



RESEARCH ARTICLE

Multiple-stressor effects on leaf litter decomposition in freshwater ecosystems: A meta-analysis

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Abstract

1. Recent years have witnessed a surge in research on the effects of multiple stressors in freshwater ecosystems. While studies have increased, the synthesis of their findings into a broader understanding of ecosystem-level effects remains an ongoing endeavour. Leaf litter decomposition, a frequently investigated and pivotal ecosystem function in freshwaters, is sensitive to changes in abiotic conditions and biotic communities, and therefore susceptible to multiple-stressor effects.
2. Here, we synthesize findings from 27 manipulative experimental studies encompassing 61 responses of litter decomposition to paired stressors such as warming, nutrient enrichment and emerging pollutants in freshwater ecosystems. We calculated the individual and overall interaction effect sizes resulting from two stressors occurring simultaneously. Furthermore, we analysed the effect of moderator variables in the size and direction of interaction effect sizes using a meta-analytical approach.
3. Although the vote-counting method showed additive interactions to dominate individual observations (91.8%), weighted random-effects meta-analysis revealed an overall antagonistic interaction between stressors (i.e. the cumulative effect of paired stressors on litter decomposition was less than the sum of their single effects). Our results emphasized the influence of experimental characteristics such as macroinvertebrate involvement, habitat type (lentic vs. lotic) and litter quality (assumed from plant mycorrhizal association) in shaping the responses of litter decomposition to multiple stressors.

Sonja C. Jähnig and Fengzhi He contributed equally to this work.

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4. Our meta-analysis highlights the need to incorporate local ecological complexities in manipulative experiments to improve predictions of multiple-stressor effects on biodiversity and ecosystem functions. The present study underscores the importance of considering biotic interactions and adopting the metacommunity framework in conservation and restoration actions to support the management of freshwater ecosystems in an era of rapid global change.

KEYWORDS

additivity, antagonism, combined stressors, organic matter decomposition, synergism, systematic review

1 | INTRODUCTION

Freshwaters are among the most diverse ecosystems and provide vital contributions to people (Lynch et al., 2023). Meanwhile, they are highly vulnerable to anthropogenic stressors and have a limited buffer capacity compared with terrestrial and marine ecosystems (Angeler et al., 2014; Revenga et al., 2005). Owing to their importance to society and topographic location (i.e. rivers, lakes and wetlands are often located at the lowest point in the landscape), freshwater ecosystems are subject to the cumulative impacts of multiple stressors in the basin (Dudgeon et al., 2006; Fluet-Chouinard et al., 2023). Stressors such as overexploitation of water and organisms, habitat fragmentation, pollution and climate change, alone or in concert, have led to drastic declines in freshwater biodiversity (He et al., 2019; Tickner et al., 2020; WWF, 2022) and altered ecosystem functions (Brauns et al., 2022; Jaiswal et al., 2021). The increasing intensity of anthropogenic impacts on freshwaters has led to a growing scientific focus on the effects and interactions of multiple stressors (Birk et al., 2020; He et al., 2023; Reid et al., 2019).

Although our knowledge of the multiple-stressor effects in freshwaters has advanced in the last two decades (Jackson et al., 2016; Orr et al., 2020), it remains challenging to predict the magnitude and direction of interactions between stressors owing to their complexity (Birk et al., 2020; Jackson et al., 2016; Piggott et al., 2015). Manipulative experiments are an effective tool to investigate stressor interactions as they allow to control the influence of other effects (e.g. abiotic and biotic variability) and help to disentangle the effects of stressor interactions on targeted responses from noise (Lange et al., 2018). To date, multiple-stressor experiments have been primarily focused on assessing the responses of species performance and community structure in freshwaters (Jackson et al., 2016; Lange et al., 2018), while research on the interactive effects of multiple stressors on ecosystem functions remains limited (He et al., 2023). Such knowledge gaps might impede our understanding of how multiple stressors interact on larger scales and, therefore, hinder the development of effective freshwater conservation and restoration actions (Vos et al., 2023).

Leaf litter decomposition is a frequently investigated ecosystem function in multiple-stressor experiments focusing on freshwaters

(He et al., 2023). Leaf litter from riparian vegetation is a key source of nutrients and energy to freshwaters and provides vital resources to heterotrophic organisms, including bacteria, fungi and invertebrates (Marks, 2019; Figure 1). Microbes, such as fungi and bacteria, rely on enzymatic mechanisms to break down litter, whereas invertebrates can influence litter decomposition directly by feeding on leaf litter (i.e. shredders; Canhoto & Graça, 2008) and indirectly through interactions with microbial decomposers (i.e. grazers; Graça, 2001; Wang et al., 2020). Therefore, the litter decomposition process is highly sensitive to changes in abiotic environment and biotic communities (Chauvet et al., 2016; Gessner et al., 2010). In addition, litter quality (e.g. carbon:nitrogen:phosphorus ratio, lignin concentration), which can influence colonization of decomposers and their interactions, also has a profound impact on this process (Graça et al., 2001; Yue et al., 2022). Moreover, a growing number of studies have suggested that mycorrhizal association of plants has a strong link with leaf chemistry (Keller & Phillips, 2019; Wu et al., 2023; Zhang et al., 2019). Plants associated with arbuscular mycorrhizae (AM) are usually associated with lower lignin and cellulose concentrations (Peng et al., 2022), and lower carbon:nitrogen ratios (Taylor et al., 2016) compared with those associated with ectomycorrhizae (EcM), and such traits can influence the rate at which leaf litter decomposes. Hence, leaf litter of AM-associated plants is often more palatable and easier to colonize for aquatic invertebrates and microbial decomposers than those associated with EcM (Yue et al., 2022). Therefore, litter types included in the multiple-stressor experiments may influence the observed effects of stressor interaction on litter decomposition. However, such impact has not yet been explicitly tested.

Various types of interactive effects on litter decomposition have been observed in multiple-stressor experiments focusing on freshwaters, including additive (Piggott et al., 2012), synergistic (Matthaei et al., 2010), antagonistic (Du et al., 2022) and reversal (Juvigny-Khenafou et al., 2021). The variability in observed interactions in multiple-stressor experiments may arise from external moderators (Lange et al., 2018), which include particular experimental settings in which ecological mechanisms might occur differently, and that can determine the magnitude and direction of the interactions (King et al., 2022), limiting our ability to

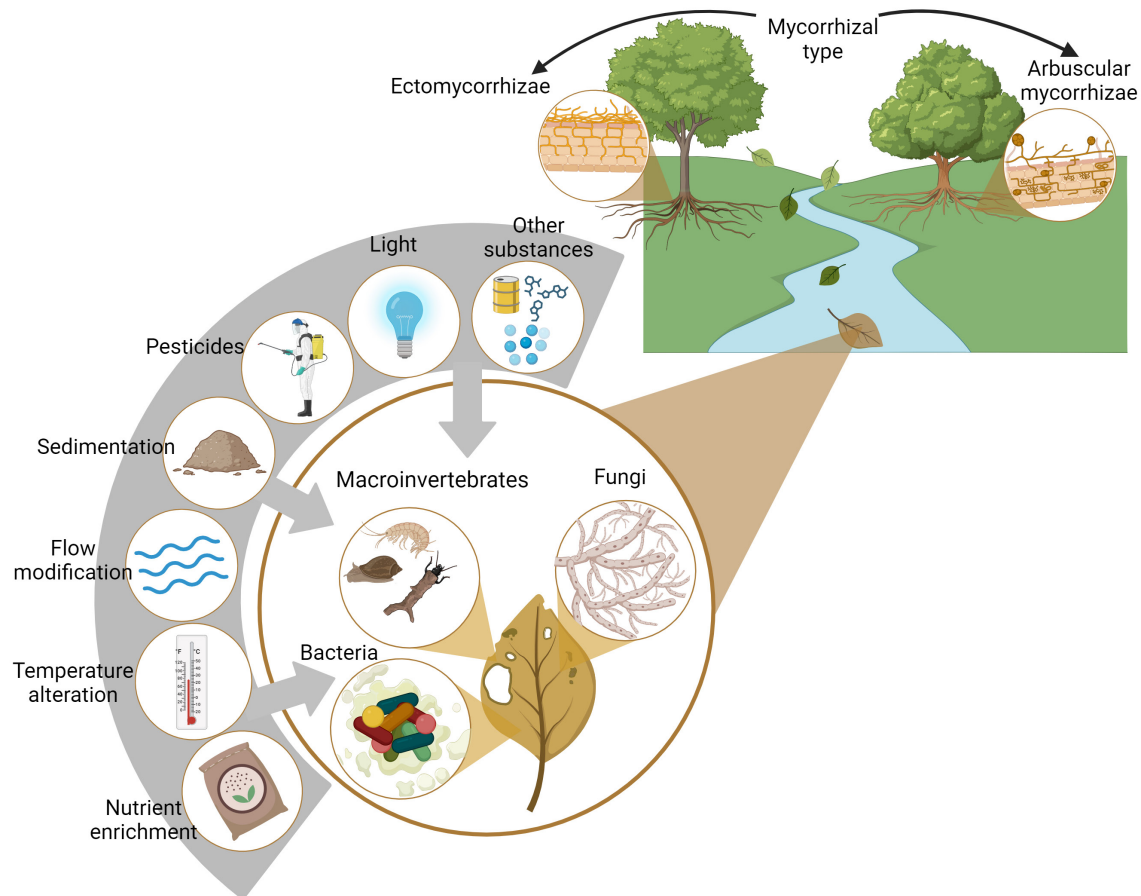


FIGURE 1 Conceptual overview of factors affecting the process of leaf litter decomposition in freshwater ecosystems. The central inner circle represents the biotic communities involved in leaf litter decomposition, while the outer semicircle represents external stressors. Note that leaf litter can originate from plants that may associate with different types of mycorrhizal fungi. Created in [BioRender.com](https://www.biorender.com) (CC-BY-NC-ND).

generalize results. Despite the surge of research about multiple-stressor impacts on litter decomposition in freshwaters, the prevailing interactive effects and recurring patterns have not been comprehensively investigated (but see Jackson et al., 2016). To our knowledge, no study has examined the potential impact of external moderators (e.g. the involvement of macroinvertebrates, dispersal potential, litter quality and quantity, habitat type and experiment duration) on the interactive effects of stressors on litter decomposition.

Here, we synthesize findings from published manipulative experimental studies to address two main research questions: (1) How do multiple stressors interact to impact litter decomposition in freshwaters? and (2) Do external moderators such as the involvement of macroinvertebrates in litter decomposition, the dispersal potential of the setup, the quality and quantity of used litter, habitat type and the duration of the experiment influence stressor interactions? We used a meta-analytic approach to investigate multiple-stressor effects on litter decomposition in freshwater ecosystems and tested hypotheses associated with these two research questions (Table 1). We discuss the potential of multiple-stressor research for enhancing conservation and restoration and

provide recommendations for future investigations and management actions to safeguard freshwater biodiversity and associated ecosystem functions.

2 | METHODOLOGY

2.1 | Literature search and data extraction

To investigate interactions between multiple stressors while controlling for changes in other target factors, we exclusively focused on manipulative experiments with a factorial design. On 19 January 2023, we performed a literature search on the Web of Science to identify relevant peer-reviewed studies published in English before 2023. In addition to the results yielded from Web of Science ($n=206$), we conducted a snowball search method (i.e. relevant studies cited in the identified articles; $n=2$) (Supporting Information). All data are available at FRED repository (<https://doi.org/10.18728/igb-fred-877.1>; Medina Madariaga et al., 2024).

Publications were checked to confirm compliance with three criteria (Figure S2). First, they should be a manipulative experimental

TABLE 1 Tested hypotheses and respective justifications. H1 is associated with the first research question, while several moderator-related hypotheses (H2.1–H2.6) are associated with the second research question.

Hypotheses	Description	Reasoning
H1	The overall stressor interaction is additive	Given the widely reported additive effects of multiple stressors on litter decomposition in freshwaters (Chará-Serna et al., 2019; Jackson et al., 2016), we expect that the overall effect size exhibits a similar pattern
H2.1	The involvement of macroinvertebrates in the experiments influences the interactive effects of multiple stressors on leaf litter decomposition	Macroinvertebrates play an important role in the leaf litter decomposition process in freshwaters (Yue et al., 2022). Shredders consume leaves and their feeding activities depend on microbial conditioning of leaves (Graça et al., 2001). Grazers feed on microbial decomposers in the biofilm on the leaf surface (Álvarez & Peckarsky, 2005; Cibils Martina et al., 2014). Therefore, the involvement of macroinvertebrates can affect litter decomposition in multiple-stressor environments by directly feeding on leaves and indirectly via their interactions with microbes
H2.2	Experiments which allow species dispersal within their design produce less additive interactions between stressors	Experiments allowing species dispersal (i.e. open systems or artificial dispersal) can reduce the dissimilarity of decomposer assemblages between different treatment groups caused by stressors (De Boer et al., 2014). Therefore, species dispersal between experimental units and the natural environment may compensate for the altered performance of decomposers by stressors, leading to a reduced magnitude of overall stressor additivity
H2.3	Mycorrhizal associations of litter-producing plants used in experiments influence the interactive effect of stressors on litter decomposition	Litter of AM-associated plants are generally more palatable and easier to colonize for aquatic decomposers under stress than that of EcM-associated plants (Zhang et al., 2019). The influence of litter quality on the feeding activity and colonization of decomposers may further modify leaf litter decomposition in a multiple-stressor context
H2.4	Stressor interactions are different between lotic ecosystems and lentic ecosystems	Flow promotes oxygen and nutrient diffusion within leaf litter packs (Cummins et al., 1980) and removes dead layers of periphytic biofilm from the litter surface (McNamara & Leff, 2004), enhancing microbial colonization and activity. In addition, strong flow can reduce periphyton abundance (Biggs et al., 1998). Hence, we expect that multiple-stressor effects on litter decomposition are different in lotic ecosystems than in lentic ecosystems
H2.5	Experiments with longer durations report fewer additive interactions	Experiments conducted during longer time spans reflect the mechanisms of resistance and resilience of the ecosystem to multiple stressors (Jackson et al., 2021), while experiments running over shorter periods of time do not allow for decomposers to adapt to changes and therefore reflect only the most magnified responses
H2.6	Experiments using larger amounts of leaf litter exhibit more antagonistic interactions	Larger amounts of litter allow for more space for decomposers to act upon and provide potential refugia in stressful conditions, which may make the overall litter decomposition process less susceptible to the changes caused by stressors

study performed in a freshwater or estuarine environment ($n=53$). Each retained publication was then checked for the second criterion (i.e. reporting a measurement of litter decomposition in response to two or more stressors; $n=37$). Finally, included studies were selected by the third criterion (i.e. providing sufficient data in the text, tables or figures to calculate effect sizes; $n=27$).

We selected responses that measured the process of litter decomposition (e.g. litter decomposition rate, mass loss, % loss). Given the large variety of stressors explored in the identified 27 studies (<https://doi.org/10.18728/igb-fred-877.1>; Medina Madariaga et al., 2024), we classified them into 10 major stressor categories (Table S1). In addition, we collected data that were directly related to our hypotheses, such as the involvement of macroinvertebrates in litter decomposition (i.e. determined by the presence of macroinvertebrates in the experiments and used mesh size), whether dispersal was allowed during the experiment, the mycorrhizal associations of plants included in the study (i.e. AM vs. EcM) according to the

FungalRoot database (Soudzilovskaia et al., 2020, 2022), initial litter mass used, habitat types that were represented by the experiments (i.e. lotic vs. lentic), and experimental duration (Table S2).

If a study included more than two stressors, data for all possible combinations of two stressors were extracted. When available, different stressor combinations were noted as different observations. When studies included more than two levels of stressor intensity, the most extreme cases of interactions were considered by selecting only the responses resulting from the exposure to the highest intensity of both stressors. The mean, standard deviation or standard error of the response related to litter decomposition, the number of replicates under treatment A (stressor 1), treatment B (stressor 2), treatment AB (both stressors together) and control treatment of each observation were extracted to calculate the effect sizes of the interactions. These data were collected from the text or tables directly or extracted from figures with the PlotDigitizer online tool (<https://plotdigitizer.com>).

TABLE 2 Replication statement table indicating scales of inference targeted in the statistical analysis.

Scale of inference	Scale at which the factor of interest is applied	Number of replicates at the appropriate scale
Individual experiments	Individual experiments	61
Individual experiments	Pooled group of individual experiments	Without macroinvertebrate involvement 20; With macroinvertebrate involvement 41
Individual experiments	Pooled group of individual experiments	With dispersal 42; No dispersal 19
Individual experiments	Pooled group of individual experiments	AM 27; EcM 33
Individual experiments	Pooled group of individual experiments	Lentic 9; Lotic 52

2.2 | Statistical analysis

2.2.1 | Replication statement

Detailed description is found in [Table 2](#).

2.2.2 | Calculation of interaction effect sizes

The factorial form of the effect size (Hedges' g) of the interactions for all observations was calculated in R (R Core Team, 2023) and classified into additive, antagonistic, synergistic or reversal, based on the approach proposed by Piggott et al. (2015; [Figure S1](#)) using the *MultipleStressR* package (Burgess & Murrell, 2022). In addition, a vote-counting approach was performed to assess the prevalence of interaction types in the dataset (Jackson et al., 2016).

2.2.3 | Publication bias

We generated funnel plots reflecting the interaction effect size against sample size, which were visually inspected to detect asymmetry (Nakagawa et al., 2022). A modified version of Egger's regression test (Egger et al., 1997; Sterne & Egger, 2005) for multivariate analysis was performed to assess potential bias ([Supporting Information](#)).

2.2.4 | Multilevel meta-analysis

To estimate the global effect size and direction of the interactions across all identified observations, statistical analyses were implemented with the *metafor* package (Viechtbauer, 2010). A multilevel meta-analysis to account for potential heterogeneity and correlation of observations that originated from the same study was performed by using the *Code_manuscript* as a random effect in the 'rma.mv' function and then proceeded with robust variance estimation (RVE; Pustejovsky & Tipton, 2022). In addition to the random-effects model, a series of mixed models were performed to test the effects of different

moderators. We only included categories with more than seven observations in the analysis (Jackson et al., 2016; Lange et al., 2018; Nakagawa & Cuthill, 2007). In addition, we explored the effect of continuous variables, such as duration and initial litter mass (centred and scaled), on the magnitude and direction of stressor interactions.

To determine the importance of each moderator variable to describe the interaction effect size, we fitted a full model including the moderator variables reported for all the studies in our analysis. We used the dredge function in *MuMIn* package (Barton, 2023) coupled with *metafor* package to obtain various models containing all possible subsets of our moderator variables. Furthermore, we determined our top model set based on the Akaike information criterion (AIC) weights (i.e. $\Delta AIC \leq 4$). We also calculated the ΔAIC for each model, which represents the degree of deviation of the model in question compared with the most parsimonious model. Finally, we obtained the relative variable importance of each moderator variable by considering the sum of the weights of the model in which the variable appeared. More detailed information on each step of the multilevel meta-analysis is found in the [Supporting Information](#).

3 | RESULTS

3.1 | Overview of the multiple-stressor studies included in the meta-analysis

Among the 27 studies included in our meta-analysis, the most frequently investigated stressor category was nutrient enrichment (e.g. nitrogen and phosphorus), followed by substrate alteration (e.g. sedimentation and substrate modification) and hydrological alteration (e.g. flow increase and drought). In terms of stressor combinations, substrate and hydrological alteration were most frequently combined ($n=8$ observations), along with the combination of temperature alteration and nutrient enrichment ($n=7$). Nutrient enrichment was also often combined with substrate alteration ($n=7$; [Figure 2a](#)). All 27 studies were published after 2009, with one to four studies published each year ([Figure 2b](#)). More studies were conducted in lotic ($n=23$) rather than in lentic ($n=4$) habitats. From the 61 extracted observations, most were obtained from experiments

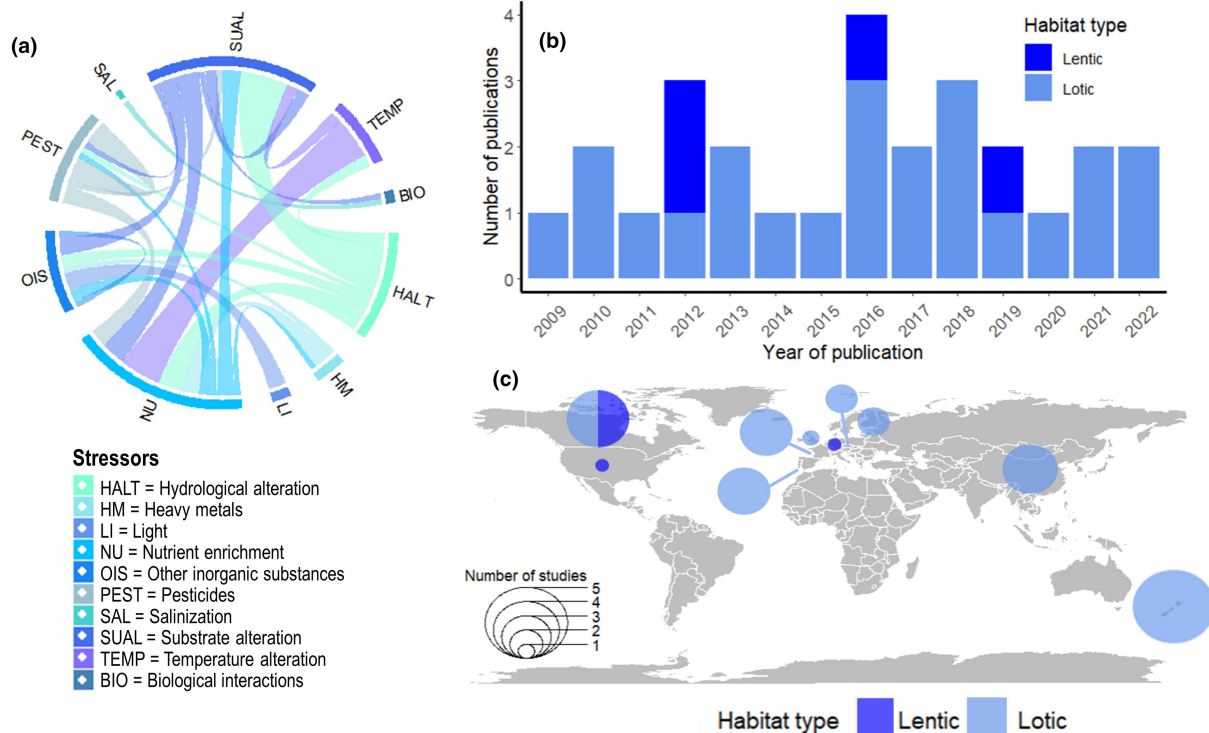


FIGURE 2 Overview of the research studies ($n=27$) exploring the effect of multiple stressors on litter decomposition that were included in the analysis by: (a) major stressor classes and their combinations, (b) year of publication, and (c) geographic location and type of habitat.

performed in flumes ($n=20$), circular mesocosms ($n=19$), indoor microcosms ($n=14$) and only a few ($n=8$) from outdoor ponds. Most studies were conducted in New Zealand ($n=5$), Canada ($n=4$), France ($n=4$), China ($n=4$) and Portugal ($n=4$) (Figure 2c). Leaves of alders (*Alnus* spp.) were predominantly used as litter in the identified experiments ($n=26$ observations), followed by mahoes (*Melycitus* spp.; $n=16$) and birches (*Betula* spp.; $n=6$).

3.2 | Interaction effects magnitudes and directions in the entire dataset

Vote counting showed that the majority of 61 interactive effect sizes had additive stressor interactions ($n=56$), followed by antagonistic ($n=3$) and synergistic ($n=2$) interactions (Figure 3). However, the overall random-effect model revealed an antagonistic interaction between stressors ($g=-0.49$, 95% CI = -0.87 to -0.12 ; Table 3). The I^2 values (i.e. 20.42%) for the overall model were below the 25% threshold, indicating a consistency among studies included in the meta-analysis.

3.3 | Publication bias

Eggers' tests revealed no significant relationships between interaction effect size and variance (intercept = -0.84 , $p=0.46$), and between interaction effect size and inverse pooled sample size

(intercept = -0.44 , $p=0.36$), suggesting no publication bias. In addition, funnel plots were also visually inspected and showed no evidence of bias (Figures S3 and S4).

3.4 | Effect of moderators on multiple-stressor interactions

Multiple stressors showed an additive interaction effect on leaf litter decomposition when macroinvertebrates were excluded, EcM-associated plant litter was used, and lentic habitats were simulated (Table 3). In contrast, multiple-stressor interactions were antagonistic when macroinvertebrates were involved in the litter decomposition process, AM-associated plant litter was used, and lotic habitats were simulated (Table 3). Experiment duration and initial litter mass showed similar trends with antagonistic interaction effect sizes, with non-significant negative trends at longer experimental spans (slope = -0.23 , 95% CI = -0.54 to 0.81), and with larger amounts of initial litter mass (slope = -0.08 , 95% CI = -0.31 to 0.14).

Thirteen models were identified from our full model fitting based on AIC values (i.e. $\Delta AIC < 4$). The plant mycorrhizal type was included in most of the identified models (Table 4) and had the greatest relative importance (0.53), followed by the duration of the experiments (0.36) (Figure 4). The involvement of macroinvertebrates, habitat type and dispersal conditions showed similar relative importance (i.e. 0.23; Figure 4).

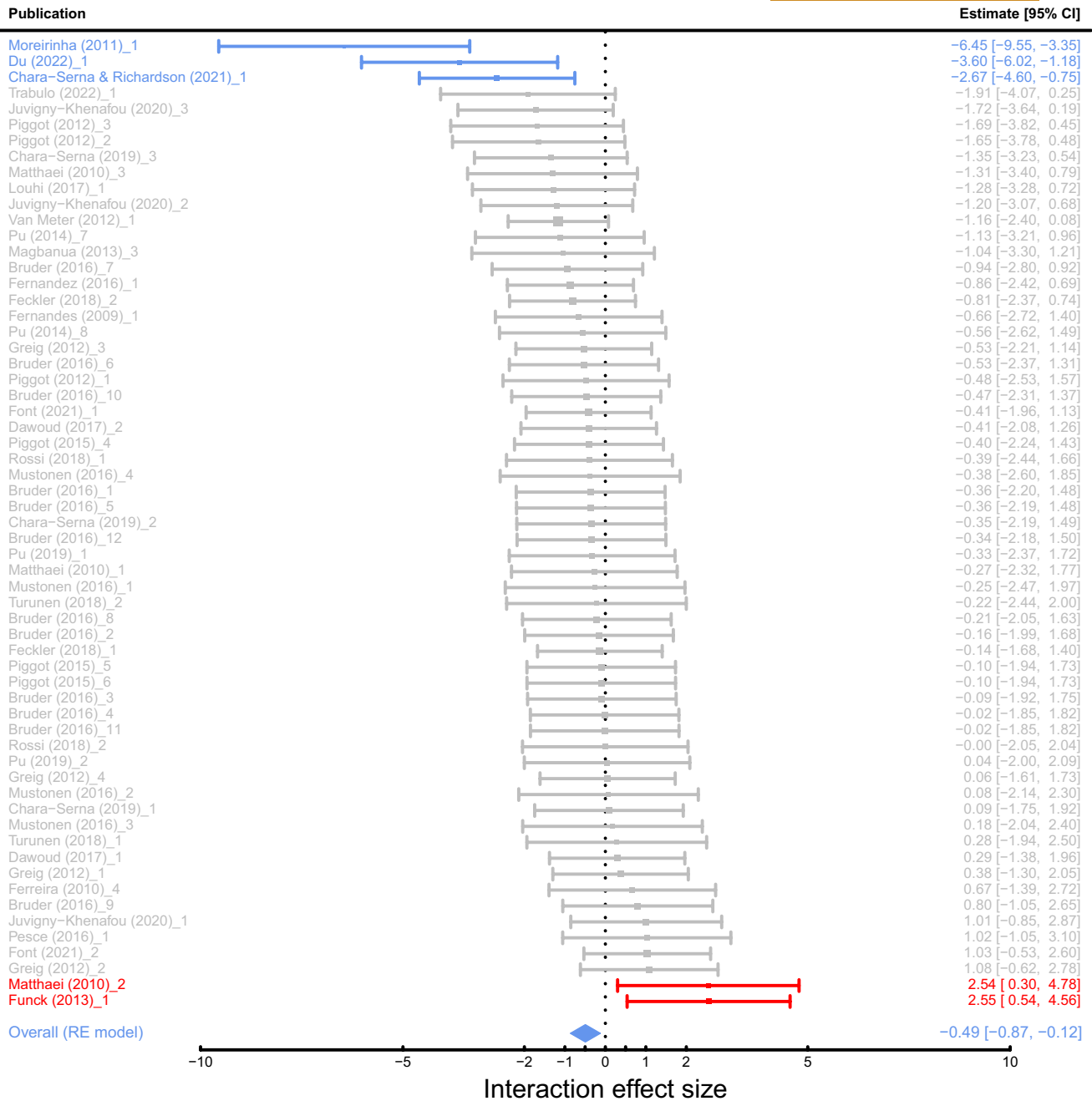


FIGURE 3 Observed interactions ($n=61$) used in this meta-analysis. Interaction effect sizes were classified as additive (95% CI overlapping zero; $n=56$; grey), antagonistic (combined effect of stressors is less than the sum of their single effects; $n=3$; blue), and synergistic (combined effect of stressors is greater than the sum of their single effects; $n=2$; red). The publication column indicates the first author, year and observation (see: Section 2.1)

4 | DISCUSSION

Our study revealed an overall antagonistic interaction of multiple-stressor effects on leaf litter decomposition in freshwaters, rejecting our first hypothesis (H1). It suggests that the cumulative effect of paired stressors on litter decomposition was less than the sum of their single effects. The result of our meta-analysis contrasts with that of a previous meta-analysis (Jackson et al., 2016), where an overall additive interaction of multiple-stressor effects on litter decomposition was detected. This difference can be attributed

to the higher sample size in our study (27 experiments containing 61 observations) compared with that of Jackson et al. (2016; 8 experiments and 14 observations). The difference in the direction between individual and overall interaction effects likely reflects an increase in statistical power resulting from combining more studies in the meta-analysis (Lange et al., 2018). Moreover, the individual responses included in our study were dominated by interaction effect sizes with negative values but confidence intervals overlapping zero. Confidence intervals are dependent on sampling variances and meta-analysis provides a more robust estimate

TABLE 3 Effect sizes and other statistics resulting from random and mixed effect meta-analysis for the moderator variables included in this study.

Moderator	Moderator level	<i>g</i>	SE	Lower 95% CI	Upper 95% CI	<i>p</i> -value	<i>I</i> ²	<i>n</i>	Interaction type
Macroinvertebrate involvement	No MI	-0.547	0.305	-1.207	0.112	0.096	21.4	20	Additive
	With MI	-0.453	0.194	-0.782	-0.034	0.036		41	Antagonistic
Dispersal potential	No dispersal	-0.586	0.333	-1.315	0.143	0.105	22.16	19	Additive
	With dispersal	-0.421	0.196	-0.851	0.009	0.054		42	Additive
Mycorrhizal type	EcM	-0.462	0.226	-0.929	0.006	0.052	19.11	33	Additive
	AM	-0.379	0.147	-0.683	-0.075	0.017		27	Antagonistic
Habitat type	Lentic	-0.540	0.341	-1.638	0.559	0.214	25.04	9	Additive
	Lotic	-0.496	0.224	-0.964	-0.028	0.039		52	Antagonistic
Experiment duration	Intercept	-0.453	0.188	-0.828	-0.078	0.019	19.52	61	Antagonistic
	Slope	-0.234	0.158	-0.549	0.081	0.143			
Initial litter mass	Intercept	-0.578	0.205	-1.010	-0.148	0.012	18.56	47	Antagonistic
	Slope	-0.083	0.111	-0.301	0.1404	0.458			
Overall		-0.494	0.183	-0.874	-0.115	0.013	20.24	61	Antagonistic

Note: From left to right: Moderator explored, moderator level, Hedges' effect size (*g*), standard error (SE), lower and upper ends of the 95% confidence interval (CI), and *p*-value (significant values ($\alpha < 0.05$) in bold), *I*² statistic for heterogeneity, sample size (*n*) and resulting interaction type according to confidence intervals. Bold should be added to *p*-values < 0.050.

Abbreviations: AM, arbuscular mycorrhizae; EcM, ectomycorrhizae; MI, macroinvertebrate involvement.

TABLE 4 Thirteen most parsimonious models after fitting our 'full model' with variables reported for all our studies.

Ranking	Macroinvertebrate involvement	Dispersal potential	Mycorrhizal type	Habitat type	Experiment duration	df	Δ AIC	Weight
1			✓			5	0.00	0.18
2						3	1.06	0.11
3					✓	4	1.14	0.10
4			✓		✓	6	2.06	0.06
5			✓	✓		6	2.38	0.05
6	✓		✓			6	2.46	0.05
7		✓	✓			6	2.46	0.05
8		✓				4	3.16	0.05
9	✓					4	3.27	0.04
10				✓		4	3.35	0.03
11		✓			✓	5	3.46	0.03
12				✓	✓	5	3.49	0.03
13	✓				✓	5	3.51	0.03

Note: Cells with a check sign (✓) represent variables that were included in the model; df = degrees of freedom; Δ AIC = performing distance to the most parsimonious model according to Akaike's information criterion. Weight refers to the Akaike weights, representing the probability of the model being the most parsimonious model.

effect size and precision compared with individual studies (Cohn & Becker, 2003).

In addition, our findings highlight that the direction of stressor interaction effects depends on experimental conditions, such as the involvement of macroinvertebrates, litter quality (i.e. assumed from plant mycorrhizal association) and habitat type. The inclusion of macroinvertebrates in the litter decomposition process led to antagonistic interactions between stressors on litter decomposition (H2.1).

The process of litter decomposition involves both microbial and macroinvertebrate communities (Gessner et al., 1999; Graça, 2001). When stressors like warming or nutrient enrichment increase the activity of microbial decomposers, shredders may further accelerate the decomposition process (i.e. leading to synergistic interactions) because they prefer litter that is well conditioned by microbes (Foucreau et al., 2013). Instead, feeding activity of grazers (and to a lesser extent of shredders because they also consume fungi and

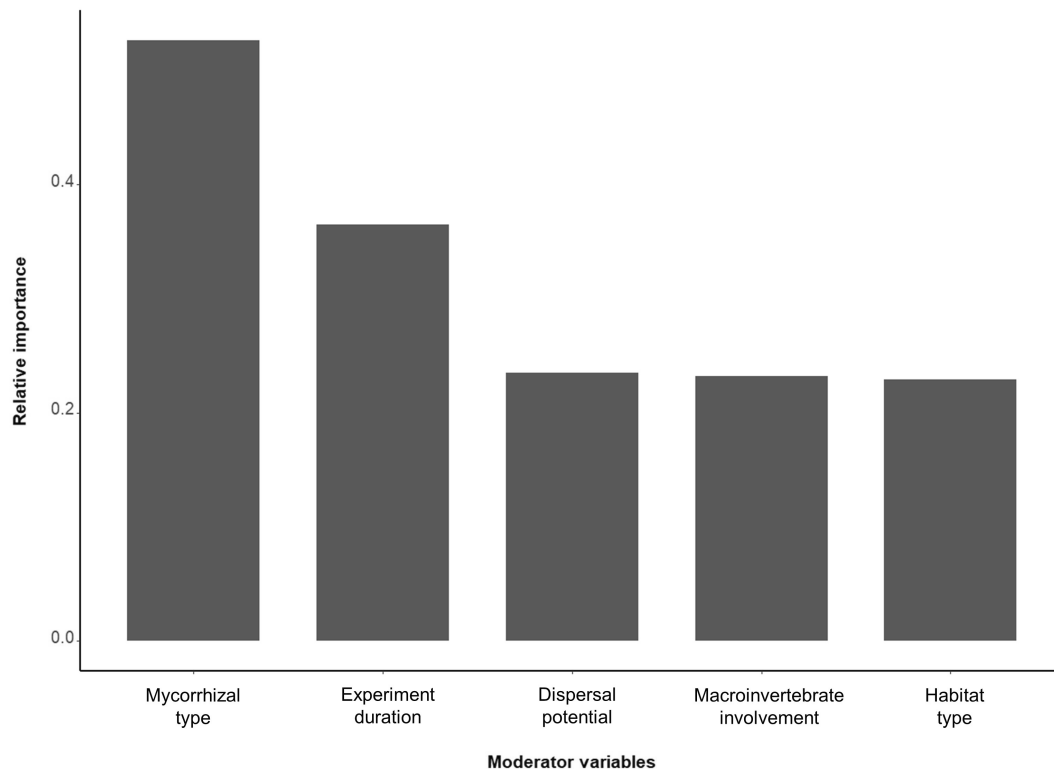


FIGURE 4 Relative importance of moderator variables in our full model (including variables reported for all studies).

bacteria when feeding on litter) can potentially control the excessive growth of microbial decomposers (Cibils Martina et al., 2014), decelerating the increased litter decomposition rate driven by stressors (i.e. causing antagonistic interactions). When stressors such as pesticides lead to increased mortality of microbial decomposers, grazers can remove dead biofilm on the surface of leaf litter and facilitate colonization of stressor-tolerant microbial decomposers (Calapez et al., 2020), enhancing litter decomposition. In addition, they may also increase nutrient availability to microbes through excretion (Schaller, 2013). Hence, the involvement of macroinvertebrates can drive multiple-stressor effects on litter decomposition into either direction, depending on the relative contributions of shredders and grazers.

The detected overall antagonistic interaction between stressors in our meta-analysis can be an amplified effect of grazer activity due to experimental settings. In multiple-stressor experimental designs, leaves are often used in small quantities and are not intensely compressed, allowing access to both grazers and shredders. In natural environments, grazers often only have access to superficial areas, and shredders are mostly responsible for the decomposition of under layers of leaf litter (Ruetz et al., 2002). The increase in relative leaf litter area exposed to grazers under experimental conditions may have amplified the effects of their interactions with microbial decomposers. In addition, the inclusion of macroinvertebrates in experiments increases the overall diversity and trophic complexity of the system and could therefore enhance its resilience capacity (Downing & Leibold, 2010; Rideout et al., 2022).

Dispersal is a major driver of local diversity and community structure in freshwater ecosystems (Cottenie & De Meester, 2004), as well as a promoter of regional recovery after disturbance (Reed et al., 2000). Theoretically, enhanced dispersal has the capacity to mask the effect of stressors due to mass effects (Heino, 2013). However, different interaction types in systems with or without dispersal were not observed in our study, rejecting our hypothesis (H2.2). Similar results have been observed in another mesocosm study (Turunen et al., 2018) where additive effects were observed despite enhanced dispersal. A reason for this could be the limited duration of manipulative experiments (mean = 33 days), which could have hampered our ability to see the effects of dispersal reducing the effects of stressors on freshwater litter decomposition. Indeed, a model designed by Traas et al. (2004) showed that the recovery of some decomposer taxa after exposure to combined stressors, might take up to 10 weeks to initiate when immigration was allowed, and recovery without immigration was observed only after 180 days. Given the importance of time to observe the effect of metacommunities under stress (Jackson et al., 2021), and the importance of metacommunity to monitor freshwater ecosystems (Cid et al., 2020), we call for more studies spanning over longer periods of time that explicitly consider dispersal and connectivity as a potential driver of stressor interactions, and for experiments that include recovery phases to better predict the responses of ecosystem functions to multiple stressors in freshwater ecosystems.

Our results supported hypothesis H2.3 and emphasized the impacts of litter quality on litter decomposition processes in

freshwaters. Litter derived from AM-associated and EcM-associated plants differ in chemical properties and decomposition rates (Keller & Phillips, 2019). Compared with EcM-associated litter, AM-associated litter could offer a continuous supply of high-quality food (e.g. higher nitrogen:carbon ratio and lower lignin concentration) to both macroinvertebrates and microbial decomposers (Yue et al., 2022). The quality of food resources for decomposers may have a strong influence on their responses to multiple stressors. For example, the better availability of high-quality food for decomposers may increase their resilience to stressors that reduce their fitness and activities. Deducing broader implications of this outcome would require further empirical studies to reveal the underlying mechanisms. For example, future studies need to investigate the influence of litter quality (e.g. litter stoichiometry) on litter decomposition processes under multiple stressors (Robbins et al., 2023).

We observed distinct stressor interactions between lotic and lentic ecosystems (H2.4), which reflects the influence of water flow on decomposer activities. Indeed, flowing waters have been associated with higher fungal biomass and therefore decomposer activity (Bruder et al., 2016; Schlieff & Mutz, 2009), increasing the palatability of leaf material for shredders. Flow can also stimulate the diffusion of oxygen within leaf packs, promoting leaf litter decomposition (Liu et al., 2022). When stressors such as sedimentation are present, flow disturbance can help remove sediment and debris from the litter surface, providing more space for microbial colonization. Some stressors (e.g. nutrient enrichment and warming) might enhance microbial activity and accelerate litter decomposition. Fast flow can reduce microbial biomass and control the excessive growth of periphytic biofilm (Biggs et al., 1998), leading to antagonistic stressor interactions.

Experimental duration presented an initial antagonistic interaction with slight trends to even more antagonistic interactions (H2.5). This trend was not statistically significant, likely due to sample size: only a handful of experiments were performed for over 60 days ($n=3$). However, ecosystem functions might have the capacity to exhibit resilience against the effects of co-occurring stressors, and develop antagonistic interactions over time (Romero et al., 2019). Some mechanisms that could play a role in counteracting additive stressor effects are related to ecological memory (Jackson et al., 2021), such as acclimation (Allison et al., 2013), or adaptation to stressors. Similarly, our hypothesis that higher litter mass is associated with more antagonistic interactions (H2.6) was not fully supported (i.e. the model slope was not statistically significant). Given that all experiments cover a relatively short time span with small amounts of leaf matter, more studies are warranted to investigate multiple-stressor effects on litter decomposition, which could help link multiple-stressor research to management actions.

Although the statistical tests supported the robustness of our meta-analysis, we acknowledge the existence of limitations in our study. The included studies were limited to only a few countries, which may restrict the generalizability of the findings to a broader range of freshwater ecosystems and climates. While there has been an increase in manipulative multiple-stressor experiments

in freshwaters (He et al., 2023), our sample size remains relatively small, which affects statistical power and the representativeness of observed responses. Classifying stressor interactions into additive, antagonistic, synergistic (Piggott et al., 2015) and reversals (Jackson et al., 2016) allows for comparability between studies and processes. However, we recognize that this approach might oversimplify things, especially for processes where any category can result in an increase or decrease compared with a control (e.g. litter decomposition). Therefore, interpretations must be done carefully, by considering the underlying mechanisms driving such responses, the organisms and stressors involved, as well as the aims of the research study, and in some cases, even re-scaling and analysing relative responses (Tekin et al., 2020) is relevant to disentangle the effects of multiple stressors on ecosystem functions.

Furthermore, limited data prevented a comprehensive assessment of the effect of the stressor categories involved in the development of interactions, which can be an important factor in determining the magnitude and direction of interaction effect sizes. Therefore, we advocate for more studies on the potential interactions of emerging stressors, which are increasingly common in freshwater ecosystems (Reid et al., 2019), and that provide more data to perform analyses that can supply important insights for the management of freshwater ecosystems. Moreover, a vast majority of multiple-stressor experiments is performed with a mesocosm setup, which could potentially bias our results to lotic conditions with similar experiment designs. Nevertheless, the variability of the studies in terms of stressor combination and litter types used remains valuable. Additionally, the temporal dynamics of stressors were rarely explored in the included studies, despite the influence of timing and duration on ecological responses (Jackson et al., 2021). Understanding how stressors manifest and interact during different trajectories of stressor increase and release is crucial for a more holistic assessment (Vos et al., 2023). Given the rapid growth in multiple-stressor studies over time (He et al., 2023), a meta-analytic approach could be a promising tool to improve our understanding of the interactive effects of multiple stressors on different ecosystem processes.

The insights derived from our meta-analysis have the potential for improving multiple-stressor research and environmental management in freshwater ecosystems. Considering the specific characteristics of an ecosystem, including the presence of particular litter species and decomposer communities, as well as the local stressor combinations, their scale and temporality can inform tailored interventions that align with the unique ecological dynamics of the system (Jackson et al., 2021). Furthermore, our study selected only extreme responses, to allow for comparability in terms of external moderators and provide inferences about the mechanisms they can influence, which could have played a role in the type of interactions observed (Schäfer & Piggott, 2018). For example, King et al. (2022) observed that the development of interactions is highly dependent on the level of the stressor and the duration it is applied. Therefore, it is advisable for multiple-stressor research studies aiming to predict interactions resulting from combined stressors, to incorporate realistic

gradient frameworks that allow to disentangle the effects of stressors in ecosystem functions (Orr et al., 2022; Turschwell et al., 2022). We emphasize the need to include more ecological complexity (Bruder et al., 2019; Simmons et al., 2021) in freshwater multiple-stressor research, to be able to communicate comprehensive and relatable results to environmental practitioners. Ecological complexity could be addressed by assessing the impact of local trophic entities (e.g. macroinvertebrates, fungi and bacteria), biological mechanisms (e.g. trophic interactions), habitat types, as well as a more diverse selection of litter species, inclusion of locally relevant stressor combinations and intensities (Lange et al., 2018). Future studies can expand the temporal and spatial scales of experimentation to resemble natural systems and improve the transferability of research results to management actions (Orr et al., 2020).

5 | CONCLUSIONS

Our study synthesized the findings of manipulative experimental studies focusing on multiple-stressor effects on litter decomposition in freshwaters. We systematically collected and analysed reported responses from published research with a meta-analytical approach. The individual interactive effects of multiple stressors on litter decomposition in freshwaters were predominantly additive (91%). However, our meta-analysis revealed an overall antagonistic interaction between stressors across all identified studies, indicating that the overall cumulative effect of paired stressors on litter decomposition was less than the sum of their single effects. The involvement of macroinvertebrates in litter decomposition, the type of habitat mimicked by the experimental system and the quality of the litter used (assumed from plant mycorrhizal association) showed the potential to shape stressor interactions. Therefore, it is important to consider characteristics of local ecosystems (e.g. habitat types, composition of riparian plants and biotic interactions) and the impacts of scales (e.g. temporal and spatial) in experimental design to improve prediction of multiple-stressor effects on litter decomposition in different freshwater ecosystems and provide insights for targeted management strategies. Finally, we highlight the need for integrated management strategies that consider local complexity to effectively address challenges posed by multiple stressors in freshwater ecosystems. Encompassing various organism groups and considering local biotic interactions can optimize conservation and restoration efforts, particularly by adopting a metacommunity framework for managing stressors and facilitating the recovery of biodiversity and ecological functions in freshwater ecosystems.

AUTHOR CONTRIBUTIONS

GMM and FH conceived the ideas and designed the methodology. GMM, RA, IM and FH collected the data. GMM analysed the data. GMM and FH led the writing of the first draft with substantial inputs from VF, GMD and SCJ. All authors contributed critically to the drafts and gave the final approval for publication.

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CONFLICT OF INTEREST STATEMENT

The authors have declared no conflicts of interest for this article. Verónica Ferreira is an Associate Editor of *Functional Ecology*, but took no part in the peer review and decision-making processes for this paper.

DATA AVAILABILITY STATEMENT

All extracted data that were used for the meta-analysis can be located in (<https://doi.org/10.18728/igb-fred-877.1>; Medina Madariaga et al., 2024).

STATEMENT OF INCLUSION

Our research involved a global review and utilized a meta-analysis of existing data instead of collecting new data. Therefore, we did not conduct data collection at a local level. Nonetheless, the authors come from diverse geographical regions, aligning with the primary regions of interest in the meta-analysis. Whenever relevant, studies published by researchers from different regions were cited.

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SUPPORTING INFORMATION

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

Table S1. Ten major stressor categories included in our meta-analysis.

Table S2. Name and levels of the categorical moderator variables included in our study with the criteria used for their classification.

Figure S1. Conceptual model of multiple stressor interactions [modified from Lange et al. (2018) and Piggott et al. (2015)].

Figure S2. PRISMA diagram depicting the information flow during the literature search and screening protocols implemented in this meta-analysis (O'Dea et al., 2021).

Figure S3. Funnel plot illustrating the interaction effect sizes (Hedges' *g*) of litter decomposition under two stressors in freshwater ecosystems against the standard error.

Figure S4. The relationship between standardized interaction effect sizes (Hedges' *g*) and pooled sample sizes.

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