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Litter quality and stream physicochemical properties drive global-scale invertebrate-mediated instream litter decomposition

Abstract

Plant litter is the major source of energy and nutrients in stream ecosystems and its decomposition is vital for ecosystem nutrient cycling and function. Invertebrates are key contributors to instream litter decomposition, yet quantification of their effects and drivers at the global scale remains lacking. Here, we synthesized data comprising 2835 observations from 141 studies of stream litter decomposition experiments to assess the contribution and drivers of invertebrates to the decomposition process within and across climate zones at the global scale. Results showed that (1) invertebrates consistently enhanced instream litter decomposition within and across tropical, temperate, and cold regions, representing an average global contribution of 70%; (2) initial litter quality and stream water physicochemical properties were equal drivers of invertebrate-mediated litter decomposition; and (3) contribution of invertebrates to litter decomposition was greatest during the early stages of litter mass loss (0−20%). Our results highlighted the global contribution of invertebrates to instream litter decomposition and provide support for their inclusion in global models of litter decomposition in streams to explore mechanisms and impacts of terrestrial, aquatic, and atmospheric carbon fluxes.

Keywords: decomposition rate, mass loss, litter quality, stream ecosystems, physicochemical properties, decomposition stage, linear-mixed model

1. Introduction

Allochthonous inputs of plant litter to stream ecosystems represent the dominant source of energy and nutrients for aquatic heterotrophic organisms that play a key role in the transport of carbon (C) and other nutrients across landscapes (Wallace et al. 1999, Graça et al. 2001). Decomposition of litter by abiotic and biotic factors drives ecosystem-level processes, such as nutrient cycling, energy flow, and trophic interactions (Chauvet et al. 2016, Lidman et al. 2017), and is essential for the maintenance of ecosystem function in streams. Climate and ambient availability of nutrients tend to exert a greater influence on litter decomposition processes in terrestrial and aquatic systems than litter quality, while it has been suggested that decomposer (bacteria, fungi, invertebrate detritivores) community structure and composition play a minor role (Aerts 1997, Cornwell et al. 2008, Frainer et al. 2014); however, recent studies indicate that the contribution of decomposer communities to litter decomposition may have been underestimated (Bradford et al. 2016, Bradford et al. 2017). For example, a meta-analysis shows average global-scale increases in litter decomposition by soil invertebrates of 37% (García-Palacios et al. 2013). While global models of litter decomposition have tended to be biased towards terrestrial ecosystems (Cole et al. 2007, Berg and McClaugherty 2014), recent models have included some drivers of instream litter decomposition (Tiegs et al. 2019, Zhang et al. 2019, Boyero et al. 2021), but neglected the contribution of invertebrates within and across climate zones.

Impacts of aquatic invertebrates on instream litter decomposition processes may be direct, through feeding, and indirect, through trophic interactions. For example, stream invertebrate detritivores, comprising shredders, grazers-scrapers, collector-filterers, and collector-gatherers

(Graça et al. 2001), contribute directly to losses in litter mass through feeding and the associated acceleration of litter fragmentation and subsequent incorporation of nutrients in secondary production through the production of fecal pellets (Graça et al. 2001, Berg and McClaugherty 2014). In contrast, macroinvertebrate-meiofauna and invertebrate-microbe interactions indirectly regulate instream litter decomposition (Wang et al. 2020) through competition for food (Ptatscheck et al. 2020) and improved palatability of litter detritus through changes in microbe community structure and activity (Hättenschwiler et al. 2005, Chambord et al. 2017), such as the preference of invertebrates to feed on leaf litter colonized by fungi and bacteria that produce enzymes, including cellulases, xilanases, and pectinases, used in the digestion of plant cell walls and liberation of simple compounds assimilated by invertebrates (Rodrigues and Graça 1997, Graça et al. 2001).

Litter quality is the dominant driver of litter decomposition processes in global terrestrial (Aerts 1997) and stream (Zhang et al. 2019) ecosystems, where it affects colonization by, and activity of invertebrate and microbe species and their subsequent interactions (Graça et al. 2001, Sales et al. 2015). For example, levels of colonization and degradation of stream litter by hyphomycetes and invertebrates are greater in litter with high nitrogen (N) concentrations or low C:N ratios (Richardson et al. 2004, Ferreira et al. 2012). However, environmental conditions of streams, such as water level, temperature, and nutrient availability, are known to mediate invertebrate and microbe community composition and biological activity, along with their interactions, that subsequently impact litter decomposition processes (García-Palacios et al. 2016a). Although litter quality and environment conditions have been shown to drive global soil litter decomposition by invertebrates (García-Palacios et al. 2013), their impacts in global stream ecosystems are unclear.

Although comparison of invertebrate effects on instream litter decomposition among studies may be problematic, due to contrasting sampling techniques (use of ~0.5 mm and ~5 mm-mesh litterbags; Graça et al. 2005) that may lead to overestimation of effects, local studies have showed changes in the relative importance of biotic and abiotic drivers of litter decomposition through the decomposition process, in which microbe and nematode communities regulate litter decomposition in the early stages (García-Palacios et al. 2016b, Yue et al. 2018), and increases in soil invertebrate litter decomposition with nutrient scarcity (Peguero et al. 2019); however, global patterns of stream litter decomposition remain unclear. Here, we test for global patterns, sampling differences, and key drivers of invertebrate-mediated instream litter decomposition in a meta-analysis to test the hypotheses that (1) globally, there is a positive relationship between instream litter decomposition and invertebrate density, biomass, and richness across and within climate zones; (2) effects of invertebrates on instream litter decomposition is driven by litter quality; and, (3) effects of invertebrates on instream litter decomposition increase during the decomposition process and are negatively related to nutrient availability.

2. Methods and materials

2.1 Data collection and compilation

We searched for peer-reviewed articles and academic theses, published in English or Chinese before March 2021, on *Web of Science*, *Google Scholar,* and *China National Knowledge Infrastructure* using the search terms (“litter decomposition” OR “litter decay” OR “litter breakdown” OR “litter processing” OR “leaf decomposition” OR “leaf decay” OR “leaf breakdown” OR “leaf processing”) AND (“stream” OR “river” OR “lotic ecosystem” OR “watercourse”). Studies were then included in our database based on the following criteria: (1) decomposition of leaf litter, excluding wood, bark, or artificial substrates, was measured in natural freshwater streams or rivers using litterbags; (2) water bodies were not experimentally manipulated, such as by nutrient enrichment, pollution, or warming; (3) litterbags contained only single species, rather than mixed species; and, (4) litter decomposition rates (*k*) either from contrasting fine and coarse litterbag mesh sizes (~0.5 mm that excludes invertebrates *vs.* ~5 mm that allows invertebrate access, respectively) or mean invertebrate values (density: individuals g^{-1} of remaining litter mass; biomass: mg of individuals g^{-1} of remaining litter mass; or, species richness: number of species) along with litter *k* or mass loss from coarse mesh size litterbags over a given decomposition period were reported or could be calculated. Most articles did not define invertebrate functional groups, hence our focus on invertebrate density, biomass, and species richness. Based on these criteria, we derived globally-distributed data comprising 2835 observations from 141 articles or academic theses (Fig. 1, Appendix 1).

We divided the derived data into three databases: database 1 (340 observations) included pairwise *k* values from coarse and fine mesh size litterbags (+/- invertebrate activity, respectively); database 2 (830 observations) contained *k* values and corresponding invertebrate density, biomass, and species richness data; and database 3 (1665 observations) represented litter mass loss and corresponding invertebrate density, biomass, and species richness data. Litter *k* was either extracted directly from primary studies or estimated based on mass loss data using the single exponential model (Olson 1963):

$$\ln\left(\frac{M_t}{M_0}\right) = -k\mathrm{t} \qquad (1)$$

where M_0 is initial litter mass and M_t is remaining mass at sampling time t (d).

To quantify drivers of invertebrate-mediated litter decomposition, we derived physicochemical (temperature; discharge rate; velocity; pH; conductivity; alkalinity; dissolved oxygen, O_2; nitrate, NO_3^-; ammonium, NH_4^+; and, phosphate, PO_4^{3-}), initial litter quality (C; N; phosphorous, P; C:N ratio; lignin; and, lignin: N ratio), and experimental condition (litterbag mesh size; initial litter mass; and, experiment duration) data from the 141 articles and theses. Study sites were organized into three climate zones, according to absolute latitude (Ferreira et al. 2015) (tropical: 0−23.5°; temperate: 23.5−60°; and, cold: >60°) and mesh size of litterbags were categorized as <5 mm, 5−10 mm, or >10 mm. Leaf litter life history and functional types were classed as either broadleaf or needle and woody or herbaceous, respectively, and mycorrhizal association of the litter was classed as arbuscular mycorrhiza (AM), ectomycorrhiza (ECM), or AM+ECM, as these are important drivers of litter decomposition (Yue et al. 2018, Keller and Phillips 2019). Data were extracted directly from the main text, tables, and appendices of the articles/theses, or digitized from figures using Engauge Digitizer (v. 11.3; http://markummitchell.github.io/engauge-digitizer).

2.2 Statistical analysis

To quantify overall (presence/absence) effects of invertebrates on litter decomposition (database 1), we used the natural log-response ratio (lnRR) (Eq. 2):

$$\mathrm{lnRR} = \ln\left(\frac{k_{coarse}}{k_{fine}}\right) \qquad (2)$$

where k_{coarse} and k_{fine} were k values for +/- invertebrates recorded using coarse and fine litterbags, respectively. We first ran an intercept-only linear mixed model using the *lme4* package in R (Bates et al. 2015) to estimate the overall effects ($\ln RR_{++}$) of invertebrates on litter decomposition, in which lnRR was fitted as a response variable and the identity of primary studies was included as a random effect factor to explicitly account for potential dependence among observations extracted from a single study. Then, we used meta-regression to assess effects on lnRR of water physicochemical characteristics, initial litter quality, and experimental condition as fixed effect factors; effects of each factor was assessed separately, to include as many observations in the model as possible. To aid interpretation, $\ln RR_{++}$ and the corresponding 95% confidence intervals (CIs) were back-transformed using the equation $(e^{lnRR_{++}} - 1) \times 100$; lack of overlap of the 95% CIs with zero indicated effects of invertebrate on litter decomposition. To evaluate the relative importance of physicochemical, leaf, and experimental condition factors that affected lnRR, we adopted mixed-effects meta-regression model selections using the *glmulti* package in R (Calcagno and de Mazancourt 2010), based on maximum likelihood estimation; the importance of each factor was computed as the sum of Akaike weights for models in which it was included, with a cutoff of 0.8 to differentiate essential from non-essential factors (Terrer et al. 2016, Yue et al. 2021).

To assess effects of invertebrate density, biomass, and species richness on litter decomposition (databases 2 and 3), we performed linear mixed effects models using the *lme4* package in R (Bates et al. 2015), with k value or litter mass loss as a response variable and invertebrate density, biomass, or richness as a fixed effect factor; the identity of primary studies was a random effect factor. We assessed the effects of each physicochemical, leaf, and experimental condition factor on invertebrate impacts on *k* value or mass loss by fitting their interaction with the invertebrate fixed effect factors. Variation in invertebrate effects on litter mass loss among stages of decomposition was tested at 10% mass loss intervals. Estimates and corresponding 95% CIs were reported, with lack of overlap of 95% CIs with zero indicating effects of invertebrate on litter decomposition.

3. Results

3.1 Overall effect of invertebrates

At the global scale, presence of invertebrates increased instream litter decomposition rates by 70%, while in tropical, temperate, and cold regions, there were increases of 64, 70, and 93%, respectively; these effects of invertebrate were consistent across climate zones, size of litter bag mesh, and type of mycorrhizal association (Fig. 2a). Initial litter C content and C:N ratios, and stream water temperature negatively affected invertebrate-mediated litter decomposition, while there were positive effects of water pH and NO_3^- concentrations, initial litter N content and (Table 1); initial litter C concentrations and stream NO_3^- concentrations and temperature were the most important drivers of invertebrate-mediated litter decomposition (Fig. 2b).

3.2 Effects of invertebrate density, biomass, and species richness

Effects of invertebrate density, biomass, and species richness on stream litter decomposition were similar to those for invertebrates in general in temperate zones; however, there were no effects in tropical regions, and no biomass or species richness data were available for cold regions (Fig. 3). Effects of invertebrate density, biomass, and species richness varied with litter bag mesh size, where there were positive effects of density were recorded using bags with mesh size <10 mm, and of biomass and species richness recorded using litterbags with 5−10 mm mesh, while decomposition of litter with AM and ECM associations was positively related to invertebrate density and biomass, and density, biomass, and species richness, respectively; there were no effects of combined AM and ECM associations on invertebrate-mediated litter decomposition (Fig. 3). Litter decomposition mediated by invertebrate density was negatively affected by pH; that mediated by invertebrate biomass was positively affected by litter N and lignin content and lignin: N ratios, whereas litter decomposition mediated by invertebrate species richness was negatively affected by discharge rate; there was a negative effect of stream flow velocity on litter decomposition mediated by both invertebrate biomass and species richness (Table 1).

We found positive effects of invertebrate density, biomass, and species richness on litter mass loss, regardless of climate zone, litter bag mesh size, and mycorrhizal association (Fig. S1). Loss of stream litter mass mediated by invertebrate density were positively affected by initial litter lignin content, and stream water dissolved oxygen and NO_3^- content, and negatively affected by water velocity and pH; litter mass loss mediated by invertebrate biomass was positively related to litter bag mesh size; and, litter mass loss mediated by invertebrate species richness was negatively related to stream water temperature and PO_4^{3-} content, and positively related to stream discharge rate (Table S1). We were unable to identify the relative importance of these litter, stream, and experimental factors on invertebrate density, biomass, or species richness effects on litter decomposition using model selection analyses, because not all factors were reported in a single study.

We found consistent negative linear relationships between log-transformed invertebrate density, biomass, and species richness with lnRR of *k* values (Fig. 4), whereas loess regression analyses of lnRR of *k* values against raw invertebrate data indicated positive to negative relationships between *k* and invertebrate density and richness, and a negative to positive relationship between *k* and invertebrate biomass (Fig. S2).

3.3 Variation in invertebrate effects with stage of decomposition

Effects of invertebrate density ($p<0.001$), biomass ($p<0.05$), and species richness ($p<0.001$) on litter mass loss varied with stage of litter decomposition, where litter decomposition was positively related invertebrate density and species richness in the early stages of decomposition (<20% loss), while invertebrate biomass was positively related to litter mass loss at the earliest stage (<10% loss) (Fig. 5). Data limitation prevented analysis of variation in effects of litter quality, stream characteristics, and experimental condition on invertebrate-mediated litter mass loss with decomposition stage.

4. Discussion

To our knowledge, this quantitative synthesis represents the most comprehensive global-scale assessment of invertebrate effects on instream litter decomposition, complementing previous site-specific studies (Graça et al. 2001, Graça et al. 2015). Our results clearly show a positive effect of invertebrates on instream litter decomposition across and within climate zones, and this effect is driven by initial litter quality and stream water characteristics; impacts of invertebrates on litter decomposition were apparent at the early stages of decomposition (<20%

mass loss) and were consistent across experimental litter bag mesh sizes and initial litter mass. Thus, our results indicate global temporal heterogeneity of invertebrate-mediated decomposition of stream litter and confirm the analyses of contrasting metrics of invertebrate biodiversity and abundance and experimental litter bag mesh sizes as a proxy measures of invertebrate effects on instream litter decomposition are appropriate.

4.1 Consistent positive effects of invertebrates on litter decomposition

Supporting our first hypothesis, we found that invertebrates consistently elicited positive effects on instream litter decomposition at the global and regional scales, although some levels of heterogeneity were found among climate zones and invertebrate metrics (density, biomass, species richness). In terrestrial systems, soil fauna represent 37% of litter decomposition (García-Palacios et al. 2013); in contrast, our results showed that invertebrates account for an average of 70% of global-scale stream litter decomposition. Rates of litter decomposition and effects of soil fauna on litter decomposition in terrestrial ecosystems are driven by environmental factors, such as temperature, moisture, and nutrient availability (Aerts 1997, García-Palacios et al. 2013); in contrast, the more stable environmental conditions of streams tend to be characterized by buffered temperature ranges, and consistent water availability and nutrient supply from upstream (Graça et al. 2015).

Climate zone affected invertebrate biomass and species richness-mediated instream litter decomposition (litter mass loss; Fig. S1b, c), and the similarity in overall effects of invertebrates on instream litter decomposition among tropical, temperate, and cold climate regions (Fig. 2a) supports recent findings that showed no climate differences in litter decomposition rates (Zhang et al. 2019). These climate variations in invertebrate biomass and richness effects on litter mass loss may be explained by contrasting environmental conditions, such as stream water temperature, pH, and dissolved oxygen across climate zones that drive invertebrate abundance and community structure (Pettit et al. 2012, Ferreira et al. 2015, Iñiguez-Armijos et al. 2016). Surprisingly, we found no effects of litterbag mesh size on invertebrate-mediated litter decomposition, with the exception of invertebrate biomass-mediated litter mass loss that was greater with larger mesh size (Fig. S1b), indicating that ~5 mm mesh litterbags, which allow access by most invertebrates, are sufficient to capture the majority of variation in invertebrate effects on instream litter decomposition. Our results also indicated there were no mycorrhizal variations in their positive effects on overall invertebrate-mediated litter decomposition, but there were differences in the degree of positive impacts of invertebrate density and richness-mediated losses in litter mass (Fig. S1), possibly as a result of differences in litter quality that were associated with mycorrhiza (Peng et al. 2020), given litter quality was found to be important driver of invertebrate-mediated instream litter decomposition.

When using pairwise observations, we found negative linear relationships between lnRR of *k* values and log-transformed invertebrate density, biomass, and species richness (Fig. 4), indicating that analyses based on litterbag mesh size differences in litter decomposition rates as a proxy for invertebrate effects may lead to underestimation of real effects. However, LOESS regression analyses of raw invertebrate data indicated that lnRR of *k* values increased with invertebrate density or species richness before decreasing (Fig. S2), possibly reflecting increases in competition for resources, due to rises in invertebrate abundance and species richness (Maraun et al. 2003) that may have led to lower levels of invertebrate-mediated litter decomposition. Despite these contrasting regression analyses, and given the small values for estimated slopes of invertebrate effects on litter decomposition (Fig. 3), we suggest that lnRR of *k* adequately describes invertebrate effects on litter decomposition.

4.2 Litter quality and stream environmental drivers of invertebrate effects

Inconsistent with our second hypothesis, that initial litter quality is the dominant driver of invertebrate-mediated instream litter decomposition, our results shows that initial litter quality plus stream water physicochemical characteristics are equally important global drivers of invertebrate-mediated instream litter decomposition, supporting previous findings from terrestrial ecosystems (García-Palacios et al. 2013). We found negative impacts of initial litter C concentrations and C:N ratios and positive impacts of N concentration on lnRR of *k* values (Table 1), reflecting their effects on litter decomposition rates in streams (Zhang et al. 2019). Litter with low levels of C and high levels of N concentrations, leading to low C:N ratios, tend to be more palatable and attractive to invertebrate consumers and microbe colonizers (Swan and Palmer 2006, Goncalves Jr et al. 2012, Ab Hamid and Rawi 2017), and higher levels of substrate colonization by microbes has been shown to render litter more accessible to invertebrates (Jinggut and Yule 2015). Previous studies have shown negative effects of litter lignin content on instream litter decomposition rates (König et al. 2014, Zhang et al. 2019); however, we found that lignin content was positively related to invertebrate biomass and density-mediated litter *k* and mass losses, respectively. We suggest two plausible explanations for this inconsistency: variation in study duration may obscure the lignin-invertebrate relationship with litter decomposition (Smith and Bradford 2003) and the relationship between litter lignin content and invertebrate effects on instream litter decomposition may depend on taxonomic and functional group preferences for level of litter lignin content (Graça et al. 2001, Graça 2001, Patoine et al. 2017). Overall, our results show that initial litter quality drives invertebrate-mediated stream litter decomposition rates at the local scale, as reported elsewhere (Yue et al. 2018, Zhang et al. 2019), and also at the global scale.

While local and global scale studies have demonstrated that initial litter quality accounts for much of the variation in litter decomposition rates in streams (Leroy and Marks 2006, Zhang et al. 2019), our findings showed that stream water physicochemical properties may represent a more important driver at the global scale (Fig. 2b). Similar to findings from terrestrial ecosystems (García-Palacios et al. 2013), we found that temperature was a key driver of invertebrate-mediated litter decomposition (negative relationship; Table 1). Activity of litter decomposers and, therefore, litter decomposition rates, tend to be positively related to temperature (Ferreira and Canhoto 2015, Ferreira et al. 2015); however, decreases in levels of dissolved O_2 in water with increasing water temperature may lead to anaerobic conditions that are known to inhibit decomposer activities (Pettit et al. 2012, Iñiguez-Armijos et al. 2016). Supporting these previous studies, our results showed a positive relationship between dissolved O_2 and invertebrate effects on litter decomposition (Table S1) and levels of stream water NO_3^- and PO_4^{3-} content, pH, velocity, were important drivers of invertebrate-mediated litter decomposition, likely because they are closely related to invertebrate metabolism and activity during the litter decomposition process (Leroy and Marks 2006, Graça et al. 2015).

4.3 Greater influence of invertebrates during early stages of decomposition

In contrast to our third hypothesis, we found evidence of invertebrate-mediated litter decomposition in the early stages of litter mass loss (<20%; Fig. 5). Previous studies of terrestrial ecosystems show the net contribution of soil invertebrates to litter decomposition increases as conditions for microbial decomposition become increasingly adverse, particularly when concentrations of N and other nutrients in the litter substrate and in the surrounding environment reduce (Peguero et al. 2019). However, our results indicate that the contribution of invertebrates to litter decomposition is greatest during the early stages, when nutrient availability is most abundant; this finding is further supported by our results that showed invertebrate-mediated litter decomposition is positively related to stream water nutrient concentrations (Table 1).

4.4 Research gaps and future studies

We identify three key research gaps in understanding of global scale contributions of invertebrates to decomposition of litter in stream ecosystems. Our study shows that initial litter quality is a major driver of invertebrate-mediated stream litter decomposition. However, of the 141 articles from which we extracted data, only 28 reported on initial litter quality in contrast to the majority that contained data on stream water physicochemical properties; this asymmetry in available data limits analysis of the relative importance of litter quality in invertebrate-mediated litter decomposition across the entire litter decomposition process (0−100% mass loss). The majority of studies included in this synthesis either compared litter decomposition rates between litterbags with contrasting mesh size or only used litterbags with larger mesh sizes to measure litter decomposition rates and invertebrate communities; this lack of pairwise data from the two approaches limits the precise assessment of effects of invertebrates on stream litter decomposition. Observations included in our synthesis tended to derive from Europe and America (Fig. 1), with other regions of the world poorly represented, possibly leading to a misrepresentation of global-scale effects and drivers of invertebrate-mediated stream litter decomposition. Thus, we suggest that future experiments should at least account for initial litter quality, stream physicochemical properties, and microbes as potential drivers of invertebrate-mediated litter decomposition, and the use of advanced approaches, such as ^{13}C labeling, may establish a correction factor to assess the “true” contribution of invertebrates to litter decomposition, by tracking fluxes in C. To ensure robust global-scale analyses of invertebrate effects on litter decomposition, we propose multisite, multispecies experimental studies distributes across all global regions that include analysis of litter quality dynamics throughout within- and between year study periods to account for temporal changes in litter chemistry (García-Palacios et al. 2016b, Yue et al. 2018) during all stages of litter decomposition.

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Author contributions

K.Y. and F.W. conceived the study. K.Y. and Y.P. collected raw data. K.Y. performed data analyses and wrote the first draft of the manuscript. All authors contributed to revisions of the manuscript.

Competing interests

The authors declared no competing interests.

Data availability

All raw data used in the study will be deposited in figshare (https://figshare.com) should the manuscript be accepted.

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Table 1 Linear mixed-effects modeling analysis of the relationship between experimental, initial litter quality, and stream physicochemical factors on the effect size of overall invertebrate-mediated stream litter decomposition (lnRR of *k*) and effects of invertebrate density, biomass, and richness on litter decomposition rate (*k*). Data were $\log_{10}$-transformed prior to analysis; bold *p*-values indicate effects at $p<0.05$.

Predictor	lnRR of *k*			Invertebrate effects on *k*								
				Density			Biomass			Richness		
	Slope	*p*	n	Slope	*p*	n	Slope	*p*	n	Slope	*p*	n
Coarse mesh size (mm)	0.0706	0.804	293	-0.0135	0.9397	323	0.6336	0.279	131	1.1476	0.191	100
Decomposition time (day)	0.2749	0.314	263	0.1043	0.380	304	0.1008	0.580	100	-0.1138	0.788	101
Initial mass (g)	-0.1891	0.155	291	0.0598	0.741	336	0.3646	0.196	135	0.7314	0.465	109
Initial C (%)	-8.8428	**0.036**	25	0.5639	0.142	40	0.793	0.128	29			
Initial N (%)	0.8462	**0.019**	53	-0.3087	0.516	47	1.0030	**0.002**	32			
Initial C:N ratio	-1.1286	**0.011**	30	0.4849	0.065	43	-0.4067	0.150	29			
Initial lignin (%)	-0.1981	0.569	33	-1.5149	0.402	12	1.8092	**0.029**	14			
Initial lignin: N ratio	-0.3040	0.204	33	-0.9660	0.348	12	1.6018	**0.009**	12			
Stream water temperature (°C)	-0.7352	**0.003**	215	-0.0272	0.884	189	-0.2165	0.208	94	-0.4845	0.294	57
Discharge (L/s)	-0.0135	0.898	48	-0.0902	0.093	107	-0.1120	0.169	62	-0.7742	**<0.001**	25
Velocity (m/s)	0.0538	0.543	83	-0.5578	**<0.001**	66	0.1189	0.355	40	-0.5371	**0.043**	46
pH	0.9186	**0.036**	234	-0.5656	**0.010**	172	-0.1124	0.432	84	-0.1786	0.763	73
Conductivity (μ/s cm)	-0.0241	0.787	236	-0.0027	0.978	163	0.1054	0.244	77	0.2279	0.468	65
Alkalinity (mg $CaCO_3$/L)	0.1950	0.182	42	-0.0959	0.506	63	-0.0359	0.404	41	-1.2082	0.651	16
Dissolved O_2 (mg/L)	0.8352	0.254	111	-0.1045	0.858	105	0.3369	0.523	30	-2.4305	0.300	45
NO_3^- (μg/L)	0.2075	**<0.001**	154	-0.0068	0.909	136	-0.0684	0.209	85	0.2264	0.346	33
NH_4^+ (μg/L)	0.2276	0.173	84	0.0831	0.276	119	-0.0471	0.696	59	0.5068	0.084	35
PO_4^{3-} (μg/L)	0.0721	0.416	99	-0.0781	0.319	123	0.0961	0.632	50	0.0474	0.891	25

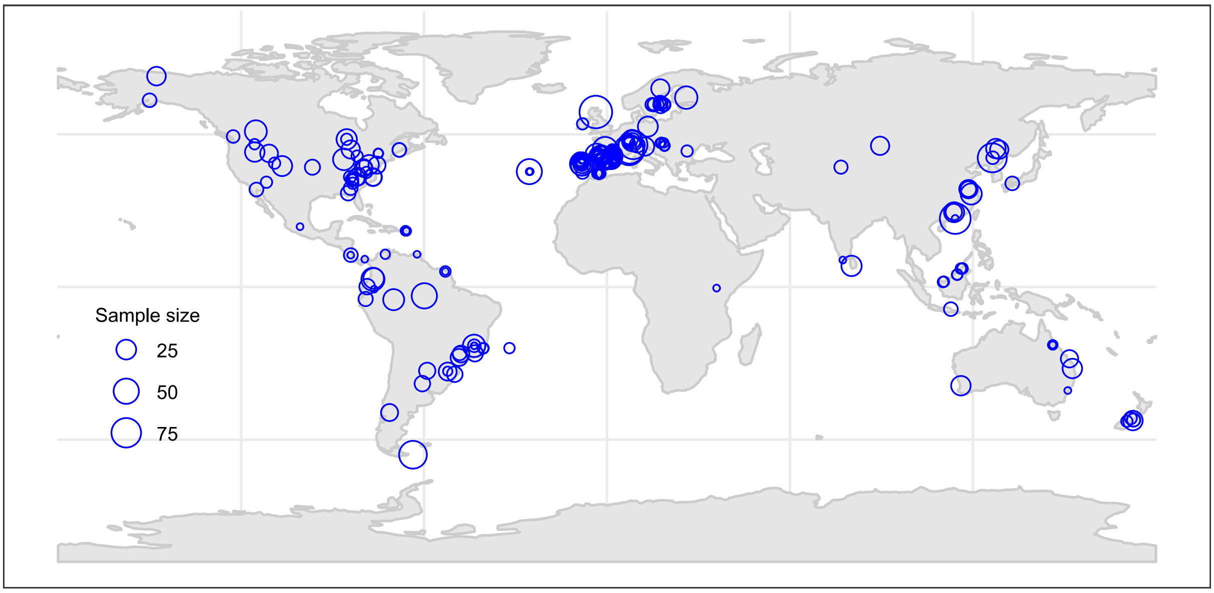

Figure 1 Global distribution of observations derived from 141 publications. The number of observations (sample size) at each site is represented by symbol size.

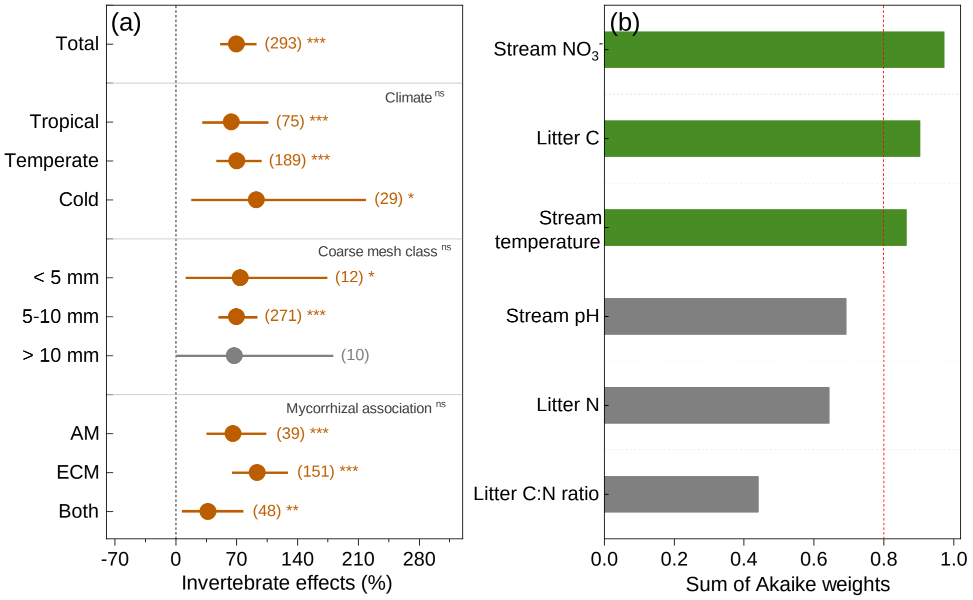

Figure 2 Overall effects of invertebrates on litter decomposition rate (*k*) in streams (a) and model-averaged importance of drivers (p<0.05) of invertebrate effects (b). Values in (a) are mean ±95% CI of the percent difference between fine and coarse meshed litterbags; number of pairwise observations are shown in parentheses. In (b), factor importance is estimated from the sum of Akaike weights, based on model selection analysis using corrected Akaike's information criteria; cutoff is set at 0.8 to differentiate essential from non-essential factors. $^{*}p$<0.05, $^{**}p$<0.01, $^{***}p$<0.001.

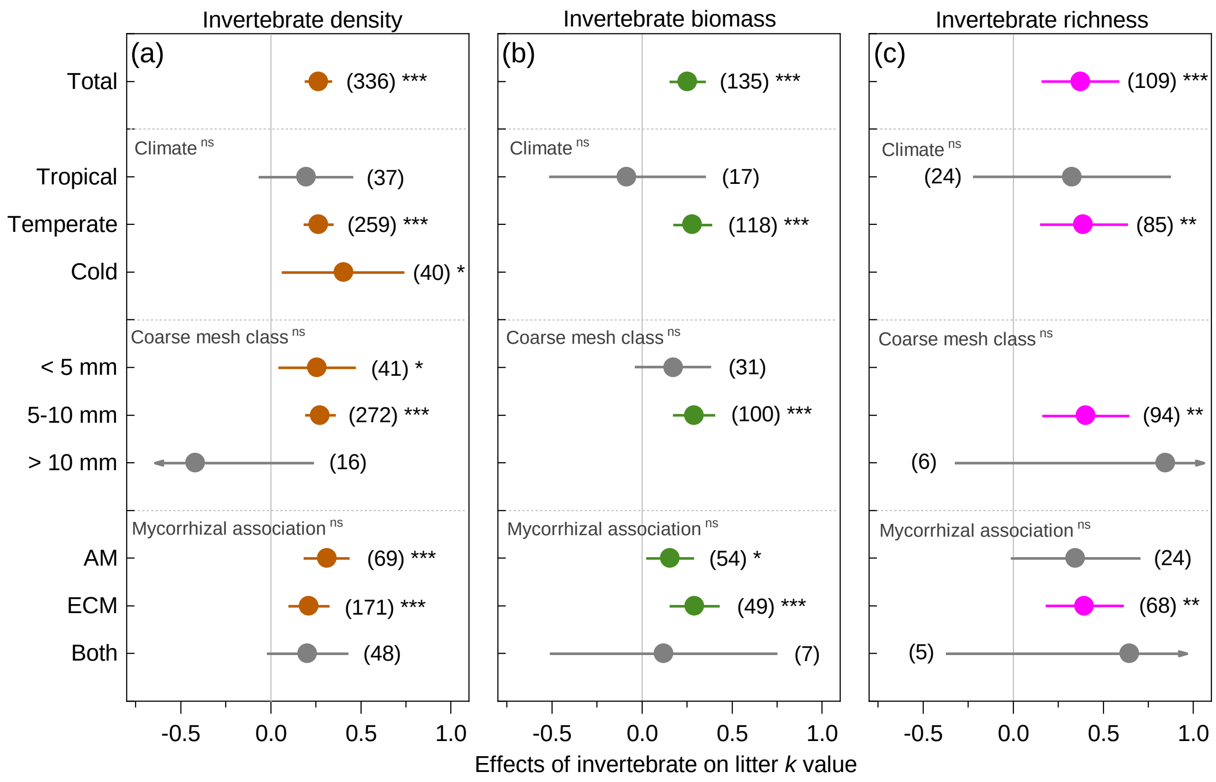

Figure 3 Effects of invertebrate density (a), biomass (b), and species richness (c) on instream litter decomposition. Values are estimated slopes and 95% CI of fixed effects of invertebrates on litter decomposition rates (*k*) from linear mixed-effects models. Data were log$_{10}$-transformed prior to analysis; number of observations is shown in parentheses. $^{*}p<0.05$, $^{**}p<0.01$, $^{***}p<0.001$.

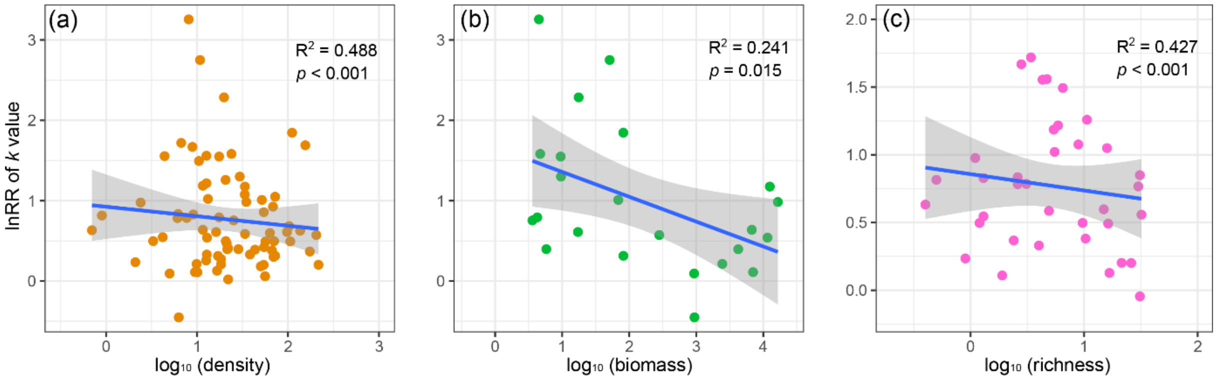

Figure 4 Relationship between invertebrate effect sizes (lnRR) on litter decomposition rates (*k*) and $\log_{10}$-transformed invertebrate density (a), biomass (b), and species richness (c) using pairwise data points. Linear fitted line and 95% CIs are shown.

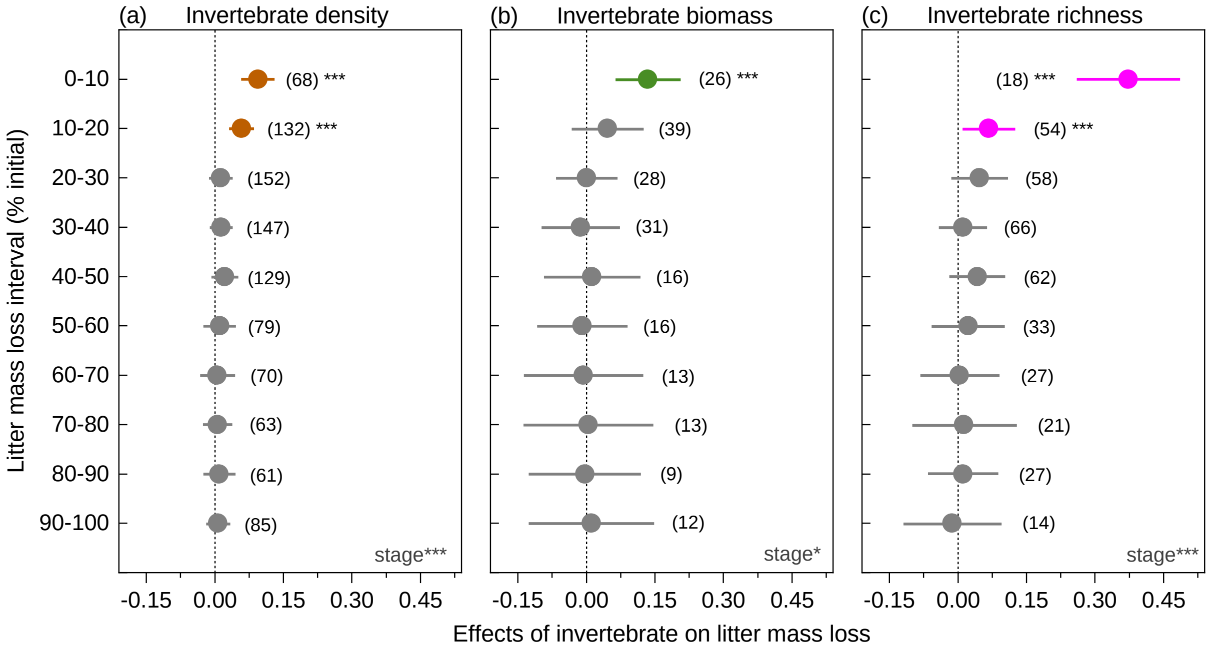

Figure 5 Effects of invertebrate density (a), biomass (b), and species richness (c) on instream litter decomposition through stages of decomposition (0−100% mass loss). Values are estimated slopes and 95% CI of fixed effects of invertebrates on litter mass loss from linear mixed-effects models. Data were log$_{10}$-transformed prior to analysis. Number of observations is shown in parentheses. $^{*}p<0.05$, $^{**}p<0.01$, $^{***}p<0.001$.