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The effects of invertebrates on wood decomposition across the world

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ABSTRACT

Invertebrates and microorganisms are important but climate-dependent agents of wood decomposition globally. In this meta-analysis, we investigated what drives the invertebrate effect on wood decomposition worldwide. Globally, we found wood decomposition rates were on average approximately 40% higher when invertebrates were present compared to when they were excluded. This effect was most pronounced in the tropics, owing mainly to the activities of termites. The invertebrate effect was stronger for woody debris without bark as well as for that of larger diameter, possibly reflecting bark- and diameter-mediated differences in fungal colonisation or activity rates relative to those of invertebrates. Our meta-analysis shows similar overall invertebrate effect sizes on decomposition of woody debris derived from angiosperms

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and gymnosperms globally. Our results suggest the existence of critical interactions between microorganism colonisation and the invertebrate contribution to wood decomposition. To improve biogeochemical models, a better quantification of invertebrate contributions to wood decomposition is needed.

Key words: bark effect, carbon cycle, dead wood, invertebrate effect, meta-analysis, woody debris.

CONTENTS

I. INTRODUCTION

Woody debris (WD) contributes 8% to total organic carbon (C) within forests globally, 17% to the total wood C pool (Pan *et al*., 2011), and stores an equivalent of 8% of atmospheric C (Friedlingstein *et al*., 2019). Estimating how quickly the carbon stored in WD returns to the atmosphere, or is transferred to long-term storage in soil through decomposition, is crucial for estimating global C fluxes and climate change (Luyssaert *et al*., 2007; Le Quéré *et al*., 2018; Seibold *et al*., 2021).

Fungi, bacteria, and invertebrates govern WD decomposition as regulated by climate (precipitation, temperature) and wood traits (Bradford *et al*., 2014, 2021; Stoklosa *et al*., 2016; Seibold *et al*., 2021). Although microorganisms are widely considered key wood decomposers, recent literature strongly suggests that the effects of invertebrates on wood decomposition have been overlooked (Griffiths *et al*., 2021). Indeed, different invertebrates utilise WD in different ways; below we use the term 'invertebrate effect' to refer to the collective contribution of multiple groups of invertebrates (e.g. termites, wood-boring insects) to WD decomposition. Most invertebrates that enhance WD decomposition do this *via* interactions with microbes, e.g. by vectoring or feeding on fungal tissues or fragmenting woody materials (Dossa *et al*., 2021; Griffiths *et al*., 2021; Zou et al., 2023). Wood-dwelling invertebrates that are responsible for wood decomposition likely accelerate the release of immobilised nutrients in fungal tissues and promote nitrogen fixation (Ulyshen, 2015). When moisture is sufficient, an increase in temperature not only promotes microbial activity, but also enhances the positive effect of invertebrates on WD decomposition (Pietsch *et al*., 2019; Seibold *et al*., 2021). However, termites (Order Blattodea) also have a strong positive effect in drier environments, e.g. savanna (Cheesman, Cernusak & Zanne, 2018; Zanne *et al*., 2022). An increase of 10 °C accelerates termite-related decomposition rates globally by a factor of 6.8, compared to a factor of 1.7 for the effect on microbial decomposition rates without termite mediation (Zanne *et al*., 2022). While previous global studies addressed climatic control over invertebrate contributions to WD decomposition (Seibold *et al*., 2021; Zanne *et al*., 2022), it remains poorly understood which other factors drive these contributions globally and how these drivers themselves might be climate dependent.

Biophysical (e.g. WD size, bark presence, wood anatomy) and chemical (e.g. nitrogen content, dry matter content, presence of secondary compounds) traits of WD may influence the invertebrate effect on WD decomposition (Harmon *et al*., 1986; Bradford *et al*., 2014, 2021; Stoklosa *et al*., 2016; Ulyshen, 2016; Seibold *et al*., 2021; Zanne *et al*., 2022). Additionally, given the previously reported differences in these traits between gymnosperms and angiosperms (Cornwell *et al*., 2009; Pietsch *et al*., 2014), the invertebrate effect on wood decomposition may vary among major tree clades. However, understanding of the factors that drive the invertebrate effect on wood decomposition represents a major research gap globally. Here, through a meta-analysis, we evaluated how climate, wood size, bark presence or absence, WD type, and species clade (gymnosperms or angiosperm) influence the invertebrate effect on WD decomposition globally (Table 1; see online

Table 1. Summary of the main hypotheses assessed in this study and the rationale behind them.

Hypothesis	Rationale	References
(H1) The invertebrate effect on WD decomposition is climate dependent and variation in deadwood traits will constrain the invertebrate effect with different effect sizes across climatic zones (stronger magnitude in tropical zone)	The biophysical (e.g. WD size, bark presence, and wood anatomy) and chemical traits of the WD may all influence the invertebrate effect on its decomposition and the magnitude of the influence is climate dependent.	Harmon *et al.* (1986); Bradford *et al.* (2014, 2021); Stoklosa *et al.* (2016); Ulyshen (2016); Dossa *et al.* (2018); Seibold *et al.* (2021); Zanne *et al.* (2022)
(H2) The invertebrate effect will be greater in WD with larger diameter	WD with larger diameter favours colonisation by more diverse groups of invertebrates than WD with smaller diameter because of its larger surface area and greater resource availability for an extended period of time.	Harmon *et al.* (1986); Edmonds & Eglitis (1989); Stoklosa *et al.* (2016)
(H3) Bark presence will increase the effect of invertebrates on wood decomposition	The vast majority of saproxylic invertebrates at some stage of their life cycle need bark and are adapted to the chemical defences of bark. Many wood-inhabiting invertebrates only occur in WD with bark. Moreover, inner bark seems to have nutritious tissues and is softer than the underlying wood; thus, bark-dependent invertebrates might consume more inner bark and also oviposit within the space between the inner bark and wood. The larvae of bark-dependent invertebrates will consume more of the underlying wood. Certain bark traits (e.g. concentrations of nutrients and phenolic compounds) may negatively influence the invertebrate effect on WD decomposition and the composition of invertebrate assemblages during decomposition. However, the net effect of bark presence is predicted to be positive.	Chomel *et al.* (2016); Ulyshen *et al.* (2016); Zuo *et al.* (2016); Dossa *et al.* (2018)
(H4) The invertebrate effect will be greater in natural (non-processed, either with or without bark) wood than in processed wood (e.g. blocks, stakes or dowels, mostly without bark) as the latter may be perceived as novel materials by invertebrates	WD structure changes during processes such as compression and drying and could result in a reduced invertebrate effect on processed wood. Processed wood usually lacks bark, and thus represents reduced resources and foraging space for invertebrates, especially invertebrates requiring bark coverage.	Ulyshen & Wagner (2013); Ulyshen (2016); Dossa *et al.* (2018)
(H5) The invertebrate effect on WD decomposition will be higher in angiosperms than in gymnosperms, as the powerful anti-herbivory defences of gymnosperms will deter invertebrate decomposers	Gymnosperms have higher concentrations of secondary protective metabolites (phenolics, flavonols, recalcitrant lignin and terpenes) than angiosperms, which act as defences against herbivory. The anti-herbivory defences in gymnosperms would thus reduce the contribution of invertebrates to the decomposition of gymnosperm WD. But exceptions exist: for example termites prefer gymnosperm wood over native angiosperm wood. Gymnosperms have guaiacyl lignin and shorter tracheids connected *via* pits whereas angiosperms have non-recalcitrant syringyl lignin and conducting vessels making angiosperms more palatable to invertebrates.	Boddy (2001); Carlquist (2001); Cornwell *et al.* (2009); Pietsch *et al.* (2014); Vogel *et al.* (2021); Cornelissen *et al.* (2023); Law *et al.* (2023)

Abbreviation: WD, woody debris.

Supporting Information, Fig. S1). We hypothesise that: (*i*) the invertebrate effect on WD decomposition is climate dependent and variations in deadwood traits will constrain the invertebrate effect with larger effect sizes in warmer climate zones (i.e. stronger in magnitude in tropical zones); (*ii*) the effect of invertebrates will be greater in WD with a larger diameter; (*iii*) bark presence will increase the effect of invertebrates on wood decomposition; (*iv*) the effects of invertebrates will be greater in natural non-processed wood, either with or without bark than in processed wood (e.g. blocks, stakes, dowels, mostly without bark) as the latter may be perceived by invertebrates as novel materials; (*v*) the effect of invertebrates on WD decomposition will be greater in angiosperms than in gymnosperms, as the powerful anti-herbivory defences present in gymnosperms will deter invertebrate decomposers (Fig. S1, Table 1).

To test these hypotheses, we conducted a meta-analysis to quantify global drivers of variation in the invertebrate effect on wood decomposition. Our literature search resulted in 1427 paired observations reporting WD decomposition in both the presence and absence of invertebrates from 20 studies across the globe (Fig. 1). We used the log response ratio [ln(RR)] and applied multi-level random-effect meta-analysis to estimate the overall effect of invertebrates on WD decomposition and quantified how this effect varied with WD diameter, bark status and taxonomic clade across multiple climate zones.

II. MATERIALS AND METHODS

(1) Data acquisition

In November 2021, we searched the literature for studies on WD decomposition and the contribution of invertebrates to WD decomposition in the *Scopus* database and ISI *Web of Science*. We used the *litsearchr* package (Grames *et al*., 2019) to refine our search string (Table S1). The search resulted in 49,352 studies. After reading titles and abstracts, and excluding studies that did not target wood decomposition, this number was reduced to 481 studies for which the full texts were read. We included studies on WD decomposition that met the following criteria: (*i*) the study explicitly reported the methods used to allow or exclude invertebrate access to WD during decomposition; (*ii*) the study reported changes in WD mass or density or volume through decomposition or associated decay rate estimates in the presence or absence of invertebrates in both inclusion or exclusion treatments; (*iii*) the study reported the tree species, bark status (present or absent) and diameter of the WD used; and (*iv*) the study reported the duration of decomposition.

We extracted data from 20 studies that met the above criteria (included studies are identified with an asterisk in the reference list; see Fig. S2 for PRISMA flow diagram). In total, we included 1427 paired observations with both an invertebrate inclusion and exclusion treatment at the tree species level. These observations were derived from 207 study sites across five continents (Fig. 1). For each paired observation, we also recorded the tree species used in the experiment

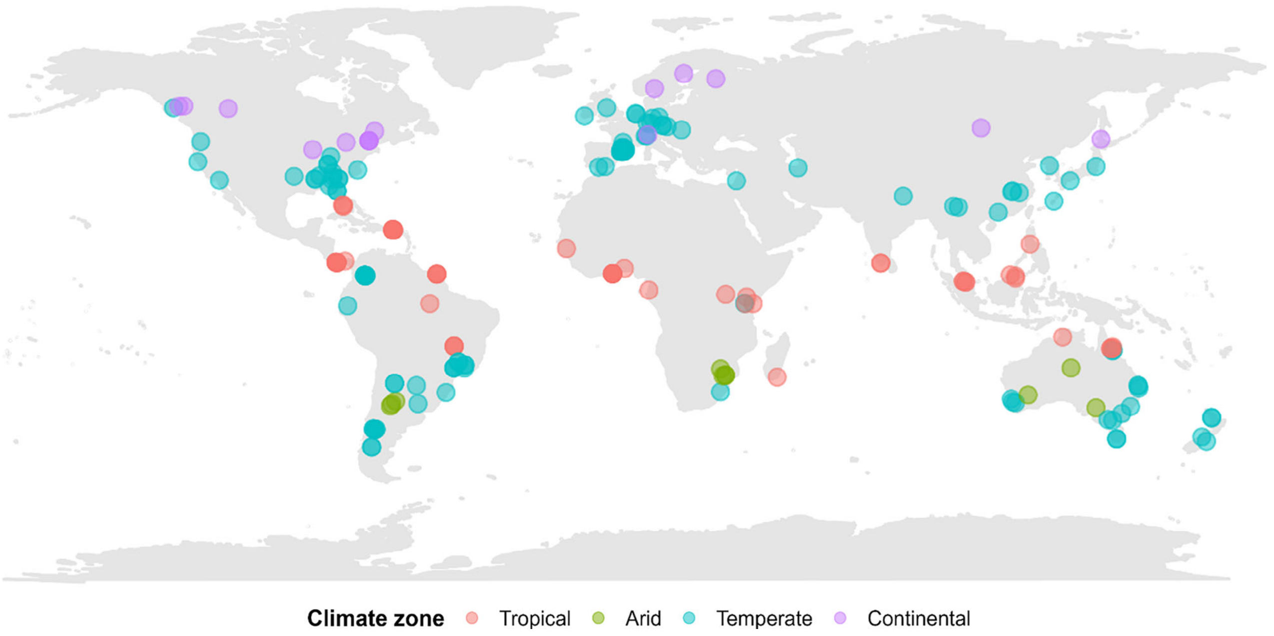

Fig. 1. Study site geographical distributions. The climate zones are based on the Köppen Geiger climate classification, which recognises five main zones: tropical, arid, temperate, continental and tundra. The continental zone also covers the boreal climate zone. Our data set included 420 paired observations for the tropical zone, 24 for the arid zone, 872 in the temperate zone and 111 in the continental zone. 51% of the paired observations used woody debris (WD) with a diameter of <3 cm, 39% used 3.1–5.0 cm diameter WD for their experiments and 10% used WD with diameters between 5.1 and 23 cm (for diameter range, see Fig. S3). All data were from downed dead wood.

yielding a data set with 162 tree species from 118 genera and 56 families. WD from the same species decomposing in the presence *versus* absence of invertebrates in each study site was considered as a paired observation across different periods of WD retrieval during the WD decomposition study. WD diameters ranged from 0.3 to 23.1 cm with a median of 3 cm (Fig. S3). For each observation reported in the study, we extracted the mass loss of the WD in the presence *versus* absence of invertebrates, the standard deviation and the number of samples used in calculating the mean rate of decay. For each paired observation, the mass loss of the WD in the presence *versus* absence of invertebrates were in the same units and measured for the same decomposition time (incubation period). This information was extracted from the text or tables in the main text or the supplementary data (e.g. data repositories). Where the information was not provided in the supplementary data or in the text, *Engauge* digitizer software 12.1 version (https://www.softpedia.com/get/Science-CAD/Engauge-Digitizer.shtml) was used to extract the data from published figures. In some studies, only the standard error was given together with the number of samples, and we then calculated the standard deviation using the following equation:

$$\text{Standard deviation} = \text{Standard error} \times \sqrt{\text{sample } N}. \tag{1}$$

When the study met our criteria for inclusion but we could not access the data, we contacted the corresponding authors directly to request the data. We did not manage to access data for six studies that met our inclusion criteria and these were excluded. From all included studies, we extracted the following information: geographical coordinates for the study sites, precipitation, temperature, WD diameter, bark status (presence/absence), invertebrates observed in the WD, duration of decomposition, and the methods used to exclude or include invertebrates. Where the geographical coordinates of experimental sites were not given, we used the site names reported in the study to search for the coordinates on *Google Earth*. Because several studies did not report precipitation and temperature at experimental sites, we used *WorldClim* to estimate climate attributes for the entire data set using the R *raster* package to obtain uniform data (Hijmans *et al.*, 2021). The majority of the studies did not report chemical traits for the WD at the onset of the experiment, neither did the studies provide a detailed description of the invertebrate communities present in the wood or site of decomposition. Therefore, we did not conduct further analyses on how chemical traits influence WD decomposition and the variations in invertebrate-mediated decomposition amongst different groups of invertebrates.

To examine how WD size affected the contribution of invertebrates to WD decomposition, we classified the WD into two diameter categories: smaller (0.3–3 cm) and larger (3.1–23.1 cm), based on the WD median diameter (3 cm) of our data set (Fig. S3). Based on whether the WD used in the experiment had bark intact or removed (without any further processing) at the onset of the decomposition experiment, we classified the data into two categories: bark present (WD with bark) and bark absent (WD without bark). The data were also classified based on whether the WD type used in the studies had undergone further processing, such as compressing or sawing to a standardised shape (e.g. wood blocks, stakes or dowels), as 'processed' or 'natural' (intact WD, not processed other than by cutting to a standardised length). Additionally, we classified the study sites into four major climate zones based on Köppen Geiger climate classifications using the *kgc* R package (Bryant *et al.*, 2017). Köppen Geiger classification is based on seasonal patterns in temperature and precipitation and recognises five climate zones: tropical, arid, temperate, continental (including boreal zones) and tundra. Our data set did not include any sites from the tundra climate zone. Therefore, only four climate zones (tropical, arid, temperate, continental) were included in our analyses. We also classified whether the WD originated from gymnosperm or angiosperm species. Finally, we examined whether there was an influence of study duration (time) on WD decomposition.

(2) Data analysis

To estimate the overall effect of invertebrates on WD, we used log response ratio [ln(RR)], because it is robust to low sample size and has a distribution that approaches normal when the standardised mean denominator is large (Hedges, Gurevitch & Curtis, 1999). We used mass loss of WD in the absence of invertebrates (exclusion) as the control while decomposition of WD in the presence of invertebrates (inclusion) was the treatment:

$$\ln(\mathrm{RR}) = \ln \frac{\mathrm{ML}_{\text{inclusion}}}{\mathrm{ML}_{\text{exclusion}}}, \tag{2}$$

where ML is the percentage change in mass.

Acceleration of WD decomposition rate by invertebrates is indicated by a positive ln(RR) while deceleration of WD decomposition rate by invertebrates is indicated by a negative ln(RR). Ln(RR) variance (V) was calculated using the following equation:

$$V(\ln(\mathrm{RR})) = \frac{(S_{\text{inclusion}})^2}{N_{\text{inclusion}}(X_{\text{inclusion}})^2} + \frac{(S_{\text{exclusion}})^2}{N_{\text{exclusion}}(X_{\text{exclusion}})^2}, \tag{3}$$

where $N_{\text{inclusion}}$ and $N_{\text{exclusion}}$ are the sample size (number of WD pieces per site, per species) for mass loss in the presence ($X_{\text{inclusion}}$) and absence ($X_{\text{exclusion}}$) of invertebrates, respectively; and $S_{\text{inclusion}}$ and $S_{\text{exclusion}}$ are the mass loss standard deviations in the presence and absence of invertebrates, respectively.

We applied multi-level random effects meta-analysis to account for non-independence and to avoid pseudoreplication in the data using the *rma.mv* function in the *metafor* package (Viechtbauer, 2010). A multi-level model accounts for both the nested structure in our data and dependency among observations (Hox, 2010). The random-effects model assumes that individual studies have their own mean estimates and that individual study effect sizes differ because of sampling differences and existing systematic differences among studies (Fernández-Castilla *et al.*, 2020; Nakagawa *et al.*, 2023). A random-effects meta-analytical model uses the inverse of within and between studies variance to weight the true effect size. A random-effects model also accounts for autocorrelation of observations within studies. The decomposition rate difference between WD decomposing in the presence and absence of invertebrates was considered significant when the 95% confidence intervals did not overlap zero. To convert the effect size (lnRR) back to percentages we used the following equation:

$$\text{Percent change} = \left(e^{\ln\text{RR}} - 1\right) \times 100\%. \qquad (4)$$

To evaluate how other factors influenced the contribution of invertebrates to WD decomposition, we used the *rma.mv* function in the *metafor* package to perform a meta-regression. As the invertebrate effect on WD decomposition could vary among species, we used tree species as a random factor nested in study (1| Study/Tree species) to account for these variations in ln(RR) among WD species. The following moderators were used as fixed effects in the meta-regressions: climatic variables (temperature and precipitation) or climate zones, bark status (presence or absence), type of WD (natural or processed), clade (gymnosperms or angiosperms), WD diameter, and incubation duration. Q_M, which tests the amount of heterogeneity explained by the variables and their related *P* values were used to estimate how individual moderators influenced invertebrate contributions to WD decomposition effect sizes [ln(RR)]. After checking for significant Pearson correlations among the moderators, we fitted linear models to evaluate which set of moderators explained variation in the invertebrate effect sizes on WD decomposition. All possible models including two-way interactions were fitted and ranked based on the Akaike information criterion (AIC) using the *glmulti* package (Calcagno & de Mazancourt, 2010). We used the genetic algorithm (GA) method in the *glmulti* package to complete model selection, as this is more computationally efficient for interaction models with large data sets and improves convergence during model selection (Calcagno & de Mazancourt, 2010). The GA method randomly explores subsets of all possible models with a bias towards better models (Calcagno & de Mazancourt, 2010). In total, 1419 observations were used in fitting the different possible models. We fitted models including climate zones or temperature and precipitation because the Köppen Geiger classification is based on temperature and precipitation patterns. The model selection including temperature and precipitation converged after 1080 generations (see Table 2 for summary results from the best model), while model selection including climate zones converged after 700 generations (see Table S2).

We used a funnel plot of effect size and the standard deviation to check for publication bias and found that the plot was relatively symmetrical but had some missing studies in the lower left (studies reporting negative effects of invertebrates on wood decomposition) (Fig. S3). To account for such biases, we performed a Rosenberg fail-safe number analysis

Table 2. Estimated effect sizes for invertebrate contribution to woody debris (WD) decomposition in the top meta-analysis model. All possible models including two-way interactions were fitted to our data (1419 paired observations with complete data) using the package *glmulti*. Study and tree species (1| Study/tree species) were used as random factors. Model selection was conducted using the genetic algorithm method in *glmulti* and model selection converged after 1080 generations. The best model was selected based on the Akaike information criterion (AIC). SE is the standard error associated with the estimates. See Table S2 for the best model using climate zones instead of temperatures and precipitation).

Variable	Estimate	SE	*Z* value	*P* value
Intercept (angiosperms without bark)	2.9650	0.6369	4.6556	**<0.0001**
Gymnosperms	0.6117	0.2372	2.5791	**0.0099**
Bark present	−0.6651	0.1385	−4.8008	**<0.0001**
Study duration	0.0150	0.0016	9.3807	**<0.0001**
WD diameter	−0.0924	0.0149	−6.2067	**<0.0001**
Temperature	−0.0187	0.0025	−7.3601	**<0.0001**
Precipitation	0.0002	0.0000	4.7197	**<0.0001**
Gymnosperm × Bark present	−0.5034	0.2124	−2.3699	**0.0178**
Study duration × WD diameter	−0.0003	0.0000	−10.6264	**<0.0001**
Study duration × Temperature	0.0000	0.0000	1.4516	0.1466
WD diameter × Temperature	0.0006	0.0001	7.3703	**<0.0001**
Study duration × Precipitation	−0.0000	0.0000	−6.9236	**<0.0001**
Temperature × Precipitation	−0.0000	0.0000	−2.7549	**0.0059**
Gymnosperm × Study duration	0.0061	0.0001	59.6614	**<0.0001**
Gymnosperms × Temperature	−0.0016	0.0007	−2.2110	**0.0270**
Bark present × Temperature	0.0028	0.0005	5.4211	**<0.0001**

(Rosenberg, 2005). This test gives an estimate of how many non-significant potential studies would be required to change our conclusion (Rosenberg, 2005). In this study, the fail-safe number was 11,325,710. Based on this number, we have confidence in our results: the fail-safe number was much greater than the recommended $5k + 10$ threshold (= 7,145), where k is the total number of observations (Rosenthal, 1979; Nakagawa *et al.*, 2022).

III. RESULTS

(1) Invertebrate contribution to WD decomposition

The presence of invertebrates accelerated WD decomposition by 40% overall [mean ± SE ln(RR) = 0.339 ± 0.148, $P = 0.022$]. The invertebrate effect varied across climate zones ranging from tropical (0.560 ± 0.036, $P < 0.001$), to arid (0.798 ± 0.25, $P = 0.001$), to temperate (0.12 ± 0.017, $P < 0.001$) zones. There was no significant effect of invertebrates on WD decomposition in the continental climate zone (0.020 ± 0.039, $P = 0.607$) (Fig. 2A).

(2) Effect of WD diameter on the invertebrate contribution to WD decomposition

WD diameter influenced the invertebrate effect on wood decomposition and this effect was greater for larger (0.371 ± 0.027, $P < 0.001$) than smaller (0.153 ± 0.020, $P < 0.001$) WD sizes (Fig. 3A). This difference was driven primarily by a higher invertebrate effect on the larger WD in the tropics (Fig. 4A).

(3) Effect of bark status on the invertebrate contribution to WD decomposition

Invertebrates accelerated WD decomposition for both WD with bark (0.1 ± 0.01, $P < 0.001$) and without bark (0.44 ± 0.03, $P < 0.001$), but the magnitude of the effect size varied with the WD bark status (bark present or absent). Bark presence reduced the magnitude of the invertebrate effect on WD decomposition (Fig. 2B). Differences between the invertebrate effect on WD with and without bark were found only in the tropical and temperate climate zones (Fig. 4B). The bark effect on invertebrate acceleration of WD decomposition did not vary with the WD size (Fig. 3B).

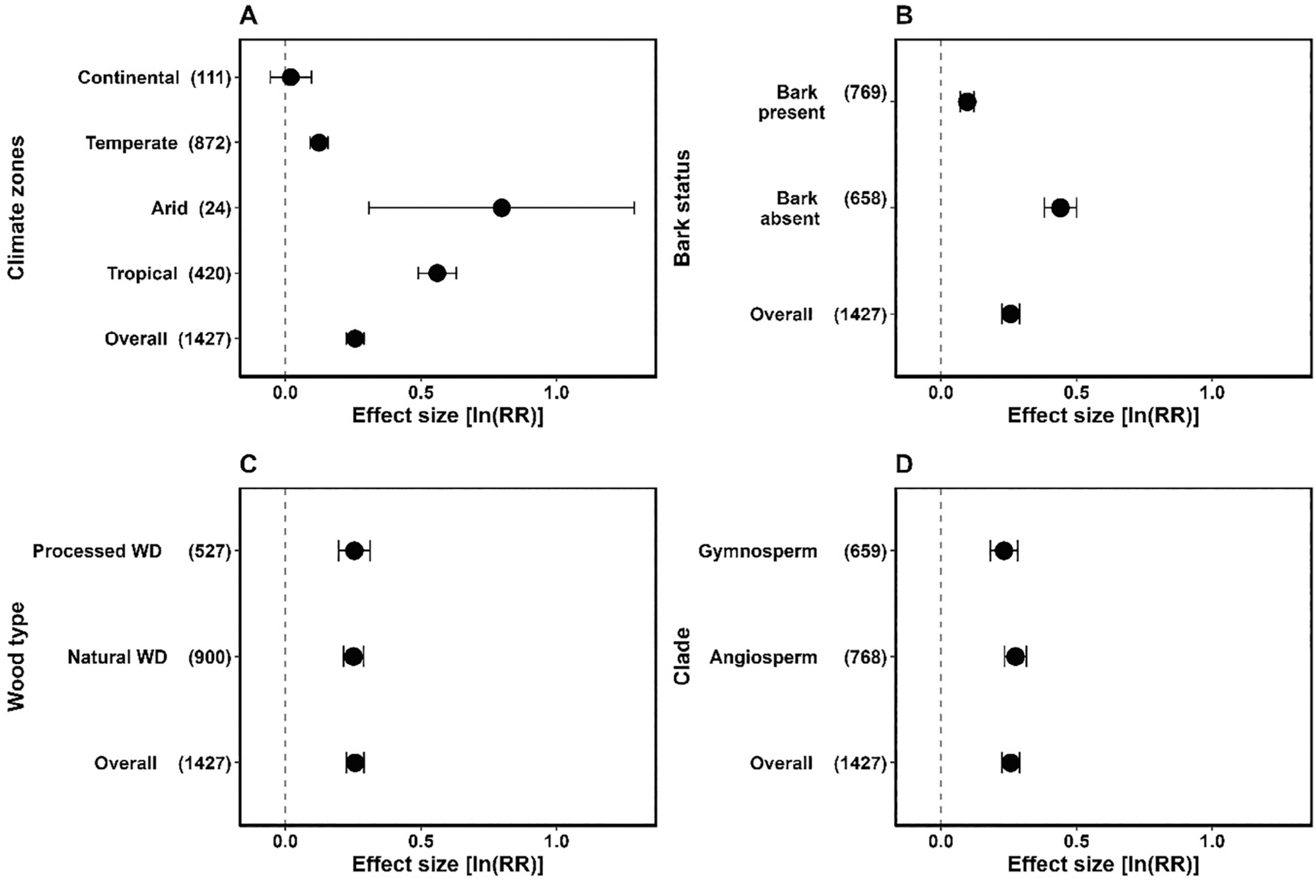

Fig. 2. Invertebrate effect on woody debris (WD) decomposition across climate zones (A), bark status (B), WD type (C), and WD clade (D). Effect sizes with error bars crossing zero (vertical dashed line) are not significantly different from zero. Numbers in parentheses are the number of observations.

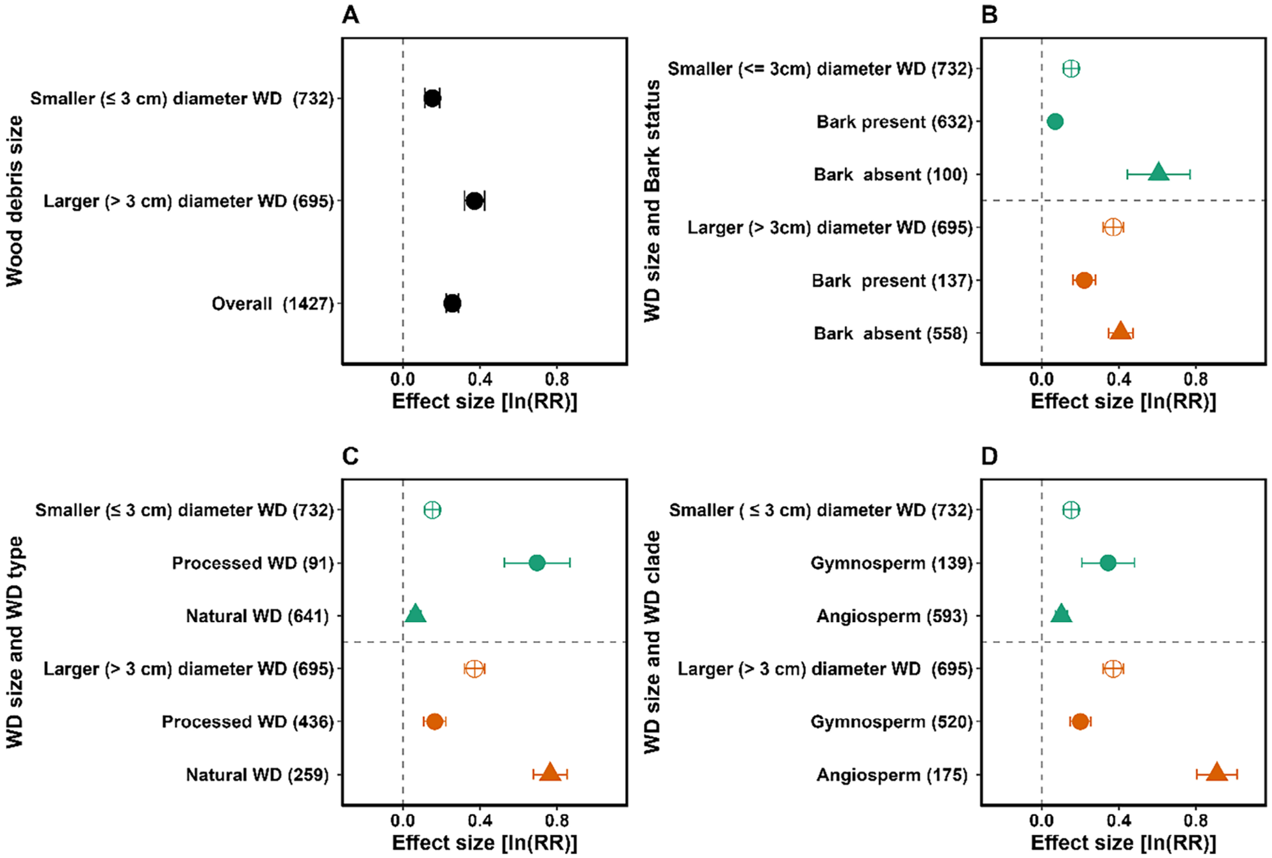

Fig. 3. Effect of woody debris (WD) diameter on the invertebrate contribution to WD decomposition (A) and its effect under different bark status (B), WD type (C), and WD clade (D). Effect sizes with error bars crossing zero (vertical dashed line) are not significantly different from zero. Numbers in parentheses are the number of observations. The WD diameter range for 'smaller' WD was 0.3–3 cm and the range for 'larger' WD was 3.1–23.1 cm.

(4) Effect of WD type on the invertebrate contribution to WD decomposition

The overall invertebrate effect on WD decomposition was positive for both processed wood (0.254 ± 0.030, $P < 0.001$) and natural wood (0.251 ± 0.019, $P < 0.001$). We found no significant differences between the magnitude of overall invertebrate effect on processed *versus* natural wood (Fig. 2C). However, when examining the effect of invertebrates on WD type within climate zones, the magnitude of invertebrate effect was higher for natural than processed WD in the tropical zone with an opposite effect in the temperate zone and no differences in the continental climate zone (Fig. 4C). Within smaller size WD, processed WD had a stronger invertebrate effect than natural WD, while within larger size WD, processed WD had a weaker invertebrate effect than natural WD (Fig. 3C).

(5) Effect of WD clade on the invertebrate contribution to WD decomposition

The presence of invertebrates accelerated wood decomposition for gymnosperms (0.232 ± 0.026, $P < 0.001$) and angiosperms (0.275 ± 0.021, $P < 0.001$) (Fig. 2D). The magnitude of the invertebrate effect on WD decomposition did not differ between gymnosperms and angiosperms across all climate zones (Fig. 4D). For smaller WD, gymnosperms showed a larger invertebrate effect than angiosperms whereas for larger WD, gymnosperms exhibited a smaller invertebrate effect than angiosperms (Fig. 3D).

(6) Effect of incubation duration on the invertebrate contribution to WD decomposition

We observed that the overall magnitude of invertebrate effect on WD decomposition decreased with incubation duration ($Q_M = 101.75$, $P < 0.001$, $R^2 = 0.0575$) (Fig. 5), but the effect was significant only in the temperate zone (slope estimates (β) = −0.04, $t = -2.5$, $P < 0.01$) (Fig. 5). Incubation duration interactions with WD diameter and precipitation also influenced the invertebrate effect on WD decomposition (Table 2, Table S2).

IV. DISCUSSION

We found that globally, invertebrates increase wood decomposition. This trend was observed in all climate zones except

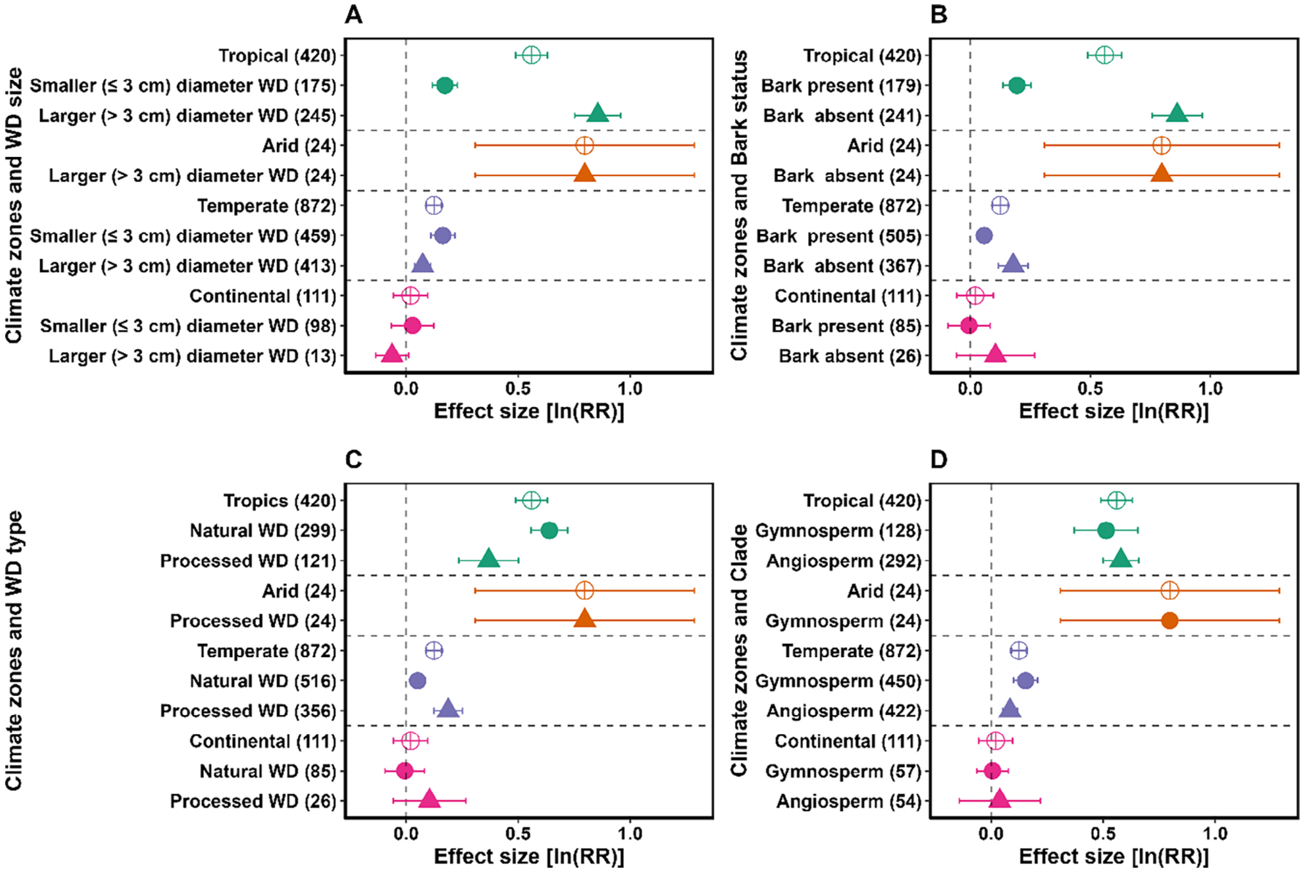

Fig. 4. Effects of woody debris (WD) diameter (A), bark status (B), WD type (C), and WD clade (D) on the invertebrate contribution to WD decomposition across climate zones. The climate zones were classified based on Köppen Geiger climate classification. Effect sizes with the error bars crossing zero (vertical dashed line) are not significantly different from zero. Numbers in parentheses are the number of observations.

areas with a continental climate. Overall, invertebrate effects on WD decomposition were higher for larger diameter WD (>3 cm, range: 3.1–23.1 cm). The invertebrate effect on wood decomposition differed between wood with and without bark, but not between processed and natural wood, and patterns differed between climate zones. Overall, the invertebrate effect did not differ between gymnosperm and angiosperm WD decomposition when the size of WD was not considered, but the invertebrate effect was greater for gymnosperms than angiosperms on smaller diameter WD and the opposite was seen for larger diameter WD. Finally, the magnitude of the invertebrate effect tended to decline with the duration of wood decomposition, which indicates that invertebrates primarily serve to accelerate the early stages of wood breakdown and decomposition.

Consistent with our first hypothesis, and consistent with previous studies (Seibold *et al.*, 2021; Zanne *et al.*, 2022), invertebrates accelerated WD decomposition at a global scale. Furthermore, the effect was positive and significant in the tropical, arid and temperate zones but not in the continental climate zone. The overall magnitude of the invertebrate effect was 40%, which substantially surpassed the ~29% found in a cross-continental experiment (Seibold *et al.*, 2021). We attribute this to differences in the methodology and modelling used to obtain these estimates. While Seibold *et al.* (2021) used empirically derived decomposition models with and without invertebrates present and applied them to a global C map to estimate the total amount of C released *via* dead wood decomposition and the contribution of invertebrates, we present an overall estimate across all sites included in our meta-analysis. In addition, whereas Seibold *et al.* (2021) utilised naturally occurring wood, our meta-analysis incorporated a large number of data points from studies examining processed wood. Processed wood lacks bark and was probably kiln dried, which may have resulted in some organic compound volatilisation and transformations, and we show here that the presence of bark reduces the effect of invertebrates on wood decomposition; therefore inclusion of data for processed wood in the meta-analysis likely increased our overall estimate.

Variation in the invertebrate effect on WD decomposition across climate zones may be explained by differences in annual average temperature from the equator towards the poles. Higher temperatures in the tropics favour a high

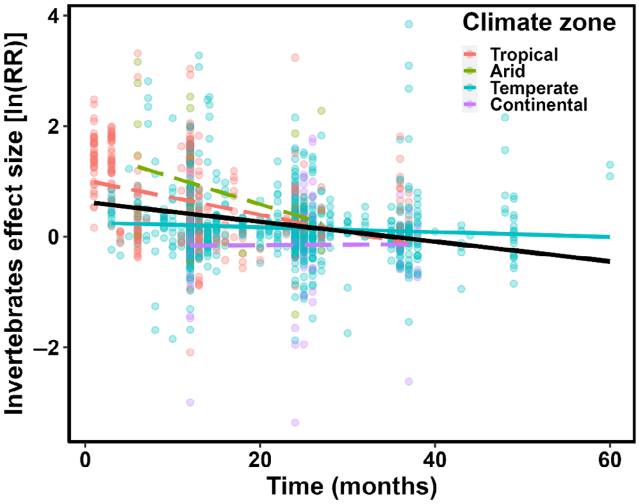

Fig. 5. Effect of incubation duration on invertebrate effect on woody debris (WD) decomposition across climatic zones. Values above *versus* below zero indicate an increase *versus* decrease, respectively, in WD decomposition by invertebrates. Climate zones are based on Köppen Geiger climate classifications. This classification recognises five main zones: tropical, arid, temperate, continental and tundra. The continental zone includes the boreal climate zones. Dashed lines are not significant, solid lines are statistically significant. The black line represents the overall trend regardless of climate zone.

abundance of invertebrates, especially termites colonising dead wood, which may promote higher decomposition rates in these zones (Tuma, Eggleton & Fayle, 2020; Liu *et al.*, 2022). Moreover, wood-feeding termites, which are a key driver of WD decomposition, occur mainly in the tropics (Rosenberg *et al.*, 2023). Higher temperatures in the tropics also govern the metabolic rates of invertebrates and hence wood consumption rate and rate of larval development in dead wood (Marshall *et al.*, 2020). The absence or rarity of termites likely explains the non-significant effect of invertebrates on WD decomposition in the continental climate zone. An effect of invertebrates in the continental climate zone would likely reflect mainly the activities of beetles, but since beetles usually attack larger wood debris (greater than the size range in this study), it is possible that studies including larger sized wood may find a significant effect.

To test hypotheses 2–5 (see Table 1), we classified the data into categories based on bark status, diameter, and tree species clade. However, we acknowledge that these potential drivers (bark status, diameter and clade) are often linked, and disentangling how they modulate the invertebrate effect on WD decomposition remains a research gap. For example, studies use WD of the same diameter, bark status, type, and species for ease of comparisons of WD decomposition across multiple sites. Thus, to compare invertebrate effects, for example, on differences among diameters of wood pieces, we have to rely on comparisons across studies. Second, the invertebrate effect on WD decomposition likely differs among groups of invertebrates based on how they utilise WD. However, studies usually do not report the invertebrate communities present in WD during the decomposition process or the invertebrate communities present at an experimental site at the onset of a study. Third, WD used in decomposition experiments had usually either been freshly cut from living trees or was industrially processed wood exposed on the forest floor. Natural WD is more heterogenous including, e.g. standing dead trees, dead branches in the canopy of living trees or slowly dying trees after windthrow or fire. Wood decomposition rates may therefore be more heterogenous than reflected by the experiments included in our meta-analysis. However, few studies compare how WD from senesced and downed living trees decomposes and how such differences may influence invertebrate contributions to WD decomposition. Consequently, there remain knowledge gaps that future studies should fill to advance our understanding on the contribution of invertebrates to WD decomposition. Future studies should focus on experiments that: (*i*) include small- and large-diameter wood at the same sites; (*ii*) compare the invertebrate effect on WD with and without bark at similar sizes; (*iii*) investigate not only insect exclusion but also record the insect communities or functional groups present (e.g. termites *versus* beetles); and (*iv*) compare the invertebrate effect on WD across a variety of deadwood types, such as standing dead trees, WD in the canopy or slowly dying trees.

In line with our second hypothesis, the global invertebrate effect on wood decomposition was on average larger for WD with larger diameters. The effect of WD diameter on the invertebrate effect varied with WD type (natural or processed) undergoing decomposition. A stronger invertebrate effect on decomposition of larger WD was found primarily in the tropics and may have resulted from rapid colonisation of WD by termites with fungal establishment slower and fungal dominance reduced in large-diameter WD. Additionally, the micro-environment in larger diameter WD is likely to be more stable as there is higher moisture retention and lower temperature variation compared to smaller diameter WD. Furthermore, larger WD may provide a wider range of resources, such as nutrients and space for more invertebrate groups to co-exist. However, we note that studies in the tropics included more WD of large diameter, while studies in the temperate and continental (boreal) zone included more WD of small diameter and thus effects of diameter could be influenced by differences in study characteristics between climate zones. We call for further studies that evaluate the effect of WD diameter on invertebrate contribution to decomposition by experimentally manipulating WD diameters and including WD of different diameters >10 cm at the same sites.

In our third hypothesis, we predicted that the invertebrate effect would be stronger when bark is present. By contrast, we observed that the absence of bark on WD resulted in stronger positive effects of invertebrates on WD decomposition. WD without bark is colonised by different species assemblages and harbours a lower diversity of insects in temperate forests (Thorn *et al.*, 2016; Hagge *et al.*, 2019*b*,*a*). Yet, WD without bark is colonised more by wood-feeding termites (Ulyshen, Müller & Seibold, 2016). Unlike other invertebrates and fungi that depend on bark for protection from microclimate fluctuations and phloem resources under the bark, termites maintain their own microclimate through shelter tubes, fortifications, and nest-building and feed directly on the wood (Oberst *et al.*, 2019). Since the absence of bark reduces the rate at which fungi colonise and establish on WD (Hagge *et al.*, 2019*a*), termites may benefit from reduced fungal dominance in WD without bark, resulting in a stronger invertebrate effect on WD decomposition, especially in the tropics where termites are more abundant. This observation suggests that removal of bark from wood could lead to an overestimation of the effect of invertebrates on wood decomposition especially in tropical zones.

We expected that the overall invertebrate effect on WD decomposition would be higher in natural than processed WD (hypothesis 4). Wood processing may change its physical and chemical traits (e.g. through kiln drying) and this could influence attractiveness to invertebrate colonisation (Ulyshen & Wagner, 2013). However, in our meta-analysis, the overall effect of invertebrates on WD decomposition did not differ between natural and processed WD. Interestingly, the magnitude of the invertebrate effect on WD decomposition was greater for natural WD than processed WD in the tropics, but showed the opposite trend in the temperate climate zone, leading to an overall non-significant difference between the two wood types. This result implies that processing wood alters WD traits which drive the effect size for the invertebrate contribution to WD decomposition, with such effect sizes inconsistent across climate zones.

Contrary to expectations in hypothesis 5, we found no significant difference between the invertebrate effect on decomposition between angiosperm and gymnosperms globally across the four climate zones studied. We hypothesised a weaker invertebrate effect in gymnosperms because of higher concentrations of anti-herbivory compounds that act as a chemical barrier to invertebrate colonisation (Pietsch *et al.*, 2014; Cornelissen *et al.*, 2023). Global meta-analyses on wood decomposition reported that under similar climatic conditions gymnosperms decompose at a slower rate than angiosperms because of their relatively low nutrient content (N, Ca and K) and different lignin chemistry (e.g. more decay-resistant guaiacyl lignin) (Cornwell *et al.*, 2009; Weedon *et al.*, 2009). However, when we categorised the data based on WD diameter, the invertebrate effect in angiosperms was higher than in gymnosperms for larger diameter WD but the opposite pattern was found for WD of smaller diameter, with a greater effect in gymnosperms than in angiosperms. The opposite patterns cancel out for the overall data set at the global scale (Fig. 4D). The stronger invertebrate effect for gymnosperm than for angiosperm WD observed for smaller WD diameters may result from reduced fungal colonisation and dominance in gymnosperms WD due to their recalcitrant chemistry and structure. Reduced fungal decomposition in gymnosperms could have resulted in greater differences between mass loss in invertebrate inclusion and exclusion treatments and hence a larger invertebrate effect than predicted by our hypothesis. Moreover, a recent study (Guo *et al.*, 2023) reported that termites preferentially fed on gymnosperm branches, resulting in an overall insignificant difference between the decomposition of gymnosperm and angiosperm branches. Similar results of higher termite consumption of *Pinus radiata* (a non-native species) compared to native angiosperms were also obtained in Australia (Law *et al.*, 2023). Invertebrates, mainly termites, are therefore likely to colonise gymnosperms earlier than fungi, resulting in a stronger invertebrate effect on decomposition in gymnosperms than in angiosperms.

The invertebrate effect on wood decomposition varied with the incubation duration and was stronger early in decomposition but declined with study duration. However, the later decay-stage data were dominated by temperate sites which could have led to a decline over time. This trend is consistent with recent findings (Taylor *et al.*, 2024), and could be explained by changes in the composition of invertebrate decomposers, which follow strong successional turnover as wood decomposes (Stokland, Siitonen & Jonsson, 2012; Ulyshen, 2018; Zuo *et al.*, 2021; Seibold *et al.*, 2023). While communities during the early stages of decomposition are dominated by wood- and bark-feeding species, mycetophagous species become increasingly dominant over time (Ulyshen, 2018; Kriegel *et al.*, 2023). In addition, the presence and abundance of wood-feeding termites could contribute to the strong invertebrate effect on decomposition in the tropical zone. Unlike other saproxylic invertebrates that need to complete their life cycle within dead wood, some termites invade WD as a colony or their workers use it to forage for food and hence exhibit high rates of consumption soon after they discover WD (Oberst, Lai & Evans, 2018). When the WD is almost completely decomposed, these termites abandon it to move to newer WD. Furthermore, nutrient dynamics during the WD decomposition process could contribute to this trend especially for non-termite invertebrates. As wood decay progresses, nutrients become homogenised and the traits that influence the invertebrate effect on the decomposing wood diminish (Oberle *et al.*, 2020). The composition of invertebrates colonising the WD could also differ with the decomposition stage (Zuo *et al.*, 2021) with more active wood feeders dominating the wood in the early stages of decomposition (Ulyshen, 2016). Finally, as decomposition progresses, fungal communities within the WD become established leading to stronger fungal decomposition, which reduces the overall contribution of invertebrates to WD decomposition as time progresses.

V. CONCLUSIONS

(1) Our study highlights the substantial role of invertebrates in accelerating wood decomposition at the global scale. We demonstrate that the invertebrate effect varies among

climate zones, with a decreasing effect from tropical to temperate zones and an insignificant effect in the continental climate zone.

(2) Wood characteristics, such as diameter, bark presence, and tree species, mediate the effect of invertebrates on wood decomposition, but disentangling the individual effects of these traits is hampered by a current lack of controlled experiments globally.

(3) Nevertheless, we demonstrate that bark presence limits the invertebrate effect on WD decomposition and thus, the use of debarked WD as experimental substrates could lead to an overestimation of the contribution of invertebrates on WD decomposition.

(4) Furthermore, we show that the overall effect of invertebrates on gymnosperm and angiosperm decomposition is similar, yet differences occur depending on wood diameter.

(5) We also demonstrate that physical (bark removal, larger diameter) and chemical barriers may likely delay WD fungal colonisation relative to that by invertebrates and favour a stronger invertebrate effect on WD decomposition.

(6) We underscore the key role played by invertebrates on biogeochemical cycles through acceleration of WD decomposition. This finding highlights the need to focus on ways to incorporate invertebrate effects into global biogeochemical models as invertebrate contributions are not parameterized yet within such models.

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VII. AUTHOR CONTRIBUTIONS

D. M. N., J. Z. and G. G. O. D. contributed equally to the conception of the study design with discussions with J. H. C. C., M. D. U., S. S., A. E. Z., B. O., R. D. H., S. L., X. L., T. B. and M. K. T. Published data collection was conducted by D. M. N., data analysis was conducted by D. M. N., G. G. O. D. and J. Z. All authors contributed to the writing of the manuscript and approved the final version.

VIII. DATA AVAILABILITY STATEMENT

All data and code used in this manuscript are available in 'The effects of invertebrates on wood decomposition across the world' at https://doi.org/10.5281/zenodo.13322590.

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X. SUPPORTING INFORMATION

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

Fig. S1. Conceptual framework on which our meta-analysis is based.

Table S1. Search string used to search for studies in the *Web of Science* and *Scopus* databases.

Fig. S2. PRISMA flow diagram showing the steps followed for the inclusion of studies in our database.

Fig. S3. Distribution of woody debris (WD) diameter in our data set.

Table S2. Estimated effect sizes for invertebrate contribution to woody debris (WD) decomposition in the top meta-analysis model using climate zones instead of temperature and precipitation.

Fig. S4. Funnel plot showing the distribution of effect sizes.

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