates in organisms, potentially altering species interactions, and the structure and energetics of food webs. However, most studies assessing warming impacts on soil invertebrates have been short-term, taxonomically narrow, or confounded by large-scale variability. We investigated how long-term warming affects soil invertebrate community structure across trophic levels. We sampled soil invertebrate along natural temperature gradients (17–40°C) of geothermal surface features of New Zealand, and we analysed community composition and population densities in relation to soil temperature, pH, water content, and microbial biomass. We found that the invertebrate community composition was significantly influenced by temperature and associated environmental variables. Total invertebrate density increased with warming, primarily driven by decomposers, while diversity metrics generally declined (except for omnivores). Decomposer diversity declined due to reductions in both dominant and rare species (Hill $q=1$ and $q=2$), whereas predator richness decreased mainly due to the loss of rare species (Hill $q=1$) that resulted in higher evenness. In contrast, omnivores exhibited increased species richness. Our results highlight that warming effects are trophic-level specific and environmentally context-dependent. This suggests that long-term warming may disrupt key ecosystem functions – such as decomposition, predator–prey interactions, and top-down control by reshaping community composition and inducing the loss of decomposer taxa and rare predatory taxa. Such alterations could compromise soil food web stability and the resilience of those communities to disturbance events in a changing climate.

Keywords: climate change, diversity, geothermal systems, soil food webs, soil invertebrates, warming

Introduction

Global warming is expected to alter soil biodiversity and its associated ecosystem functioning and stability (Campbell et al. 2009, Schwarz et al. 2017, O’Gorman et al.



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2019, Barnes et al. 2024). Soil biodiversity plays a crucial role in maintaining ecosystem processes, such as decomposition and nutrient cycling, thereby supporting ecosystem services such as food production, water regulation, waste decomposition and carbon sequestration (Bardgett and van der Putten 2014, Wagg et al. 2014, Pereira et al. 2018). Temperature, together with water availability, is one of the main factors driving the activity of soil communities (Wardle 2002, Lindo 2015). However, predicting how soil organisms respond to warming is challenging since previous research has shown contrasting responses (Blankinship et al. 2011, Pritchard 2011, Lang et al. 2014, Holmstrup et al. 2018, Barreto et al. 2021) due to many differential factors, such as the spatial and temporal variability of soil biodiversity, environmental context, and trophic interactions. Additionally, short-term and long-term warming studies can show contrasting results, as immediate responses of soil communities to higher temperatures may then change to more gradual adaptations or shifts over time (Bradford et al. 2008, Holmstrup et al. 2018). Responses may also differ with specific taxa or trophic level due to variation in temperature sensitivity that underlies different temperature responses in growth rates, reproduction rates, and interactions (Dell et al. 2011). These different attributes of soil ecosystems pose significant challenges for making generalized predictions of how warming will impact soil biodiversity and ecosystem functioning.

Warming may induce direct changes to soil invertebrate densities and species composition through two major mechanisms occurring simultaneously. Firstly, soil organisms have different thermal tolerances depending on their evolutionary histories (Jensen et al. 2019, Bennet et al. 2021). Some species of ectotherms, particularly those adapted to cooler environments, may have reduced tolerance to heat due to oxidative stress, which can lead to population decline or extinction at higher temperatures (Brown et al. 2004, Somero 2010, Saito et al. 2021). Consequently, warming could alter community composition and reduce diversity by filtering for species with higher temperature optima (O’Gorman et al. 2012, Sharp et al. 2014).

Secondly, organisms metabolic rates increase with temperature as warming accelerates molecular kinetics, driving faster physiological processes such as growth, mortality, and reproduction (Gillooly et al. 2002, Brown et al. 2004, Meehan 2006, Saito et al. 2021). The increase in metabolic rates imposes higher energetic demands, driving an increase in foraging and feeding rates of soil invertebrates (Lang et al. 2014, Jensen et al. 2017, Schwarz et al. 2017). However, resource availability in a warming system may become a limiting factor, particularly if resource quantity or quality is also temperature-dependant (Fierer et al. 2005). Lower trophic level consumers, such as decomposers, are expected to be more resistant to warming due to less limiting access to basal resources (Wardle 2002, Schwarz et al. 2017). In contrast, predators depend on fluctuating prey populations and may struggle to meet their energetic needs as warming could simultaneously impact prey availability (Brose et al. 2012). In the case of ectotherms, warming is expected to

favour small-bodied individuals over large-bodied ones due to the higher energetic demands of larger bodied organisms (Gardner et al. 2011, Vucic-Pestic et al. 2011, Thakur et al. 2017, Meehan et al. 2021, 2022). Since predators are generally larger than their prey, higher trophic levels will likely experience greater energetic constraints under warming conditions. These differential impacts of warming across trophic levels may lead to declining predation rates while decomposition rates are expected to increase. Consequently, shifts in top-down and bottom-up forces could drive significant changes in the stability of soil food webs in response to warming (Schwarz et al. 2017, Thakur et al. 2017, Barnes et al. 2024).

While laboratory and field micro- and mesocosms are useful for isolating the effects of temperature, they often lack environmental complexity. Moreover, their typically short duration can introduce additional limitations, potentially leading to ‘overreacted’ responses of the soil communities to warming in comparison with long-term experiments (Walker et al. 2020). However, long-term, large-scale studies are rare due to logistical challenges, and global-scale analyses incorporating data from different biomes are limited by confounding environmental variables that are difficult to control (De Boeck et al. 2015, Barreto et al. 2023). Hence, there is a pressing need for long-term, in situ warming experiments to establish causal temperature effects under future climate warming scenarios (Rustad 2008, De Boeck et al. 2015). In addition, most studies have focused on warming responses either at a broad community level or within specific taxonomic groups (e.g. Oribatida, Mesostigmata, Collembola) (Kardol et al. 2011, Barreto et al. 2023), and very few have examined trophic group-specific responses (Barreto et al. 2024). However, there is considerable evidence that global change impacts vary significantly across different trophic levels, which carry out unique ecosystem functions, highlighting the need to investigate multitrophic responses to warming (Hunt and Wall 2002, Soliveres et al. 2016). Furthermore, warming studies typically apply only few experimental temperatures (e.g. ambient versus warmed, Briones et al. 2009, Kardol et al. 2011, Thakur et al. 2023), which may fail to detect more fine-scaled community responses that emerge along continuous temperature gradients.

Geothermal systems are increasingly used as natural warming experiments to test ecosystem response to warming (O’Gorman et al. 2014, Sigurdsson et al. 2016). These ‘natural laboratories’ with diverse underlying temperature gradients allow for partial control of confounding environmental variables, while maintaining more realistic abiotic conditions. Furthermore, geothermal systems can provide decades of natural warming (Seward et al. 2015, van de Laar 2021). As a result, soil communities are able to undergo long-term natural assembly processes along thermal gradients. There have been recent studies using geothermal features in sub-Arctic regions that provide valuable insights into soil communities responses to long-term warming (Robinson et al. 2018, 2022, Dahl et al. 2023, Ferrin et al. 2023, Thakur et al. 2023), but we still lack experimental studies that 1) incorporate

continuous temperature gradients in geothermally warmed soils, 2) use standardized community metrics (e.g. density per square meter of soil) that can be used to compare the structure and composition of soil communities across studies, and 3) that investigate trophic level-specific responses to warming, given their unique roles in supporting ecosystem functions.

In this study, we investigate the long-term effects of soil warming on soil invertebrate communities by analyzing shifts in species density and diversity, considering both the whole soil invertebrate community and individual trophic levels along continuous natural geothermal gradients in Aotearoa New Zealand, where mean annual soil temperatures (MAT) range from 17 to 40°C. We hypothesized that warming 1) increases the overall density of the soil invertebrate community, driven by increased productivity; 2) decreases overall soil invertebrate diversity, as some species with lower thermal tolerances or higher metabolic needs may be lost, reducing species richness and evenness; and 3) induces differential responses across trophic levels, with predators showing the strongest declines in density and diversity due to higher energetic constraints.

Material and methods

Study site

The study was conducted at two geothermal sites within the Taupō Volcanic Zone, located in the northwest of New Zealand's North Island. One site was situated at the Arikikapakapa golf course in Rotorua (38°09'46.54"S, 176°14'56.90"E), while the other site was located at the Ngāpouri Research Farm in Waiotapu (38°21'51"S, 176°21'30"E). These sites were selected due to their geographic proximity and similar environmental features, minimizing potential biotic and abiotic variability, and due to their long-term historically geothermal activity reported (van de Laar 2021, Land Information New Zealand 2025). Both sites are managed grasslands with open exposure to sunlight and featuring no substantial slopes. Each site contained a single geothermal feature classified as 'heated ground' by GNS surveys (Seward et al. 2015), that exhibited a thermal gradient where soil temperatures were highest at the outer edges and gradually declined with distance from the edge. At the Arikikapakapa golf course, the geothermal feature measured 5 × 4 m with temperatures ranging from a mean annual soil temperature (MAT) of ~32°C at the hotspot edge to ~17°C, over a linear distance of 12 m. The site was uniformly covered mostly by *Axonopus fissifolius* (40%) and *Elymus repens* (15%), with lesser amounts of *Hypochaeris radicata* (5%) and *Leptospermum scoparium* (3%), which were regularly mowed, along with a few unidentified scattered mosses. At the Ngāpouri Research Farm site, a pasture regularly grazed by ovine and bovine cattle, the geothermal feature measured 4.2 × 4.0 m with temperatures ranging from a MAT of ~38°C at the hotspot edge to ~18°C at 20 m distance. The site, classified as High Producing Exotic Grassland (Manaaki

Whenua – Landcare Research 2020), was dominated by the presence of *Trifolium* spp., *Lolium* spp. and *Dactylis glomerata*, among other pasture species. The plant nomenclature follows the Biota of New Zealand database (Manaaki Whenua – Landcare Research 2025). Soils at both sites were classified as Typic Tephric Recent Soils (RTT), characterized by tephra-based deposits derived from rhyolitic rock, with loamy texture, and a very stony topsoil layer (0–10 cm). These soils have a good drainage, moderate permeability and soil moisture, deep rock depth, and low topsoil phosphorus retention (Lilburne et al. 2012, Manaaki Whenua – Landcare Research 2019). The Ngāpouri Research Farm site is located within the rohe (tribal district) of Ngāti Tahu-Ngāti Whaoa, who have mana whakahaere (authority) over the geothermal features located throughout this region.

Soil temperature monitoring and sampling

We conducted preliminary soil temperature monitoring at each site for five months prior to sampling to characterize the temperature gradients around the geothermal hotspots. The temperature was recorded using HOBO (Onset Corporation 2017–2021) and iButton (Maxim Integrated 2013) data loggers buried at 7.5 cm depth across multiple locations around the hotspots. Based on these profiles, we established 10 plots per site (n = 20) to capture the widest possible range of temperatures along the gradient. The temperature monitoring continued at each plot over the following year (June 2023 to July 2024, Fig. 1). We maintained a minimum distance of 2 m between plots to reduce potential non-independence of soil communities while simultaneously ensuring homogeneity of soil conditions by avoiding areas with varying vegetation composition, swampy conditions, or steep slopes.

Sampling was conducted in early December 2022 and repeated in December 2023, at the spring-summer transition, to capture the soil invertebrate community structure under conditions of high productivity, when water availability was not limiting and environmental temperatures are warmer. For each site, we collected one 10 cm depth × 5 cm diameter soil core per plot (n = 40) to target the soil invertebrate community, and five 10 cm depth × 2.2 cm diameter cores per plot (n = 100) for microbial respiration and biomass analyses, and to determine soil chemical properties. Cores were taken in close proximity within each plot to maintain consistent temperature conditions (Cesarz et al. 2019).

Soil microbial biomass and soil chemical properties

Soils from the 10.0 × 2.2 cm cores were sieved (<2 mm diameter), homogenized and used to determine soil microbial biomass, pH, water content and C:N ratios. Relative soil microbial biomass was estimated using the substrate-induced respiration (SIR) method, where glucose was added in the soil as an easily metabolizable carbon source to stimulate microbial activity (Anderson and Domsch 1978, Alster et al. 2023). Following a 5-h incubation at 20°C, we quantified CO₂ production (µg CO₂ h⁻¹ g⁻¹ soil dry weight) using an infrared gas analyzer (LI-7000 CO₂/H₂O Analyzer, LI-COR). Microbial biomass (µg C_{mic} g⁻¹ soil dry weight) was then estimated

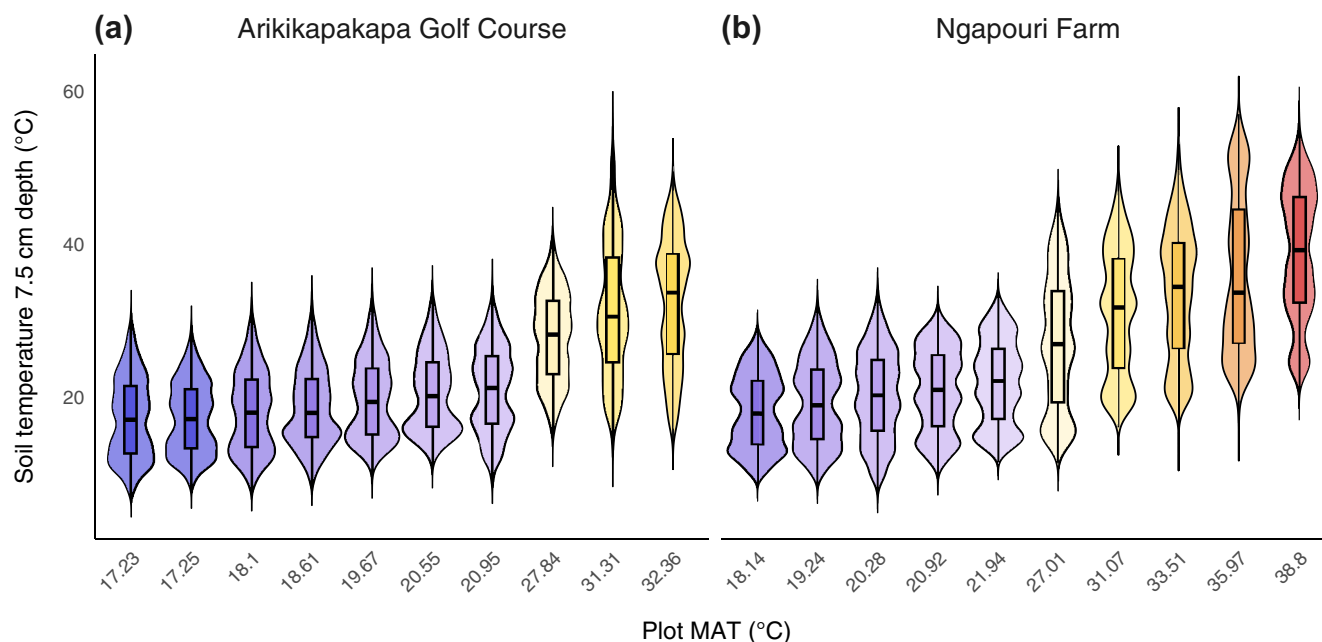


Figure 1. Range of soil temperatures (7.5 cm depth) monitored hourly during an entire year (June 2023 to July 2024) across two geothermal warming gradients in New Zealand; 1) Arikikapakapa Golf Course and 2) Ngāpouri Farm sites. Each violin plot represents the temperature distribution within an individual sampling plot, ordered by mean annual temperature (MAT, °C). Violin widths indicate the density of observed temperatures, with inner boxplots showing the interquartile range and median. Colours transition from blue (cooler plots) to red (warmer plots) based on MAT, illustrating the full range of geothermal warming within each site.

from respiration rates by applying established equations from Anderson and Domsch (1978) and Sparling et al. (1990). Soil water content (WC) was determined gravimetrically, where fresh soil subsamples were weighed, oven-dried at 105°C for 24 h until constant weight, and reweighed. Water content was then represented as the percentage of weight loss between dry soils and the initial fresh soils. Soil pH was measured by adding a standardized quantity of air-dried soil to Falcon tubes (10 g dry soil: 25 ml distilled water), mixing thoroughly, and allowing the suspension to settle for 30 min. pH was then recorded from the supernatant using a Denver Instrument UB-10 pH/mV meter. C:N ratios were determined by air-drying and grinding the soil, followed by total carbon and nitrogen analysis (vario EL cube; Elementar Analysensysteme).

Soil invertebrate extraction and identification

The soil invertebrate individuals were extracted from the 10 × 5 cm cores within 24 h of soil sampling using a Macfayden high-gradient heat extraction method (Macfayden 1953), where samples are placed in a multi-chamber apparatus and subjected to a heat gradient over 11 days, with temperatures gradually increasing from 20 to 55°C. Extracted organisms were preserved in 70% ethanol until sorted and identified. Extracted invertebrates were counted and identified to the family level and, where possible, to morphospecies level using stereo and compound microscopes (up to ×100 magnification level), and with the usage of taxonomic keys (Hopkin 2007, Shepherd and Crotty 2022, Lucidcentral 2022). Taxonomic groups were then assigned to trophic levels within the soil

food web primarily following Potapov et al. (2022) based on the feeding habits and preferences of soil invertebrate species, families, and orders: decomposers (feeding on soil organic matter, detritus, and microbes), predators (preying on other invertebrates), omnivores (consuming multiple resource types), and herbivores (feeding primarily on algae and plants) (Supporting information).

Data analysis

We conducted a two-way permutational multivariate analysis of variance (PERMANOVA) based on Bray–Curtis dissimilarity using the ‘vegan’ package (Oksanen et al. 2025) in R (www.r-project.org) to assess how soil temperature, water content, pH, C:N ratio, and microbial biomass influenced the species composition (i.e. relative abundances) of the whole soil invertebrate communities as well as for each trophic level individually. Non-metric multidimensional scaling (NMDS) plots were used to visualize compositional dissimilarity across the temperature gradient. To investigate specific measures of soil invertebrate density and diversity, we analysed the effects of temperature on soil invertebrate abundance per soil core (~20 cm²), observed species richness, Pielou’s evenness, and Hill diversity numbers (Shannon, $q=1$; Simpson, $q=2$) as measures of the effective number of species, using the ‘hillR’ package (Li 2018). Each metric was modelled for the whole soil invertebrate community and separately for each trophic level (predators, omnivores, and decomposers) using generalised linear mixed effects models (GLMMs), using the ‘glmmTMB’ package (Brooks et al. 2017), which allows flexibility in mixed-effects structures for Gaussian or non-Gaussian

data. Soil temperature and its interactions with water content, pH, C:N ratio, and microbial biomass were included as fixed effects, while experimental plot was treated as a random effect to avoid pseudoreplication from the repeated sampling (2022 and 2023). Due to collinearity issues, C:N ratios were excluded from the models. Field site (representing spatial variation) and sampling round (representing temporal variation) were included in initial models, but these variables were excluded from the final models as they did not improve model fit. Invertebrate density and species richness, which are overdispersed count data, were modelled using a negative binomial distribution. Evenness, expressed as a continuous proportion, was modelled using a beta distribution, while Shannon ($q=1$) and Simpson ($q=2$) diversity indices were modelled using Gaussian errors. All model predictors were mean-centred and scaled by their SD (z-transformed) to resolve model convergence issues and avoid structural multicollinearity. Model simplification was performed by applying the *dredge* function in the 'MuMin' package (Bartoń 2023) to construct models with all possible predictor combinations, where the maximal models included all predictors and their interactions with temperature and the simplest possible model included soil temperature only. We then identified the best model as the one with the lowest Akaike information criterion (AIC) score (by at least 2 AIC units). If two or more models yielded the lowest scores within 2 AIC units of each other, we selected the model with the fewest parameters as the top model. Model assumptions were checked and met for all the models corresponding to their respective distributions. We excluded herbivores from the community structure and diversity analyses of specific trophic levels, due to their low and patchy representation in the overall soil community, which also prevented us from fitting statistically reliable models for this trophic group.

Results

Soil invertebrate densities, temperature and other soil properties

A total of 4124 invertebrates from 131 morphospecies were collected across the experiment (Supporting information). From those, 2640 invertebrates (64%) from 68 morphospecies were classified as decomposers, 921 (22%) from 23 morphospecies as omnivores, 451 (11%) from 36 morphospecies as predators, and 112 (3%) from 12 morphospecies as herbivores. Mean annual soil temperature was negatively correlated with soil water content ($r=-0.67$, $p < 0.001$) and with soil C:N ratios ($r=-0.45$, $p=0.004$), but not with soil pH ($r=0.08$, $p=0.64$). At the same time, soil C:N ratios were positively correlated with soil water content ($r=0.36$, $p=0.021$) and negatively correlated with soil pH ($r=-0.79$, $p < 0.001$) (see the Supporting information for raw environmental data). Soil microbial biomass ($\mu\text{g C}_{\text{mic}} \text{g}^{-1}$ soil dry weight), as estimated by soil microbial respiration, showed a negative relationship with soil temperature ($\beta=-172.78$, $p=0.02$) and C:N ratios ($\beta=-215.24$, $p < 0.001$) and a

positive relationship with soil water content ($\beta=377.2$, $p < 0.001$) (Supporting information).

Soil invertebrate community compositional responses to temperature

We found distinct patterns in clustering of communities between warmer and cooler soils, indicating notable shifts in species relative abundances in response to temperature (Fig. 2). Results from the PERMANOVA analyses (Supporting information) indicated significant shifts in species composition in response to mean annual soil temperature, alongside soil pH, C:N ratio, water content and microbial biomass ($p < 0.05$) for the whole soil invertebrate community (Fig. 2a). We also observed significant effects for each of the three trophic levels analysed (Fig. 2b–d), with the exception of non-significant effects of soil water content and microbial biomass on omnivores and predators.

Soil invertebrate density and diversity responses to temperature

The total density of the whole soil invertebrate community (Fig. 3a, Table 1) increased significantly with soil temperature ($\beta=0.196$, $p=0.018$) and soil pH ($\beta=0.329$, $p < 0.001$). Additionally, there was a marginally significant negative interaction between soil temperature and pH ($\beta=-0.183$, $p=0.063$), suggesting that the positive effect of temperature on the total density was weaker at higher pH levels. Species richness increased with soil pH ($\beta=0.141$, $p=0.043$) and microbial biomass ($\beta=0.092$, $p=0.043$) but did not respond significantly to soil temperature. However, a significant negative interaction between temperature and pH ($\beta=-0.118$, $p=0.007$) indicates that the positive effect of pH on richness was diminished under higher temperatures. Species evenness was not directly affected by temperature ($\beta=-0.031$, $p > 0.05$) but increased significantly with water content ($\beta=0.213$, $p=0.023$). Similarly, Shannon (Hill $q=1$) and Simpson (Hill $q=2$) diversity showed no significant response to temperature ($\beta=-0.994$, $p > 0.05$ and $\beta=-1.072$, $p > 0.05$, respectively), though both increased significantly with microbial biomass ($\beta=1.651$, $p=0.007$ and $\beta=1.072$, $p=0.033$, respectively) (Fig. 4a, Table 1). Notably, decomposers numerically dominated the community (Supporting information) and exhibited response patterns similar to those observed at the whole-community level, suggesting they drive the overall trends.

At the trophic level, decomposers (Fig. 2b, Table 1) increased in density with soil temperature ($\beta=0.228$, $p=0.016$) and pH ($\beta=0.344$, $p < 0.001$). Decomposer species richness remained unchanged along the temperature gradient ($\beta=-0.046$, $p > 0.05$) but increased with pH ($\beta=0.362$, $p < 0.001$). A significant negative interaction between temperature and pH ($\beta=-0.133$, $p=0.024$) suggests that higher pH buffered potential negative effects of temperature on decomposer richness. Decomposer evenness was also unaffected by temperature ($\beta=0.399$, $p > 0.05$) but increased with microbial biomass ($\beta=0.640$, $p=0.007$). Furthermore, a strong positive interaction between microbial

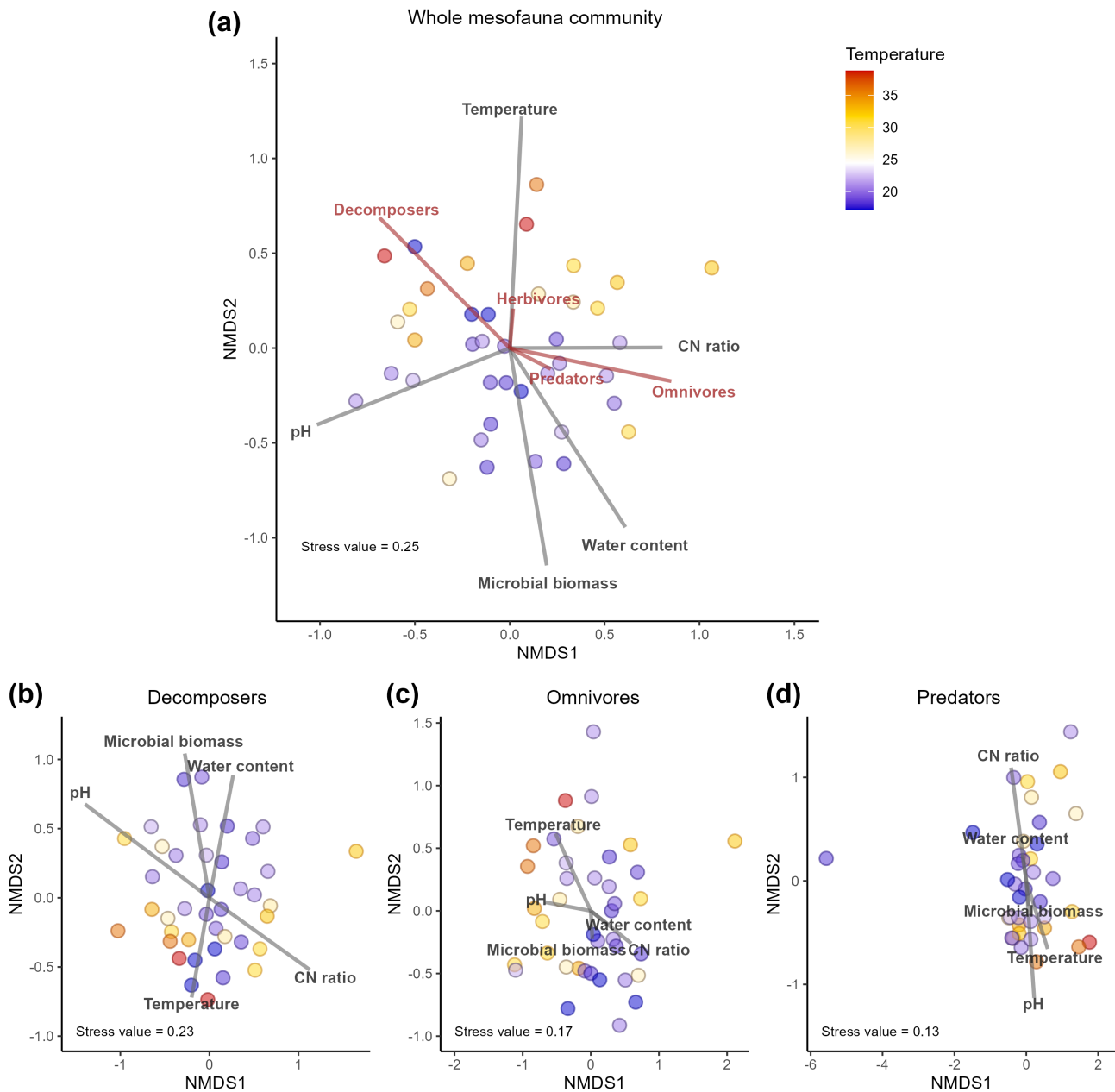


Figure 2. Nonmetric multidimensional scaling (NMDS) ordinations of species composition for (a) the whole soil invertebrate community and of individual trophic levels (b) decomposers, (c) omnivores, and (d) predators along the geothermal temperature gradient, based on Bray–Curtis dissimilarity. Each point represents one soil invertebrate community from an individual plot and sampling time ($n = 40$). Grey arrows (a–d) represent fitted vectors for each of the environmental factors (temperature, C:N ratio, water content, pH and microbial biomass) that significantly ($p < 0.05$) contribute to dissimilarities in species composition among plots. Red arrows (a) represent fitted vectors for soil invertebrate trophic levels within whole soil communities.

biomass and temperature ($\beta = 1.540$, $p < 0.001$) indicates that temperature effects on evenness were amplified at higher microbial biomass levels. Both Shannon (Hill $q = 1$) and Simpson (Hill $q = 2$) diversity significantly decreased with warming ($\beta = -0.938$, $p = 0.005$ and $\beta = -0.837$, $p = 0.005$, respectively) and strongly increased with pH ($\beta = 1.948$, $p < 0.001$ and $\beta = 1.142$, $p < 0.001$, respectively), with negative interactions with temperature ($\beta = -1.012$, $p = 0.003$ and $\beta = -0.569$, $p > 0.05$, respectively) (Fig. 4b, Table 1).

For omnivores (Fig. 3c, Table 1), species richness increased significantly with temperature ($\beta = 0.246$, $p = 0.028$), but neither density ($\beta = 0.276$, $p > 0.05$) nor evenness ($\beta = -0.151$, $p > 0.05$) responded to temperature changes. Microbial biomass positively affected both omnivore density ($\beta = 0.449$, $p = 0.011$) and species richness ($\beta = 0.255$, $p = 0.022$), with a positive interaction between temperature and pH on richness, suggesting that warmer conditions favoured omnivore richness more under higher pH levels. Both Shannon (Hill $q = 1$)

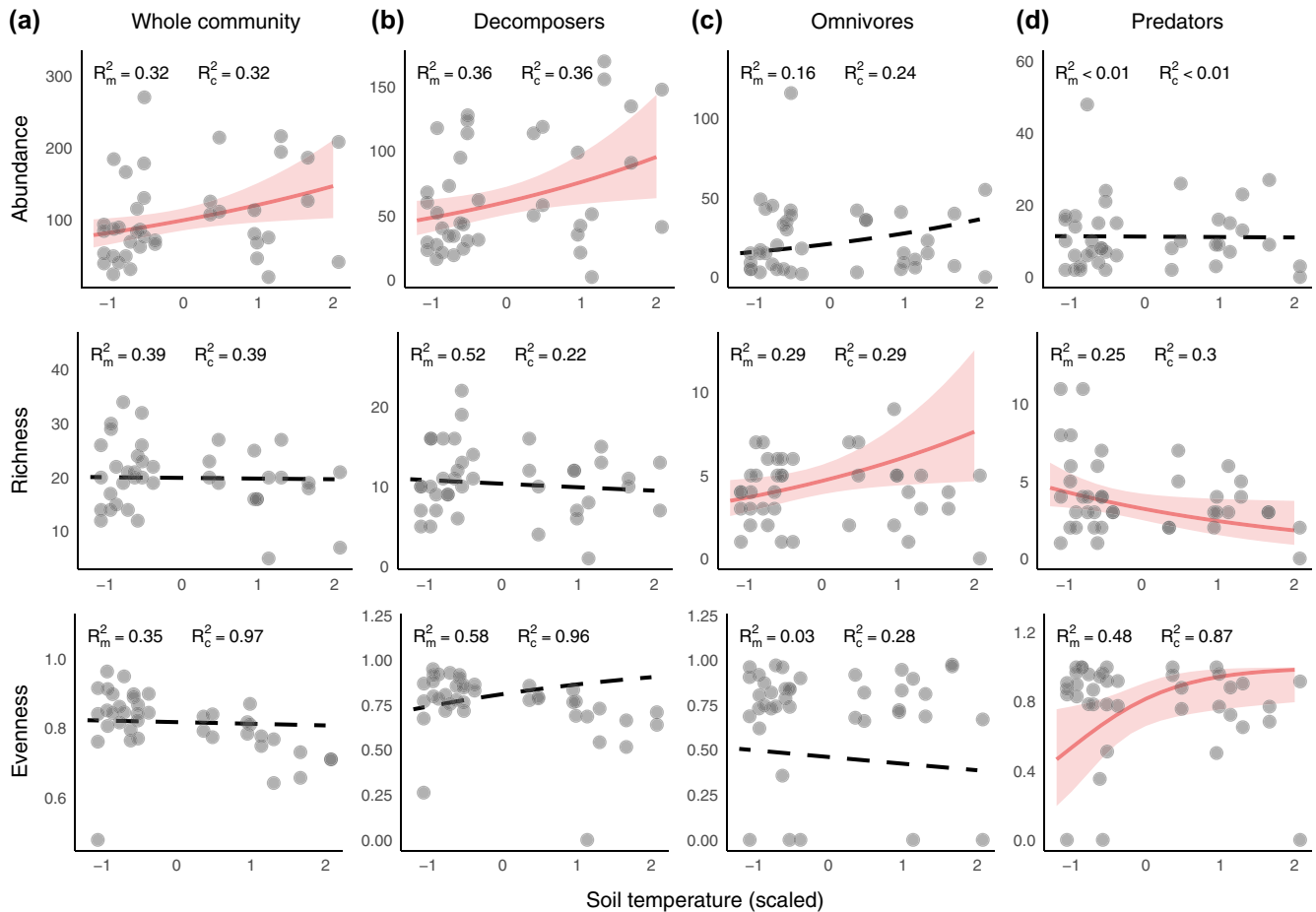


Figure 3. Soil invertebrate community responses in densities, observed species richness and species evenness along the geothermal temperature gradients for (a) the whole soil invertebrate community, (b) decomposer, (c) omnivore, and (d) predator trophic levels. Predicted partial effects of temperature from the mixed effects models are shown ($n=40$), whereby solid red trend lines and 95% confidence intervals represent statistically significant relationships and black dashed lines represent non-significant relationships. Marginal R^2 (R_m^2) represents variance explained by fixed effects alone, and conditional R^2 (R_c^2) represents variance explained by both fixed and random effects combined.

and Simpson (Hill $q=2$) diversity were directly unaffected by temperature ($\beta=0.377$, $p > 0.05$ and $\beta=0.205$, $p > 0.05$, respectively). However, both diversity facets significantly decreased with pH ($\beta=-0.460$, $p=0.01$ and $\beta=-0.369$, $p=0.022$, respectively) and increased with microbial biomass ($\beta=0.712$, $p < 0.001$ and $\beta=0.529$, $p=0.005$, respectively) (Fig. 4c, Table 1).

Predator responses to temperature were distinct from other trophic groups (Fig. 3d, Table 1). While predator density remained unaffected ($\beta=-0.010$, $p > 0.05$), species richness declined significantly with increasing temperature ($\beta=-0.289$, $p=0.041$). A significant negative interaction between microbial biomass and temperature ($\beta=-0.318$, $p=0.038$) suggests that microbial biomass buffered temperature effects on predator richness (Table 1). However, predator evenness increased with temperature ($\beta=1.365$, $p=0.024$) and soil water content ($\beta=0.766$, $p=0.045$). A positive interaction between microbial biomass and temperature ($\beta=1.577$, $p < 0.001$) suggests that the increase in predator evenness under warming was more pronounced

when microbial biomass was higher. Shannon (Hill $q=1$) diversity declined with increasing temperature ($\beta=-0.816$, $p=0.030$), but this relationship was dependent on microbial biomass, such that the negative effect of temperature was reduced at higher microbial biomass ($\beta=-0.923$, $p=0.028$). In contrast, Simpson (Hill $q=2$) diversity was not affected by temperature ($\beta=-0.150$, $p > 0.05$), though it decreased with pH ($\beta=-0.399$, $p=0.049$) and increased with microbial biomass ($\beta=0.562$, $p=0.019$) (Fig. 4d, Table 1).

Discussion

We explored the long-term effects of soil geothermal warming on the composition, density and diversity of soil invertebrate communities. Our results confirm that while temperature strongly influences soil invertebrate communities, its effects are highly variable across trophic levels and modulated by other environmental properties, such as soil water content, pH and microbial biomass (Fig. 2a).

Table 1. Partial effects from generalized linear mixed-effects models (GLMMs) assessing the influence of mean annual soil temperature and additional environmental covariates (soil pH, water content, microbial biomass) with their interaction with temperature on invertebrate density, species richness, evenness (Pielou's index), Shannon (Hill q = 1) and Simpson (Hill q = 2) diversity both for the whole community and by trophic group (decomposers, omnivores, predators). Statistically significant effects (p < 0.05) are shown in bold.

	Response (model)	Mean annual soil temperature		Soil pH		Temperature: pH		Soil water content		Temperature: WC		Microbial biomass		Temperature: Microbial biomass	
		Estimate	p-value	Estimate	p-value	Estimate	p-value	Estimate	p-value	Estimate	p-value	Estimate	p-value	Estimate	p-value
Whole community	Density	0.196	0.018	0.329	<0.001	-0.183	0.063								
	Richness	-0.006	0.892	0.141	0.002	-0.118	0.007					0.093	0.043		
	Evenness	-0.031	0.812					0.213	0.023			1.651	0.007		
	Shannon (Hill q = 1)	-0.994	0.149												
	Simpson (Hill q = 2)	-1.072	0.063									1.072	0.033		
	Density	0.228	0.016	0.344	<0.001										
Decomposers	Richness	-0.044	0.420	0.362	<0.001	-0.133	0.024								
	Evenness	0.399	0.188					0.080	0.767	-0.061	0.008	0.640	0.008	1.547	<0.001
	Shannon (Hill q = 1)	-0.938	0.005	1.948	<0.001	-1.012	0.003								
	Simpson (Hill q = 2)	-0.837	0.005	1.142	<0.001	-0.569	0.066								
	Density	0.276	0.141												
	Richness	0.246	0.028			0.258	0.018					0.449	0.011		
Omnivores	Evenness	-0.151	0.523								0.255	0.022			
	Shannon (Hill q = 1)	0.377	0.063	-0.460	0.010						0.712	<0.001			
	Simpson (Hill q = 2)	0.205	0.259	-0.369	0.022						0.529	0.005			
	Density	-0.010	0.937												
	Richness	-0.289	0.041												
	Evenness	1.365	0.024					0.766	0.045			0.069	0.536	-0.318	0.038
Predators	Shannon (Hill q = 1)	-0.816	0.030								0.220	0.510	1.577	<0.001	
	Simpson (Hill q = 2)	-0.150	0.513	-0.399	0.049						0.297	0.352	-0.923	0.028	
	Density														
	Richness														
	Evenness														
	Shannon (Hill q = 1)														

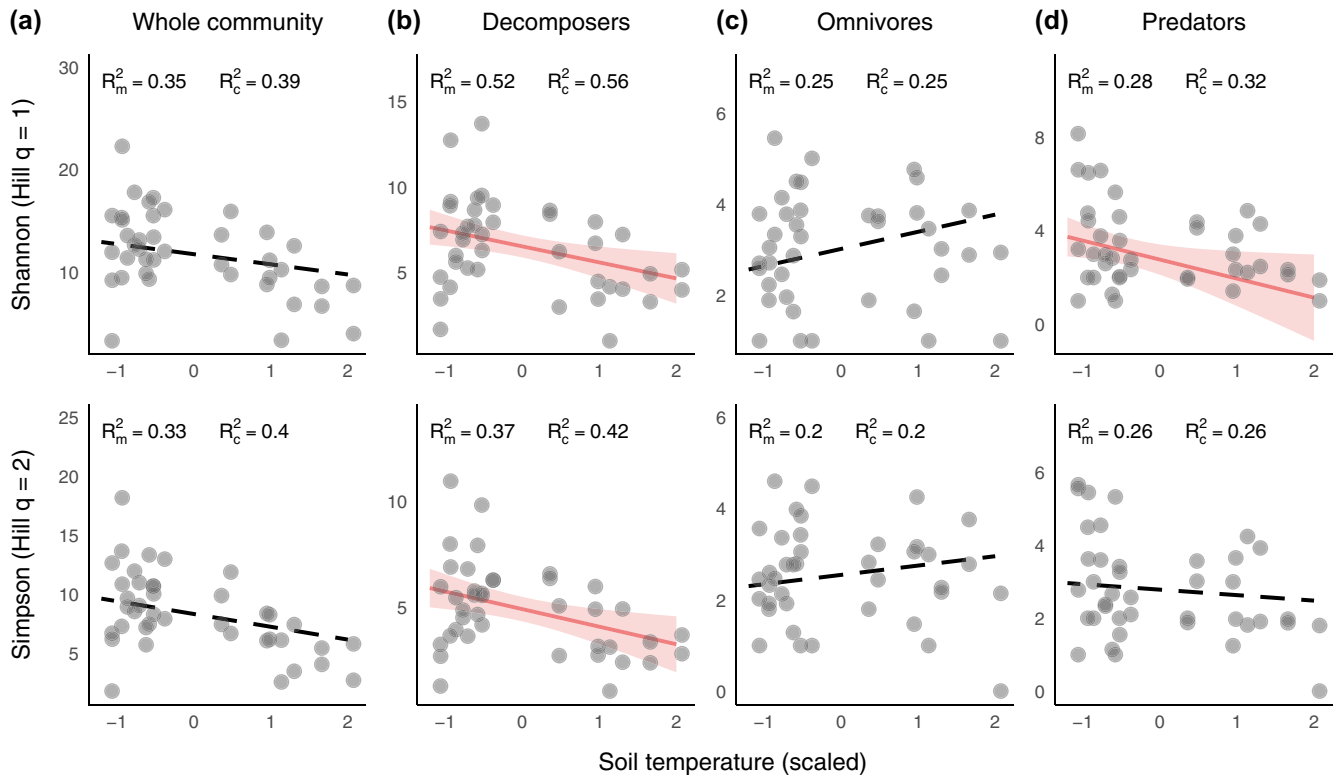


Figure 4. Soil invertebrate community responses for Shannon (Hill $q = 1$) and Simpson (Hill $q = 2$) diversity along the geothermal temperature gradients for (a) the whole soil invertebrate community, (b) decomposer, (c) omnivore, and (d) predator trophic levels. Predicted partial effects of temperature from the mixed effects models are shown ($n = 40$), whereby solid red trend lines and 95% confidence intervals represent statistically significant relationships and black dashed lines represent non-significant relationships. Marginal R^2 (R_m^2) represents variance explained by fixed effects alone, and conditional R^2 (R_c^2) represents variance explained by both fixed and random effects combined.

Trophic-level differences emphasize that warming impacts are not uniform across functional groups, with decomposers largely driving whole-community responses with overall increases in densities (Fig. 2b–d). We found that diversity metrics generally declined under warming, with the exception of omnivores. Although decomposer richness and evenness remained unchanged, both their more dominant and rare species appear to decrease significantly with warming (reflected by declines in Hill $q = 1$ and $q = 2$ indices), indicating a reciprocal increase in the number of species with intermediate abundances. In contrast, omnivores exhibited higher species richness under warming, whereas predators showed declines in Shannon diversity (Hill $q = 1$) and species richness but increases in evenness (Fig. 3b–d, 4b–d). These divergent trends suggest that although certain trophic levels may benefit from increased temperatures, others – predators in particular – are more susceptible to species loss, potentially due to metabolic constraints and changes in prey dynamics. These findings contribute to an increasing body of research demonstrating that the increase of temperatures due to global warming will alter soil communities' structure and composition (Briones et al. 2009, Pritchard 2011).

As we predicted, the total density of soil invertebrate communities increased significantly with temperatures (Fig. 3a), suggesting that warming enhances overall

invertebrate productivity, and is consistent with previous geothermal studies showing sustained density increases under direct warming (Robinson et al. 2018, Thakur et al. 2023). We also expected total species richness and evenness to decline due to temperature driven effects, such as the loss of taxa with lower thermal tolerance and the rise of thermally advantaged ones with faster growth rates. Additionally, warming-induced metabolic demands might intensify foraging and competition, leading to differential competitive performance among taxa (Englund et al. 2011, Brose et al. 2012, Reuman et al. 2014). Instead, our findings suggest that soil pH, a well-established determinant of soil microbial community composition (Hågvar et al. 1980, Fierer and Jackson 2006), was a strong driver of species richness and density for the whole invertebrate community rather than temperature alone, with strong negative interactions with temperature. Additionally, we found that declining water content along the thermal gradient likely drove the decrease in overall species evenness, mirroring climate projections predicting increased drought frequency in warming scenarios (Ranasinghe et al. 2021). This is in line with what many previous long-term warming studies found, that shifts in soil invertebrate diversity are mediated by temperature-mediated shifts in other environmental variables, such as water content (Barreto et al. 2023), carbon and nitrogen availability (Ferrín et al. 2023), pH, and

plant community densities and composition (Robinson et al. 2018).

When we examined temperature responses within trophic levels, decomposer responses dominated the whole-community trends, which accounted for 64% of the whole soil invertebrate community. This dominance reflects a typical soil food web pyramidal structure, where decomposers generally dominate the vast majority of biomass (Wardle 2002, Bardgett and van der Putten 2014). The significant increase in decomposer densities aligns with some studies reporting specific decomposer taxa increase with warming (e.g. Oribatid mites increase in a short-term mesocosm experiment, Briones et al. 2009), but contrasts with others (e.g. declines in Collembola biomass in geothermally warmed sub-Arctic soils, Thakur et al. 2023). More complex temperature effects have also been shown, such as a unimodal response in mite biomass, with increases in moderately warmed soils but declines in highly warmed soils (Thakur et al. 2023). In contrast, we found a linear response along the thermal gradient. In addition, another study in Icelandic geothermally warmed soils found that soil organic matter, rather than soil temperature, was the main driver of decomposer community shifts (Robinson et al. 2022). Instead, our analyses detected temperature effects on decomposer densities, after accounting for environmental covariates. These findings suggest that warming, alone, can drive shifts in decomposer community composition and density, possibly due to enhanced population growth rates followed by temperature-dependent increases in metabolism (Dell et al. 2011). The contrasting findings of our study compared to these previous geothermal soil experiments may partly arise because the taxa in our system lack the same physiological constraints of high-latitude species, which often exhibit lower thermal thresholds (Nielsen and Wall 2013), allowing them to thrive under elevated temperatures. In addition, decomposers are expected to be less affected by perturbations than consumers at higher trophic levels, whose survival depends mainly on prey availability (Bardgett and van der Putten 2014). Decomposers feed on diverse soil basal resources such as soil litter, soil organic matter and microbes, with some taxa being more generalist feeders and other taxa more specialised on a particular resource. Thus, despite finding that microbial biomass decreased with temperature, likely due to a potential temperature-mediated decrease in water content, we did not find that microbial biomass influenced decomposer responses to temperature. Instead, microbial biomass surprisingly appeared to increase Shannon ($q=1$) and Simpson ($q=2$) diversity of omnivores and predators. While decomposer species richness was not directly affected by temperature, we found a consistent decrease in Shannon (Hill $q=1$) and Simpson (Hill $q=2$). This suggests that temperature redistributed the relative abundances of decomposers, where the loss of dominant or rare species is compensated by the increase of intermediately abundant taxa, consequently reducing the effective number of species. In addition, species evenness varied significantly with microbial biomass, suggesting that some taxa, probably microbial feeders, might have perished along the thermal gradient due to limitation in their

primary food resource. As a result, higher decomposer densities but reduced microbial biomass introduces uncertainties around the overall effect of warming on decomposition rates and nutrient cycling, which raises important questions about whether warming will accelerate or destabilize nutrient release.

In contrast, omnivores densities were invariant with temperature differences but exhibited a significant rise in species richness with temperature. This suggested that trophic flexibility (i.e. the capacity of omnivores to exploit both animal prey and basal resources) could buffer them against the energetic constraints imposed by higher temperatures. By feeding opportunistically on other invertebrates and on organic matter, omnivores may have maintained or even expanded their niche space under warming conditions. However, recent evidence suggests that greater foraging flexibility could ultimately increase the extinction probability of consumers with warming, because of reduced consumption efficiency under more adverse conditions (Gauzens et al. 2024). Whether this is the case for omnivorous consumers that forage across basal resources and animal prey, however, is still unclear.

Despite the significant increase in decomposer densities, predator densities remained unchanged, a pattern also observed by some previous studies (Briones et al. 2009), but also in contrast with others reporting predator increases (Thakur et al. 2018). However, we found that predator richness and Shannon (Hill $q=1$) diversity decreased alongside an increase in predator evenness. This suggests that warming may have filtered out particularly vulnerable taxa with lower thermal tolerance or specialized predatory species, while allowing more warming-tolerant or generalist predatory taxa to persist by switching to alternative prey sources. This could be explained by warming-induced increases in predator metabolic demands outweighing the energetic gains from increased prey densities (Fussmann et al. 2014, Meehan and Lindo 2023). While warming might enhance invertebrate activity and mobility that could lead to greater predator-prey encounters and attack rates and lower prey handling times (Kruse et al. 2008, Lang et al. 2012), prey may simultaneously improve escape abilities with warming, potentially reducing predatory attacks and offsetting predation success (Grigaltchik et al. 2012). Furthermore, if predators modify their foraging habits or dietary preferences in response to warming, this may compromise predator persistence in warmer environments. Recent empirical models suggest that predators may shift from selecting prey based on traits (e.g. size, energy content) to density-based prey selection (Gauzens et al. 2024). This shift to more abundant but less energetically rewarding prey selection may fail to meet their energetic demands in the long-term, ultimately leading to species extinctions. At the same time, warming-induced increases in decomposer availability could favour predators capable of exploiting abundant but lower-energy rewarding prey, reducing the dominance of specific taxa and increasing evenness.

Shifts in other environmental properties, such as water content, may further influence predator species distributions, disproportionately affecting some taxa while redistributing

density among others. These results suggest that warming restructures predator communities by decreasing taxonomic diversity, where certain consumer taxa are lost while promoting a more balanced distribution of surviving species with the observed increase in evenness. This aligns with recent theoretical and empirical findings showing that warming, and the consequential increase in metabolic demands, may strengthen interactions but also increase extinction risks, particularly for higher trophic levels when energetic needs outpace prey availability (Fussmann et al. 2014, Barnes et al. 2024). Such shifts may lead to food web simplification (O’Gorman et al. 2019), where warming would reduce trophic complexity (O’Gorman et al. 2023), alter energy flux pathways (Schwarz et al. 2017) and predator–prey dynamics (Meehan and Lindo 2023, Gauzens et al. 2024), and weaken the structural stability of soil communities. As a result, their resistance and resilience to additional climate change related disturbances may be compromised, ultimately diminishing the capacity of soil ecosystems to sustain multifunctionality under environmental change (Barnes et al. 2024).

This study provides evidence that temperature effects vary across trophic levels in soil food webs, and that long-term warming may have complex, environmentally context-dependent effects on soil invertebrate communities. In contrast to previous studies that have found weak or contrasting effects of temperature on soil communities, we were able to distinguish the main effects of temperature on soil food webs, after accounting for variation in other soil environmental factors due to key methodological advantages in our experimental design. First, the use of a wide and continuous temperature gradient enabled us to detect continuous responses to temperature that may have been obscured in shorter temperature gradients. Second, the use of a natural, long-term warming system ensured that the soil communities were not influenced by short-term disturbance artifacts, which might appear in manipulative experiments. Third, by setting up entire sampling sites along temperature gradients radiating from a single geothermal hotspot, we were able to control for confounding soil variables – such as pH, water content, and microbial biomass – which allowed us to isolate the direct effects of temperature. Lastly, with our multi-trophic taxonomic approach we were able to detect differential warming responses across trophic levels, with decomposers, omnivores, and predators showing diverse patterns in density, richness, and evenness. In doing so, our research contributes to the growing recognition that soil biodiversity and ecosystem functions are at risk under climate change, and highlights the need for long-term multi-trophic studies that disentangle warming effects on soil biodiversity. Such approaches are essential to predicting future shifts in the stability and multifunctionality of soil ecosystems under ongoing global change.

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Author contributions

Estela Folch Chaos: Conceptualization (equal); Data curation (lead); Formal analysis (lead); Investigation (lead); Methodology (lead); Resources (lead); Writing – original draft (lead). **Charlotte Alster:** Resources (supporting); Supervision (supporting); Validation (supporting); Writing – review and editing (supporting). **Louis Schipper:** Funding acquisition (lead); Project administration (equal); Resources (supporting); Supervision (supporting); Validation (supporting); Writing – review and editing (supporting). **Andrew D. Barnes:** Conceptualization (equal); Formal analysis (supporting); Methodology (supporting); Project administration (supporting); Resources (supporting); Supervision (lead); Validation (lead); Writing – review and editing (supporting).

Data availability statement

Data are available at Zenodo: <https://doi.org/10.5281/zenodo.17904996> (Chaos and Barnes 2025)

Supporting information

The Supporting information associated with this article is available with the online version.

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