# Soil invertebrates are the key drivers of litter decomposition in tropical forests

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## Abstract

Forest litter decomposition is an essential component of global carbon and nutrient turnover. Soil invertebrates play important roles in litter decomposition, but the regional pattern of their effects is poorly understood. We examined 476 case studies across 93 sites and performed a meta-analysis to estimate regional effects of invertebrates on forest litter decomposition. We then assessed how invertebrate diversity, climate and soil pH drive regional variations in invertebrate-mediated decomposition. We found that (1) invertebrate contributions to litter decomposition are 1.5 times higher in tropical forests than forests outside the tropics, with an overall contribution of 31% to global forest litter decomposition; and (2) invertebrate diversity, particularly of termites, together with warm, humid and acidic environments in the tropics are positively associated with forest litter decomposition by soil invertebrates. Our results demonstrate the significant difference in invertebrate effects on mediating forest litter decomposition between the tropics and elsewhere. We demonstrate, also, the significance of termites in driving litter mass loss in the tropics. These results are particularly pertinent in the tropics where climate change and human disturbance threaten soil invertebrate biodiversity and the ecosystem services it provides.

## INTRODUCTION

Plant litter is important in the formation of soil organic matter in terrestrial ecosystems (Pan *et al.* 2011). Decomposition of plant litter is fundamental in maintaining soil health, carbon sequestration and plant productivity (Hättenschwiler *et al.* 2005). Litter decomposition is primarily caried out by microbes (fungi and bacteria), microfauna (e.g. nematodes), mesofauna (e.g. collembola and mites) and macrofauna (e.g. termites, earthworms, isopods and millipedes) (Lehmann & Kleber 2015). These organisms break down plant materials to small particles, mineral salts, carbon dioxide and water which are then used by plants and soil organisms for nutrients and energy (Swift *et al.* 1979; Griffiths *et al.*2021a). Generally in ecology microbes are considered the major decomposers since they can produce cellulase and lignases that degrade structural polysaccharides in plant litter (i.e. cellulose and lignin) (Papanikolaou et al. 2010; Pausas & Bond 2020). Another important component of the soil biome is the invertebrates whose effects on litter decomposition are often underestimated (Filser *et al.* 2016; Pausas & Bond 2020). However, micro-organisms are the only soil biota currently included in global biogeochemistry models (Cotrufo *et al.* 2010; Wieder *et al.* 2015). This omission limits our ability to model global nutrient and carbon budgets, which are crucial for understanding the links between climate change and ecosystem services (Grandy *et al.* 2016; Bishop *et al.* 2021).

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Recently there has been an increase in understanding of invertebrate decomposer assemblages and how they affect carbon cycling and nutrient availability (Chang & Lai 2018; Shelomi *et al.* 2019; Joly*et al.* 2020). Studies have shown decomposer invertebrates can increase litter mass loss and nutrient release either in partnership with symbiotic microbes or using endogenous cellulases (Eggleton & Tayasu 2001; Ashton *et al.* 2019; Griffiths *et al.* 2019). Earthworms, beetles, isopods and millipedes can produce extracellular cellulases in partnership with gut symbionts (Pauchet *et al.*2010; Ni'matuzahroh *et al.* 2022). In addition and apart from gut symbionts, some of these groups are also capable of producing endogenous cellulases to digest dead organic matter through invertebrate-enzymatic decomposition without the support of microbes (Pauchet *et al.*2010; Griffiths *et al.* 2021a).

In addition to affecting litter decomposition directly through the breakdown of organic material, soil invertebrates are important bioturbators that enhance microbial decomposition by reshaping soil physical and chemical properties. Termites and earthworms, for example, build huge networks of soil galleries that promote water infiltration and transportation (Jouquet *et al.* 2011; Hoeffner *et al.*2019). These water-filled pores and water films are ideal habitats for aquatic microbiota, such as protists, nematodes, bacteria and fungi (Hoeffner *et al.* 2019). Foraging and nesting behaviors of invertebrates improve soil nutrient heterogeneity, creating hotspots of essential plant-nutrients such as nitrogen and phosphorus (Griffiths *et al.* 2018; Ashton *et al.* 2019; Phillips *et al.* 2021). Invertebrate faeces influence soil nutrients and ambient microbial communities (David 2014). The wide-ranging ways in which invertebrates influence soil properties are complex, with ecosystem-wide effects mediating microbial decomposition and plant growth (Swift *et al.* 1979; Adejuyigbe *et al.*2006). Although a growing body of work highlights the importance of soil invertebrates in decomposition, there remains large gaps in our understanding of the biogeography of soil invertebrate contributions to carbon and nutrient cycling.

The ecological functions carried out by soil invertebrates vary across regions, such as the tropics and non-tropics (Brussaard *et al.*2012; Phillips *et al.* 2021; Kass *et al.* 2022). Evolutionary history and habitat have led to regional differences in soil faunal taxa (van den Hoogen*et al.* 2020). In tropical forests, macrofauna (e.g. termites, earthworms, isopods and millepedes) dominate the decomposer invertebrate assemblages (Swift *et al.* 1979; Lavelle *et al.* 2022). The termites are especially important for decomposition yet are a group that is largely absent from temperate regions. Termites remove large quantities of dead organic material from the forest floor (Bignell & Eggleton 2000). In forests outside the tropics (e.g. temperate, subtropical, and boreal) where microbes are accepted as the dominant decomposers, the mesofauna (e.g. mites and collembolas) and macrofauna (e.g. earthworms, isopods and millepedes) are also important contributors to litter decomposition (Anderson 1978; Korboulewsky*et al.* 2016; Heděnec *et al.* 2022). The quality and palatability of plant-derived resources affect soil invertebrate diversity (Cebrian 1999; Kurokawa *et al.* 2010; Bastida *et al.* 2020). Plant materials with a high proportion of nitrogen relative to structural polysaccharides (e.g. low C:N or lignin:N ratios) usually shows high palatability and decomposability (Swift *et al.* 1979; Kurokawa & Nakashizuka 2008). In addition, most invertebrates are sensitive to climate. They are usually more active in warm or humid biomes such as tropical forests, limited by cold and dry conditions (García-Palacios *et al.* 2013). As most published observations are from non-tropical regions (Xu *et al.* 2020; McCary & Schmitz 2021), current models and their conceptual framework may not assess invertebrate effects on decomposition accurately. Accordingly, an understanding of the regional differences in invertebrate-mediated decomposition and how specific decomposer invertebrates, climate, and soil mediate regional differences are important for us to estimate invertebrate effects on biogeochemistry.

We have performed a meta-analysis to compare the effects of soil invertebrate on leaf litter decomposition in forests contrasting the tropics and the non-tropics. We then analyzed whether and how invertebrate diversity, litter traits, climate, and soil pH influence the global patterns of soil invertebrate-mediated decomposition. Using this approach, we address whether soil invertebrate contributions to forest leaf litter decomposition vary across regions. Based on previous work on soil invertebrate-mediated decomposition, we hypothesize that (1) soil invertebrate effects on forest litter decomposition will be significantly higher in tropical forests than non-tropical forests; (2) high termite diversity, warm and humid environments will be the major drivers

of high tropical invertebrate contributions to forest litter decomposition.

## MATERIALS AND METHODS

### Data collection

We synthesized studies related to soil invertebrate effects on forest leaf litter decomposition and searched articles published in the Web of Science, Elsevier ScienceDirect, SpringerLink, and Wiley. The keywords used for the literature searches were ('decomposition' OR 'breakdown' OR 'degradation' OR 'decay') AND ('leaf' OR 'foliar' OR 'litter') AND ('forest' OR 'wood land') AND ('litterbag' OR 'naphthalene' OR 'mesh size') AND ('soil animal' OR 'soil fauna' OR 'soil invertebrate' OR 'soil detritivore'). We initially selected 2278 contributions based on the keyword list. Studies were included in our database when fulfilling all three of the following requirements:

(1) conducted leaf litter decay experiments in natural forests;

(2) used graded mesh sizes (fine (mesh size [?] 1 mm) vs coarse (mesh size >1 mm)) or chemical agents (dose vs control) to establish treatments including invertebrate inclusion and exclusion under the same abiotic and biotic conditions; and,

(3) measured litter decomposition in terms of mass loss, mass remaining, or decomposition rate over a known decay duration.

### Data extraction

For invertebrate exclusion and/or inclusion treatments of each article, we recorded sample sizes (n), means of mass loss or decomposition rates, and standard deviations (SD) from tables directly or extracted data from figures by performing Web-PlotDigitizer (Burda *et al.* 2017). Standard errors (SE) reported in the original articles were converted into SD using the formula $\mathbf{SD = SE \times \sqrt{n}}$. Means of mass loss were converted into annual decomposition rates using the negative exponential decomposition equation described by Olson (1963). Other information we recorded from the original articles include latitude, longitude, biome, mean annual temperature (MAT, degC), mean annual precipitation (MAP, mm yr$^{-1}$), soil pH, litter traits (carbon (C), nitrogen (N), C:N ratio, lignin:N ratio), duration of decomposition, and the method to exclude invertebrates (physical vs. chemical).

All sites were classified into geographic groups for testing regional variations. First, we grouped sites into 'the tropics' and 'the non-tropics' based on biomes as stated in the original articles which we further checked by spatial coordinates. Specifically, tropical wet and dry forests were grouped into 'the tropics' (96% belonged to tropical wet forests); other forest biomes were grouped into 'the non-tropics'. Biomes are powerful biogeographic units for studying large-scale patterns of carbon and energy fluxes (Yi *et al.* 2010; Mucina 2019). Our classification of biomes followed Dinerstein *et al.*(2017). Fig. 1 was plotted using ArcGIS (version 10.2, ESRI, 2020). We also assigned sites into zoogeographic realms to explore potential biogeographic effects (e.g. dispersal and evolutionary histories). Zoogeographic information of each observation followed Holt *et al.* (2013) which is based on vertebrates but is generally pertinent to the assessment of invertebrate distributions (Liria *et al.* 2021).

To explore potential moderators of regional variation of the effects of invertebrate son decomposition, we tested several potential explanatory factors: termite diversity (a decomposer group the diversity of which is different in the tropics and non-tropics), litter traits (C, N, C:N and lignin:N ratios), climate and soil pH. Termite diversity values were extracted from a corresponding prediction model. The diversity predictions are estimated from a model which was 'trained' using alpha-diversity values from 700 sites (Woon et al., in preparation). We acknowledge that species diversity and richness do not always confer higher contribution to ecosystem services compared with functional diversity, but, currently, this is the best proxy we have to identify global patterns of species distribution of the group. Where data were absent from focal studies we obtained missing litter quality data from the TRY plant trait database (Kattge *et al.* 2020), missing soil

pH data from the Harmonized World Soil Database (https://www.fao.org/soils-portal/en/, resolution = 5'), and missing climate data (mean annual temperature, MAT and mean annual precipitation, MAP) from the Worldclim database (http://www.worldclim.org/, resolution = 5').

**Statistical analysis**

We first predicted the relative contributions of soil invertebrates and microbes across absolute latitude using weighted least square models controlled for the random effects of references. The relative contribution of microbes in each case was calculated as one minus the invertebrate contribution. We then used a natural log-transformed response ratio (LRR) to estimate invertebrate effect size of each observation (Hedges *et al.* 1999), *viz* :

$LRR = \ln(K_c/K_f)$

where $K_c$ and $K_f$ are the mean decay rates under invertebrate inclusion and exclusion treatments, respectively. $LRR > 0$ indicates that soil invertebrates contribute positively to forest litter decomposition. The within-study variance ($v_i$) of each effect size was calculated as:

$$v_i = \frac{S_c^2}{n_c K_c^2} + \frac{S_f^2}{n_f K_f^2}$$

where $n_c$ and $n_f$ are the sample sizes of invertebrate inclusion and exclusion treatments, respectively, and $S_c$ and $S_f$ are the standard deviations of invertebrate inclusion and exclusion treatments. We calculated the effect size and $v_i$ using the 'escalc' function in the R package 'metafor' (Xu *et al.* 2020). We estimated missing $S_c$ and $S_f$ values using random number simulation (10000 repetitions) and estimated the missing $v_i$ using the 'impute_SD' function in the 'metagear' package (Bracken & Sinclair 1992). Invertebrate contributions (%) to forest leaf litter decomposition were calculated as:

Invertebrate contribution (%) = $[1 - 1/\exp(LRR)] \times 100\%$

In our meta-data, a single reference usually reported multiple observations, which means the observations are nested in the reference. This nested data structure may cause non-independent response variables. Thus, we applied an inverse variance-weighted hierarchical random-effects model (rma.mv) with a random part (~ 1| reference / observation) to estimate the weighted mean effect size (LRR$_{++}$) with 95% confidence intervals (Viechtbauer 2010). Confidence intervals not crossing zero indicate significant mean effect sizes. We first estimated the mean invertebrate effect sizes at spatial scales and then performed a driving factor analysis to assess the relationships between moderators and invertebrate effect sizes. For categorical moderators (i.e., region, biome, and realm), we used the hierarchical model to calculate the mean effect sizes at different levels and compared them by employing multiple comparisons using the 'multcomp' package (Bretz *et al.* 2010). For continuous moderators (i.e. termite diversity, earthworm richness, microbial biomass carbon, MAT, MAP, and soil pH), we used mixed-effects meta-regression to assess the relationships between effect sizes and moderators. We also tested the effects of decomposition duration and protocol (mesh vs. chemical) of invertebrate exclusion on invertebrate effect sizes.

We used a Q-statistic to evaluate the heterogeneity of effect sizes, which is based on a chi-squared test. Total heterogeneity (Qt) can be divided into the variance explained by the moderators (Qm) and the residual error variance (Qe). A significant Qm ($P < 0.05$) indicates that the moderator significantly influences effect sizes (Viechtbauer 2010). Publication bias arises from a preponderance of articles presenting 'favorable' results which can impact the reliability of our assessment. We tested the possibility of publication bias using a funnel plot and performed Egger's regression test to examine, quantitatively, the funnel symmetry (Su *et al.* 2021). A p value greater than 0.05 for Egger's test indicates that the result is less affected by publication bias. All analyses were performed in R 4.2.0.

**RESULTS**

**Meta-data in this study**

A total of 62 articles, encompassing 476 observations across 93 study sites met our criteria (for detailed references see supporting material S1). Eighty-five per cent of case studies used graded mesh sizes to exclude soil invertebrates, with 15% using chemical agents. Observations were distributed across all continents on Earth except Antarctica: Asia (37%), Europe (32%), South America (24%), North America (5%), and Australia and Africa (2% for both) (Fig. 1). For litter traits and environmental variables, 36% of leaf litter traits (C, N, C: N and lignin:N ratios), 50% of soil pH, 90% of mean annual temperature (MAT, degC), and 91% of mean annual precipitation (MAP, mm $yr^{-1}$) were taken from the original articles.

**Spatial distribution of soil invertebrate effects on forest leaf litter decomposition**

Forest litter decomposition by invertebrates was the highest in the tropics and decreased with increasing absolute latitude (Fig. 2a). Although overall microorganism effect (69% on average) on forest litter decomposition twice that of invertebrate effect (31% on average), the contribution of invertebrates to litter decomposition in the tropics approaches that of microorganisms. In boreal forests, the invertebrate contribution is low, with microorganisms acting as the major decomposers (Fig. 2a). Overall, invertebrates had significantly positive effects on forest litter decomposition, leading to a 31% increase in decomposition where there was invertebrate access ($LRR_{++}$ = 0.368, Qt = 37687.144, df = 475, P < 0.001) (Fig. 2b, Table S1). Soil invertebrates increased litter decomposition significantly by an average of 40% in tropical forests ($LRR_{++}$ = 0.513, df = 161, P < 0.001) compared with 26% in non-tropical forests ($LRR_{++}$ = 0.303, df = 311, P < 0.001), respectively (Fig. 2b, Tables S1, S2). Tropical invertebrates contributed 1.5 times more to forest litter decomposition *in situ* than did non-tropical invertebrates (Fig. 2b, Table S2).

Across different forest biomes, soil invertebrates contributed significantly to litter decomposition in all forest biomes, increasing decomposition by 43% in tropical wet forests ($LRR_{++}$ = 0.554, P < 0.001), 28% in evergreen broadleaf forests ($LRR_{++}$ = 0.323, P = 0.001), 26% in deciduous forests ($LRR_{++}$ = 0.303, P < 0.001), 25% in coniferous forests ($LRR_{++}$ = 0.293, P < 0.001), and 24% in cold or dry woodlands ($LRR_{++}$ = 0.274, P < 0.001) (Fig. 2b). Compared with non-tropical forests, tropical wet forests held the highest invertebrate-mediated litter decomposition (Table S2). Among forests in different zoogeographic realms measured, we found the higher soil invertebrate effects on decomposition in Neotropical forests (48%, $LRR_{++}$ = 0.656, P < 0.001) compared with those in the Nearctic (29%, $LRR_{++}$ = 0.338, P = 0.001), the Palearctic (25%, $LRR_{++}$ = 0.292, P < 0.001), and the Sino-Japanese forests (22%, $LRR_{++}$ = 0.247, P < 0.001), respectively (Fig. 3, Table S2). There were no significant differences in invertebrate effects in the Neotropical forests compared with forests in the Oriental (29%, $LRR_{++}$ = 0.344, P < 0.001), Panamanian (46%, $LRR_{++}$ = 0.625, P < 0.001), and Australian (35%, $LRR_{++}$ = 0.426, P = 0.004) data, respectively (Table S2).

**Drivers of soil invertebrate effects on forest leaf litter decomposition**

Mixed-effect meta regression showed a significantly positive relationship between termite diversity and invertebrate effect sizes (Qm = 17.842, P < 0.001, df = 446, Fig. 4a). For litter traits, our meta regressions showed significantly negative relationships between invertebrate effect sizes and C: N ratios in litter (Qm = 5.475, P = 0.019, df = 266, Fig. 4b) and lignin: N ratios (Qm = 5.634, P = 0.018, df = 153, Fig. 4c), whereas no significant relationships were observed between effect sizes and litter C, N, P contents (as percentage of dry litter weight) (Table S1). In terms of climatic variables, there were significant positive relationships between invertebrate effect sizes and mean annual temperature (Qm = 8.133, P = 0.004, df = 474, Fig. 4d) and mean annual precipitation (Qm = 25.672, P < 0.001, df = 475, Fig. 4e). We also found that soil pH negatively correlated with invertebrate effects on forest litter decomposition (Qm = 11.226, P = 0.001, df = 450, Fig. 4f).

In our dataset, the decomposition durations of 73% of observations are [?] 1 year, and the remaining 23% are from 1 to 2 years. Mixed-effect meta regression showed that soil invertebrate effects weakened with the increasing of decomposition duration (Qm = 5.942, P = 0.015, Table S1), indicating soil invertebrates contribute differentially to the early stages of leaf litter decomposition (Fig. S1a). We did not find a

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significant impact of faunal exclusion protocol (chemical vs. physical) on invertebrate effects (Table S1). The reliability of our results was supported by Egger's test for funnel plot asymmetry (z = 0.8708, P = 0.3838), showing that invertebrate effect sizes were not affected by publication bias (Fig. S2).

## DISCUSSION

### Soil invertebrates contribute to forest litter decomposition across the globe

Soil invertebrates make considerable contributions to the decomposition of forest litter. Our synthesis shows 31% of litter decomposition, globally, is mediated by invertebrates. Our estimate is in line with the previous estimates ranging from 27% to 35% of invertebrate effects on decomposition (Kampichler & Bruckner 2009; Garcia-Palacios *et al.* 2013; Xu *et al.* 2020). Based on the overall estimates, our analysis further shows a regional pattern of invertebrate effects on litter decomposition and particular invertebrate groups driven the regional difference. We have shown that the invertebrate contribution to litter decomposition in tropical forests is 1.5 times higher than in forests outside the tropics. This latitudinal pattern was observed consistently across all zoogeographic realms except the Ethiopian (Afrotropical) and all biomes. The pattern is supported both historically and ecologically. The presence of particular decomposer groups (e.g. termites) may explain the strong effects of soil invertebrate on decomposition in the tropics. The so-called 'tropical conservatism hypothesis' suggests that, in the past, when the Earth was warmer, tropical lineages had wider distributions. Long-term cooling since the late Eocene has restricted distributions of tropical fauna and driven their extinctions in now non-tropical regions (Wiens & Donoghue 2004; Guenard *et al.* 2015). This history over deep time may well underpin current ecological functions. Major biogeographic differences in soil invertebrate species pools must be considered when discussing the major drivers of decomposition globally. Plant community and environmental conditions also drive soil invertebrate activities and abundance in tropical forests. Diverse plant communities create rich food resources for soil invertebrates and is the basis for maintaining their abundance and activities (Cebrian 1999; Kurokawa *et al.* 2010; Lavelle *et al.* 2022). Humid and warm environment in tropical regions are generally favorable for the activities of specific decomposer invertebrates, which are crucial for their corresponding ecological functions, which includes litter decomposition (Tan *et al.* 2020).

### Drivers mediate regional variation in soil invertebrate effects on forest litter decomposition

Soil invertebrate fauna

We have shown that termites are important decomposers responsible for a significant component of mass loss of litter. Termites specializing in the decomposition of dead plant material and are diverse in the tropics but not in temperate regions (Lavelle *et al.* 2022). The Termitidae, for example, are litter-feeders with high diversity in tropical forests (Eggleton & Tayasu 2001), well adapted to breaking down organic matter (Hogan *et al.* 1988; Bignell 2019). Many termite species are able to produce endogenous cellulase predominantly in the midgut enabling them to digest cellulose (Hogan *et al.* 1988). They also produce extracellular enzymes that digest cell wall polysaccharides cooperatively with symbiotic protozoa (e.g. Kalotermitidae) or microbial symbionts (e.g. the Termitidae) (Eggleton & Tayasu 2001). Our results provide further evidence that termites are key decomposers in the tropics, shaping nutrient turnover with ecosystem-wide implications for carbon flux and soil modification (Ashton *et al.*2019; Griffiths *et al.* 2021b). Understanding the links among termite biodiversity, ecosystem processes and environmental change such as climate and land use change is key for understanding biogeochemical cycles.

Climatic variables

We demonstrated that soil invertebrate contributions to forest litter decomposition are positively related to temperature and precipitation. Climate can moderate faunal decomposition through its impacts upon invertebrate activities (Thakur *et al.* 2018). Low temperature or water-limited conditions in subtropical, temperate, and boreal forests limit soil invertebrate activities and their decomposing effects (David & Handa 2010; Castanho *et al.* 2012). The behaviour of some invertebrate decomposers are directly sensitive to temperature. Foraging termites, for example, show increasing discovery rates with increasing temperature

(Zanne *et al.* 2022). For precipitation, many soil organisms are sensitive to low soil moisture. Protozoa, nematodes and mites, for instance, live within water droplets or films and are directly affected by water potential (Hoeffner *et al.* 2019). Some soft-bodied meso- or macro-invertebrates (e.g. earthworms) are also susceptible to moisture stress (Swift *et al.* 1979). In contrast, invertebrates that mainly occupy the litter layer or air-filled soil spaces (e.g. termites, isopods, millipedes and beetles), have lower water sensitivity and are more resistant to desiccation (Swift *et al.* 1979; Berg & McClaugherty 2020). Foraging discovery rates and activities of termites may even be enhanced with increasing drought, enhancing their ecological importance in extreme droughts (Ashton *et al.* 2019). Any loss of decomposer organisms driven by climate change, therefore, may lead to a decrease in future litter decomposition (Wall *et al.* 2010), but the relative magnitude of termite impacts on biogeochemistry may increase at the Earth's surface with increasing tropicalization (Zanne *et al.*2022).

Soil pH

Soil pH shows a negative relationship with invertebrate effects on forest litter decomposition. Microbiota within water films, were clearly the most sensitive to soil pH (Tao *et al.* 2019). Tropical soils are usually acidic due to high leaching intensity driven by high precipitation (Zhang *et al.* 2019), with pH levels ranging from 3.8 to 6.2 in our meta-data. In the tropics, litter-feeders with high acidity tolerance, such as termites, can reach high abundance levels and so have a competitive advantage over microorganisms, especially bacteria (Lavelle *et al.* 1995). Reduced vegetation cover caused by deforestation leads to soil acidification as lack of organic matter and root systems lead to loss of soil nutrients (Birhanu *et al.*2016). Increased land-use intensity with concomitant loss of tree cover, therefore, threatens soil biodiversity not only through habitat loss but also by changing soil properties by acidification. This negative effect may undermine the ecological functions of both microbial and faunal decomposers, while some highly adapted invertebrates, such as invasive earthworms and termites, may be responsible for more litter decomposition in disturbed areas (Liu & Zou 2002; Huang *et al.*2020).

## FUTURE WORK

Including regional variations in soil invertebrate effects on biogeochemistry to conceptual and predicting models. The temperate bias of studies examining the role of invertebrates in decomposition means that much of the raw data for existing biogeochemical models are from non-tropical zones, which may result in an underestimation of soil invertebrate effects on carbon flux and nutrient turnover. Moreover, invertebrate biodiversity has been under tremendous pressure, with knock-on effects on soil health, plant growth and climate regulation. The tropics represent 36% of earth's landmass and support the majority of aboveground plant biomass (Crowther *et al.* 2019). The regional differences in invertebrate functions we have reported suggests that the loss of invertebrate biodiversity could be particularly catastrophic in the Tropics.

More empirical studies needed in Africa and Australia. As with many meta-analyses in ecology, only a small number of studies have occurred in Australia and Africa, where large areas of tropical dry forests and rainforests are located (Pan *et al.* 2013). We have repeatedly stressed the relative importance of the termites in driving tropical decomposition. Termites are diverse in both Australia and Africa. Africa, indeed, is the evolutionary cradle of termites and hosts the highest number of termite species (Buitenwerf *et al.* 2011; Bignell 2019). The lack of observations in these areas suggests that we may have underestimated tropical invertebrate effects on forest litter decomposition. We urge, extensive data collection in the tropics, especially in Africa, as essential for future assessments of global carbon cycling and nutrient turnover.

Detailed information on litter traits and environmental variables are needed. We suggest that detailed measurements of leaf litter traits need to be included in further studies of litter decomposition. We advocate for the establishment of a global dataset of leaf litter traits. No such comprehensive global dataset for leaf litter traits exists. Contrasts with living leaves (for which global data bases do exist (Kattge*et al.* 2020)) will be informative. In addition, information on plant communities, plot-based microclimates and soil properties should accompany future studies since they are important factors driving the ecological functions of soil invertebrate. Collecting such data at a local scales is essential (Bradford *et al.* 2014).

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Protocol used to exclude soil invertebrates. To date, most studies have used physical methods (i.e. litterbags and mesocosms) to exclude soil invertebrates in field experiments, accounting for 85% of observations in our meta-data. Sixteen percent of observations in our meta-data showed negative effects of invertebrates on litter mass loss. These negative faunal effects on decomposition have not been well tested. Possible explanations would be non-target effects of chemicals (e.g. naphthalene) on both invertebrates and microbes (Lan *et al.*2020). Within the observations of negative faunal effects in our meta-data, 62% of observations were from the use of naphthalene to exclude invertebrates. The inclusion of fungivores such as Collembola and Nematoda may affect microbial decomposition negatively (Johnson*et al.* 2005) in cold or dry regions where invertebrate activity is constrained by temperature and water availability (Wall *et al.*2008). Our analysis shows an insignificant relationship between exclusion method and invertebrate effects on forest litter decomposition. The potential non-target effects of chemicals such as naphthalene on soil organisms and environments (Lan *et al.* 2020), however, leads us to advocate use of physical exclusion methods (Lan*et al.* 2019), particularly in highly stochastic tropical rainforests and in regions with high precipitation.

## CONCLUSION

We have demonstrated conclusively that soil invertebrates are important components of global forest leaf litter decomposition, especially in the tropics, from both biogeographical and ecological perspectives. Termites in particular are major decomposers mediating the regional variation in animal-driven decomposition. Soil invertebrates are experiencing remarkable diversity loss and functional changes driven by multiple disturbances including climate change, habitat loss and environmental pollution (Cifuentes-Croquevielle *et al.* 2020). Potentially, this loss will decrease the release of carbon and plant-available nutrients from dead organic matter significantly with cascading effects on plant nutrient uptake and soil health (Handa*et al.* 2014; Griffiths *et al.* 2021a). Future climate change and other human disturbance has the potential to reshape the relative contributions of soil invertebrates and microbes in global litter decomposition with unknown but undoubtedly serious consequences.

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## COMPETING INTERESTS

The authors declare that they have no known competing financial interests or personal relationships that could have influenced the work reported in this article.

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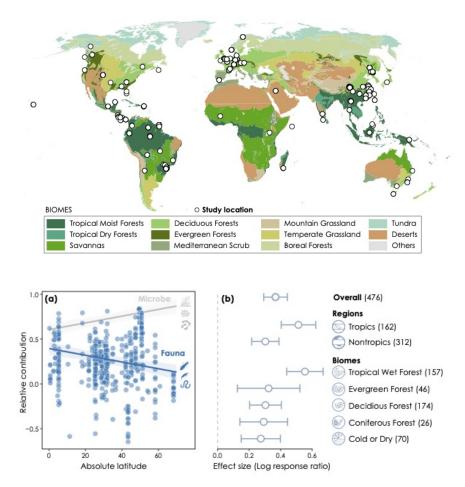
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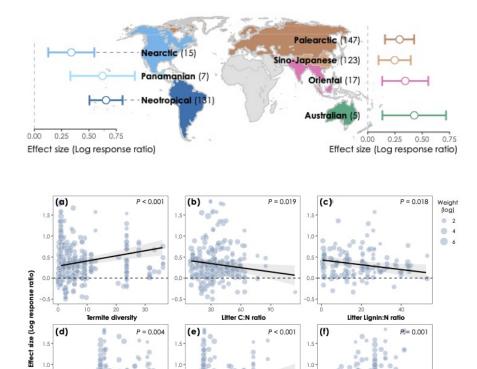
**Figure 1** Global distribution of forest leaf litter decomposition experiment used in this study. The map indicates a total of 476 observations at 93 sites across the world superimposed on the background of biome patterns.

**Figure 2** Soil invertebrate contributions to forest litter decomposition across regions. **(a)** Relative contributions of soil invertebrates (blue) and microorganisms (grey) to forest litter decomposition against absolute

latitude. **(b)** Effect sizes of soil invertebrates on forest litter decomposition at global, regional, and biome scales. The errors represent 95% confidence intervals. The numbers of observations are in the brackets. Positive mean effect sizes indicate soil invertebrates significantly contribute to forest litter decomposition.

**Figure 3** Soil invertebrate effect sizes on forest leaf litter decomposition across zoogeographic realms. The numbers of observation are in the brackets. Realms with [?] 5 observations are included. Colors are identical in forest plot and map, realms with observations less than 5 are indicated by the grey color. The errors represent 95% confidence intervals.

**Figure 4** Influence of **(a)** termite diversity, **(b)** litter C: N ratio, **(c)** litter lignin: N ratio, **(d)** mean annual temperature (MAT), **(e)** mean annual precipitation (MAP), and **(f)** soil pH on invertebrate effect sizes determined using mixed-effect meta regressions. Point sizes represent the relative weights (log) of corresponding observations. Significant correlations (P < 0.05) are shown with solid regression lines with 95% confidence intervals.



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