SOIL ORGANISMS **97** (3) · 2025

Online First
https://doi.org/10.25674/444

Soil fauna community body size structure mediates litter loss responses to temperature and plant litter treatments in ecological microcosms

Zhaoxing Li[1], Nick T. Girkin[1,2,†], Jacqueline A. Hannam[1,3,†] and Alice S.A. Johnston[1,*]

[1] Cranfield Environment Centre, Faculty of Engineering and Applied Sciences, Cranfield University, Bedfordshire, MK43 0AL, UK
[2] Agricultural and Environmental Sciences, School of Biosciences, University of Nottingham, Nottingham, LE12 5RD, UK
[3] Natural Resource Institute, Faculty of Engineering and Science, University of Greenwich, Kent, ME4 4TB, UK
[*] Corresponding author, email: a.s.johnston@cranfield.ac.uk
[†] Authors contributed equally

Received 09 January 2025 | Accepted 25 June 2025 | Published online 20 October 2025

Abstract

Litter decomposition is strongly influenced by soil communities, composed of soil biota which display large variations in body size. Body size plays a central role in metabolism and mediates the functional potential of soil biota, but the influence of soil community body size structure on litter decomposition is unresolved. Here, we conduct ecological microcosm experiments to investigate how soil fauna community body size structure mediates litter loss in response to temperature and plant litter availability. Community-weighted mean body mass (CWMBM) calculations are taken as an indicator of structural shifts in soil fauna community body size across treatments. Structural equation models revealed that CWMBM was strongly influenced by Collembola body mass and exhibited a non-linear response to temperature, with convergence at intermediate temperatures. Collembola CWMBM mediated a portion of the temperature effect on CWMBM, while Nematode responses were opposite and weakly correlated. Litter loss was jointly driven by CWMBM and plant litter input, with no direct effect of temperature. Sensitivity and mediation analyses confirmed the central role of Collembola in linking temperature to soil fauna community shifts but identified plant litter availability as the dominant driver of litter loss. Linear mixed effects models of relative litter loss, however, highlight a key role of the soil fauna community across temperature treatments when the effects of plant litter availability are controlled. Our experiment included extreme low plant litter availability (0 g) and high temperature (30°C) treatments to detect critical thresholds for the functioning of soil communities, but high variation in temperature responses between 20 and 30°C require exploration in future studies. Although our experiment did not isolate body size effects independently of treatments, our findings suggest an important role of soil fauna body size structure in soil functioning. Future work, experiments and statistical models should be designed to test the causal mechanisms driving emergent shifts in soil community structure and soil function in response to environmental perturbations. Such an understanding could guide management practices which buffer against potentially detrimental effects of environmental change.

Keywords soil mesofauna | community structure | functional traits | litter decomposition | ecosystem functioning

1 Introduction

Litter decomposition is a critical component of the global net land carbon sink and is strongly influenced by climate, plant litter availability and quality, and soil community composition at a global scale (Heděnec et al., 2022; Swift, 1979). Syntheses of litter bag field studies across globally distributed ecosystems have identified a significant climate-dependent effect of soil fauna on litter decomposition in temperate and wet tropical regions (Frouz et al., 2015; García-Palacios et al., 2013; Wall et al., 2008). However, the complex interplay between soil fauna communities with site-specific climatic and plant conditions in field experiments limits current insights

ISSN 1864-6417 · **eISSN** 2509-9523

into the general relationship between soil community composition and litter decomposition. The role of soil fauna communities in mediating litter decomposition is also not well known.

Climate directs litter decomposition rates through well-known reaction kinetics (Swift, 1979), and by constraining both plant and soil biota (microbial and faunal) distribution and metabolism (Joly et al., 2023). For instance, the temperature sensitivity of soil biota metabolism (Johnston & Sibly, 2018) relative to resource availability and quality constrains soil community composition across latitudinal gradients (Johnston & Sibly, 2020). Nutrient availability (e.g. soil carbon:nitogen (C:N) and phosphorous (C:P) ratios) modulates litter decomposition rates by directing plant carbon allocation above- or below-ground (Gill & Finzi, 2016), with consequences on the availability of food resources for different soil biota groups. Nutrient availability and correlated edaphic variables such as soil pH and soil organic carbon (SOC) thus show strong relationships with the composition of soil communities at a global scale (Johnston, 2019; Johnston & Sibly, 2020; Phillips et al., 2021; Tedersoo et al., 2014). The influence of both climate and nutrient availability on the role of soil fauna in litter decomposition have most often been studied according to their effect on microbial activity, and differences between bacterial- and fungal-dominated food webs (Geisen, 2016; Lavelle et al., 1997; Wardle et al., 2006). Soil food web interactions, however, are complicated by the effects of abiotic factors (e.g. temperature) on various trophic groups and feedbacks between bottom-up and top-down food web control (Sauvadet et al., 2016).

Soil community groups (e.g. bacteria, fungi, microfauna and microarthropods) respond differently to environmental perturbations such as climate extremes and changing resource availability, leading to novel shifts in the functional composition of soil communities (Bardgett & Caruso, 2020; Cifuentes-Croquevielle et al., 2020; Siebert et al., 2020). Different environmental perturbations can also influence soil community groups via different mechanisms and at different levels of biological organisation (Johnston, 2024). For instance, in an experimental field study of the interactive effects of climate and land use changes on soil microarthropods at the Global Change Experimental Facility in Central Germany, Yin et al. (2020) found climate change (increased temperature and precipitation) to reduce individual body size and land use intensification to reduce population density. In a sub-Arctic dwarf shrub heathland, Bokhorst et al. (2012) found extreme winter warming events to have a disproportionate effect on smaller body sized soil microarthropods (Prostigmata and eu-edaphic Collembola) that was not apparent from species-level metrics. Enhanced and reduced litter decomposition rates in warm and cold climates are also typically facilitated by soil communities composed of soil biota with larger and smaller body sizes respectively (Petersen & Luxton, 1982; Swift, 1979). The interactive effects of climate and plant controls on soil fauna and litter decomposition could thus be explained by the functional composition of soil communities.

Body size is widely adopted for the functional classification of soil community groups and is strongly related to numerous life history traits such as metabolic and ingestion rates, generation times and population size (Bonfanti et al., 2018; Luan et al., 2020; Tan et al., 2021). The functional roles of soil communities are strongly influenced by their body size ranges within functional groups (Zhu et al., 2024) but less evidence is available across functional groups as this relationship is complicated by complex food web interactions. Larger soil mesofauna (e.g. collembola) break down plant litter into smaller fragments, while soil microfauna (e.g. nematodes) are typically classified as fungal or bacterial feeders, regulating litter decomposition and nutrient mineralization through the soil microbial community (Beare et al., 1992; Szanser et al., 2011). Species richness has also been shown to decline with increasing body size, making larger sized biota more rare and thus more functionally unique, and potentially more functionally important in determining decomposition dynamics due to their higher population biomass (Andriuzzi et al., 2020; Potapov et al., 2019). Larger soil biota are also typically more susceptible to environmental perturbations (e.g. land management practices and climate extremes) via reductions in body size and/or population density (Yin et al., 2020). Together, these observations suggest that the role of soil fauna in litter decomposition, across environmental gradients, could be explained by accounting for the body size structure of soil communities.

Here, we use ecological microcosms to investigate the interactive effects of temperature and plant litter availability on the body size structure and community composition of soil communities (bacteria, fungi, nematodes, mites and collembola) and litter loss. We use extreme ranges in our temperature and plant litter treatments to identify critical thresholds in energy availability and expenditure conditions on soil fauna with different body size ranges. The central hypothesis we test is that larger soil mesofauna are more sensitive to extreme temperatures and resource limitation, and that their reduced representation in the soil community structure will correlate with decreased litter decomposition.

2 Methods

2.1 Site description and experimental treatments

Ecological microcosms (n = 3 replicates for each treatment and timepoint (n = 5)) were prepared with soils (Endostagnic Luvisols, clay loam, pH 6.8) collected from an arable farm in Shefford, southeast England in October 2022. Air temperature during soil collection was 15°C, and gravimetric soil moisture was between 38 and 43%. 150 L of soil was collected from four randomly designated areas in a field planted with winter wheat. Soil was collected between 5 and 20 cm depth as soil mesofauna are most abundant at this depth (Petersen & Luxton, 1982). During collection, fresh soil samples were passed through a 5 mm diameter mesh sieve to remove large debris such as stones and roots. Winter wheat litter from the same site was collected and stored separate to the soil. All soil and litter were transported to Cranfield University and maintained at an air temperature of 15°C and 40% gravimetric soil moisture for three weeks prior to experimental setup. The homogenised soil was stored in two bulk containers and air flow was maintained to ensure soil community survival. A sample of the soil was used to measure the soil community composition on the collection day to monitor soil community composition during the storage period. On the day of the experimental setup, the bulk soil was homogenised again and 500g of soil placed in 1L plastic containers, which were randomly assigned a treatment code and replicate number.

Experimental treatments were designed to disentangle the effects of broad temperature and resource availability ranges on soil community composition and litter decomposition. Experimental treatments included four temperatures (4, 12, 20 and 30°C) and three plant litter availability treatments (0, 2.5 and 5 g of dried plant material in litter bags), with three replicates of each treatment combination. Temperature levels were selected to reflect a wide gradient from suboptimal to extreme conditions based on seasonal soil temperatures in temperate agricultural regions, with 30°C intentionally high to represent a functional stress threshold and test whether resource availability from the high plant litter treatment alleviated the detrimental effects of extreme temperatures. To destructively sample three replicates of each treatment across multiple timepoints (0, 30, 60, 90, 120 days) throughout the experiment, experimental set up was for a total of 180 containers. Microbial and soil chemical properties were measured at the start and end of the 16-week experimental period, while soil fauna metrics were measured at each timepoint. For the main statistical analysis we use the final timepoint to reflect the cumulative experimental treatment effects. 4°C treatments were maintained in fridges and 12 and 30°C treatments were maintained at constant temperatures using two incubators. To avoid the risk of a high temperature shock for the 30°C treatment we increased the temperature of the incubator incrementally from ~15°C by 1°C per 48 hours over 30 days. The 20°C treatment was maintained at room temperature, and soil temperature variations monitored using a Mcbazel soil temperature meter. Initial microcosm soil bulk density was 1.69 g cm^{-3}. Soil moisture was checked every 48 hours for the 4, 12 and 20°C treatments or every 24 hours for the 30°C treatment and maintained at 40% using distilled water. Lighting across treatments was not controlled. Plant litter treatments were instigated following a 30 day temperature incubation period (see Figure S1 for a comparison of soil CWMBM between day 0 of the experiment (when plant litter treatments were established, after temperature incubation) and day -30 (when microcosms were established, prior to temperature incubation periods). Litter bags were stainless steel with a 1.2 mm size mesh, with nylon wire stitches. Additional non-toxic plastic balls were packed into litter bags with 0g or 2.5g plant litter to provide an equal weight of 5 g across all treatments. Each experimental microcosm was sampled every 30 days over a 16-week period to monitor changes in soil community body size structure over time. Soil microbial communities, extractable N, available P and soil organic matter (SOM) content were measured twice, at the start and end of experimental period, together with plant litter loss.

Experimental microcosms do have some limitations, deviating from real world conditions, and thus potentially compromising the ability to compare or upscale findings to the field (Chen et al., 2023). For example, fixed temperature and moisture conditions do not replicate the daily to seasonal dynamics of natural environments. However, crucially, they do allow isolation and investigation of individual and interactive environmental conditions on soil fauna community composition (Kitagami et al., 2020), the focus of this study.

2.2 Soil community composition

Soil fauna were extracted from each replicate soil sample using Tullgren and Bearman funnels for soil microarthropods (mites and collembola) and nematodes, respectively. The abundance of soil fauna in three different body size ranges (< 0.5mm, between 0.5-1mm, and > 1 mm) were identified and measured by micro rulers under a dissecting microscope. Body size ranges were used to classify fauna into micro- and meso-faunal groups, which informed CWMBM calculations and group-level analyses. All individuals were measured and identified to the family level if it was not possible to identify the functional groups below. The Tullgren funnel method adopted here placed 300g of fresh soil in each funnel, which were maintained under 40W lights for 72 hours to create a desiccation gradient. Each funnel was sampled every 24 hours to extract soil mites and collembola in containers placed beneath the funnels. Soil nematodes were extracted using 50 g of fresh soil from mesocosm replicates in Bearman funnels, which were maintained at ambient temperature (> 15°C) for 72 hours and sampled once every 24 hours.

Soil micro- and meso-fauna in each body size group were identified to family level and classified according to the following functional groups: fungivore mites, predator mites, decomposer collembola, plant parasitic nematodes, bacterivore nematodes, fungivore nematodes, omnivore nematodes and predatory nematodes (Briones, 2014; Rusek, 1998). Soil fauna were identified according to existing online databases (Balogh & Balogh, 1992; G. O. Evans & Till, 1979; Kalúz & Fenďa, 2005; Skvarla et al., 2014) and their abundances recorded for each body size and functional group for aggregation in taxonomic group CWMBM calculations. Body lengths (*L*, µm for nematodes and mm for mites and collembola) of individuals in each functional and body size group were measured using a micro ruler under the microscope for a subset of at least 20 identifiable individuals (van den Hoogen et al., 2019). Body mass (*M*, mg dry weight) was then estimated from *L* according to $M = aL^b$, where the parameters a and b were 0.153 and 2.300 for collembola, 0.053 and 2.494 for mites, and 0.00113 and 12.387 for nematodes (Douce, 1976; Hódar, 1996; van den Hoogen et al., 2020; Zhao et al., 2019).

2.3. Microbial community composition

Phospholipid fatty acid analysis (PLFA) was used to assess the soil microbiome. Fresh soil samples were frozen at -80°C and freeze-dried below -20°C to maintain the structure of the living soil microbiome. PLFA biomarkers were extracted followed the methodology of (Frostegård et al., 1991), based on the modified (Bligh & Dyer, 1959) protocol, using 5 g of freeze-dried soil from each replicate, as described in detail in (Girkin et al., 2020). PLFA markers were assigned according to (Frostegård et al., 1991) and updated classifications (Joergensen, 2022; Ruess & Chamberlain, 2010; Zelles, 1997). 18:2ω6, 9c biomarkers were used for saprotrophic fungi, 16:1ω5c for arbuscular mycorrhizal fungi, i15:0, a15:0, i16:0, i17:0, a17:0 for gram-positive bacteria, 16:1ω7c, 18:1ω7c, cy17:0 and cy19:0 for gram-negative bacteria (Ruess & Chamberlain, 2010; Zelles, 1997). We used mol% to calculate the ratio between saprotrophic fungi and bacteria (F:B ratio).

2.4 Soil properties and litter loss

Soil organic matter (SOM) was measured via loss on ignition by drying 10g of fresh soil at 105°C for 24 hours and combusted at 450°C (Roper et al., 2019). SOM was measured at the beginning and end of the experimental treatments. SOM was converted to SOC using a conversion factor of 1.724 (Pribyl, 2010) and used in calculating soil C:N:P ratios across experimental treatments. Bulk density was measured by drying a known volume of soil at 105°C for 24 hours. Soil available P was measured by the Olsen P method and was extracted using 0.5M $NaHCO_3$ solution, pH 8.5 (Olsen, 1954), and analysed colorimetrically via the molybdate blue–ascorbic acid colorimetric method (Murphy & Riley, 1962). Total C and N of plant litter and total soil N were determined by an elemental analyser (Seal Analytical AA3 Segmented Flow Multi-Chemistry Analyzer). Field collected plant litter was dried at 65°C for 48 hours for use in litter bags during the experimental treatments (Isaac et al., 2005). Initial plant litter C:N was 27.06 ±2.36. Litter mass loss was taken by measuring the residual litter after drying at the end of the 16-week experiment.

2.5 Data analyses

All data analyses were performed in R v 4.3.2 (R Core Team, 2024). Soil fauna data from all samples were first summarised to investigate total community responses to the experimental treatments (plant litter availability: n = 3; temperature: n = 4, with 3 replicates). CWMBM was calculated for given treatments as the mean body mass (mg) for all sampled soil fauna groups, weighted by species abundance. An increase in CWMBM reflects a community increasingly composed of individuals with larger body masses and so provides a relative composition of large versus small soil fauna groups in the community. Here, we use CWMBM as an indicator of shifts in soil fauna community structure in response to treatments. CWMBM responses were consistent across the experimental duration, and so we use average measurements across the experimental period in our analyses. CWMBM's were calculated for the overall soil fauna community, taxonomic groups (nematodes, mites, collembola) and functional groups (e.g. predators, fungivores).

The interactive effects of plant litter and temperature treatments on soil community (total abundance and biomass, overall soil fauna, taxonomic and functional group CWMBM and F:B ratio, summarised as the ratio of fungal to bacterial PFLAs) and soil function (litter loss, SOC, soil C:N and C:P ratios) response variables were investigated using two-way ANOVA. Significant interaction effects were further explored by applying post-hoc pairwise comparisons using estimated marginal means with Tukey's adjustment for multiple testing to identify which specific combinations of temperature and plant litter treatments differed in their effects on soil community and function responses.

To assess the moderating effect of soil community structure responses to treatments on litter loss (N = 36), we constructed a piecewise structural equation model (SEM) using the piecewiseSEM package in R. The SEM was used to test causal pathways from temperature, quadratic temperature (T^2), and plant litter inputs to various soil community and soil function metrics. These terms, alongside residual correlations to account for unmeasured shared responses, were tested in a stepwise approach which started with the null model (Litter loss ~ Temperature + Plant Litter) and added additional terms. Maximum-likelihood estimation was applied and model fit evaluated using Fisher's *C* statistic, with a $P > 0.05$ for Fisher's C indicating an adequate model fit, alongside degrees of freedom (df), and Akaike's Information Criterion (AIC). Model parsimony was also accounted for by setting the condition that additional df's should result in $\Delta \mathrm{AIC}_{\mathrm{df}} < -5$.

Mediation analysis was consequently applied to the final SEM model to decompose the total effect of predictor variables into direct effects and average causal mediation effects (ACMEs). Nonparametric bootstrap sampling (n = 1000 simulations) was used to estimate confidence intervals and assess significance. Statistical significance of mediation was evaluated using the proportion mediated and associated *p* values. We further evaluated the robustness of the final SEM by conducting a leave-one-out sensitivity analysis to test the effect of removing key structural paths on model fit and explanatory power. Each reduced model retained the same overall structure as the final SEM but excluded a single causal effect or predictor, and alternative models were compared based on changes in R^2 for key response variables, Fisher's *C* statistic, AIC and df.

Linear mixed effect models were applied to examine the relationship between relative litter loss (proportion of litter mass loss, compared to the starting plant litter mass, N = 24) and soil community variables. Models were fitted using the nlme package (Pinheiro et al., 2023), with initial plant litter mass included as a random effect to account for variation in litter availability. This structure controls for baseline differences in input mass while isolating the effects of soil community predictor variables on litter decomposition. All soil community and edaphic variables were tested as predictors of relative litter loss and the best fitting models selected based on their goodness of fit via AIC and the $\Delta \mathrm{AIC}_{\mathrm{df}} < -5$ model parsimony condition. Pseudo-marginal (fixed effect) and conditional (fixed and random effect) R^2 values for models were calculated using the MuMIn package in R (Bartoń, 2023). To better visualise litter loss according to changes in soil community composition across treatments, effect sizes were calculated according to changes in variables (V) between the 2.5 and 5g plant litter treatments (V_{PL}) and no plant litter treatments (V_0) as standardised mean differences (SDMs): $\ln(V_{PL}/ V_0)$.

3 Results

3.1 Treatment effects on soil community composition and soil function

The interactive effects of experimental treatments (plant litter and temperature) were tested using two-way ANOVA's (Table 1, see Supplementary Table S1 for the data summary). Results demonstrate variable significant main and interactive effects of temperature and plant litter on both soil community composition and soil functions. Total soil fauna community abundance, biomass and CWMBM were strongly influenced by both treatment factors and their interaction ($p < 0.0001$), with high variance explained ($R^2_{\mathrm{adj}} > 0.95$). Similarly, Collembola CWMBM showed significant main effects of both temperature and litter, as well as a strong interaction (all $p \leq 0.001$), suggesting trait shifts in community composition across treatments. Nematode CWMBM was especially sensitive to temperature ($F = 113.00$, $p < 0.0001$) and exhibited a significant interaction with plant litter ($F = 32.06$, $p < 0.0001$), but not plant litter ($p > 0.05$). In contrast, mite and fungivorous mite CWMBM showed no significant responses. Litter loss was significantly affected by plant litter ($F = 38.00$, $p < 0.0001$) and its interaction with temperature ($F = 6.42$, $p < 0.0001$), but not by temperature alone. Soil C:N ratio also responded significantly to all terms, whereas soil C:P ratio was significantly influenced by temperature. Overall, the results highlight strong, trait-specific responses of the soil community to warming and resource availability, with consistent evidence for interactive effects on both soil community structure and soil function.

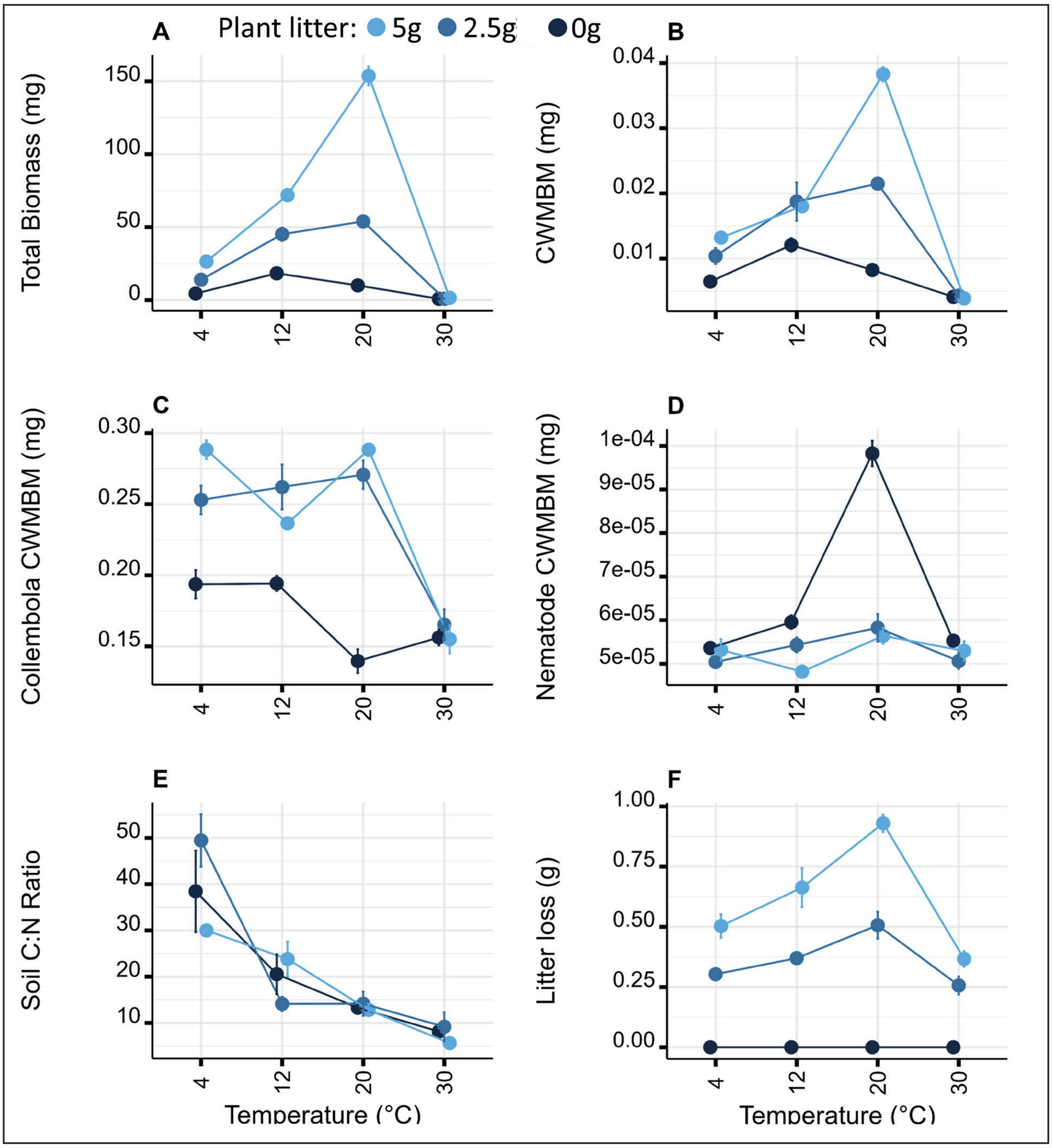

Figure 1. Interaction plots showing the effects of temperature (4, 12, 20, 30 °C) and plant litter (0 , 2.5, 5 g) treatments on (**A**) total soil fauna community biomass, (**B**) overall soil fauna community-weighted mean body mass (CWMBM), (**C**) Collembola CWMBM, (**D**) nematode CWMBM, (**E**) soil C:N ratio, and (**F**) litter loss (g). Symbols represent treatment means and error bars show standard errors (N = 36).

Significant treatment interactions are visualised in Figure 1. Total soil fauna community biomass and overall CWMBM (Fig. 1A-B, also see Supplementary Figure S2) showed strong interactive responses, with both variables peaking at 20°C under high plant litter availability and declining sharply at 30°C across all plant litter treatments. CWMBM responses indicate that the largest individuals occurred under high litter and moderate temperature (Fig. 1B), also evident for collembola CWMBM (Fig. 1C) and nematode CWMBM (Fig. 1D) (also see Supplementary Figure S3). Collembola CWMBM decreased with increasing temperature, especially under low and no litter treatments, whereas nematode CWMBM (Fig. 1D) peaked sharply at 20°C regardless of litter addition, suggesting a distinct thermal optimum for nematode body size. Soil C:N ratio declined markedly with temperature (Fig. 1E) and was only modestly influenced by plant litter availability at lower temperatures. Litter loss (Fig. 1F) showed a pronounced temperature and plant litter interaction, with maximum decomposition at 20 °C under high litter, paralleling biomass and CWMBM patterns. These results indicate strong interactive effects of temperature and resource availability on soil community structure and soil function, with evidence of trait–function coupling around intermediate temperatures.

3.2 The role of soil fauna community in observed litter loss

The final SEM provided a very good fit to the data (Fisher's $C = 12.43$, $p = 0.572$, df = 14; AIC = –1212.26), with no evidence of significant missing pathways. The model explained a substantial proportion of variance in Collembola CWMBM ($R^2 = 0.64$), Nematode CWMBM ($R^2 = 0.39$), overall mean CWMBM ($R^2 = 0.84$), and litter loss ($R^2 = 0.93$) (Figure 2, also see Table S2 of

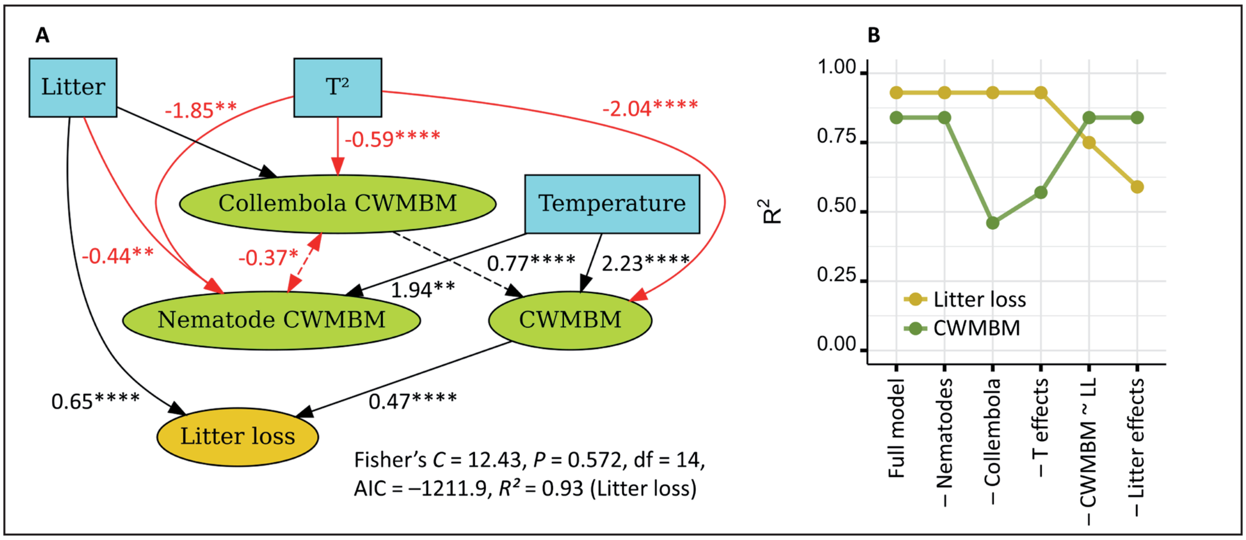

Figure 2. Final structural equation model (SEM) showing (**A**) significant pathways (arrows) linking environmental drivers (blue), soil fauna community traits (green), and soil function (gold). Arrow thickness reflects standardized effect size; red arrows represent negative relationships. Residual correlation (dashed red arrow) indicates an unmodelled, but significant association and the dashed black arrow indicates a partially mediation pathway from T^2 to CWMBM via Collembola CWMBM. The full SEM and mediation analysis are presented in Table S2 and Table S3 of the supplementary material, respectively. Sensitivity analysis of the SEM in (**B**) shows the impact of removing individual paths or effects on the explained variance (R^2) of litter loss (gold) and CWMBM (green) (also see Table S4).

Table 1. Two-way ANOVA results testing the effects of temperature and plant litter treatments and their interaction (T × PL) on soil community composition and litter loss, SOC and soil C:N and C:P ratios. F values and significance levels (ns: $p > 0.05$; *: $p < 0.05$; **: $p < 0.01$, ***: $p < 0.001$, ****: $p < 0.0001$) for each term alongside the adjusted R^2 for the general linear model.

	Temperature	Plant Litter	T × PL	R^2_{adj}
Total Abundance	38.24****	39.18****	22.19****	0.978
Total Biomass	8.38**	17.42****	152.16****	0.989
CWMBM	9.66***	9.78***	39.34****	0.963
Collembola CWMBM	9.27***	28.19****	15.36****	0.921
Mite CWBMB	ns	ns	ns	
Fungivorous mite CWMBM	ns	ns	ns	
Nematode CWMBM	113.00****	ns	32.06****	0.936
Fungivorous nem. CWMBM	15.85****	3.15*	ns	0.645
F:B ratio	9.33***	ns	2.83*	0.604
Litter loss (g)	ns	38.00****	6.42***	0.952
SOC (%)	ns	ns	ns	
Soil C:N ratio	12.69****	6.89**	2.65*	0.788
Soil C:P ratio	10.15***	ns	ns	0.739

the supplementary material). Collembola CWMBM increased significantly with plant litter input ($\beta = 0.53$, $p < 0.001$) and showed a nonlinear relationship with T^2 ($\beta = -0.59$, $p < 0.001$). The final SEM excluded the non-significant direct path from temperature to Collembola CWMBM, as temperature effects were sufficiently captured by T^2, with removal of the linear term improving overall model fit without compromising explanatory power. Nematode CWMBM was also sensitive to temperature and declined with increasing litter ($\beta = -0.44$, $p = 0.003$), suggesting contrasting responses across taxa. A significant residual correlation between the collembola and nematode CWMBM ($r = -0.38$, $p = 0.014$) indicated shared but opposing trait responses to environmental conditions. Overall soil fauna CWMBM was strongly driven by Collembola CWMBM ($\beta = 0.79$, $p < 0.001$) and responded positively to temperature ($\beta = 2.23$, $p < 0.0001$) and negatively to T^2 ($\beta = -2.04$, $p < 0.0001$), reflecting trait convergence around intermediate temperatures. Litter loss was significantly predicted by both mean CWMBM ($\beta = 0.47$, $p < 0.001$) and litter addition ($\beta = 0.65$, $p < 0.001$), indicating that community body size structure and resource availability jointly enhanced litter loss. Mediation analysis revealed a partially mediated pathway from T^2 to CWMBM via Collembola CWMBM (Table S3), while other pathways showed limited evidence of mediation. Sensitivity analysis using leave-one-out SEM variants (Fig. 5B, also see Table S4) confirmed the importance of Collembola CWMBM and temperature effects as removing these paths resulted in the largest drop in R^2 for CWMBM. Removing nematode or litter pathways had minimal impact, indicating a more limited role for those predictors in the final model structure. Litter loss R^2 was sensitive to the removal of the pathway between CWMBM and Litter Loss, but mostly explained by plant litter mass (Litter, although note this was both Litter and Litter Loss was 0 for n = 13 for the 36 measurements included).

3.2 The influence of soil body size structure on litter loss

We further tested the independent and interactive effects of explanatory variables on relative litter loss across treatments (excluding treatments with no plant litter as no litter loss occurred) using mixed effect models and testing linear and quadratic terms. The best predictor of litter loss was a quadratic term for overall soil community CWMBM (Figure 3A, ΔAIC compared to the null model = -30.08). No additional terms increased model likelihood, with the condition of $\Delta\text{AIC} < -5$ for additional degrees of freedom. Model predictions are compared to experimental observations in Figure 3B, and alongside the relationship between the model residuals and experimental temperature in Figure 3C, indicate a slight under-prediction of litter loss at low temperature (4 and 12°C) and an over-prediction of litter loss at 20°C when overall soil CWMBM is the only fixed effect. Plant litter quantity was used as a random effect and explained around 19% of the variation in litter loss observations (conditional compared to marginal R^2 values presented in Figure 3A). Alternative random-effect structures were tested but this formulation provided the best explanatory power.

To further visualise effect sizes between the plant litter treatments on soil community body size structure, we calculated standardised mean differences between the plant litter and no litter treatments (Figure 4). Regres-

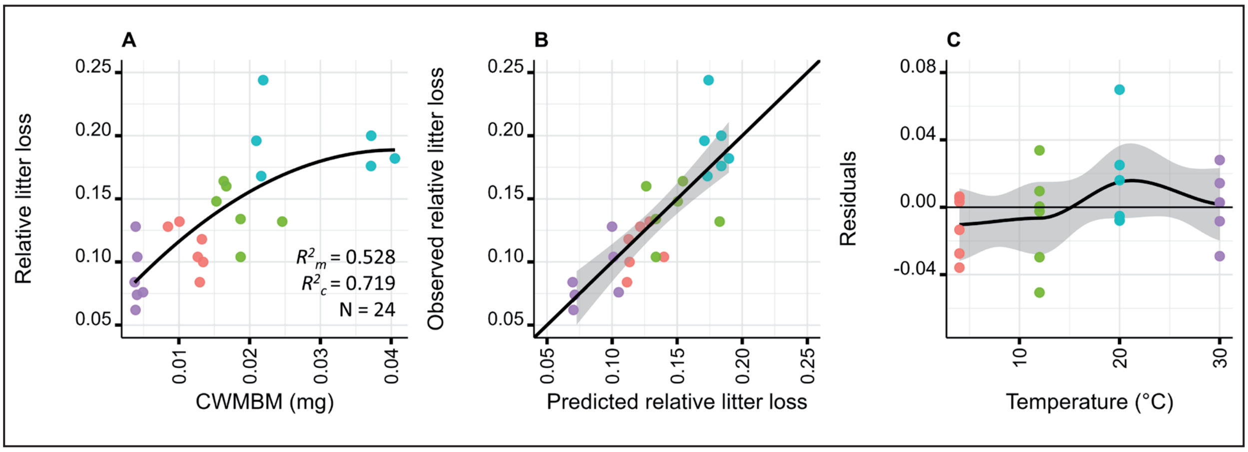

Figure 3. Best fitting mixed effect model for predicting relative litter loss (proportion litter loss compared to initial plant litter (2.5 and 5g treatments), showing (**A**) a quadratic relationship between soil community weighted mean body mass (CWMBM) and relative litter loss (N = 24, also see Table S5), (**B**) model predictions compared to observed litter loss (the solid line shows a 1:1 relationship), and (**C**) model residuals against experimental temperature with loess fit (black line with shaded area showing standard error). Symbol colours in the order coral, green, blue, magenta indicate experimental temperatures of 4, 12, 20 and 30°C respectively (shown alongside temperature in C).

sion analysis revealed changes in nematode CWMBM to be more strongly related to relative litter loss (F = 25.93, p < 0.0001) (Figure 4A) than changes in overall soil CWMBM (F = 16.50, p = 0.0005) and collembola CWMBM (F = 21.44, p < 0.0001). However, a strong positive linear relationship appeared between changes in total soil and collembola CWMBM (F = 133.57, p < 0.0001, Figure 4B) and negative linear relationship between collembola CWMBM and nematode CWMBM (F = 25.57, p < 0.0001, Figure 4C).

4. Discussion

Across a broad gradient of plant litter and temperature treatments, our results show that variation in soil fauna CWMBM significantly mediates litter decomposition (Figures 2-4). The final SEM revealed that collembola CWMBM was a key driver of overall CWMBM, and that it responded positively to plant litter and non-linearly to temperature, declining at both temperature extremes (Figure 2A, Table S2). Mediation analysis further confirmed that collembola CWMBM partially mediated the effect of T^2 on CWMBM (Table S3), supporting the role of collembola as a critical link between environmental conditions and soil community structure. A significant residual correlation between collembola and nematode CWMBM (r = –0.38, p = 0.014) indicate shared but opposing trait responses to environmental conditions. Although the SEM sensitivity analysis (Figure 2A, Table S4) indicates a minimal impact of nematode or litter pathways, the linear mixed effect model applied to relative litter loss (which accounts for initial plant litter variation, Figure 3 and Table S5) demonstrates a large influence of the soil fauna CWMBM and of collembola and nematode CWMBM (Figure 4).

Taken together, our results suggest an important and distinct role of both large and small soil fauna in litter decomposition, whereby the removal of larger body sized biota at extreme temperature and resource conditions can reduce top-down control on smaller body sized biota. For instance, highly variable soil community and litter loss measurements in the 20°C temperature treatments reflected a low collembola CWMBM in the no plant litter treatment, which coincided with a greater nematode CWMBM under these experimental conditions (Figure 4). The SEM further identified overall CWMBM to peak at intermediate temperatures under high litter availability (Table S2), reflecting taxonomic convergence around optimal conditions. However, while litter loss was strongly predicted by soil fauna CWMBM and plant litter availability no direct pathway with temperature was identified (Figure 2A), supporting the finding that temperature effects on litter decomposition are mediated through changes in soil community structure, particularly body size composition.

Dissimilar temperature responses between taxonomic and functional groups (Figure 6) require a higher resolution understanding to enable predictions of how shifting soil community composition will alter soil functions such as litter decomposition. Similarly, the role of CWMBM as a causal mechanism remains unresolved. While our experiment was not designed to manipulate CWMBM independently, mixed-effects modelling of relative litter loss (Figure 3) supports a unimodal (quadratic) relationship between CWMBM and decomposition, consistent with trait–function coupling

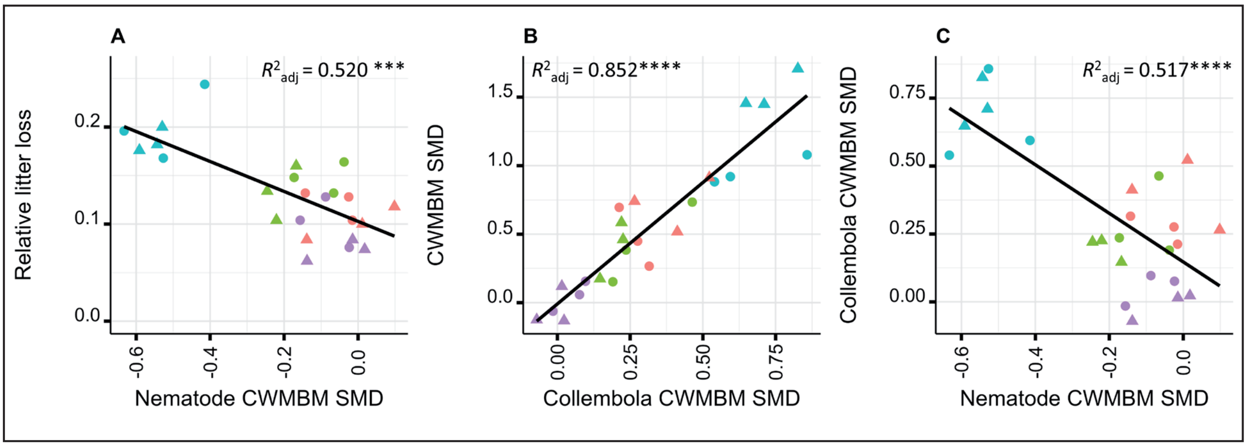

Figure 4. Significant linear effect size relationships, calculated as standardised mean differences (SMD), between (**A**) relative litter loss and overall soil fauna community weighted mean body mass (CWMBM, mg); (**B**) SMD's between overall soil and collembola CWMBM, and (**C**) SMD's between collembola and nematode CWMBM (N = 24 for all plots). Symbol colours represent experimental temperatures as in Figure 3 and symbol shapes represent plant litter treatments for which relative litter loss can be calculated (circle: 2.5g, triangle: 5g plant litter).

(REF). This implies that intermediate community body size distributions, composed of both small (e.g. nematodes) and large (e.g. collembola) taxa, may play an important role in litter decomposition. Future work should experimentally separate soil fauna body size classes to test this relationship mechanistically.

Temperature has been extensively shown to strongly influence the body size structure of ecological communities (Angilletta et al., 2004; Evans et al., 2020), but co-occurring shifts in resource availability can lead to context-specific community effects when temperature responses differ between community groups (Tabi et al., 2019; Tan et al., 2021). For instance, Thakur et al. (2023) found climate warming of a sub-Arctic grassland soil by 3-6°C to decrease collembola biomass and abundance, whereas mites showed a unimodal response to warming thereby shifting the overall soil body size structure. Changes in resource availability, for instance through land use intensity and management, can also shift the body size structure and trophic processing of energy and nutrients without immediate effects on soil functions like litter decomposition by favouring larger body size soil fauna (Potapov et al., 2019). Here, we find distinct taxa-specific responses to our temperature and plant litter treatments that lead to shifts in the body size structure of soil communities that mediate litter loss across treatments (Table 1). Litter loss, however, may reflect treatment-induced changes in body size structure. For instance, temperature effects on CWMBM were observed following incubation periods and prior to plant litter treatments (Figure S1). Future experiments exploring the causal mechanisms linking soil communities and litter decomposition thus need to tightly control for treatment effects.

The fundamental influence of temperature and body size on metabolism is well known, but biota are also known to display varying temperature sensitivities to their metabolic rates (Brown et al., 2004). In soil communities, this temperature sensitivity (the magnitude with which metabolic rates increase with a rise in temperature) has been shown to increase from smaller (microbial) to larger (macrofauna) biota (Johnston & Sibly, 2018). Whether different sized soil biota can meet their metabolic demands, and so increase their population growth, also depends on the availability of energy from food resources. In a natural experiment on stream food webs, for instance, nutrient supply offset the effects of temperature on primary producers to support larger body sized animals at higher trophic levels (O'Gorman et al., 2017). Greater SOM content under grazing has also been observed to enhance nematode CWMBM via greater biomass transfer through the soil food web (Andriuzzi & Wall, 2018). Our results identify a much stronger influence of temperature compared to plant litter availability on overall community CWMBM, potentially reflecting different resource preferences for smaller and larger fauna in our study.

Soil macrofauna play a key role in litter decomposition (Delgado-Baquerizo et al., 2020; Sagi & Hawlena, 2023), but their abundances and distributions often decline substantially in response to environmental perturbations (e.g. land management practices and climate extremes) (Ge et al., 2021; Sünnemann et al., 2023; Yin et al., 2022). Here, we collected arable soil and plant litter and focused on the soil microfauna and mesofauna community as they are typically more abundant than soil macrofauna across gradients of agricultural management intensity but play a central role in litter decomposition (Hanisch et al., 2022). The application of our results is thus mainly to soils in which soil macrofauna are absent or reduced, either due to land management (e.g. arable, urban) or climate (e.g. tundra, alpine). Within an arable context, our results reinforce the observed benefits of land management practices, such as cover cropping, on soil multifunctionality (Garland et al., 2021) through the provision of resources for larger body sized soil fauna which have higher metabolic demands as temperatures rise. That is, greater resource availability could buffer the effects of extreme temperatures on soil community composition and the soil functions that are strongly influenced by larger body sized soil fauna.

Soil mesofauna are thought to influence litter decomposition both directly through fragmentation and digestion of plant litter, but also indirectly through regulation of soil bacterial and fungal communities (Hättenschwiler et al., 2005). Here, we observed limited inter-relationships between soil taxonomic or functional groups to suggest an effect of temperature and/or plant litter treatments on the overall soil food web. For instance, F:B ratio showed limited response to the microcosm treatments and was not selected in the SEM (Table 1, Table S1). This may be an artifact of the relatively short experimental period, or finer-resolution scale-dependency of smaller biota responses. However, clear relationships between soil mesofauna and microbial communities have been observed in shorter, similar-scale, microcosm experiments (Coulibaly et al., 2019). Several other environmental factors, aside from resource availability and temperature, are also important in regulating soil community structure and litter decomposition. For instance, precipitation, soil water content and other measures of aridity are key filters for soil microbial activity, nematode body size and detrivore abundance (Andriuzzi et al., 2020; Siebert et al., 2023; Zheng et al., 2023). Here, our focus was on the ability of greater plant litter availability to alleviate extreme temperature effects on the bottom-up processes regulating litter decomposition. Future research would benefit from the study of smaller temperature increments, particularly between 20 and 30°C, together with the inclusion and exclusion of macrofauna and interactive soil moisture effects.

Conclusion

Overall, our study demonstrates variable sensitivity of soil fauna taxonomic and functional groups to temperature and resource availability, which results in a non-linear response of overall soil fauna CWMBM to temperature. We find a significant influence of soil fauna CWMBM on litter loss and relative litter loss and a strong influenced of both large (collembola) and small (nematode) taxa on soil fauna CWMBM across treatments. In response to high temperatures, our results show that larger soil mesofauna are particularly sensitive to reduced resource availability, which through mediated pathways could have cascading effects on soil functioning. Continued efforts are needed to quantitatively formulate a higher resolution, mechanistic, understanding of soil communities in a way that can be scaled-up to the landscape scales at which the effects of global drivers influence soil structure and function.

References

Andriuzzi, W. S., Franco, A. L. C., Ankrom, K. E., Cui, S., de Tomasel, C. M., Guan, P., Gherardi, L. A., Sala, O. E. & Wall, D. H. (2020). Body size structure of soil fauna along geographic and temporal gradients of precipitation in grasslands. *Soil Biology and Biochemistry*, *140*, 107638. https://doi.org/10.1016/j.soilbio.2019.107638

Andriuzzi, W. S. & Wall, D. H. (2018). Grazing and resource availability control soil nematode body size and abundance–mass relationship in semi-arid grassland. *Journal of Animal Ecology*, *87*(5), 1407–1417. https://doi.org/10.1111/1365-2656.12858

Angilletta, M. J., Jr., Steury, T. D. & Sears, M. W. (2004). Temperature, Growth Rate, and Body Size in Ectotherms: Fitting Pieces of a Life-History Puzzle1. *Integrative and Comparative Biology*, *44*(6), 498–509. https://doi.org/10.1093/icb/44.6.498

Balogh, J. & Balogh, P. (1992). *The oribatid mites genera of the world* (Vol. 1). Hungarian National Museum Press.

Bardgett, R. D. & Caruso, T. (2020). Soil microbial community responses to climate extremes: Resistance, resilience and transitions to alternative states. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *375*(1794), 20190112. https://doi.org/10.1098/rstb.2019.0112

Bartoń, K. (2023, March 22). *MuMIn: Multi-Model Inference*. R Package Version 1.47.5. https://cran.r-project.org/web/packages/MuMIn/index.html

Beare, M. H., Parmelee, R. W., Hendrix, P. F., Cheng, W., Coleman, D. C. & Crossley Jr., D. A. (1992). Microbial and Faunal Interactions and Effects on Litter Nitrogen and Decomposition in Agroecosystems. *Ecological Monographs*, *62*(4), 569–591. https://doi.org/10.2307/2937317

Bligh, E. G. & Dyer, W. J. (1959). A rapid method of total lipid extraction and purification. *Canadian Journal of Biochemistry and Physiology*, *37*(8), 911–917. https://doi.org/10.1139/o59-099

Bokhorst, S., Phoenix, G. K., Bjerke, J. W., Callaghan, T. V., Huyer-Brugman, F. & Berg, M. P. (2012). Extreme winter warming events more negatively impact small rather than large soil fauna: Shift in community composition explained by traits not taxa. *Global Change Biology*, *18*(3), 1152–1162. https://doi.org/10.1111/j.1365-2486.2011.02565.x

Bonfanti, J., Hedde, M., Joimel, S., Krogh, P. H., Violle, C., Nahmani, J. & Cortet, J. (2018). Intraspecific body size variability in soil organisms at a European scale: Implications for functional biogeography. *Functional Ecology*, *32*(11), 2562–2570. https://doi.org/10.1111/1365-2435.13194

Briones, M. J. I. (2014). Soil fauna and soil functions: A jigsaw puzzle. *Frontiers in Environmental Science*, *2*. https://www.frontiersin.org/articles/10.3389/fenvs.2014.00007

Brown, J. H., Gillooly, J. F., Allen, A. P., Savage, V. M. & West, G. B. (2004). Toward a metabolic theory of ecology. *Ecology*, *85*(7), 1771-1789. https://doi.org/10.1890/03-9000

Chen, J., Zhang, Y., Kuzyakov, Y., Wang, D. & Olesen, J. E. (2023). Challenges in upscaling laboratory studies to ecosystems in soil microbiology research. *Global Change Biology*, *29*(3), 569–574. https://doi.org/10.1111/gcb.16537

Cifuentes-Croquevielle, C., Stanton, D. E. & Armesto, J. J. (2020). Soil invertebrate diversity loss and functional changes in temperate forest soils replaced by exotic pine plantations. *Scientific Reports*, *10*(1), Article 1. https://doi.org/10.1038/s41598-020-64453-y

Coulibaly, S. F. M., Winck, B. R., Akpa-Vinceslas, M., Mignot, L., Legras, M., Forey, E. & Chauvat, M. (2019). Functional Assemblages of Collembola Determine Soil Microbial Communities and Associated Functions. *Frontiers in Environmental Science*, *7*. https://www.frontiersin.org/articles/10.3389/fenvs.2019.00052

Delgado-Baquerizo, M., Reich, P. B., Trivedi, C., Eldridge, D. J., Abades, S., Alfaro, F. D., Bastida, F., Berhe, A. A., Cutler, N. A., Gallardo, A. et al. (2020). Multiple elements of soil biodiversity drive ecosystem functions across biomes. *Nature Ecology & Evolution*, *4*(2), 210–220. https://doi.org/10.1038/s41559-019-1084-y

Douce, G. K. (1976). Biomass of Soil Mites (Acari) in Arctic Coastal Tundra. *Oikos*, *27*(2), 324–330. https://doi.org/10.2307/3543914

Evans, G. O. & Till, W. M. (1979). Mesostigmatic mites of Britain and Ireland (Chelicerata: Acari-Parasitiformes): An introduction to their external morphology and classification. *The Transactions of the Zoological Society of London*, *35*(2), 139–262. https://doi.org/10.1111/j.1096-3642.1979.tb00059.x

Evans, L. E., Hirst, A. G., Kratina, P. & Beaugrand, G. (2020). Temperature-mediated changes in zooplankton body size: Large scale temporal and spatial analysis. *Ecography*, *43*(4), 581–590. https://doi.org/10.1111/ecog.04631

Frostegård, Å., Tunlid, A. & Bååth, E. (1991). Microbial biomass measured as total lipid phosphate in soils of different organic content. *Journal of Microbiological Methods*, *14*(3), 151–163. https://doi.org/10.1016/0167-7012(91)90018-L

Frouz, J., Roubíčková, A., Heděnec, P. & Tajovský, K. (2015). Do soil fauna really hasten litter decomposition? A meta-analysis of enclosure studies. *European Journal of Soil Biology*, *68*, 18–24. https://doi.org/10.1016/j.ejsobi.2015.03.002

García-Palacios, P., Maestre, F. T., Kattge, J. & Wall, D. H. (2013). Climate and litter quality differently modulate the effects of soil fauna on litter decomposition across biomes. *Ecology Letters*, *16*(8), Article 8.

Garland, G., Edlinger, A., Banerjee, S., Degrune, F., García-Palacios, P., Pescador, D. S., Herzog, C., Romdhane, S., Saghai, A., Spor, A. et al. (2021). Crop cover is more important than rotational diversity for soil multifunctionality and cereal yields in European cropping systems. *Nature Food*, *2*(1), Article 1. https://doi.org/10.1038/s43016-020-00210-8

Ge, B., Zhou, J., Yang, R., Jiang, S., Yang, L. & Tang, B. (2021). Lower land use intensity promoted soil macrofaunal biodiversity on a reclaimed coast after land use conversion. *Agriculture, Ecosystems & Environment*, *306*, 107208. https://doi.org/10.1016/j.agee.2020.107208

Geisen, S. (2016). The bacterial-fungal energy channel concept challenged by enormous functional versatility of soil protists. *Soil Biology and Biochemistry*, *102*, 22–25. https://doi.org/10.1016/j.soilbio.2016.06.013

Gill, A. L. & Finzi, A. C. (2016). Belowground carbon flux links biogeochemical cycles and resource-use efficiency at the global scale. *Ecology Letters*, *19*(12), 1419-1428. https://doi.org/10.1111/ele.12690

Girkin, N. T., Lopes dos Santos, R. A., Vane, C. H., Ostle, N., Turner, B. L. & Sjögersten, S. (2020). Peat Properties, Dominant Vegetation Type and Microbial Community Structure in a Tropical Peatland. *Wetlands*, *40*(5), 1367–1377. https://doi.org/10.1007/s13157-020-01287-4

Hanisch, J., Engell, I., Linsler, D., Scheu, S. & Potthoff, M. (2022). The role of Collembola for litter decomposition under minimum and conventional tillage. *Journal of Plant Nutrition and Soil Science*, *185*(4), 529–538. https://doi.org/10.1002/jpln.202200077

Hättenschwiler, S., Tiunov, A. V. & Scheu, S. (2005). Biodiversity and Litter Decomposition in Terrestrial Ecosystems. *Annual Review of Ecology, Evolution, and Systematics*, *36*(1), 191–218. https://doi.org/10.1146/annurev.ecolsys.36.112904.151932

Heděnec, P., Jiménez, J. J., Moradi, J., Domene, X., Hackenberger, D., Barot, S., Frossard, A., Oktaba, L., Filser, J., Kindlmann, P. & Frouz, J. (2022). Global distribution of soil fauna functional groups and their estimated litter consumption across biomes. *Scientific Reports*, *12*(1), Article 1. https://doi.org/10.1038/s41598-022-21563-z

Hódar, J. A. (1996). The use of regression equations for estimation of arthropod biomass in ecological studies. *Acta (Ecologica, 1996, 17 (5)*, *421*, 433.

Isaac, M. E., Gordon, A. M., Thevathasan, N., Oppong, S. K. & Quashie-Sam, J. (2005). Temporal changes in soil carbon and nitrogen in west African multistrata agroforestry systems: A chronosequence of pools and fluxes. *Agroforestry Systems*, *65*(1), 23–31. https://doi.org/10.1007/s10457-004-4187-6

Joergensen, R. G. (2022). Phospholipid fatty acids in soil—Drawbacks and future prospects. *Biology and Fertility of Soils*, *58*(1), 1–6. https://doi.org/10.1007/s00374-021-01613-w

Johnston, A. S. A. (2019). Land management modulates the environmental controls on global earthworm communities. *Global Ecology and Biogeography*, *28*(12), 1787–1795. https://doi.org/10.1111/geb.12992

Johnston, A. S. A. (2024). Predicting emergent animal biodiversity patterns across multiple scales. *Global Change Biology*, *30*(7), e17397. https://doi.org/10.1111/gcb.17397

Johnston, A. S. A. & Sibly, R. M. (2018). The influence of soil communities on the temperature sensitivity of soil respiration. *Nature Ecology & Evolution*, *2*(10), 1597-1602. https://doi.org/10.1038/s41559-018-0648-6

Johnston, A. S. A. & Sibly, R. M. (2020). Multiple environmental controls explain global patterns in soil animal communities. *Oecologia*, *192*(4), 1047-1056. https://doi.org/10.1007/s00442-020-04640-w

Joly, F.-X., Scherer-Lorenzen, M. & Hättenschwiler, S. (2023). Resolving the intricate role of climate in litter decomposition. *Nature Ecology & Evolution*, *7*(2), https://doi.org/10.1038/s41559-022-01948-z

Kalúz, S. & Fenďa, P. (2005). *Mites (Acari: Mesostigmata) of the family Ascidae of Slovakia*. Institute of Zoology, Slovak Academy of Sciences Bratislava.

Kitagami, Y., Tanikawa, T. & Matsuda, Y. (2020). Effects of microhabitats and soil conditions on structuring patterns of nematode communities in Japanese cedar (Cryptomeria japonica) plantation forests under temperate climate conditions. *Soil Biology and Biochemistry*, *151*, 108044. https://doi.org/10.1016/j.soilbio.2020.108044

Lavelle, P., Bignell, D., Lepage, M., Wolters, V., Roger, P., Ineson, P., Heal, O. W. & Dhillion, S. (1997). Soil function in a changing world: The role of invertebrate ecosystem engineers. *European Journal of Soil Biology*, *33*(4), 159-193.

Luan, L., Jiang, Y., Cheng, M., Dini-Andreote, F., Sui, Y., Xu, Q., Geisen, S. & Sun, B. (2020). Organism body size structures the soil microbial and nematode community assembly at a continental and global scale. *Nature Communications*, *11*(1), 6406. https://doi.org/10.1038/s41467-020-20271-4

Murphy, J. & Riley, J. P. (1962). A modified single solution method for the determination of phosphate in natural waters. *Analytica Chimica Acta*, *27*, 31–36. https://doi.org/10.1016/S0003-2670(00)88444-5

O'Gorman, E. J., Zhao, L., Pichler, D. E., Adams, G., Friberg, N., Rall, B. C., Seeney, A., Zhang, H., Reuman, D. C. & Woodward, G. (2017). Unexpected changes in community size structure in a natural warming experiment. *Nature Climate Change*, *7*(9), 659-663. https://doi.org/10.1038/nclimate3368

Olsen, S. R. (1954). *Estimation of Available Phosphorus in Soils by Extraction with Sodium Bicarbonate*. U.S. Department of Agriculture.

Petersen, H. & Luxton, M. (1982). A Comparative Analysis of Soil Fauna Populations and Their Role in Decomposition Processes. *Oikos*, *39*(3), 288-388. https://doi.org/10.2307/3544689

Phillips, H. R. P., Bach, E. M., Bartz, M. L. C., Bennett, J. M., Beugnon, R., Briones, M. J. I., Brown, G. G., Ferlian, O., Gongalsky, K. B., Guerra, C. A. et al. (2021). Global data on earthworm abundance, biomass, diversity and corresponding environmental properties. *Scientific Data*, *8*(1), 136. https://doi.org/10.1038/s41597-021-00912-z

Pinheiro, J., Bates, D., DebRoy, S., Sarkar, D., Heisterkamp, S., Van Willigen, B., Ranke, J. & R Core Team. (2023, November 27). *nlme: Linear and Nonlinear Mixed Effects Models*. R Package Version 3.1-164. https://cran.r-project.org/web/packages/nlme/index.html

Potapov, A. M., Klarner, B., Sandmann, D., Widyastuti, R. & Scheu, S. (2019). Linking size spectrum, energy flux and trophic multifunctionality in soil food webs of tropical land-use systems. *Journal of Animal Ecology*, *88*(12), 1845–1859. https://doi.org/10.1111/1365-2656.13027

Pribyl, D. W. (2010). A critical review of the conventional SOC to SOM conversion factor. *Geoderma*, *156*(3), 75–83. https://doi.org/10.1016/j.geoderma.2010.02.003

R Core Team. (2024). *R: The R Project for Statistical Computing*. https://www.r-project.org/

Roper, W. R., Robarge, W. P., Osmond, D. L. & Heitman, J. L. (2019). Comparing Four Methods of Measuring Soil Organic Matter in North Carolina Soils. *Soil Science Society of America Journal*, *83*(2), 466–474. https://doi.org/10.2136/sssaj2018.03.0105

Ruess, L. & Chamberlain, P. M. (2010). The fat that matters: Soil food web analysis using fatty acids and their carbon stable isotope signature. *Soil Biology and Biochemistry*, *42*(11), 1898–1910. https://doi.org/10.1016/j.soilbio.2010.07.020

Rusek, J. (1998). Biodiversity of Collembola and their functional role in the ecosystem. *Biodiversity & Conservation*, *7*(9), 1207–1219. https://doi.org/10.1023/A:1008887817883

Sagi, N. & Hawlena, D. (2023). Climate dependence of the macrofaunal effect on litter decomposition—A global meta-regression analysis. *Ecology Letters*, *27*(1), e14333. https://doi.org/10.1111/ele.14333

Sauvadet, M., Chauvat, M., Cluzeau, D., Maron, P.-A., Villenave, C. & Bertrand, I. (2016). The dynamics of soil micro-food web structure and functions vary according to litter quality. *Soil Biology and Biochemistry*, *95*, 262–274. https://doi.org/10.1016/j.soilbio.2016.01.003

Siebert, J., Ciobanu, M., Schädler, M. & Eisenhauer, N. (2020). Climate change and land use induce functional shifts in soil nematode communities. *Oecologia*, *192*(1), 281–294. https://doi.org/10.1007/s00442-019-04560-4

Siebert, J., Sünnemann, M., Hautier, Y., Risch, A. C., Bakker, J. D., Biederman, L., Blumenthal, D. M., Borer, E. T., Bugalho, M. N., Broadbent, A. A. D. et al. (2023). Drivers of soil microbial and detritivore activity across global grasslands. *Communications Biology*, *6*(1), 1220. https://doi.org/10.1038/s42003-023-05607-2

Skvarla, M. J., Fisher, J. R. & Dowling, A. P. G. (2014). A review of Cunaxidae (Acariformes, Trombidiformes): Histories and diagnoses of subfamilies and genera, keys to world species, and some new locality records. *ZooKeys*, *418*, 1–103. https://doi.org/10.3897/zookeys.418.7629

Sünnemann, M., Beugnon, R., Breitkreuz, C., Buscot, F., Cesarz, S., Jones, A., Lehmann, A., Lochner, A., Orgiazzi, A., Reitz, T. et al. (2023). Climate change and cropland management compromise soil integrity and multifunctionality. *Communications Earth & Environment*, *4*(1), 394. https://doi.org/10.1038/s43247-023-01047-2

Swift, M. J. (1979). *Decomposition in terrestrial ecosystems*. University of California Press.

Szanser, M., Ilieva-Makulec, K., Kajak, A., Górska, E., Kusińska, A., Kisiel, M., Olejniczak, I., Russel, S., Sieminiak, D. & Wojewoda, D. (2011). Impact of litter species diversity on decomposition processes and communities of soil organisms. *Soil Biology and Biochemistry*, *43*(1), 9–19. https://doi.org/10.1016/j.soilbio.2010.08.031

Tabi, A., Petchey, O. L. & Pennekamp, F. (2019). Warming reduces the effects of enrichment on stability and functioning across levels of organisation in an aquatic microbial ecosystem. *Ecology Letters*, *22*(7), 1061–1071. https://doi.org/10.1111/ele.13262

Tan, H., Hirst, A. G., Atkinson, D. & Kratina, P. (2021). Body size and shape responses to warming and resource competition. *Functional Ecology*, *35*(7), 1460–1469. https://doi.org/10.1111/1365-2435.13789

Tedersoo, L., Bahram, M., Põlme, S., Kõljalg, U., Yorou, N. S., Wijesundera, R., Ruiz, L. V., Vasco-Palacios, A. M., Thu, P. Q. et al. (2014). Global diversity and geography of soil fungi. *Science*, *346*(6213), 1256688. https://doi.org/10.1126/science.1256688

Thakur, M. P., Sigurðsson, B. D., Sigurðsson, P. & Holmstrup, M. (2023). Warming shifts the biomass distribution of soil microarthropod communities. *Soil Biology and Biochemistry*, *177*, 108894. https://doi.org/10.1016/j.soilbio.2022.108894

van den Hoogen, J., Geisen, S., Routh, D., Ferris, H., Traunspurger, W., Wardle, D. A., de Goede, R. G. M., Adams, B. J., Ahmad, W., Andriuzzi, W. S. et al. (2019). Soil nematode abundance and functional group composition at a global scale. *Nature*, *572*(7768), 194-198. https://doi.org/10.1038/s41586-019-1418-6

van den Hoogen, J., Geisen, S., Wall, D. H., Wardle, D. A., Traunspurger, W., de Goede, R. G. M., Adams, B. J., Ahmad, W., Ferris, H., Bardgett, R. D. et al. (2020). A global database of soil nematode abundance and functional group composition. *Scientific Data*, *7*(1), 103. https://doi.org/10.1038/s41597-020-0437-3

Wall, D. H., Bradford, M. A., St. John, M. G., Trofymow, J. A., Behan-Pelletier, V., BIGNELL, D. E., Dangerfield, J. M., Parton, W. J., Rusek, J. & Voigt, W. (2008). Global decomposition experiment shows soil animal impacts on decomposition are climate-dependent. *Global Change Biology*, *14*(11), 2661-2677.

Wardle, D. A., Yeates, G. W., Barker, G. M. & Bonner, K. I. (2006). The influence of plant litter diversity on decomposer abundance and diversity. *Soil Biology and Biochemistry*, *38*(5), 1052–1062. https://doi.org/10.1016/j.soilbio.2005.09.003

Yin, R., Kardol, P., Eisenhauer, N. & Schädler, M. (2022). Land-use intensification reduces soil macrofauna biomass at the community but not individual level. *Agriculture, Ecosystems & Environment*, *337*, 108079. https://doi.org/10.1016/j.agee.2022.108079

Yin, R., Siebert, J., Eisenhauer, N. & Schädler, M. (2020). Climate change and intensive land use reduce soil animal biomass via dissimilar pathways. *eLife*, *9*, e54749. https://doi.org/10.7554/eLife.54749

Zelles, L. (1997). Phospholipid fatty acid profiles in selected members of soil microbial communities. *Chemosphere*, *35*(1), 275–294. https://doi.org/10.1016/S0045-6535(97)00155-0

Zhao, Q., Van den Brink, P. J., Carpentier, C., Wang, Y. X., Rodríguez-Sánchez, P., Xu, C., Vollbrecht, S., Gillissen, F., Vollebregt, M. & Wang, S. (2019). Horizontal and vertical diversity jointly shape food web stability against small and large perturbations. *Ecology Letters*, *22*(7), 1152-1162. https://doi.org/10.1111/ele.13282

Zheng, L., Wu, S., Lu, L., Li, T., Liu, Z., Li, X. & Li, H. (2023). Unraveling the interaction effects of soil temperature and moisture on soil nematode community: A laboratory study. *European Journal of Soil Biology*, *118*, 103537. https://doi.org/10.1016/j.ejsobi.2023.103537

Zhu, G., Luan, L., Zhou, S., Dini-Andreote, F., Bahram, M., Yang, Y., Geisen, S., Zheng, J., Wang, S. & Jiang, Y. (2024). Body size mediates the functional potential of soil organisms by diversity and community assembly across soil aggregates. *Microbiological Research*, *282*, 127669. https://doi.org/10.1016/j.micres.2024.127669