

Global contribution of invertebrates to forest litter decomposition

Xiaoyi Zeng¹ | Huilin Gao² | Runxi Wang¹ | Bartosz M. Majcher¹ | Joel S. Woon^{3,4} | Cheng Wenda⁵  | Paul Eggleton⁴ | Hannah M. Griffiths⁶ | Louise A. Ashton¹ 

¹School of Biological Sciences, University of Hong Kong, Hong Kong, China

²Faculty of Business and Economics, University of Hong Kong, Hong Kong, China

³School of Environmental Sciences, University of Liverpool, Liverpool, UK

⁴Department of Life Sciences, Natural History Museum, London, UK

⁵School of Ecology, Sun Yat-Sen University, Guangdong, China

⁶School of Biological Sciences, University of Bristol, Bristol, UK

Correspondence

Louise A. Ashton, School of Biological Sciences, University of Hong Kong, Hong Kong, China.

Email: lashton@hku.hk

Funding information

General Research Fund, Hong Kong Research Grants Council, Grant/Award Number: 17101021

Editor: Akira S Mori

Abstract

Forest litter decomposition is an essential component of global carbon and nutrient turnover. 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 1.4 times higher in tropical and subtropical forests than in forests elsewhere, with an overall contribution of 31% to global forest litter decomposition; and (2) termite diversity, together with warm, humid and acidic environments in the tropics and subtropics are positively associated with forest litter decomposition by invertebrates. Our results demonstrate the significant difference in invertebrate effects on mediating forest litter decomposition among regions. We demonstrate, also, the significance of termites in driving litter mass loss in the tropics and subtropics. These results are particularly pertinent in the tropics and subtropics where climate change and human disturbance threaten invertebrate biodiversity and the ecosystem services it provides.

KEY WORDS

climate, earthworms, forests, invertebrates, litter decomposition, meta-analysis, soil condition, termites

INTRODUCTION

Soil organisms in the process of plant litter decomposition

Plant litter is important in the formation of soil organic matter in terrestrial ecosystems (Aerts, 1997; 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 carried 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 (Griffiths, Ashton, et al., 2021; Swift et al., 1979). Generally, in ecology, microbes are considered the major decomposers since they can produce cellulase and lignases that degrade structural polysaccharides in plant litter (e.g. cellulose and lignin) (Papanikolaou et al., 2010; Pausas & Bond, 2020). However, another important component of the soil biome are the invertebrates whose effects on litter decomposition are often underestimated (Filser et al., 2016; Pausas & Bond, 2020) and are not currently included in global biogeochemical models (Cotrufo et al., 2010; Wieder et al., 2015). This omission limits our ability to understand and predict global nutrient and carbon budgets, which are crucial for determining the links between climate change and ecosystem services (Bishop et al., 2021; Grandy et al., 2016).

This is an open access article under the terms of the [Creative Commons Attribution-NonCommercial](https://creativecommons.org/licenses/by-nc/4.0/) License, which permits use, distribution and reproduction in any medium, provided the original work is properly cited and is not used for commercial purposes.

© 2024 The Authors. *Ecology Letters* published by John Wiley & Sons Ltd.

Invertebrates chemically decompose dead organic material

Recently, there has been an increase in understanding of invertebrate decomposer assemblages and how they affect carbon cycling and nutrient availability (Chang & Lai, 2018; Joly et al., 2020; Shelomi et al., 2019). Studies have shown decomposer invertebrates can increase litter mass loss and nutrient release either in partnership with symbiotic microbes or using endogenous cellulases (Ashton et al., 2019; Eggleton & Tayasu, 2001; Griffiths et al., 2019). Earthworms, beetles, isopods and millipedes can produce extracellular cellulases in partnership with gut symbionts (de Jonge et al., 2023; Ni'matuzahroh et al., 2022; Pauchet et al., 2010). In addition, and apart from gut symbionts, some termite groups are also capable of producing endogenous cellulases to digest dead organic matter through invertebrate-enzymatic decomposition without the support of microbes (Griffiths, Ashton, et al., 2021; Pauchet et al., 2010).

Invertebrates contribute indirectly to plant litter decomposition

In addition to affecting litter decomposition directly through the breakdown of organic material, 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 (Hoeffner et al., 2019; Jouquet et al., 2011). 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 behaviours of invertebrates improve soil nutrient heterogeneity, creating hotspots of essential plant nutrients such as nitrogen and phosphorus (Ashton et al., 2019; Phillips et al., 2021), while invertebrate faeces influence soil nutrients and ambient microbial communities (David, 2014). In addition, invertebrates can interact with vertebrates through trophic ways (e.g. predation), enhancing vertebrate contributions to litter decomposition (Tuo et al., 2024). The wide-ranging ways in which invertebrates influence soil properties are complex, with ecosystem-wide effects mediating microbial decomposition and plant growth (Adejuyigbe et al., 2006; Swift et al., 1979). Although a growing body of work highlights the importance of invertebrates in decomposition, there remain large gaps in our understanding of the biogeography of invertebrate contributions to carbon and nutrient cycling.

Ecological functions of invertebrates are affected by their evolutionary history and biomes

The ecological functions carried out by invertebrates vary across regions (Brussaard et al., 2012; Kass et al., 2022;

Phillips et al., 2021). Evolutionary history and biomes have led to regional differences in faunal taxa (van den Hoogen et al., 2020). In tropical and subtropical forests, macrofauna (e.g. termites, earthworms, isopods and millepedes) dominate the decomposer invertebrate assemblages (Lavelle et al., 2022; Swift et al., 1979). Termites remove large quantities of dead organic material from the forest floor (Bignell & Eggleton, 2000) making them especially important for decomposition where they occur in high abundances. A key regional difference between global decomposer assemblages is that termites are largely absent from temperate and boreal regions. However, in cool temperate and boreal forests where microbes are accepted as the dominant decomposers, mesofauna (e.g. mites and collembolas) and non-termite macrofauna (e.g. earthworms, isopods and millepedes) are also important contributors to litter decomposition (Anderson, 1978; Heděneć et al., 2022; Korboulewsky et al., 2016). The quality and palatability of plant-derived resources affect invertebrate diversity (Bastida et al., 2020; Cebrian, 1999; Kurokawa et al., 2010). Plant materials with a high proportion of nitrogen relative to structural polysaccharides (e.g. low C:N or lignin:N ratios) usually show high palatability and decomposability (Kurokawa & Nakashizuka, 2008; Swift et al., 1979). As most published observations are from temperate regions (McCary & Schmitz, 2021; Xu et al., 2020), 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, soil and plant resources mediate regional differences are important for us to estimate invertebrate effects on biogeochemistry.

We have performed a meta-analysis to compare the effects of invertebrates on leaf litter decomposition in forests among regions. We then analysed whether and how invertebrate diversity, litter traits, climate and soil pH influence the global patterns of invertebrate effects on forest litter decomposition. Based on previous work on invertebrate-mediated decomposition, we use this approach to address the following questions: (1) are invertebrate effects on litter decomposition significantly higher in tropical forests than in forests elsewhere? And (2) are invertebrate diversity, climate and soil properties major moderators driving the regional pattern of invertebrate-mediated decomposition?

MATERIALS AND METHODS

Data collection

We synthesized studies related to 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 (For PRISMA Workflow, see Figure S4). Studies were included in our database when fulfilling all three of the following requirements:

1. conducted leaf litter decomposition experiments in natural and less disturbed 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 $SD = SE \times \sqrt{n}$. We extracted annual decomposition rates calculated by the negative exponential decomposition equation described by Olson (1963). If the original article did not present these decomposition rates, we extracted the means of the mass loss and converted these into annual decomposition rates using Olson's equation. Other information we recorded from the original articles include latitude, longitude, forest type, mean annual temperature (MAT, °C), mean annual precipitation (MAP, mm year⁻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. We classified forest life zones based on the classification described by Holdridge (1947). We then, according to Holdridge's latitudinal regions, grouped the forest life zones into different forest types: 'Tropical forest' (i.e. tropical moist, wet and dry forests), 'Subtropical forest' (i.e. subtropical moist and wet forests), 'Temperate forest' (i.e. warm temperate moist, wet and dry forests; cool temperate moist and wet forests) and 'Other forest' (e.g. boreal wet forest, polar woodland, alpine forest, subalpine wet forest and montane moist forest). To assess the differences in invertebrate-mediated

forest decomposition between the tropics-subtropics and regions elsewhere, we grouped temperate and other forests into 'Other regions'. Figure 1 was plotted using ArcGIS (version 10.2, ESRI, 2020) with a background map described by Dinerstein et al. (2017). 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 also broadly applicable to the assessment of invertebrate distributions (Liria et al., 2021).

To explore potential moderators of the effects of invertebrates on decomposition, we tested several potential explanatory factors: termite diversity (a decomposer group the diversity of which is different in the tropics-subtropics and other regions), litter traits (C, N, C:N and lignin:N ratios), climate and soil pH. We extracted termite diversity values (alpha-diversity calculated by species richness and proportional species abundance) of the corresponding locations from the raster layer of predictive models of global termite diversity using QGIS (version 3.24.2). The diversity predictions were constructed using random forest models with data from 672 termite transects which were modelled against a suite of environmental and location variables (Woon, 2022). 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 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 invertebrates contribute positively

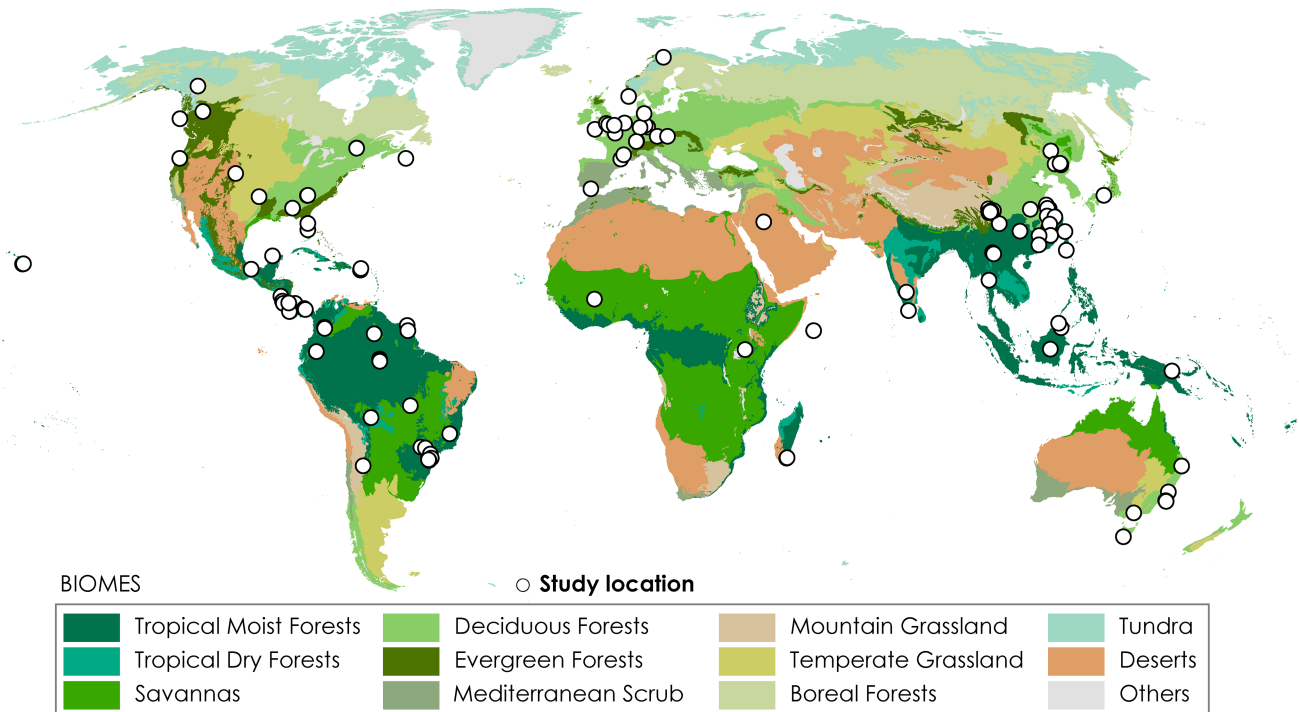


FIGURE 1 Global distribution of forest leaf litter decomposition experiment used in this study. The map indicates a total of 476 observations at 93 sites across the world superimposed on the background of biome patterns.

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' (version 3.8-1) (Xu et al., 2020). We estimated the missing v_i using the 'impute_SD' function in the 'metagear' package (version 0.7) (Bracken & Sinclair, 1992). Invertebrate contributions (%) to forest leaf litter decomposition were calculated as:

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

In our 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 factor (~ 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. We modelled the relationship between effect size (the invertebrate contribution to litter decomposition rates: the dependent variable) and each moderator (e.g. region, forest type, realm, termite diversity, MAT, MAP, litter traits and soil pH: the independent variables). For categorical moderators (i.e. region, forest type 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 (version 1.4-20) (Bretz et al., 2010). For continuous moderators (i.e. termite diversity, MAT, MAP, soil pH and litter traits), we used mixed-effect 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 (Q_t) can be divided into the variance explained by the moderators (Q_m) and the residual error variance (Q_e). A significant Q_m ($p < 0.05$) indicates that the moderator significantly influences effect sizes (Viechtbauer, 2010). Publication bias arises from a preponderance of articles presenting 'favourable' 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 4.2.1.

RESULTS

Data collection in this study

A total of 60 articles, encompassing 476 observations across 93 study sites, met our criteria (Figure S4). Eighty-five percent of case studies used graded mesh sizes to exclude 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) (Figure 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, °C) and 91% of mean annual precipitation (MAP, mm year⁻¹) were taken from the original articles.

Spatial distribution of invertebrate effects on forest leaf litter decomposition

Forest litter decomposition by invertebrates was the highest in the tropics and decreased with increasing absolute latitude (Figure 2a). Although the overall microorganism effect (69% on average) on forest litter decomposition was more than twice that of the invertebrate effect (31% on average), tropical invertebrates show considerable contributions to litter decomposition. In boreal forests, the invertebrate contribution is low, with microorganisms acting as the major decomposers (Figure 2a). Overall, invertebrates had significantly positive effects on forest litter decomposition, leading to a 31% increase in global decomposition, where there was

invertebrate access ($LRR_{++}=0.367$, $Q_t=37,767$, $df=475$, $p<0.001$) (Figure 2b). Invertebrates increased forest litter decomposition in situ significantly by 38% in the tropics-subtropics ($LRR_{++}=0.474$, $df=184$, $p<0.001$), which was 1.4 times than in other regions (by 26%, $LRR_{++}=0.304$, $df=289$, $p<0.001$) (Figure 2b; Tables S1 and S2).

Across forest types, invertebrates increased decomposition by 37% in tropical forests ($LRR_{++}=0.458$, $p<0.001$), 40% in subtropical forests ($LRR_{++}=0.498$, $p<0.001$), 27% in temperate forests ($LRR_{++}=0.320$, $p<0.001$) and 24% in other forests ($LRR_{++}=0.275$, $p<0.001$) (Figure 2b). Among forests in different zoogeographic realms measured, we found the higher invertebrate effects on decomposition in the Neotropical forests (48%, $LRR_{++}=0.660$, $p<0.001$) compared with those in the Palaeartic (26%, $LRR_{++}=0.295$, $p<0.001$) and the Sino-Japanese forests (23%, $LRR_{++}=0.259$, $p<0.001$) respectively (Figure 3; Table S2). There were no significant differences in invertebrate effects in the Neotropical forests compared with forests in the Nearctic (31%, $LRR_{++}=0.367$, $p=0.001$), Oriental (30%, $LRR_{++}=0.359$, $p<0.001$), Panamanian (41%, $LRR_{++}=0.536$, $p<0.001$) and Australian (32%, $LRR_{++}=0.386$, $p=0.004$) respectively (Table S2).

Drivers of invertebrate effects on forest leaf litter decomposition

Mixed-effect meta regression showed a significantly positive relationship between termite diversity and invertebrate effect sizes ($Q_m=17.859$, $p<0.001$, $df=446$, Figure 4a). For litter traits, our meta regressions showed significantly negative relationships between invertebrate

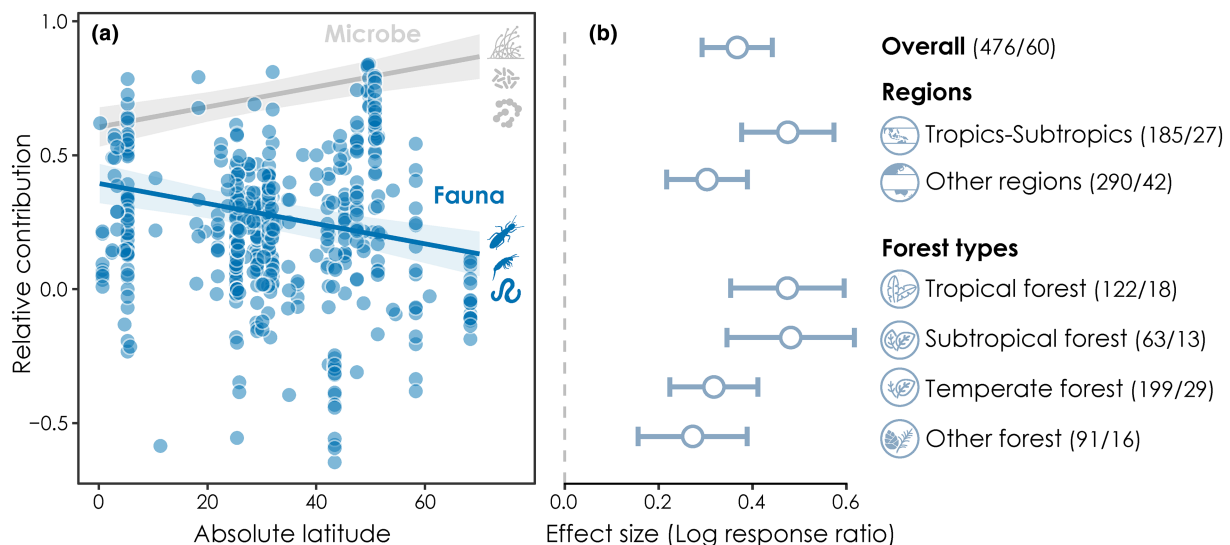


FIGURE 2 Soil invertebrate contributions to forest litter decomposition across regions. (a) Relative contributions of invertebrates (blue) and microorganisms (grey) to forest litter decomposition against absolute latitude. (b) Effect sizes of invertebrates on forest litter decomposition at global, regional and biome scales. The errors represent 95% confidence intervals. The numbers of observations (left) and studies (right), separated by slash, are in brackets. Positive mean effect sizes indicate soil invertebrates significantly contribute to forest litter decomposition.

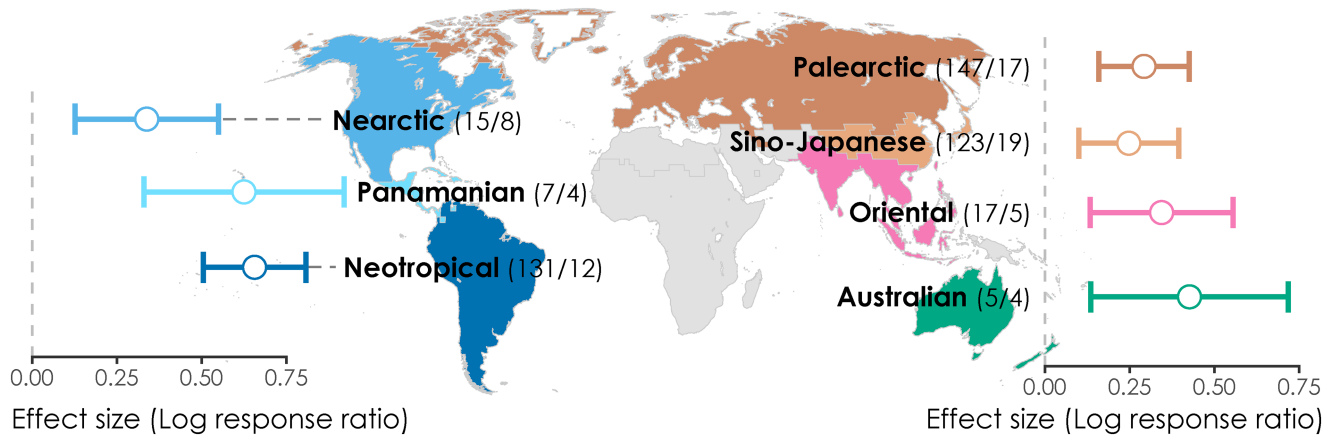


FIGURE 3 Invertebrate effect sizes on forest leaf litter decomposition across zoogeographic realms. The numbers of observations (left) and studies (right), separated by slash, are in brackets. Realms with ≥ 5 observations are included. Colours are identical in forest plot and map, realms with observations less than 5 are indicated by the grey colour. The errors represent 95% confidence intervals.

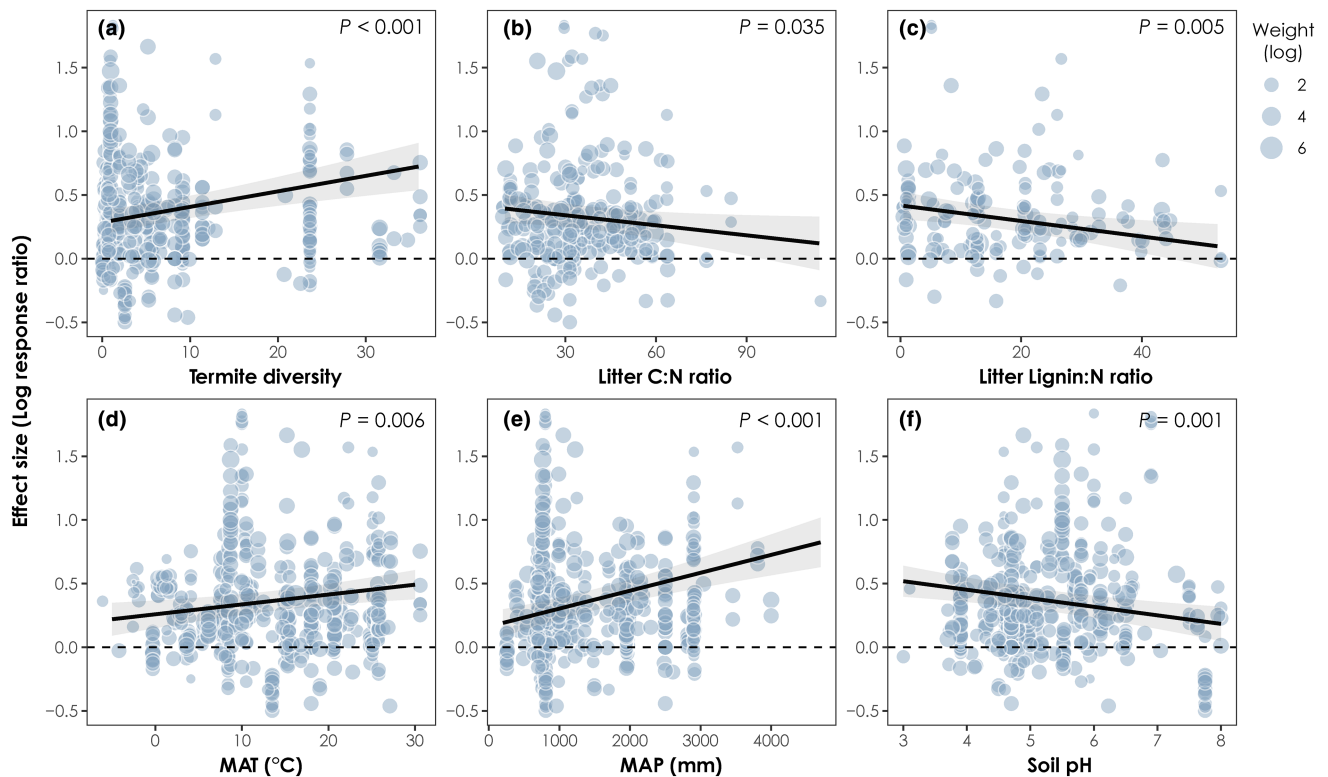


FIGURE 4 Influence of (a) termite diversity, (b) litter C:N ratio, (c) litter lignin:N ratio, (d) mean annual temperature (MAT), (e) mean annual precipitation (MAP) and (f) soil pH on invertebrate effect sizes determined using mixed-effect meta regressions. Point sizes represent the relative weights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

effect sizes and C:N ratios in litter ($Q_m = 4.447$, $p = 0.035$, $df = 252$, **Figure 4b**) and lignin:N ratios ($Q_m = 7.816$, $p = 0.005$, $df = 142$, **Figure 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 ($Q_m = 7.479$, $p = 0.006$, $df = 474$, **Figure 4d**) and mean annual

precipitation ($Q_m = 24.170$, $p < 0.001$, $df = 475$, **Figure 4e**). We also found that soil pH was negatively correlated with invertebrate effects on forest litter decomposition ($Q_m = 10.713$, $p = 0.001$, $df = 450$, **Figure 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 invertebrate effects weakened with the increasing of decomposition duration ($Q_m = 5.356$, $p = 0.021$,

Table S1), indicating invertebrates contribute differentially to the early stages of leaf litter decomposition (Figure S1a). We did not find a 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 ($z=0.907$, $p=0.364$), showing that invertebrate effect sizes were not affected by publication bias (Figure S2).

DISCUSSION

Invertebrates contribute to forest litter decomposition across the globe

Invertebrates make considerable contributions to the decomposition of forest litter. Our synthesis shows 31% of forest leaf litter decomposition, globally, is mediated by invertebrates. Our estimate is in line with the previous estimates of invertebrate effects on litter decomposition in terrestrial biomes (27%–40%) (García-Palacios et al., 2013; Kampichler & Bruckner, 2009; Sagi & Hawlena, 2023; Xu et al., 2020), but lower than instreams (74%) (Yue et al., 2022). Based on the existing findings, for example, the pattern of macrofaunal-mediated decomposition across terrestrial ecosystems reported by Sagi and Hawlena (2023). We further quantified a regional variation that the invertebrate effect in tropical and subtropical forests (38% on average) is 1.4 times higher than in forests elsewhere (26% on average). In addition, we have shown a positive relationship between termite diversity and invertebrate-mediated decomposition, indicating the potential for termites to drive this spatial variation as key invertebrate decomposers. Our results are important additions to existing syntheses of invertebrate effects on litter decomposition in not only terrestrial ecosystems but also water bodies where this regional variation has not been found (Yue et al., 2022).

We have shown the regional difference was observed consistently across all zoogeographic realms measured. The pattern is supported both historically and ecologically. The presence of particular decomposer groups (e.g. termites) may explain the strong effects of invertebrate on decomposition in the tropics and subtropics. 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, such as temperate and boreal regions (Guénard et al., 2015; Wiens & Donoghue, 2004). This history over deep time may well underpin current ecological functions. Major biogeographical differences in invertebrate species pools must be considered when discussing the major drivers of decomposition globally. In addition, diverse plant communities in tropical and

some subtropical forests, for instance, create rich food resources for invertebrates and are the basis for maintaining their abundance and activities (Cebrian, 1999; Kurokawa et al., 2010; Lavelle et al., 2022). Climatic conditions in tropical and subtropical forests are generally favourable for the activities of specific decomposer invertebrates, which are crucial for their corresponding ecological functions, which include litter decomposition (Sagi & Hawlena, 2023; Tan et al., 2020).

Invertebrate contributions to forest litter decomposition are biome dependent

Invertebrate fauna

We have shown that termites are important decomposers responsible for a significant component of mass loss of litter. The contribution of termites to plant litter decomposition is diversity and abundance dependent (Zanne et al., 2022). Termite diversity and abundance peak in the tropics are high in some areas of subtropics but not in temperate and northern regions (Lavelle et al., 2022; Liu 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 (Bignell, 2019; Hogan et al., 1988). 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, especially in the tropics, shaping nutrient turnover with ecosystem-wide implications for carbon flux and soil modification (Ashton et al., 2019; Griffiths, Eggleton, et al., 2021). 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, overall, invertebrate contributions to forest litter decomposition are positively related to temperature and precipitation. Climate can moderate faunal decomposition through its impacts on the abundance and activity of invertebrates (Thakur et al., 2018). Decomposer invertebrates are usually abundant and active in warm biomes (e.g. tropical forests) due to high metabolic and physiological processes (Castanho et al., 2012; David & Handa, 2010; Lavelle et al., 2022). For example, termite activity is three times higher in warm habitat than at cool sites (Bradford et al., 2021). Unlike

temperature, the impact of precipitation on decomposer invertebrates appears to be taxa dependent. For instance, invertebrates that live within water droplets or films (e.g. nematodes and mites) are directly affected by water potential (Hoeffner et al., 2019). Some soft-bodied meso- or macroinvertebrates (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 and isopods), have lower water sensitivity and are more resistant to desiccation (Berg & McLaugherty, 2020; Swift et al., 1979) and may in fact contribute a great amount to decomposition rates in warm dry environments (Sagi & Hawlena, 2023; Veldhuis et al., 2017).

Climate change can directly drive litter decomposition. Mori et al. (2020) reported the net effects of global warming on forest litter decomposition, showing that decomposition rates increase by 14% and 26% under the increases in mean annual temperature in the next 50 years predicted by CMIP5 RCP 2.6 and 8.5 respectively. Climate change also affects the decomposition process hierarchically by shifting decomposer communities. For example, a recent meta-analysis reported by Goncharov et al. (2023) showed a 1°C temperature rise results in a 12.5% increase in Acari but a 9.6% decrease in Collembola abundance. Figueroa et al. (2021) found declines in invertebrate abundance with increasing temperature in cool temperate forests, while Zanne et al. (2022) found that termite wood discovery rates increased with increasing temperature in the tropics. In addition, increasing drought limits the activities of free-living microflora (de Jonge et al., 2023) and below-ground invertebrates (e.g. nematodes and springtails) (Nielsen & Ball, 2015). Conversely, foraging discovery rates and abundance of termites increased with increasing drought, enhancing their ecological importance in extreme droughts (Ashton et al., 2019). The overall increase in forest litter decomposition mediated by invertebrates (31%) we estimated is similar in magnitude to that mediated by climate warming (14%–26%) predicted by Mori et al. (2020). As there are a range of predictions that indicate changes in the diversity of decomposer organisms under climate change, we could see significant shifts in litter decomposition in the future; however, the direction and magnitude of this change remain unclear (Goncharov et al., 2023; Wall et al., 2010). Given the different responses of invertebrate taxa to a changing climate, understanding the roles of key decomposer invertebrate groups and their responses to climate change is essential for predicting future biogeochemistry.

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). Soils in tropical wet forests 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 dataset. 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 results in the 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 (Huang et al., 2020; Liu & Zou, 2002).

FUTURE WORK

Introducing invertebrate functions to conceptual framework and biogeochemical models

Existing biogeochemical models generally employ climate, vegetation and soil characteristics to explain carbon and nitrogen turnover in terrestrial ecosystems, which could explain <50% of variations (Bradford et al., 2017). Multiple drivers of decomposition, currently missing from Earth System Models (ESM), include invertebrates which contribute to a large but often overlooked proportion of energy cycling pathways (Fry et al., 2019). We stress the need to integrate invertebrate functions into ESM as they contribute around 31% of global forest litter decomposition. Other drivers of decomposition such as vertebrate effects which make up around 6.7% of global litter decomposition, must also be included to increase model accuracy (Tuo et al., 2024). Invertebrate-mediated litter decomposition shows unique regional differences. However, available data exhibit a major temperate bias, challenging the power of model predictions (Figures 1 and 2b). Omitting invertebrate effects in ESM overlooks not only direct effects but also effects driven by invertebrate interactions with microbes, vertebrates and environmental variables. We acknowledge that there are several reasons why invertebrate effects have not yet been included in model predictions of biogeochemistry: (1) Researchers tend to simplify descriptors to avoid overfitting models using climate and vegetation profiles to represent functions of soil biomes (Bradford et al., 2017); (2) The importance of decomposer invertebrates has been underestimated (Filser et al., 2016; Pausas & Bond, 2020); (3) We lack empirical data for global distribution of invertebrate functional groups

(e.g. decomposers) (Fry et al., 2019) and (4) the high heterogeneity of invertebrate fauna at local scales of space and time may cause the uncertainty for long-term model predictions (Grandy et al., 2016).

Introducing invertebrate effects improves the biotic pools that drive biogeochemistry (e.g. invertebrate direct effects, invertebrate-microbial effects, invertebrate-vertebrate effects, etc.) creating more accurate ESM, as highlighted by Fry et al. (2019) and Ren et al. (2022). Future research can adjust models to describe the decomposing effects of invertebrates for the prediction of carbon and nitrogen dynamics but to get to this new level of detail will require extensive model training and ground-truthing data (Fry et al., 2019; Wieder et al., 2018). Although the introduction of biota pools would greatly increase the complexity and instability of the models, we believe that such attempts are of great value. Introducing invertebrate decomposing effects into ESM will be possible with global data on the distribution of decomposer invertebrates, decomposition rates and their diverse characteristics. To achieve this, we can classify dominant invertebrate taxa associated with litter decomposition using widely accepted classifications (Hedde et al., 2022). Assessing the global distribution of the decomposer invertebrate taxa according to integrative disciplines to minimize methodological bias of empirical studies. For instance, combining molecular approaches like environmental DNA with traditional morphology will facilitate the collection of global data (Arribas et al., 2022; Geisen et al., 2019). Additionally, global collaboration networks will facilitate the management and sharing of these global data.

More empirical studies are needed in tropical and boreal regions

As with many meta-analyses in ecology, only a small number of studies on invertebrate-mediated forest litter decomposition have occurred in the African, Australian, Oriental and realms in boreal regions where large areas of tropical dry forests, tropical rainforests and taiga are located (Pan et al., 2013). We have emphasized the importance of realm-based invertebrate distribution and climate variables in driving invertebrate effects on forest litter decomposition. For example, termites are diverse and abundant across Africa, South America, South East Asia and Australia. Africa, indeed, is the evolutionary cradle of termites and hosts the highest number of termite species (Bignell, 2019; Buitenwerf et al., 2011). The lack of observations in these areas suggests that we may have underestimated tropical invertebrate effects on forest litter decomposition. In addition, boreal forests are dominated by coniferous trees with different litter traits than those from broad-leaved deciduous trees (Swift et al., 1979). Therefore, wider data collection across the African, Australian, Nearctic and Palearctic realms is

essential for better understanding of global decomposition pathways.

Detailed information on leaf litter traits and environmental variables is 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 databases 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 invertebrates. Collecting such data at a local scale is essential (Bradford et al., 2014).

Physical protocol used to exclude invertebrates is encouraged

To date, most studies have used physical methods (i.e. litterbags and mesocosms) to exclude invertebrates in field experiments, accounting for 85% of observations in our dataset. Thirteen percent of observations in our dataset showed negative effects of invertebrates on litter mass loss. Seventy percent of negative faunal effects in our dataset were from biomes with long-term winter (e.g. cool temperate, boreal and alpine forests). These negative faunal effects on decomposition have not been well tested. Possible explanation would be 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). We did not find a significant difference in effects on invertebrate effect sizes between physical and chemical protocols. The potential non-target effects of chemicals such as naphthalene on soil organisms and environments (Lan et al., 2020), however, leads us to advocate the 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 invertebrates are important components of global forest litter decomposition, especially in the tropics-subtropics, from both biogeographical and ecological perspectives. Termites in particular are major decomposers mediating the regional variation in animal-driven decomposition. Invertebrates

are experiencing remarkable diversity shifts and functional changes driven by multiple disturbances including climate change, habitat loss and environmental pollution (Cifuentes-Croquevielle et al., 2020). Potentially, this shift will alter the turnover of carbon and plant-available nutrients significantly with cascading effects on plant nutrient uptake and soil health (Griffiths, Ashton, et al., 2021; Handa et al., 2014). Future climate change and other human disturbances have the potential to reshape the relative contributions of invertebrates and microbes in global litter decomposition with unknown but undoubtedly serious consequences.

AUTHOR CONTRIBUTIONS

XYZ, LAA and HMG designed this study. XYZ, HLG, BMM and JSW collected and organized the data. XYZ, HLG, RXW and WDC performed the statistical analyses. RXW plotted the data. XYZ wrote the first draft of the manuscript and all authors contributed to manuscript revision.

ACKNOWLEDGEMENTS

We gratefully acknowledge Prof. Jonathan Chase, Prof. Timothy Bonebrake, Dr. Michael Boyle and Prof. Roger Kitching for helpful comments on the manuscript.

CONFLICT OF INTEREST STATEMENT

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

PEER REVIEW

The peer review history for this article is available at <https://www.webofscience.com/api/gateway/wos/peer-review/10.1111/ele.14423>.

DATA AVAILABILITY STATEMENT

The data supporting the results and the code used to generate the figures can be accessed via the Figshare repository using the following link: <https://doi.org/10.6084/m9.figshare.24654966>.

ORCID

Cheng Wenda  <https://orcid.org/0000-0002-2596-3028>

Louise A. Ashton  <https://orcid.org/0000-0001-6471-0827>

REFERENCES

- Adejuyigbe, C.O., Tian, G. & Adeoye, G.O. (2006) Microcosmic study of soil microarthropod and earthworm interaction in litter decomposition and nutrient turnover. *Nutrient Cycling in Agroecosystems*, 75, 47–55.
- Aerts, R. (1997) Climate, leaf litter chemistry and leaf litter decomposition in terrestrial ecosystems: a triangular relationship. *Oikos*, 79, 439–449.
- Anderson, J.M. (1978) Inter- and intra-habitat relationships between woodland cryptostigmata species diversity and the diversity of soil and litter microhabitats. *Oecologia*, 32, 341–348.
- Arribas, P., Andújar, C., Bohmann, K., de Waard, J.R., Economo, E.P., Elbrecht, V. et al. (2022) Toward global integration of biodiversity big data: a harmonized metabarcoding data generation module for terrestrial arthropods. *GigaScience*, 11, giac065.
- Ashton, L.A., Griffiths, H.M., Parr, C.L., Evans, T.A., Didham, R.K., Hasan, F. et al. (2019) Termites mitigate the effects of drought in tropical rainforest. *Science*, 363, 174–177.
- Bastida, F., Eldridge, D.J., Abades, S., Alfaro, F.D., Gallardo, A., García-Velázquez, L. et al. (2020) Climatic vulnerabilities and ecological preferences of soil invertebrates across biomes. *Molecular Ecology*, 29, 752–761.
- Berg, B. & McClaugherty, C. (2020) *Plant litter: decomposition, humus formation, carbon sequestration*. Berlin: Springer Press, pp. 17–25.
- Bignell, D.E. (2019) Termite ecology in the first two decades of the 21st century: a review of reviews. *Insects*, 10, 60.
- Bignell, D.E. & Eggleton, P. (2000) Termites in ecosystems. In: Abe, T., Bignell, D.E. & Higashi, M. (Eds.) *Termites: evolution, sociality, symbioses, ecology*. Dordrecht, Netherlands: Springer, pp. 363–387.
- Birhanu, I., Muktar, M. & Kibebew, K. (2016) Impact of deforestation and subsequent cultivation on soil fertility in Komto, Western Ethiopia. *Journal of Soil Science and Environmental Management*, 7, 212–221.
- Bishop, T.R., Griffiths, H.M., Ashton, L.A., Eggleton, P., Woon, J.S. & Parr, C.L. (2021) Clarifying terrestrial recycling pathways. *Trends in Ecology & Evolution*, 36, 9–11.
- Bracken, M.B. & Sinclair, J.C. (1992) *Statistical methods for analysis of effects of treatment in overviews of randomized trials. Effective care of the newborn infant*. Oxford: Oxford University Press.
- Bradford, M.A., Maynard, D.S., Crowther, T.W., Frankson, P.T., Mohan, J.E., Steinrueck, C. et al. (2021) Belowground community turnover accelerates the decomposition of standing dead wood. *Ecology*, 102, e03484.
- Bradford, M.A., Veen, G.F., Bonis, A., Bradford, E.M., Classen, A.T., Cornelissen, J.H.C. et al. (2017) A test of the hierarchical model of litter decomposition. *Nature Ecology & Evolution*, 1, 1836–1845.
- Bradford, M.A., Warren, R.J., Baldrian, P., Crowther, T.W., Maynard, D.S., Oldfield, E.E. et al. (2014) Climate fails to predict wood decomposition at regional scales. *Nature Climate Change*, 4, 625–630.
- Bretz, F., Hothorn, T., Westfall, P., Heiberger, R.M., Schuetzenmeister, A. & Scheibe, S. (2010) Simultaneous inference in general parametric models. In: Bretz, F., Hothorn, T. & Westfall, P. (Eds.) *Multiple comparisons using R*. Boca Raton: CRC Press, p. 44.
- Brussaard, L., Aanen, D., Briones, M., Decaëns, T., Deyn, G.B., Fayle, T. et al. (2012) Biogeography and phylogenetic community structure of soil invertebrate ecosystem engineers: global to local patterns, implications for ecosystem functioning and services and global environmental change impacts. In: *Soil ecology and ecosystem services*. Oxford: Oxford University Press, pp. 201–231.
- Buitenwerf, R., Stevens, N., Gosling, C.M., Anderson, T.M. & Olf, H. (2011) Interactions between large herbivores and litter removal by termites across a rainfall gradient in a south African savanna. *Journal of Tropical Ecology*, 27, 375–382.
- Burda, B.U., O'Connor, E.A., Webber, E.M., Redmond, N. & Perdue, L.A. (2017) Estimating data from figures with a web-based program: considerations for a systematic review. *Research Synthesis Methods*, 8, 258–262.
- Castanho, C.T., Lorenzo, L. & de Oliveira, A.A. (2012) The importance of mesofauna and decomposition environment on leaf decomposition in three forests in southeastern Brazil. *Plant Ecology*, 213, 1303–1313.
- Cebrian, J. (1999) Patterns in the fate of production in plant communities. *The American Naturalist*, 154, 449–468.
- Chang, W.H. & Lai, A.G. (2018) Mixed evolutionary origins of endogenous biomass-depolymerizing enzymes in animals. *BMC Genomics*, 19, 483.

- 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, 7762.
- Cotrufo, M.F., Ngao, J., Marzaioli, F. & Piermatteo, D. (2010) Inter-comparison of methods for quantifying above-ground leaf litter decomposition rates. *Plant and Soil*, 334, 365–376.
- David, J.F. (2014) The role of litter-feeding macroarthropods in decomposition processes: a reappraisal of common views. *Soil Biology and Biochemistry*, 76, 109–118.
- David, J.-F. & Handa, I.T. (2010) The ecology of saprophagous macroarthropods (millipedes, woodlice) in the context of global change. *Biological Reviews*, 85, 881–895.
- de Jonge, I.K., Veldhuis, M.P., Cornelissen, J.H.C., Berg, M.P. & Olf, H. (2023) The metamicrobiome: key determinant of the homeostasis of nutrient recycling. *Trends in Ecology & Evolution*, 38, 183–195.
- Dinerstein, E., Olson, D., Joshi, A., Vynne, C., Burgess, N.D., Wikramanayake, E. et al. (2017) An ecoregion-based approach to protecting half the terrestrial realm. *Bioscience*, 67, 534–545.
- Eggleton, P. & Tayasu, I. (2001) Feeding groups, lifestyles and the global ecology of termites. *Ecological Research*, 16, 941–960.
- Figuerola, L.L., Maran, A. & Pelini, S.L. (2021) Increasing temperatures reduce invertebrate abundance and slow decomposition. *PLoS One*, 16, e0259045.
- Filser, J., Faber, J.H., Tiunov, A.V., Brussaard, L., Frouz, J., de Deyn, G. et al. (2016) Soil fauna: key to new carbon models. *Soil-Germany*, 2, 565–582.
- Fry, E.L., de Long, J.R., Álvarez Garrido, L., Alvarez, N., Carrillo, Y., Castañeda-Gómez, L. et al. (2019) Using plant, microbe, and soil fauna traits to improve the predictive power of biogeochemical models. *Methods in Ecology and Evolution*, 10, 146–157.
- 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, 1045–1053.
- Geisen, S., Briones, M.J.I., Gan, H., Behan-Pelletier, V.M., Friman, V.-P., de Groot, G.A. et al. (2019) A methodological framework to embrace soil biodiversity. *Soil Biology and Biochemistry*, 136, 107536.
- Goncharov, A.A., Leonov, V.D., Rozanova, O.L., Semenina, E.E., Tsurikov, S.M., Uvarov, A.V. et al. (2023) A meta-analysis suggests climate change shifts structure of regional communities of soil invertebrates. *Soil Biology and Biochemistry*, 181, 109014.
- Grandy, A.S., Wieder, W.R., Wickings, K. & Kyker-Snowman, E. (2016) Beyond microbes: are fauna the next frontier in soil biogeochemical models? *Soil Biology and Biochemistry*, 102, 40–44.
- Griffiths, H.M., Ashton, L.A., Evans, T.A., Parr, C.L. & Eggleton, P. (2019) Termites can decompose more than half of deadwood in tropical rainforest. *Current Biology*, 29, R118–R119.
- Griffiths, H.M., Ashton, L.A., Parr, C.L. & Eggleton, P. (2021) The impact of invertebrate decomposers on plants and soil. *The New Phytologist*, 231, 2142–2149.
- Griffiths, H.M., Eggleton, P., Hemming-Schroeder, N., Swinfield, T., Woon, J.S., Allison, S.D. et al. (2021) Carbon flux and forest dynamics: increased deadwood decomposition in tropical rainforest tree-fall canopy gaps. *Global Change Biology*, 27, 1601–1613.
- Guénard, B., Perrichot, V. & Economo, E.P. (2015) Integration of global fossil and modern biodiversity data reveals dynamism and stasis in ant macroecological patterns. *Journal of Biogeography*, 42, 2302–2312.
- Handa, I.T., Aerts, R., Berendse, F., Berg, M.P., Bruder, A., Butenschoen, O. et al. (2014) Consequences of biodiversity loss for litter decomposition across biomes. *Nature*, 509, 218–221.
- Hättenschwiler, S., Tiunov, A.V. & Scheu, S. (2005) Biodiversity and litter decomposition in terrestrial ecosystems. *Annual Review of Ecology, Evolution, and Systematics*, 36, 191–218.
- Hedde, M., Blight, O., Briones, M.J.I., Bonfanti, J., Brauman, A., Brondani, M. et al. (2022) A common framework for developing robust soil fauna classifications. *Geoderma*, 426, 116073.
- Heděnc, P., Jiménez, J.J., Moradi, J., Domene, X., Hackenberger, D., Barot, S. et al. (2022) Global distribution of soil fauna functional groups and their estimated litter consumption across biomes. *Science Reports*, 12, 17362.
- Hedges, L.V., Gurevitch, J. & Curtis, P.S. (1999) The meta-analysis of response ratios in experimental ecology. *Ecology*, 80, 1150–1156.
- Hoeffner, K., Santonja, M., Cluzeau, D. & Monard, C. (2019) Epianecic rather than strict-aneic earthworms enhance soil enzymatic activities. *Soil Biology and Biochemistry*, 132, 93–100.
- Hogan, M., Veivers, P.C., Slaytor, M. & Czolij, R.T. (1988) The site of cellulose breakdown in higher termites (*Nasutitermes walkeri* and *Nasutitermes exitiosus*). *Journal of Insect Physiology*, 34, 891–899.
- Holdridge, L.R. (1947) Determination of world plant formations from simple climatic data. *Science*, 105, 367–368.
- Holt, B.G., Lessard, J.-P., Borregaard, M.K., Fritz, S.A., Araujo, M.B., Dimitrov, D. et al. (2013) An update of Wallace's zoogeographic regions of the world. *Science*, 339, 74–78.
- Huang, W., González, G. & Zou, X. (2020) Earthworm abundance and functional group diversity regulate plant litter decay and soil organic carbon level: a global meta-analysis. *Applied Soil Ecology*, 150, 103473.
- Johnson, D., Krsek, M., Wellington, E.M., Stott, A.W., Cole, L., Bardgett, R.D. et al. (2005) Soil invertebrates disrupt carbon flow through fungal networks. *Science*, 309, 1047.
- Joly, F.-X., Coq, S., Coulis, M., Jean-François, D., Hättenschwiler, S., Mueller, C.W. et al. (2020) Detritivore conversion of litter into faeces accelerates organic matter turnover. *Communications Biology*, 3, 660.
- Jouquet, P., Traoré, S., Choosai, C., Hartmann, C. & Bignell, D. (2011) Influence of termites on ecosystem functioning. Ecosystem services provided by termites. *European Journal of Soil Biology*, 47, 215–222.
- Kampichler, C. & Bruckner, A. (2009) The role of microarthropods in terrestrial decomposition: a meta-analysis of 40 years of litterbag studies. *Biological Reviews*, 84, 375–389.
- Kass, J.M., Guénard, B., Dudley, K.L., Jenkins, C.N., Azuma, F., Fisher, B.L. et al. (2022) The global distribution of known and undiscovered ant biodiversity. *Science Advances*, 8, eabp9908.
- Kattge, J., Bönsch, G., Díaz, S., Lavorel, S., Prentice, I.C., Leadley, P. et al. (2020) TRY plant trait database—enhanced coverage and open access. *Global Change Biology*, 26, 119–188.
- Korboulewsky, N., Perez, G. & Chauvat, M. (2016) How tree diversity affects soil fauna diversity: a review. *Soil Biology and Biochemistry*, 94, 94–106.
- Kurokawa, H. & Nakashizuka, T. (2008) Leaf herbivory and decomposability in a Malaysian tropical rain forest. *Ecology*, 89, 2645–2656.
- Kurokawa, H., Peltzer, D.A. & Wardle, D.A. (2010) Plant traits, leaf palatability and litter decomposability for co-occurring woody species differing in invasion status and nitrogen fixation ability. *Functional Ecology*, 24, 513–523.
- Lan, L., Yang, F., Zhang, L., Yang, W., Wu, F., Xu, Z. et al. (2019) Non-target effects of naphthalene on the soil microbial biomass and bacterial communities in the subalpine forests of western China. *Science Reports*, 9, 9811–9818.
- Lan, L.Y., Zhang, L., Shen, Y., Zhang, J., Yang, W.Q., Xu, Z.F. et al. (2020) Naphthalene exerts non-target effects on the abundance of active fungi by stimulating basidiomycete abundance. *Journal of Mountain Science*, 17, 2001–2010.
- Lavelle, P., Chauvel, A. & Fragoso, C. (1995) Principles and management: proceedings of the third international symposium on plant–soil interactions at low pH. In: Date, R.A., Grundon, N.J., Rayment, G.E. & Probert, M.E. (Eds.) *Faunal activity in acid soils*. Dordrecht, Netherlands: Springer, pp. 201–211.
- Lavelle, P., Mathieu, J., Spain, A., Brown, G., Fragoso, C., Lapied, E. et al. (2022) Soil macroinvertebrate communities: a world-wide assessment. *Global Ecology and Biogeography*, 31, 1261–1276.

- Lehmann, J. & Kleber, M. (2015) The contentious nature of soil organic matter. *Nature*, 528, 60–68.
- Liria, J., Szumik, C.A. & Goloboff, P.A. (2021) Analysis of endemism of world arthropod distribution data supports biogeographic regions and many established subdivisions. *Cladistics*, 37, 559–570.
- Liu, S., Xia, S., Wu, D., Behm, J.E., Meng, Y., Yuan, H. et al. (2022) Understanding global and regional patterns of termite diversity and regional functional traits. *iScience*, 25, 105538.
- Liu, Z.G. & Zou, X.M. (2002) Exotic earthworms accelerate plant litter decomposition in a Puerto Rican pasture and a wet forest. *Ecological Applications*, 12, 1406–1417.
- McCary, M.A. & Schmitz, O.J. (2021) Invertebrate functional traits and terrestrial nutrient cycling: insights from a global meta-analysis. *The Journal of Animal Ecology*, 90, 1714–1726.
- Mori, A.S., Cornelissen, J.H.C., Fujii, S., Okada, K.-I. & Isbell, F. (2020) A meta-analysis on decomposition quantifies after-life effects of plant diversity as a global change driver. *Nature Communications*, 11, 4547.
- Nielsen, U.N. & Ball, B.A. (2015) Impacts of altered precipitation regimes on soil communities and biogeochemistry in arid and semi-arid ecosystems. *Global Change Biology*, 21, 1407–1421.
- Ni'matuzahroh, Affandi, M., Fatimah, Trikurniadewi, N., Khiftiyah, A.M., Sari, S.K. et al. (2022) Comparative study of gut microbiota from decomposer fauna in household composter using metataxonomic approach. *Archives of Microbiology*, 204, 210.
- Olson, J. (1963) Energy storage and balance of producers and decomposers in a young scots pine stand in central Sweden. *Oikos*, 34, 322–331.
- Pan, Y., Birdsey, R.A., Fang, J., Houghton, R., Kauppi, P.E., Kurz, W.A. et al. (2011) A large and persistent carbon sink in the world's forests. *Science*, 333, 988–993.
- Pan, Y., Birdsey, R.A., Phillips, O.L. & Jackson, R.B. (2013) The structure, distribution, and biomass of the world's forests. *Annual Review of Ecology, Evolution, and Systematics*, 44, 593–622.
- Papanikolaou, N., Britton, A.J., Helliwell, R.C. & Johnson, D. (2010) Nitrogen deposition, vegetation burning and climate warming act independently on microbial community structure and enzyme activity associated with decomposing litter in low-alpine heath. *Global Change Biology*, 16, 3120–3132.
- Pauchet, Y., Wilkinson, P., Chauhan, R. & Ffrench-Constant, R.H. (2010) Diversity of beetle genes encoding novel plant cell wall degrading enzymes. *PLoS One*, 5, e15635.
- Pausas, J.G. & Bond, W.J. (2020) On the three major recycling pathways in terrestrial ecosystems. *Trends in Ecology & Evolution*, 35, 767–775.
- Phillips, H.R.P., Bach, E.M., Bartz, M.L.C., Bennett, J.M., Beugnon, R., Briones, M.J.I. et al. (2021) Global data on earthworm abundance, biomass, diversity and corresponding environmental properties. *Scientific Data*, 8, 136.
- Ren, L., Jensen, K., Porada, P. & Mueller, P. (2022) Biota-mediated carbon cycling—a synthesis of biotic-interaction controls on blue carbon. *Ecology Letters*, 25, 521–540.
- Sagi, N. & Hawlena, D. (2023) Climate dependence of the macrofaunal effect on litter decomposition—a global meta-regression analysis. *Ecology Letters*, 27, 1–11.
- Shelomi, M., Wipfler, B., Zhou, X. & Pauchet, Y. (2019) Multifunctional cellulase enzymes are ancestral in Polyneoptera. *Insect Molecular Biology*, 29, 124–135.
- Su, H., Feng, Y., Chen, J., Chen, J., Ma, S., Fang, J. et al. (2021) Determinants of trophic cascade strength in freshwater ecosystems: a global analysis. *Ecology*, 102, e03370.
- Swift, M.J., Heal, O.W. & Anderson, J.M. (1979) *Decomposition in terrestrial ecosystems*. Oxford: Blackwell Scientific Publications.
- Tan, B., Yin, R., Zhang, J., Xu, Z., Liu, Y., He, S. et al. (2020) Temperature and moisture modulate the contribution of soil fauna to litter decomposition via different pathways. *Ecosystems*, 24, 1142–1156.
- Tao, J., Zuo, J., He, Z., Wang, Y., Liu, J., Liu, W. et al. (2019) Traits including leaf dry matter content and leaf pH dominate over forest soil pH as drivers of litter decomposition among 60 species. *Functional Ecology*, 33, 1798–1810.
- Thakur, M.P., Reich, P.B., Hobbie, S.E., Stefanski, A., Rich, R., Rice, K.E. et al. (2018) Reduced feeding activity of soil detritivores under warmer and drier conditions. *Nature Climate Change*, 8, 75–78.
- Tuo, B., García-Palacios, P., Guo, C., Yan, E.-R., Berg, M.P. & Cornelissen, J.H.C. (2024) Meta-analysis reveals that vertebrates enhance plant litter decomposition at the global scale. *Nature Ecology & Evolution*, 8(3), 411–422.
- van den Hoogen, J., Geisen, S., Wall, D.H., Wardle, D.A., Traunspurger, W., de Goede, R.G.M. et al. (2020) A global database of soil nematode abundance and functional group composition. *Scientific Data*, 7, 103.
- Veldhuis, M.P., Laso, F.J., Olf, H. & Berg, M.P. (2017) Termites promote resistance of decomposition to spatiotemporal variability in rainfall. *Ecology*, 98, 467–477.
- Viechtbauer, W. (2010) Conducting meta-analyses in R with the metafor package. *Journal of Statistical Software*, 36, 1–48.
- Wall, D.H., Bardgett, R.D. & Kelly, E. (2010) Biodiversity in the dark. *Nature Geoscience*, 3, 297–298.
- Wall, D.H., Bradford, M.A., St John, M.G., Trofymow, J.A., Behan-Pelletier, V., Bignell, D.E. et al. (2008) Global decomposition experiment shows soil animal impacts on decomposition are climate-dependent. *Global Change Biology*, 14, 2661–2677.
- Wieder, W.R., Grandy, A.S., Kallenbach, C.M., Taylor, P.G. & Bonan, G.B. (2015) Representing life in the Earth system with soil microbial functional traits in the MIMICS model. *Geoscientific Model Development*, 8, 1789–1808.
- Wieder, W.R., Hartman, M.D., Sulman, B.N., Wang, Y.-P., Koven, C.D. & Bonan, G.B. (2018) Carbon cycle confidence and uncertainty: exploring variation among soil biogeochemical models. *Global Change Biology*, 24, 1563–1579.
- Wiens, J.J. & Donoghue, M.J. (2004) Historical biogeography, ecology and species richness. *Trends in Ecology & Evolution*, 19, 639–644.
- Woon, J.S. (2022) *Out of the forest: how the environment affects termite distributions, physiology and contribution to ecosystem processes* (Doctoral dissertation, University of Liverpool).
- Xu, X., Sun, Y., Sun, J., Cao, P., Wang, Y., Chen, H.Y.H. et al. (2020) Cellulose dominantly affects soil fauna in the decomposition of forest litter: a meta-analysis. *Geoderma*, 378, 114620.
- Yue, K., de Frenne, P., van Meerbeek, K., Ferreira, V., Fornara, D.A., Wu, Q. et al. (2022) Litter quality and stream physicochemical properties drive global invertebrate effects on instream litter decomposition. *Biological Reviews of the Cambridge Philosophical Society*, 97, 2023–2038.
- Zanne, A.E., Flores-Moreno, H., Powell, J.R., Cornwell, W.K., Dalling, J.W., Austin, A.T. et al. (2022) Termite sensitivity to temperature affects global wood decay rates. *Science*, 377, 1440–1444.
- Zhang, Y.-Y., Wu, W. & Liu, H. (2019) Factors affecting variations of soil pH in different horizons in hilly regions. *PLoS One*, 14, e0218563.

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

How to cite this article: Zeng, X., Gao, H., Wang, R., Majcher, B.M., Woon, J.S., Wenda, C. et al. (2024) Global contribution of invertebrates to forest litter decomposition. *Ecology Letters*, 27, e14423. Available from: <https://doi.org/10.1111/ele.14423>