Litter quality and stream physicochemical properties drive global invertebrate effects on instream litter decomposition

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ABSTRACT

Plant litter is the major source of energy and nutrients in stream ecosystems and its decomposition is vital for ecosystem nutrient cycling and functioning. Invertebrates are key contributors to instream litter decomposition, yet quantification of their effects and drivers at the global scale remains lacking. Here, we systematically synthesized data comprising 2707 observations from 141 studies of stream litter decomposition to assess the contribution and drivers of invertebrates to the decomposition process across the globe. We found that (1) the presence of invertebrates enhanced instream litter decomposition globally by an average of 74%; (2) initial litter quality and stream water physicochemical properties were equal drivers of invertebrate effects on litter decomposition, while invertebrate effects on litter decomposition were not affected by climatic region, mesh size of coarse-mesh bags or mycorrhizal association of plants providing leaf litter; and (3) the contribution of invertebrates to litter decomposition was greatest during the early stages of litter mass loss (0−20%). Our results, besides quantitatively synthesizing the global pattern of invertebrate contribution to instream litter decomposition, highlight the most significant effects of invertebrates on litter decomposition at early rather than middle or late decomposition stages, providing support for the inclusion of invertebrates in global dynamic models of litter decomposition in streams to

explore mechanisms and impacts of terrestrial, aquatic, and atmospheric carbon fluxes.

Key words: decomposition rate, mass loss, climatic region, litterbag, decomposition stage, meta-analysis.

CONTENTS

I. INTRODUCTION

Allochthonous inputs of plant litter to stream ecosystems represent the major source of energy and nutrients for stream heterotrophic organisms, which play a key role in the transport of carbon (C) and nutrients to higher trophic levels across landscapes (Swan, Boyero & Canhoto, 2021; Wallace *et al*., 1999). 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 important for the maintenance of ecosystem functioning in streams. Climate and nutrient availability were traditionally thought to exert a greater influence on litter decomposition in terrestrial and freshwater systems than does litter quality, while it has been suggested that decomposers (bacteria, fungi, and invertebrates) play a minor role (Aerts, 1997; Cornwell *et al.*, 2008; Frainer, McKie & Malmqvist, 2014; Griffiths *et al.*, 2021); however, recent studies from terrestrial ecosystems indicated that the contribution of decomposer communities to litter decomposition may have been underestimated (Bradford *et al.*, 2016, 2017). For example, a meta-analysis showed an average global-scale increase in litter decomposition of 37% with presence of soil invertebrates (García-Palacios *et al.*, 2013), indicating the important role of invertebrates in the decomposition process when compared with climate and litter quality. While global models of litter decomposition have been biased towards terrestrial ecosystems (Cole *et al.*, 2007), recent models have included some drivers of instream litter decomposition (Boyero *et al.*, 2021; Tiegs *et al.*, 2019; Zhang *et al.*, 2019), but a comprehensive assessment of the contribution and drivers of aquatic invertebrates to instream litter decomposition at the global scale is still lacking.

Impacts of aquatic invertebrates on instream litter decomposition may be direct through feeding, and indirect through trophic interactions (Graça, Ferreira & Coimbra, 2001). For example, stream shredders contribute directly to losses in litter mass through feeding and the associated acceleration of litter fragmentation (Raposeiro *et al.*, 2018; Graça, 2001). Grazers–scrapers can contribute to litter decomposition by scraping the litter surface while feeding on the biofilm, thus promoting litter mass loss directly, and indirectly by facilitating microbial colonization (Wang *et al.*, 2020). Predators can also affect litter decomposition indirectly by controlling the abundance and activity of shredders (Lecerf & Richardson, 2011). Invertebrates can also affect litter decomposition indirectly by modifying the structure and activity of microbial decomposer communities (Bärlocher & Sridhar, 2014; Canhoto & Graça, 2008). One example is that invertebrates prefer to feed on leaf litter colonized by fungi and bacteria, which can produce cellulases, xilanases, pectinases, and other enzymes able to digest plant cell walls and to liberate digestible compounds that can be assimilated by invertebrates (Graça, Ferreira & Coimbra, 2001; Rodrigues & Graça, 1997).

Invertebrate effects on litter decomposition can be controlled by a variety of factors, including litter quality, stream physicochemical properties, and climate. Litter quality was recently found to be the dominant driver of litter decomposition in stream ecosystems globally (Zhang *et al.*, 2019), where it affects colonization by, and activity of, invertebrate and microbe species and their interactions (De Schrijver *et al.*, 2012; Graça, Ferreira & Coimbra, 2001; Sales *et al.*, 2015). In fact, levels of colonization and degradation of litter by aquatic hyphomycetes and invertebrates are greater in litter with high nitrogen (N) concentration and low lignin concentration or low C:N ratio than in more recalcitrant litter (Ostrofsky, 1997; Ramos, Graça & Ferreira, 2021). Plants associated with different mycorrhizae generally vary in leaf litter quality, with a general pattern of higher quality for arbuscular mycorrhizal (AM) than ectomycorrhizal (ECM) litter (Shi *et al.*, 2020). Therefore, the type of mycorrhizal association may be an important factor controlling litter quality, and consequently controlling the litter decomposition process. Given that the effects of invertebrates are generally larger for higher quality litter (e.g. low C:N and lignin:N ratios) in stream ecosystems (Hieber &

Gessner, 2002; Ramos, Graça & Ferreira, 2021), invertebrate effects on instream litter decomposition could be higher for litter from AM than ECM trees, but this has not yet been tested at the global scale.

Stream physicochemical properties, such as water temperature, pH, dissolved oxygen and nutrient concentration, are known to mediate invertebrate and microbial community composition and biological activity, strongly affecting litter decomposition (Amani, Graça & Ferreira, 2019; Ferreira *et al.*, 2015*a*; Ferreira & Guérold, 2017; Gomes *et al.*, 2018), but their relative importance in controlling invertebrate effects on litter decomposition at the global scale is unknown. Climate is another important factor, as it determines environmental conditions (e.g. higher water temperature in the tropics), leaf litter quality (e.g. lower leaf litter quality in the tropics) (Boyero *et al.*, 2017), and detritivore distribution (e.g. lower litter-associated shredder density and diversity in the tropics) (Boyero *et al.*, 2011*a*), which can significantly alter invertebrate effects on litter decomposition (Boyero *et al.*, 2011*b*; Ferreira, Encalada & Graça, 2012; Gonçalves, Graça & Callisto, 2007). For example, temperature may be positively correlated with the effects of invertebrates on litter decomposition, as higher temperatures would favour invertebrate activity (Ferreira & Canhoto, 2015; Follstad Shah *et al.*, 2017). Although litter quality, environmental conditions, and climate have been shown to drive global soil litter decomposition by invertebrates (García-Palacios *et al.*, 2013), their impacts and relative importance on invertebrate effects on litter decomposition in global stream ecosystems are unclear.

To assess invertebrate effects on instream litter decomposition, researchers generally contrast litter enclosed into fine-mesh bags that exclude invertebrates with litter enclosed into coarse-mesh bags that allow invertebrates to enter (Bärlocher, Gessner & Graça, 2020). The mesh size used in coarse-mesh bags controls the size of the invertebrates allowed to access the litter, and thus may be a vital factor controlling the effects of invertebrates on litter decomposition (Handa *et al.*, 2014). Therefore, it is important to assess whether the difference in litter decomposition between coarse- and fine-mesh bags can account for invertebrate effects quantified by invertebrate community data such as density, biomass, and species richness (Bärlocher *et al.*, 2020). In addition, the effects of invertebrates on litter decomposition can vary over the decomposition process in response to changes in litter quality, which decreases with increasing concentrations of recalcitrant components such as lignin (Berg & McClaugherty, 2020; Yue *et al.*, 2018). This was supported by studies that have found higher invertebrate contribution to the decomposition of high- than low-quality litter species (Hieber & Gessner, 2002). This has been tested in terrestrial ecosystems where nematodes regulate litter decomposition in the early decomposition stages (García-Palacios *et al.*, 2016). In contrast to invertebrate communities in soils where meiofauna such as collembolans, nematodes, and acarina that feed on fungi account for a large proportion of the total soil fauna community (Swift, Heal & Anderson, 1979), the majority of invertebrates in streams are macroinvertebrates that feed on leaf litter and the associated fungi, indicating potential different temporal patterns of invertebrate effects on litter decomposition in streams compared with terrestrial ecosystems.

Here, by systematically synthesizing 2707 observations from 141 publications, we searched for global patterns, key drivers, and temporal dynamics of invertebrate-mediated instream litter decomposition to test the following hypotheses: (1) invertebrates would show consistent positive effects on instream litter decomposition globally and within different climatic regions; (2) effects of invertebrates on instream litter decomposition are jointly driven by litter quality and environmental factors that are closely related to invertebrate community and activities; and (3) effects of invertebrates on instream litter decomposition are higher in the early and intermediate stages of decomposition where nutrients are most rich and accessible and the colonization of microbes is high.

II. METHODS

(1) Data collection and compilation

Data collection and compilation were carried out following the PRISMA statement, which is an evidence-based minimum set of items for reporting in systematic reviews and meta-analysis (Moher *et al.*, 2009). Specifically, we searched for peer-reviewed articles, academic theses, and book chapters, published in English or Chinese before March 2021, in *Web of Science*, *Google Scholar*, and *China National Knowledge Infrastructure* using the following search string [("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")] and their equivalents in Chinese. Studies were included in our database if they complied with the following criteria: (1) decomposition of leaf litter, excluding wood, bark, or artificial substrates, was measured in natural streams or rivers using litterbags; (2) water bodies where decomposition studies were carried out were not affected by pollution or artificial nutrient enrichment experiments; (3) litterbags contained litter of only a single plant species, rather than mixed species; and (4) litter decomposition rates (k) and corresponding standard deviations (SD) or standard errors (SE) from contrasting fine-mesh (≤0.5 mm, which excludes invertebrates) and coarse-mesh (ranged from 1 to 25 mm in this study, which allows all invertebrate access) bags were reported or could be calculated; or (5) litter k or mass loss from coarse-mesh litterbags and corresponding mean invertebrate values (density: individuals g^{-1} of remaining litter mass; biomass: mg of invertebrates g^{-1} of remaining litter mass; or species richness: number of species) over a given decomposition period were reported or could be calculated. Most articles did not define invertebrate functional groups, hence we only focused on total invertebrate density, biomass, and species richness. Based on these criteria, we derived globally distributed data comprising 2707 observations from 141 (135 in English and 6 in Chinese) independent publications (Fig. 1; see references identified with asterisks in the reference list).

We divided the resulting data into three separate databases: database 1 (281 observations from 45 publications) included pairwise *k* values from coarse- and fine-mesh litterbags (with and without invertebrate activity, respectively), which was used to calculate the overall invertebrate effects; database 2 (761 observations from 89 publications) contained *k* values and corresponding invertebrate density, biomass, and/or species richness data from coarse-mesh litterbags, which was used to assess the overall relationships between litter decomposition and invertebrate community; and database 3 (1665 observations from 69 publications) represented litter mass loss from coarse-mesh litterbags and corresponding invertebrate density, biomass, and/or species richness data, which was used to evaluate the temporal dynamics of invertebrate effects at different stages of litter decomposition. The difference between database 2 and database 3 is the variable used for litter decomposition, where database 2 included *k* values while database 3 included litter mass loss. Litter *k* was either extracted directly from primary studies or estimated based on mass-remaining data using the single exponential model (Olson, 1963):

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

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

To quantify drivers of invertebrate effects on litter decomposition, we extracted data on stream physicochemical properties [water temperature, discharge rate, current velocity, pH, conductivity, alkalinity, and levels of dissolved oxygen (O_2), nitrate (NO_3^-), ammonium (NH_4^+) and phosphate (PO_4^{3-})], initial litter quality [levels of C, N, and phosphorus (P); C:N ratio, lignin concentration and lignin:N ratio], and experimental conditions (litterbag mesh size, initial litter mass, and experiment duration). Table S1 details the range of these variables obtained from the 141 publications, where available. Study sites were organized into three climatic regions (Ferreira *et al.*, 2015*a*), according to the absolute latitude of the study area (tropical: 0−23.5°; temperate: 23.5−55°; and boreal: >55°) and mesh size of coarse-mesh litterbags was categorized as 1−5 (including 1 and 5) mm, 5−10 (including 10) mm, or 10−25 (including 25) mm. Mycorrhizal association of the plant contributing litter was classed as AM, ECM, or AM+ECM. 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) Statistical analysis

To quantify overall (presence/absence) effects of invertebrates on litter decomposition (database 1), we calculated the individual natural logarithm response ratio (lnRR):

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

where k_{coarse} and k_{fine} were k values recorded in coarse- and fine-mesh litterbags, respectively. The variance (v) associated with each lnRR was estimated as:

$$v = \frac{s_{\mathrm{coarse}}^2}{n_{\mathrm{coarse}} k_{\mathrm{coarse}}^2} + \frac{s_{\mathrm{fine}}^2}{n_{\mathrm{fine}} k_{\mathrm{fine}}^2} \qquad (3)$$

where n_{coarse} and n_{fine} are the sample sizes, and s_{coarse} and s_{fine} are the SDs of k in coarse- and fine-mesh litterbags, respectively. The weight of each lnRR estimate in the analyses was calculated as the inverse of its variance (1/v). We first ran an intercept-only linear mixed model using the *lme4* package in R (Bates *et al.*, 2015) to estimate the overall weighted effects (lnRR_{++}) 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 account explicitly for potential dependence among observations extracted from a single study. Then, we used meta-regression to assess effects of stream physicochemical properties, initial litter quality, and experimental conditions on lnRR by fitting them as fixed effect factors; the effects of each factor were assessed separately, aiming to include as many observations in the model as possible. To aid interpretation, lnRR_{++} 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 indicates significant effects of invertebrates on litter decomposition. To evaluate the relative importance of stream physicochemical properties, litter quality, and experimental conditions that affected lnRR, we adopted mixed-effects meta-regression model selections using the *glmulti* package in R (Calcagno & 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 following previous studies (Jiang *et al.*, 2019; Terrer *et al.*, 2016).

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 litter *k* or litter mass loss as a response variable, invertebrate density, biomass, or richness as a fixed effect, and the identity of primary studies as a random effect. Although an issue with endogeneity is not likely to occur in each model because we assessed each variable individually (Angrist & Pischke, 2009), we are aware that the relationship between the response variable and predictor may not be a causal relationship or ‘effect’. Nevertheless, the relationships between litter decomposition and invertebrate variables can explain, at least to a certain degree, how invertebrates may affect litter decomposition. Therefore, for easy description and understanding, we use the term ‘effect’ in this study. We assessed the impacts of each stream physicochemical, leaf litter, and experimental condition factor on invertebrate effects on *k* or mass loss by fitting their interaction with the invertebrate fixed-effect factors. Linear regression was used to detect the relationships between lnRR of *k* and invertebrate density, biomass, and species richness. Variation in invertebrate effects on litter mass loss among stages of decomposition was tested with a 10% mass loss interval using database 3, i.e. data were allocated to 10% mass loss intervals (0–10, 10–20, 20–30, …, 80–90, and 90–100%) and differences in invertebrate effects among mass loss intervals were then assessed. Estimates and corresponding 95% CIs are reported, with lack of overlap of 95% CIs with zero indicating significant effects of invertebrates on litter decomposition.

(3) Publication bias

To address potential publication bias that can arise when studies published and included in our database are not a random subset of the total number of performed studies, we used Egger's regression test along with a funnel plot (Egger *et al.*, 1997) and trim-and-fill test (Duval & Tweedie, 2000). Both Egger's regression and trim-and-fill tests were applied using the meta-analytic residuals, which consist of sampling errors as well as the effect-size-level effects that are equivalent to normal residuals (Nakagawa & Poulin, 2012). The R_0 estimator was used and implemented with the *trimfill* function in the R package *metafor* to perform the trim-and-fill test (Viechtbauer, 2010). Egger's regression test on the meta-analytic residuals showed potential funnel asymmetry ($p = 0.047$; Table S2), but the trim-and-fill test suggested no evidence for publication bias (Fig. S1). Taken together, it is likely that publication bias in the data used for our study is very limited and the studies included in the database are a representative sample of available studies.

III. RESULTS

(1) Overall effects of invertebrates

At the global scale, the presence of invertebrates increased instream litter *k* by an average of

74% (database 1; Fig. 2A). Invertebrate effects on instream litter *k* were not affected by climatic region (34–103% increase across regions), litterbag mesh size (73–89% increase across sizes), or type of mycorrhizal association (50–98% increase across types) (Fig. 2A). Initial litter lignin concentration and C:N ratio, and stream water temperature negatively influenced the effect of invertebrates on litter *k*, while initial litter N concentration and stream water pH, dissolved O_2, and NO_3^- concentration had a positive influence (Table 1). Initial litter C:N ratio, stream water pH and dissolved O_2 were the most important drivers of invertebrate effects on litter *k* (Fig. 2B).

(2) Effects of invertebrate density, biomass, and species richness

Invertebrate density, biomass, and species richness all had positive effects on instream litter *k* (database 2; Fig. 3). These effects were not affected by climate, coarse litterbag mesh size, or mycorrhizal association, even though non-significant slopes were identified for tropical regions, the largest mesh size (10–25 mm), and litter species associated with both types of mycorrhizae (Fig. 3). Litter *k* mediated by invertebrate density was negatively affected by current velocity and pH, that mediated by invertebrate biomass was positively affected by initial litter N and lignin concentrations and lignin:N ratios, whereas litter *k* mediated by invertebrate species richness was negatively affected by discharge rate and current velocity (Table 1).

We found positive effects of invertebrate density, biomass, and species richness on litter mass loss (database 3), regardless of climatic region, litterbag mesh size, and mycorrhizal association, although there were differences in the magnitude of invertebrate effects between levels of these factors (Fig. S2). Litter mass loss mediated by invertebrate density was positively affected by initial litter lignin concentration, and water dissolved O_2 and NO_3^- concentration, and negatively affected by current velocity and pH; litter mass loss mediated by invertebrate biomass was positively related to litterbag mesh size; and litter mass loss mediated by invertebrate species richness was negatively related to stream water temperature and PO_4^{3-} concentration, and positively related to stream discharge rate (Table S3). 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 *k* or mass loss using model selection analyses, because not all factors were reported in a single study. In addition, we found consistent negative linear relationships between log-transformed invertebrate density, biomass, and species richness and lnRR of *k* (Fig. 4).

(3) Variation in invertebrate effects with stage of litter 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, with litter decomposition being positively related to invertebrate parameters only in the <20% mass loss interval for invertebrate density and species richness and <10% mass loss interval for invertebrate biomass (Fig. 5). Limitations in the available data prevented analysis of effects and relative importance of litter quality, stream physicochemical properties, and experimental conditions on invertebrate-mediated litter mass loss with decomposition stages.

IV. DISCUSSION

(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 heterogeneity was found among climatic regions and invertebrate metrics (density, biomass, and species richness). In terrestrial systems, soil fauna increased global litter decomposition by 37% (García-Palacios *et al.*, 2013), while our results showed that invertebrates accounted for an average increase of 74% of global-scale instream litter decomposition. Differences in the invertebrate communities between soils and streams may be the main explanation for this difference (Graça, 2001; Swift *et al.*, 1979), because a large proportion of soil invertebrates are micro- and mesofauna (e.g. millions of collembolans and Acarina) that feed on fungi rather than on leaf litter (except for Isopoda and some Gastropoda), whereas in small forest streams macroinvertebrate shredders that feed directly on leaf litter represent an important proportion of invertebrate communities (Vannote *et al.*, 1980, Wallace *et al.*, 1997), contributing to a larger litter mass loss. Also, 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). By contrast, the environmental conditions of streams tend to be characterized by buffered temperature ranges, and generally consistent water availability and nutrient supply from upstream (Graça *et al.*, 2015), making these unlikely limiting factors for invertebrate activities across an annual period in streams compared with soil systems, and potentially leading to a higher contribution of invertebrates to litter decomposition in streams than in terrestrial ecosystems.

Climate only influenced invertebrate biomass and species richness effects on instream litter decomposition (litter mass loss; Fig. S2B, C). Invertebrate effects on litter decomposition showed a non-significant trend to increase from tropical to boreal regions (Fig. 2A), although previous evidence showed that this pattern can be significant (Boyero *et al.*, 2011*b*). Climate variations in invertebrate biomass and species richness effects on litter mass loss (Fig. S2B, C) may be explained by contrasting environmental conditions, such as stream water temperature, pH, nutrients and dissolved O_2 across climatic regions that drive invertebrate abundance and community structure (Ferreira *et al.*, 2015*a*; Iñiguez-Armijos *et al.*, 2016; Pettit *et al.*, 2012).

Surprisingly, we found no effects of litterbag coarse-mesh size on invertebrate-mediated litter decomposition, with the exception of invertebrate biomass-mediated litter mass loss that was greater with larger mesh sizes (Fig. S2B). Given the unique environmental conditions in streams, comparing litter *k* between coarse- and fine-mesh litterbags to account for invertebrate effects may overestimate their real effects if litter mass loss due to physical abrasion by current velocity and fine sediments is substantial in coarse-mesh litterbags, and if litter mass loss is impaired by the reduced water exchange and low-oxygen environment in fine-mesh litterbags. On the other hand, this method may underestimate invertebrate effects if large shredders are unable to reach litter inside bags. However, our results indicated that our methods capture the majority of variation in invertebrate effects on instream litter decomposition: results from comparing litter *k* between coarse- and fine-mesh litterbags (Fig. 2) and from assessing the relationships between litter *k*/mass loss (Fig. 3 and Fig. S2) and invertebrate communities were similar, and there was a consistently non-significant effect of litterbag coarse mesh size. The observed non-significant effects of invertebrate density, biomass, or species richness on litter *k* (Fig. 3) may perhaps be attributed to the low sample sizes that limited the statistical power of our analyses (Loladze, 2014).

When using pairwise observations, we found negative linear relationships between lnRR of *k* and log-transformed invertebrate density, biomass, and species richness (Fig. 4). Potential mechanisms explaining these results may be that not all invertebrates make a direct contribution to litter decomposition (Graça, 2001), thus the total density, biomass, and richness of invertebrates may not be an accurate reflection of the effects assessed by lnRR of *k*. However, because of the lack of data on shredders, we cannot directly assess the relationships between lnRR of *k* and the shredder community. It is noteworthy that invertebrate effects quantified by the slope of the relationships shown in Fig. 4 may also be affected by other factors such as environmental gradients regulating both litter decomposition and invertebrates, which could bias the assessment of 'real' invertebrate effects. Nevertheless, given the consistent positive effects of invertebrates by both methods and the consistently non-significant effects of litterbag mesh size, it is likely that lnRR of *k* can, at least to a certain degree, accurately describe invertebrate effects on litter decomposition.

(2) Litter quality and stream environmental drivers of invertebrate effects

Consistent with our second hypothesis, our results show that initial litter quality and stream water physicochemical properties are equally important global drivers of invertebrate effects on instream litter decomposition. We found negative impacts of initial litter lignin concentration and C:N ratio and positive impacts of N concentration on lnRR of *k* (Table 1), reflecting their effects on litter *k* in streams (Zhang *et al.*, 2019). Litter with low levels of lignin and low C:N ratios tends to be more palatable and attractive to invertebrate consumers and microbial colonizers (Ab Hamid & Rawi, 2017; Gonçalves *et al*., 2012; Swan & Palmer, 2006), and higher levels of substrate colonization by microbes have been shown to render litter more digestible to invertebrates (Jinggut & Yule, 2015). In contrast to the negative effects of lignin concentration on overall invertebrate effects, we also found that lignin concentration was positively related to invertebrate biomass and density-mediated litter *k* and mass loss, respectively (Tables 1 and S3). One plausible explanation for this inconsistency may be that the relationship between litter lignin concentration and invertebrate effects on instream litter decomposition may depend on taxonomic and functional group preferences for specific litter lignin concentrations (Graça, Ferreira & Coimbra, 2001; Graça, 2001; Patoine *et al.*, 2017). When invertebrates of specific taxonomic groups that account for a high proportion of biomass or density of the whole invertebrate community prefer some particular types of litter with high lignin concentration, invertebrate effects on litter decomposition can be positively related to litter lignin concentration. In addition, we found that positive effects of invertebrates on litter decomposition did not depend on mycorrhizal associations of the litter producing taxa, but there were differences in the degree of positive impacts of invertebrate density and richness in litter mass loss according to these mycorrhizal associations (Fig. S2). This is possibly a result of differences in litter quality from taxa with different types of mycorrhizal association (Shi *et al.*, 2020), given that litter quality was found to be an important driver of invertebrate effects on instream litter decomposition. Overall, our results show that initial litter quality, besides controlling litter *k* as reported elsewhere (Yue *et al.*, 2018; Zhang *et al.*, 2019), also drives invertebrate effects on instream litter decomposition at the global scale.

While local- and global-scale studies have demonstrated that initial litter quality accounts for much of the variation in litter *k* in streams (Boyero *et al.*, 2016; Leroy & Marks, 2006; Zhang *et al.*, 2019), our findings showed that stream water physicochemical properties may represent an equally important driver of invertebrate effects 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). Previous studies suggested that activity of litter decomposers and, therefore, litter *k*, tends to be positively related to temperature (Ferreira & Canhoto, 2015; Ferreira *et al.*, 2015*a*). However, decreases in levels of dissolved O_2 in water with increasing water temperature may be detrimental to decomposer activities (Iñiguez-Armijos *et al.*, 2016; Pettit *et al.*, 2012). Supporting these previous studies, our results showed a positive relationship between dissolved O_2 and invertebrate effects on litter decomposition (Tables 1, S3). In addition, stream water NO_3^- and PO_4^{3-} concentrations, pH, and current velocity, were also important drivers of invertebrate effects on litter decomposition, likely because they are directly or indirectly related to invertebrate metabolism and activity during the litter decomposition process (Graça *et al.*, 2015; Leroy & Marks, 2006). For example, higher concentrations of NO_3^- were found to stimulate litter-associated fungal biomass (Ferreira, Gulis & Graça, 2006), which would make litter more palatable to invertebrates. By contrast, a recent meta-analysis suggested that excess amounts of N and P have negative effects on invertebrate populations (Nessel *et al.*, 2021), indicating the importance of ambient N and P in regulating invertebrate effects on instream litter decomposition.

(3) Greater effects of invertebrates during the early stages of decomposition

Partly consistent with our third hypothesis, we found evidence for the most significant effects of invertebrates only during the early stages of litter mass loss (< 20% mass loss; Fig. 5). Previous studies of terrestrial ecosystems show that 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 decline (Peguero *et al.*, 2019). In contrast to this finding in terrestrial ecosystems, however, our results indicate that the contribution of invertebrates to instream litter decomposition is greatest during the early stages. Although heavy leaching can contribute to 10–20% of initial litter mass loss in the early decomposition stages (Gessner, Chauvet & Dobson, 1999), this does not conflict with our findings of higher invertebrate effects in the early decomposition stages when nutrient availability is higher, because previous local-scale studies showed that invertebrate effects on litter decomposition are greater for species with higher litter quality (Hieber & Gessner, 2002). This result is further supported by a positive relationship between invertebrate effects and stream water nutrient concentrations (Table 1). Another potential explanation may be that microbes were found to regulate early-to-middle litter decomposition (0–40% mass loss interval; García-Palacios *et al.*, 2016), and the relatively higher colonization and effects of microbes during the early stages of decomposition could render the litter more digestible to invertebrates

(Jinggut & Yule, 2015), and thus stimulate the effects of invertebrates.

(4) Research gaps and recommendations

We identify three key research gaps in our understanding of the global contributions of invertebrates to decomposition of litter in stream ecosystems. First, our study shows that initial litter quality is a major driver of invertebrate effects on stream litter decomposition. However, of the 141 articles from which we extracted data, only 28 reported initial litter quality whereas the majority contained data on stream water physicochemical properties. This asymmetry in the available data limits any analysis of the relative importance of litter quality *versus* stream physicochemical properties on invertebrate effects on litter decomposition among different stages of the litter decomposition process. Secondly, the majority of studies included in this synthesis either compared litter *k* between litterbags with contrasting mesh size or only used litterbags with larger mesh sizes to measure litter *k* and invertebrate communities. This lack of pairwise data from the two approaches limits the precise assessment of the effects of invertebrates on stream litter decomposition. The majority of primary studies only used fine-mesh litterbags of ~0.5 mm to exclude invertebrates, although such a mesh remains accessible for micro- and meso-invertebrates. Thus, the effects of micro- and meso-invertebrates on instream litter decomposition are generally not assessed, and were therefore not considered in the present study. More importantly, in future studies different functional groups, especially shredders, should be evaluated independently in order to allow a precise assessment of invertebrate effects on instream litter decomposition. Thirdly, the results included in our synthesis were focussed on Europe and the Americas (Fig. 1), with other regions of the world poorly represented, possibly leading to a misrepresentation of global-scale effects and drivers of invertebrate-mediated instream litter decomposition. Overall, we suggest that future experiments should describe initial litter quality, stream physicochemical properties, and microbial communities as potential drivers of invertebrate effects, and employ advanced approaches, such as ^{13}C labelling, which may allow the derivation of correction factors to assess the 'true' contribution of invertebrates to litter decomposition by tracking fluxes in C. To ensure future robust global-scale analyses of invertebrate effects on litter decomposition, we further propose multisite, multi-species experiments distributed across all global regions and running for multiple years to account for temporal changes in litter chemistry during all stages of litter decomposition (Boyero *et al.*, 2021; Yue *et al.*, 2018).

V. CONCLUSIONS

(1) 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, Ferreira & Coimbra, 2001) and a recent global study that included few study sites (Boyero *et al.*, 2021). Our results clearly show a positive effect of invertebrates on instream litter decomposition globally, increasing litter *k* by an average of 74%, and that this effect is driven jointly by initial litter quality and stream physicochemical properties.

(2) Invertebrate effects were not affected by climatic region, litterbag mesh size, or type of mycorrhizal association across the whole decomposition stage, but the magnitude and significance of the relationship between invertebrate parameters (density, biomass, and species richness) and litter mass loss depended on these factors. Effects of invertebrates on litter decomposition were most apparent during the early stages of decomposition (<20% mass loss).

(3) Our results not only quantitatively synthesize global patterns of invertebrate contributions to instream litter decomposition, but also show that the most significant effects of invertebrates on litter decomposition are at early rather than middle or late decomposition

stages. The results highlight the importance of the inclusion of invertebrates in global dynamic models of litter decomposition in streams to explore the mechanisms and impacts of terrestrial, aquatic, and atmospheric carbon fluxes.

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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. All authors contributed to revisions.

Data availability: the raw data used in the review have been deposited in the online digital repository figshare (https://doi.org/10.6084/m9.figshare.19137389.v1).

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VIII. SUPPORTING INFORMATION

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

Table S1. The range of variables for stream physicochemical properties, litter quality, and experimental conditions used in this study.

Table S2. Results of publication bias analysis using Egger's regression tests on the meta-analytic residuals and trim-and-fill tests from the multi-level meta-analytical model.

Fig. S1. Funnel plot displaying the residuals from the mixed-effect model plotted against the inverse standard error (precision) of invertebrate effects.

Fig. S2. Effects of invertebrate density, biomass, and species richness on instream litter decomposition.

Table S3. Univariate linear mixed-effects modelling analysis of relationships between experimental condition, initial litter quality, and stream physicochemical properties and litter mass loss mediated by invertebrate density, biomass, and species richness.

Table 1. Univariate linear mixed-effects modelling analysis of the relationship between experimental condition, initial litter quality, and stream physicochemical properties and the effect of invertebrates on instream litter decomposition [natural logarithm response ratio (lnRR) of litter decomposition rate (*k*); database 1] and the effects of their interactions with invertebrate density, biomass, and species richness on *k* (database 2). Data were $\log_{10}$-transformed prior to analysis; bold *p*-values indicate significant effects.

	lnRR of *k*			**Invertebrate effect on *k***								
				Density			**Biomass**			**Species richness**		
Predictor	**Slope**	***p***	***N***	**Slope**	***p***	***N***	**Slope**	***p***	***N***	**Slope**	***p***	***N***
Experimental condition												
Litterbag coarse mesh size (mm)	–0.034	0.760	293	–0.014	0.940	323	0.634	0.279	131	1.148	0.191	100
Experimental duration (days)	–0.086	0.347	263	0.104	0.380	304	0.101	0.580	100	–0.114	0.788	101
Initial litter mass (g)	0.176	0.252	291	0.056	0.741	336	0.365	0.196	135	0.731	0.465	109
Initial litter quality												
C concentration (%)	–0.734	0.807	25	0.564	0.142	40	0.793	0.128	29			
N concentration (%)	0.273	**0.024**	53	–0.309	0.516	47	1.003	**0.002**	32			
C:N ratio	–0.759	**< 0.001**	30	0.485	0.065	43	–0.407	0.150	29			
Lignin concentration (%)	–0.196	**0.046**	34	–1.515	0.402	12	1.809	**0.029**	14			
Lignin:N ratio	–0.123	0.077	34	–0.966	0.348	12	1.602	**0.009**	12			
Stream physicochemical properties												
Water temperature (°C)	–0.333	**0.001**	216	–0.027	0.884	189	–0.217	0.208	94	–0.485	0.294	57
Discharge rate (l/s)	0.007	0.881	48	–0.090	0.093	107	–0.112	0.169	62	–0.774	**< 0.001**	25
Current velocity (m/s)	–0.028	0.398	83	–0.558	**< 0.001**	66	0.119	0.355	40	–0.537	**0.043**	46
pH	0.752	**< 0.001**	222	–0.566	**0.010**	172	–0.112	0.432	84	–0.179	0.763	73
Conductivity (μ/s cm)	–0.011	0.758	224	–0.003	0.978	163	0.105	0.244	77	0.228	0.468	65
Alkalinity (mg $CaCO_3$/l)	0.084	0.208	43	–0.096	0.506	63	–0.036	0.404	41	–1.208	0.651	16
Dissolved O_2 (mg/l)	0.591	**0.028**	111	–0.105	0.858	105	0.337	0.523	30	–2.431	0.300	45
$[NO_3^-]$ (μg/l)	0.104	**< 0.001**	155	–0.007	0.909	136	–0.068	0.209	85	0.226	0.346	33
$[NH_4^+]$ (μg/l)	0.100	0.122	85	0.083	0.276	119	–0.047	0.696	59	0.507	0.084	35
$[PO_4^{3-}]$ (μg/l)	0.026	0.376	100	–0.078	0.319	123	0.096	0.632	50	0.047	0.891	25

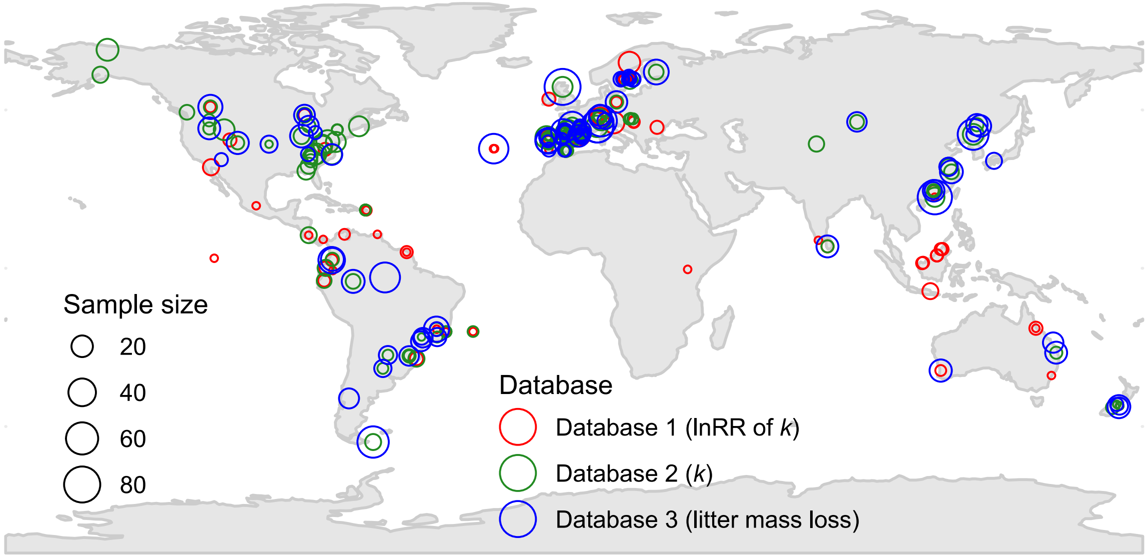

Fig. 1. Global distribution of observations derived from the 141 publications used in our meta-analysis (see references marked with an asterisk in the reference list). The number of observations (sample size) at each site is represented by symbol size, and different colours indicate different databases (the full data set is available in figshare, see Section VI). *k*, litter decomposition rate; lnRR, natural logarithm response ratio.

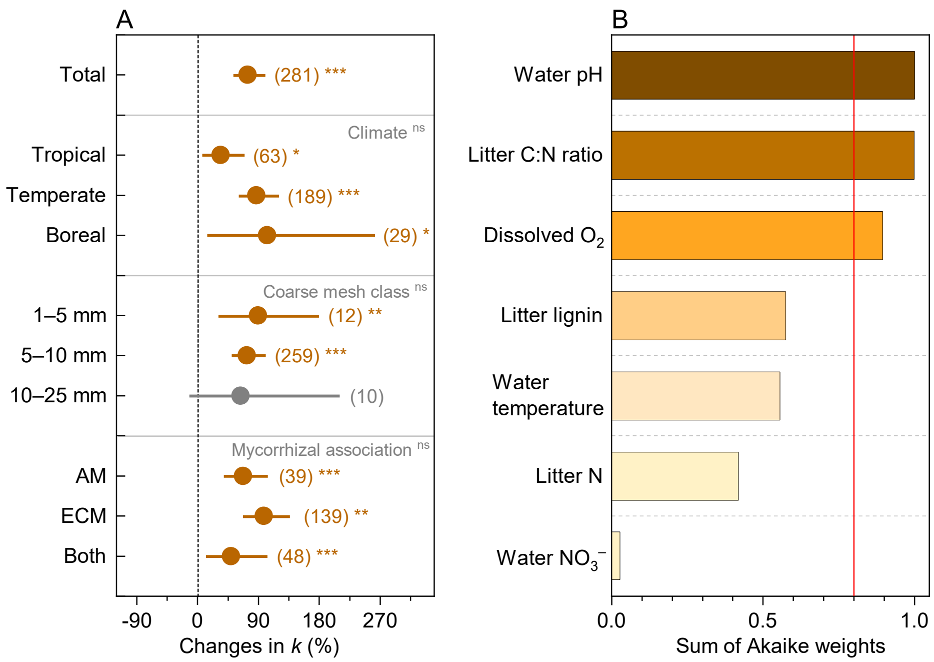

Fig. 2. Overall effects of invertebrates (presence *versus* absence in coarse- *versus* fine-mesh litterbags) on litter decomposition rate (k) in streams (A) and model-averaged importance of drivers ($p < 0.05$) of invertebrate effects (B) assessed using database 1. Values in A are mean ± 95% confidence intervals of the per cent difference between fine- and coarse-mesh litterbags; number of pairwise observations are shown in parentheses; values on the x-axis indicate per cent changes in litter k due to the presence of invertebrates. In B, factor importance is estimated from the sum of Akaike weights, based on model selection analysis using corrected Akaike's information criteria; the cut-off (red vertical line) is set at 0.8 to differentiate essential from non-essential factors. Coloured symbols depict significant effects; grey and/or ns indicates a statistically non-significant result. AM, arbuscular mycorrhizal; ECM, ectomycorrhizal. $^{*}p < 0.05$, $^{**}p < 0.01$, $^{***}p < 0.001$.

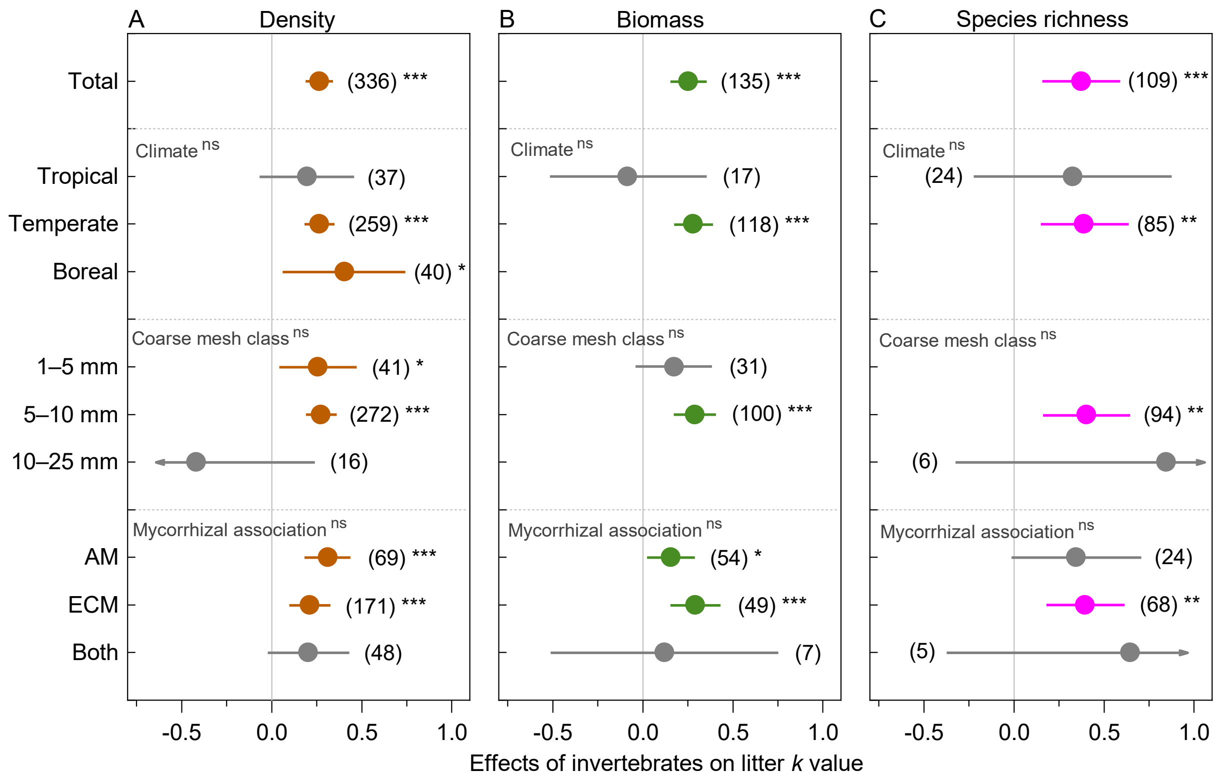

Fig. 3. Effects of invertebrate density (A), biomass (B), and species richness (C) on instream litter decomposition assessed using database 2. Values are estimated slopes and 95% confidence intervals of fixed effects of invertebrate variables on litter decomposition rates (*k*) from linear mixed-effects models. Invertebrate data were $\log_{10}$-transformed prior to analysis; number of observations is shown in parentheses. Coloured symbols represent significant effects of invertebrate density, biomass, and species richness on litter decomposition ($^{*}p <$ 0.05, $^{**}p < 0.01$, $^{***}p < 0.001$); grey and/or ns indicates a statistically non-significant result. AM, arbuscular mycorrhizal; ECM, ectomycorrhizal.

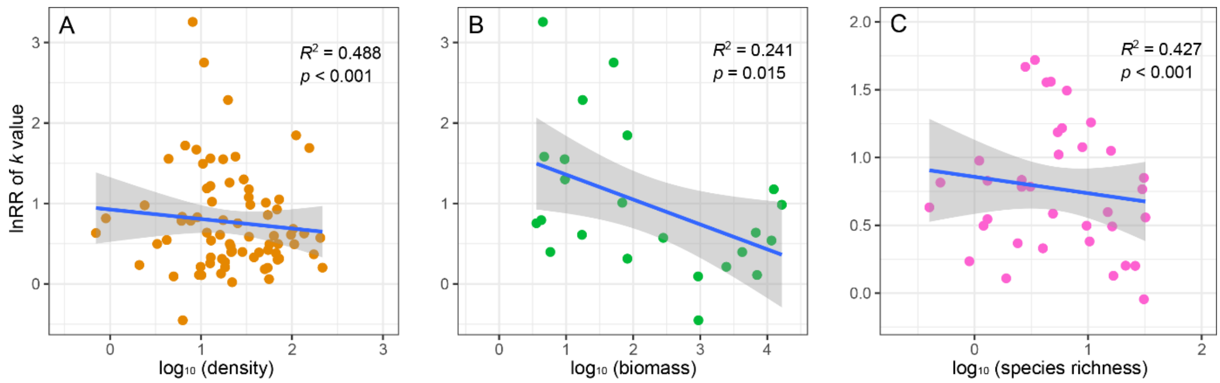

Fig. 4. Relationship between invertebrate effect sizes on litter decomposition rates [natural logarithm response ratio (lnRR) of litter decomposition rate (k)] and $\log_{10}$-transformed invertebrate density (A), biomass (B), and species richness (C) using pairwise data points from databases 1 and 2. Linear fitted lines and 95% confidence intervals are shown.

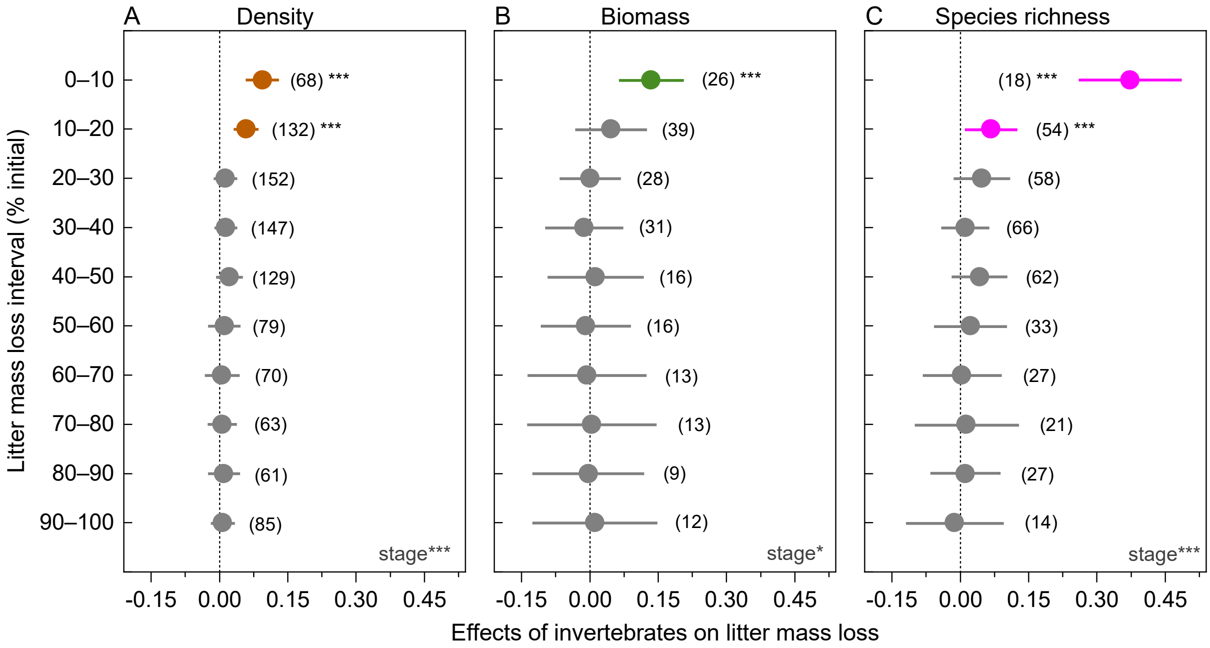

Fig. 5. Effects of invertebrate density (A), biomass (B), and species richness (C) on instream litter decomposition over the stages of decomposition (0−100% mass loss) assessed using database 3. Values are estimated slopes and 95% confidence intervals of fixed effects of invertebrates on litter mass loss from linear mixed-effects models. Data were log_{10}-transformed prior to analysis. Number of observations is shown in parentheses. Coloured symbols represent significant effects of invertebrate density, biomass, and species richness ($^{*}p < 0.05$, $^{**}p < 0.01$, $^{***}p < 0.001$); grey symbols indicate a statistically non-significant slope.