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Effects of elevated atmospheric CO_2 concentration and temperature on litter decomposition in streams: A meta-analysis

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Abstract
The metabolism of forest streams depends on the decomposition of plant litter of terrestrial origin. In turn, the rate at which litter decomposes depends on litter characteristics, decomposer activity, environmental characteristics, and their interactions. Atmospheric changes, such as increases in atmospheric carbon dioxide concentration ([CO_2]) and in temperature, may affect all these variables. Here, we report the results of a meta-analysis of 41 studies conducted worldwide between 1993 and 2017 on the effects of elevated atmospheric [CO_2], elevated temperature, or both (temperature + [CO_2]) on litter decomposition in streams. Elevated temperature significantly increased litter decomposition rates, whereas elevated [CO_2] and temperature + [CO_2] did not significantly affect litter decomposition rates. The effect of elevated temperature did not depend on the type of study (i.e., laboratory or field study, correlative field or manipulative field study) but in correlative field studies, the temperature effect was stronger over latitudinal than altitudinal gradients. Effects of elevated temperature also did not depend on the type of decomposer community (microbial or microbial and macroinvertebrates) but effects were always significant for total litter decomposition (both microbes and macroinvertebrates involved), whereas microbial-driven litter decomposition was significantly affected only in manipulative studies. Effects of elevated temperature did not depend on the litter identity, although significant effects were found for some litter genera but not others. In terrestrial ecosystems, the elevated temperature was found to increase litter decomposition rates, whereas elevated [CO_2] decreased litter decomposition rates. Study type (laboratory or field) and litter identity were important moderators of the response of litter decomposition to elevated temperature and [CO_2] in terrestrial ecosystems. These differences between soil and stream ecosystems may be partially due to intrinsic differences (such as moisture that is not limiting in streams) between these ecosystems. In addition, our meta-analysis is geographically biased with most studies being conducted in Europe. More studies in other parts of the world could allow for a better understanding of the effects of climate warming and [CO_2] increases on litter decomposition, the global carbon cycle, and biochemistry in streams.

KEYWORDS
climate change, detritivores, effect size, moderators, systematic review

1 | INTRODUCTION

Between 1750 and 2011, atmospheric [CO_2] has increased by approximately 40%, from 280 parts per million (ppm) to 391 ppm and it is expected to reach 936 ppm by the end of the 21st century (IPCC, 2013). If the emissions of greenhouse gases (particularly CO_2) continue at the current pace, temperature is expected to rise by up to 4.8°C by the end of this century (IPCC, 2013). Global warming will likely lead to changes in global species distribution (Hufnagel & Garamvölgyi, 2014), phenology (Miller-Rushing & Primack, 2008; Parmesan, 2006), and reduction in body size of organisms (Gardner, Peters, Kearney, Joseph, & Heinsohn, 2011). Global warming and increases in atmospheric [CO_2] are also likely to affect organisms' metabolism (Brown, Gillooly, Allen, Savage, & West, 2004) and tissue chemistry (Rier, Tuchman, Wetzel, & Teeri, 2002; Tuchman, Wahtera, Wetzel, & Teeri, 2003), which, in turn, may eventually affect the ecosystem processes.

One process potentially affected by elevated [CO_2] and temperature is litter decomposition in soils and streams. Allochthonous plant litter is the main source of energy and carbon for woodland streams (Minshall et al., 1985; Vannote, Minshall, Cummins, Sedell & Cushing, 1980; Wallace et al. 1997). This litter is incorporated into aquatic food webs or mineralized by microbes and detritivores (Abelho 2001; Graça, 2001; Hieber & Gessner, 2002).

Under elevated atmospheric [CO_2], plants invest the surplus carbon in primary and secondary carbon-based molecules resulting in the overproduction of recalcitrant compounds (Peñuelas & Estiarte, 1998; Poorter et al., 1997; Stiling & Cornelissen, 2007). This overinvestment in recalcitrant compounds is more significant in plant species that generally produce fast-decomposing litter under ambient atmosphere (Hemming & Lindroth, 1995; Kinney, Lindroth, Jung, & Nordheim, 1997) and C_4 plant species are less responsive to elevated CO_2 than C_3 species (Reich, Hobbie, Lee, & Pastore, 2018). Recalcitrant compounds decrease the palatability of plant litter to consumers (Rier et al., 2002; Tuchman et al., 2003), which decreases the rate at which plant litter decomposes (Fernandes, Seena, Pascoal, & Cássio, 2014; Ferreira, Castagneyrol, et al., 2015; Ferreira, Chauvet, & Canhoto, 2015; Martínez et al., 2016).

However, studies that addressed the effects of elevated [CO_2] on litter decomposition rates have found contrasting results. Although plants grown under elevated [CO_2] were reported to produce slow-decomposing litter (i.e., higher concentrations of phenolic compounds, condensed tannins, lignin, and C:N; Rier et al., 2002; Tuchman et al., 2003) some authors have reported that although phytochemical composition was affected by increases in [CO_2], this did not result in measurable changes on litter decomposition rates (Ferreira & Chauvet, 2011a; Martins, Melo, Gonçalves, Campos, & Hamada, 2017; Monroy et al., 2016).

A second effect of elevated [CO_2] is the increase in temperature. Temperature rise may increase litter decomposition by stimulating metabolic and consumption rates of litter microbial decomposers and detritivores (Azevedo-Pereira, Graça, & González, 2006; Ferreira & Chauvet, 2011a, 2011b; González & Graça, 2003). Increases in temperature can also accelerate litter decomposition by stimulating the leaching of secondary refractory compounds, such as polyphenols (Mas-Martí, Muñoz, Oliva, & Canhoto, 2015), which have antimicrobial activity (Canhoto & Graça, 1999). Accordingly, both field (Fabre & Chauvet, 1998; Martínez, Larrañaga, Pérez, Descals, & Pozo, 2014; Taylor & Chauvet, 2014) and laboratory studies (Dang, Schindler, Chauvet, & Gessner, 2009; Ferreira & Chauvet, 2011a, 2011b; Martínez et al., 2014) have shown litter decomposition rates to increase with temperature.

The decomposition of different organic substrates may exhibit differences in their sensitivity to temperature increase. Fast-decomposing litter types (i.e., those rich in nutrients and poor in recalcitrant compounds) may be more sensitive to elevated temperatures than slow-decomposing litter types for which decomposers' activities may be nutrient limited (Ferreira, Castagneyrol, et al., 2015; Ferreira, Chauvet, et al., 2015; Martínez et al., 2016) but this is still under debate (Rier et al., 2002). Temperature increase may also affect microorganisms and insect detritivores in different ways. Total litter decomposition (driven by microbial decomposers plus detritivores) was stimulated by elevated temperature to a larger extent than microbial-driven litter decomposition (Friberg et al., 2009; Martínez et al., 2016).

The effect of increases in temperature may, however, depend on ambient temperature. For instance, experimental warming in a forest stream stimulated litter decomposition rates in colder but not in warmer months (Ferreira & Canhoto, 2014, 2015). Although moderate warming accelerates the metabolism of microbial decomposers, litter decomposition may nevertheless decrease under a warming scenario because of the inhibitory effects on stream detritivores (Boyero, Pearson, Gessner, et al., 2011; Graça et al., 2015).

These contrasting results among primary studies could result from small sample sizes, relatively small ranges of [CO_2] or temperature differences between elevated and ambient treatments, differences in experimental settings or from confounding environmental variables. Here, we combine the results of published primary studies in a meta-analysis. These studies were published between 1993 and 2017 and analyzed the effects of elevated [CO_2] and temperature on litter decomposition in streams. Specifically, the objectives of this study are: (a) to estimate the magnitude and direction of effect size of elevated [CO_2], elevated temperature, or both (temperature + [CO_2]) on litter decomposition and (b) to test the effects of study characteristics (such as experimental approach, decomposer community involved, and litter identity) on litter decomposition. Specific questions addressed and hypotheses tested are listed in Table 1.

2 | METHODS

2.1 | Literature search and inclusion criteria

This meta-analysis summarizes the findings of primary studies that addressed the effects of elevated atmospheric [CO_2] and/or elevated

TABLE 1 Questions and hypotheses addressed and the data sets used by the present systematic review

Questions	Hypotheses	Data set	Results
1. Do atmospheric changes (elevated temperature, elevated [CO_2] or both) affect the decomposition of litter in streams, and do the effects depend on the type of change?	H_{1a}: Elevated [CO_2] concentrations are expected to slow down litter decomposition because plants should invest more in structural and secondary compounds under elevated [CO_2] and litter rich in such compounds is known to be of low palatability and to be colonized and decomposed slower compared with litter with a lower concentration of such compounds	[CO_2]	Figure 2
	H_{1b}: Elevated temperature is expected to stimulate plant litter decomposition by stimulating metabolic activities of microbes and detritivores involved in litter decomposition	Temperature	Figure 2
	H_{1c}: Elevated temperature increases litter decomposition while elevated [CO_2] inhibits litter decomposition, the combined effect of temperature + [CO_2] should be nonsignificant	Temperature + [CO_2]	Figure 2
2. Does the response of litter decomposition to elevated temperature depend on the type of study (laboratory vs. field; type of field study)?	H_2: Litter decomposition in laboratory studies may be more strongly affected by increases in temperature than litter decomposition in field studies due to better replication and control in the laboratory. For field studies, this effect may be stronger for manipulative studies than for correlative studies	Temperature	Figure 3a
3. Does the response of litter decomposition to elevated temperature depend on litter identity (genus)?	H_3: Fast-decomposing litter (i.e., soft with high nutrient concentration) may be more responsive to elevated temperature than slow-decomposing litter as the potentially stimulatory effect of elevated temperature could be limited in the latter (e.g., due to nutrient limitation)	Temperature, laboratory studies	Figure 3b
		Temperature, correlative altitudinal field studies	Figure 4
		Temperature, correlative seasonal field studies	Figure 4
4. Does the response of litter decomposition to elevated temperature depend on the type of decomposers involved (microbes only or microbes plus invertebrates)?	H_4: Litter decomposition mediated by both macroinvertebrates and microorganisms may be more sensitive to elevated temperature than microbial-driven litter decomposition as the effect of warming on microbes might be amplified by invertebrates, which are strongly affected by the conditioning level of the detritus	Temperature, manipulative field studies	Figure 3b
		Temperature, correlative altitudinal field studies	Figure 4
		Temperature, correlative seasonal field studies	Figure 4
5. Does the response of litter decomposition to elevated temperature depend on the magnitude of increase?	H_5: The higher the increase in temperature the stronger the effects on litter decomposition	Temperature	Table 2

temperature (by at least 1°C, the smallest temperature increase predicted by the end of the 21st century; IPCC, 2013) on allochthonous plant litter decomposition in streams. Studies published in international and national journals or as theses were located using personal databases, electronic journal indices, and electronic reference databases (Google Scholar and Web of Science) considering the time period between January 1970 and November 2017.

In Google Scholar and Web of Science, primary studies were found using combinations of the following keywords: "decomposition OR processing OR breakdown OR decay" for the process, AND "litter OR leaf OR leaves OR bark OR wood OR organic matter" for the substrate, AND "temperature OR warming OR carbon dioxide OR CO_2" for the stressor, AND "freshwater" for the system. Publication lists of researchers known to work on litter decomposition and reference lists in papers were surveyed as well for potentially relevant primary studies.

Different experimental approaches were used across studies and thus data were shown (a) as the comparison of two groups (e.g., ambient vs. "elevated" conditions) in terms of continuous variables (e.g., litter decomposition) or (b) as the relationship between two continuous variables (e.g., litter decomposition rates across a gradient of temperature). Only primary studies that fulfilled the following criteria were selected: In the first case (a), studies had to report decomposition of natural litter (in any unit) in at least one ambient and one elevated condition, sample sizes (n) for both ambient and elevated conditions, and measurements of variance (i.e., standard deviation [SD], standard error [SE], or confidence limit [CL]) for litter decomposition estimates for both ambient and elevated conditions (not necessarily mandatory in all cases); in the second case (b), studies had to report the Pearson r (or enough information to allow its estimation) and sample size. The application of these criteria resulted in the selection of 41 studies (marked with "*" in the Reference section).

2.2 | Data extraction

Data were obtained from graphs, tables, text, or directly from authors. When the means and measurements of dispersion (generally *SE*) were available in graphs only, they were extracted using WebPlotDigitizer v4.1 (Rohatgi, 2018). For studies that reported decomposition data at multiple dates, data of the latest date were considered. For studies that reported multiple decomposition data along with temperature gradients, the Pearson *r* was estimated by correlating litter decomposition to temperature. When available, *SE* values were converted into *SD*s. In the few cases in which no measure of dispersion associated with mean values was provided, *SD* values were imputed considering the mean *SD* values from other similar conditions for which mean values and *SD* values were provided (Lajeunesse, 2013). Extracting, estimating, and imputing data might introduce errors and bias the results, but excluding studies with missing information would have limited the analyses. Thus, an effort was made to include the maximum number of ambient—elevated comparisons. The potential for bias due to the inclusion of "estimated" cases was assessed using sensitivity analyses.

2.3 | Effect size

The effect size is a value that reflects the magnitude of the effect of a treatment or the strength of the relationship between two variables (Borenstein, Hedges, Higgins, & Rothstein, 2009). Where primary studies reported data as the comparison of two groups in terms of continuous variables ($n = 35$), effect sizes were calculated as the standardized mean difference Hedges' *g*, using the mean decomposition values (X_{ambient} and X_{elevated}), associated standard deviation (SD_{ambient} and SD_{elevated}), and sample size (n_{ambient} and n_{elevated}) (Borenstein et al., 2009), which resulted in 175 effect sizes (Table S1). The variance associated with Hedges' *g* (*Vg*) was calculated to weight the effect size by its precision in the analysis. For studies that reported data as the correlation between litter decomposition and continuous variables (i.e., temperature; $n = 6$), the Pearson *r* was taken (or estimated) as the effect size and then converted to Hedges' *g* (Borenstein et al., 2009), which resulted in 10 effect sizes (Table S1). Many studies contributed with multiple effects sizes to the database, which might affect the results if the nonindependence of effect sizes is a problem. However, not considering them would have restricted the analyses by reducing sample size (i.e., number of available effect sizes) and moderators. Multiple effect sizes per study were thus considered but their impact on the results was assessed using sensitivity analyses.

2.4 | Moderators

Variables that might affect the magnitude and direction of the response are called moderators (Borenstein et al., 2009). These can be environmental or methodological factors that vary across studies (Ferreira, Castagneyrol, et al., 2015; Ferreira, Chauvet, et al., 2015). The moderators we included (Table 1) were the type of change (elevated temperature, elevated [CO_2], or both), type of study (laboratory or field), type of field study (correlative or manipulative), type of correlative study (altitudinal, geothermal, latitudinal, or seasonal), type of aquatic decomposer community (microbial or total: microbes plus invertebrates), and litter genus (Table S2). The origin of data was not included in the hypotheses, but it was used in sensitivity analyses (reported or estimated; Table S2).

2.5 | Statistical analyses

Meta-analysis is a statistical approach that allows for a quantitative synthesis of primary studies, taking into account their precision, to produce a summary of the findings and assess causes of heterogeneity among them (Borenstein et al., 2009; Hedges, Gurevitch, & Curtis, 1999; Suurmond, van Rhee, & Hak, 2017). The random-effects model of meta-analysis was used, with between-study variance estimated by the restricted maximum likelihood (REML) method. Statistical analyses were performed using the *metaphor* package (Viechtbauer, 2010) on RStudio (R Core Team, 2013).

2.5.1 | Subgroup meta-analysis

The effects of categorical moderators on the response of litter decomposition to environmental changes were assessed for subsets of the database according to our questions (Table 1), available sample size (only levels with $n \geq 3$ were tested within a given moderator), and robustness of the data subset to publication bias. Mean effect sizes (Hedges' *g*) for the levels within given moderators were estimated and compared by subgroup analyses, using the random-effects model of meta-analysis (REML method). To avoid potential confounding factors, moderators were tested hierarchically (Figure 1). The overall differences between the three stressors (elevated temperature, elevated [CO_2], and elevated temperature + [CO_2]) were tested first using the entire database. For the temperature data set, we then first tested for differences in the overall effect size between laboratory and field studies (Figure 1). Thereafter, analyses were performed separately for both laboratory and field studies. For field studies, the difference between manipulative and correlative studies was tested. Further analyses were performed separately for both manipulative and correlative studies. No further analyses were possible for the elevated [CO_2] data set due to low sample size for levels within moderators ($n < 3$) and for the temperature + [CO_2] subset as it was potentially affected by publication bias (i.e., the effect size lacked statistical robustness; see Section 2.5.4).

2.5.2 | Meta-regression

Weighted metaregressions, which are equivalent to regular regressions, with the difference that more precise studies are assigned a larger weight, were used to investigate the relationship between effect sizes (Hedges' *g*) and temperature increase within given data subsets: laboratory, field correlative studies, and field manipulative studies.

Moderator										
		All (n=175)								
Stressor	Temp+[CO_2] (n = 19)	[CO_2] (n = 8)	Temp (n = 148)							
Study type			Laboratory (n = 57)	Field (n = 91)						
Field type				Manipulative (n = 20)	Correlative (n = 71)					
Correlative type					Altitudinal (n = 32)	Latitudinal (n = 22)	Geothermal (n = 2)	Seasonal (n = 15)		
Community type								Total (n = 12)	Microbial (n = 3)	
Litter genus								*Alnus* (n = 5)	*Populus* (n = 6)	*Quercus* (n = 4)
Study type			Laboratory (n = 57)							
Litter genus			*Alnus* (n = 31)	*Quercus* (n = 9)	*Eucalyptus* (n = 4)	*Melicytus* (n = 7)	*Vitis* (n = 1)	*Platanus* (n = 1)	*Nothofagus* (n = 2)	*Betula* (n = 2)
Field type				Manipulative (n = 20)						
Community type				Total (n = 7)	Microbial (n = 13)					
Correlative type					Altitudinal (n = 32)					
Community type					Total (n = 19)	Microbial (n = 13)				
Litter genus					*Alnus* (n = 13)	*Quercus* (n = 6)	*Fagus* (n = 4)	*Acer* (n = 5)	*Macaranga* (n = 2)	*Liriodendron* (n = 2)
Stressor		[CO_2] (n = 8)								
Study type		Laboratory (n = 2)	Field (n = 6)							
Community type			Microbial (n = 4)	Total (n = 2)						
Stressor	Temp+[CO_2] (n = 19)									
Litter genus	*Eperua* (n = 6)	*Goupia* (n = 6)	*Hevea* (n = 6)	*Alnus* (n = 1)						

FIGURE 1 Schematic design of the database indicating the number of cases per moderator variable. *n*: number of effect sizes (refer to Table S2 for descriptions of moderator variables)

2.5.3 | Sensitivity analysis

Sensitivity analyses allow assessment of how decisions undertaken during the main analyses may have affected the results (Borenstein et al., 2009). To account for the potential effect of nonindependence of effect sizes on the results (given that several studies contributed with multiple effect sizes), the analyses were repeated using a single effect size per study. Using subgroup analysis (with “study” as the categorical moderator), single effect size was estimated per study, which was used to create a new data set with sample size (i.e., available effect sizes) equal to the number of studies. The analyses were repeated to the extent possible using this new data set and the significance and direction of the results were compared with those obtained using the main data set. The bias that might be introduced due to data estimation was also assessed by comparing results based on reported and estimated effect sizes by subgroup analyses.

2.5.4 | Publication bias

Sensitivity to publication bias in the data sets used in the analyses was assessed by the Rosenthal's fail-safe number (N_{fs}). When N_{fs} is larger than the threshold given by $5 \times n + 10$ (n is the number of effect sizes), the data set is robust to publication bias (Borenstein et al., 2009).

3 | RESULTS

3.1 | Data description

Thirty out of 41 (73%) studies included in this meta-analysis were conducted in Europe, three (7%) studies in the United States, two (5%) in Brazil, and one (2.4%) in each of Canada, Chile, Malaysia, New Zealand, and USA–Costa Rica (this study was conducted in both the

United States and Costa Rica). One study covered latitudes ranging from 0.37° to 47.80° in both hemispheres. Most studies (88%) were conducted in temperate, 7% in tropical, and 5% simultaneously in temperate and tropical regions. Thirty-three, six, and three studies addressed, respectively, the effects of elevated temperature, elevated [CO_2], and elevated temperature + [CO_2] on litter decomposition in streams. For stressors, the study Ferreira and Chauvet (2011a) was used twice because it provided enough data to be considered for both the temperature and temperature + [CO_2] data sets.

Twenty-five (61%), fifteen (36.6%), and one (2.4%) studies were carried out in the field, laboratory and both laboratory and field, respectively. Total litter decomposition, that is, driven by both microbes and invertebrates, was reported in 57% of the studies whereas microbial-driven decomposition was reported in 43%. Four of the 41 studies were conducted between 1990 and 1999, six studies between 2000 and 2009, and 31 studies between 2010 and 2017.

3.2 | Effects of moderators on the response of litter decomposition to elevated [CO_2] and temperature

Elevated temperature (Hedges' g = 1.20, 95% CL: 0.96–1.43) significantly and strongly stimulated litter decomposition whereas elevated [CO_2] (Hedges' g = –0.11, 95% CL: –1.13–0.91) and elevated temperature + [CO_2] (Hedges' g = –0.11, 95% CL: –0.75–0.54) did not significantly affect litter decomposition (Figure 2 and Table S3).

The effect of elevated temperature on leaf litter decomposition did not depend on the type of study (Q_B = 1.38, df = 1, p = 0.240), with a significant strong stimulation for both laboratory and field studies (Figure 3a and Table S3). The type of field study also did not affect the response of litter decomposition to an elevated temperature (Q_B = 0.38, df = 1, p = 0.536), with a significant strong stimulation for both manipulative and correlative studies (Figure 3a and Table S3). The type of correlative study significantly affected the response of litter decomposition to an elevated temperature (Q_B = 14.19, df = 2, p < 0.001), with stronger stimulation over latitudinal than over altitudinal gradients (Figure 3a and Table S3).

For laboratory studies, the response of litter decomposition to elevated temperature did not depend on plant identity (Q_B = 3.26, df = 3, p = 0.353), although the decomposition of *Alnus* and *Quercus* leaves was significantly stimulated, whereas that of *Eucalyptus* and *Melicytus* was not (Figure 3b and Table S3). For manipulative studies, the response of leaf litter decomposition to elevated temperature did not depend on the type of aquatic community involved in litter decomposition (Q_B = 2.32, df = 1, P = 0.128), with both microbial-driven and total litter decomposition being stimulated (Figure 3b and Table S3).

For studies conducted along altitudinal gradients, the elevated temperature had a significant stimulatory effect on microbial-driven litter decomposition and on the decomposition of *Fagus* leaves (Figure 4 and Table S3). For studies conducted across seasons, the elevated temperature had a significant stimulatory effect on total litter decomposition and on the decomposition of *Alnus* leaves (Figure 4 and Table S3).

There was no correlation between the response of litter decomposition and the magnitude of temperature increase for laboratory (p = 0.123) and manipulative studies (p = 0.245) (Table 2). There was a positive relationship between the response of litter decomposition and the magnitude of temperature increase for correlative studies (slope = 0.13, p < 0.001; Table 2).

3.3 | Sensitivity analysis

The magnitude of effect sizes for subgroup analyses considering a single effect size per study was generally similar or became smaller when compared with that found using the overall larger matrix but the direction and significance of the findings did not change and, consequently, conclusions remain largely the same. Thus, results based on the original matrix, which contains multiple effect sizes per study, are robust to the potential nonindependence of effect sizes.

Analyses comparing mean effect sizes based on reported and estimated data showed that the trends and interpretations remained generally the same, although stronger mean effect sizes were generally found based on reported data. The smaller mean effect sizes based on estimated data suggest that the results based on the original database are conservative (Table S5).

4 | DISCUSSION

Here, we address the effects of elevated [CO_2] and temperature on litter decomposition in streams. Elevated temperature significantly stimulated litter decomposition, whereas elevated [CO_2] and the

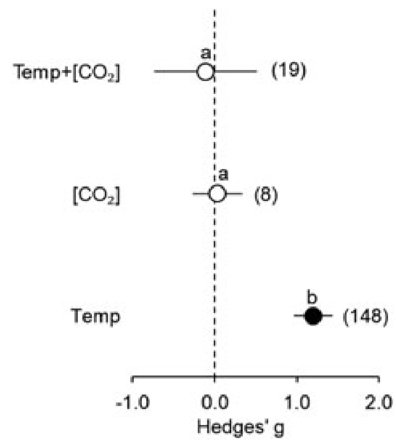

FIGURE 2 Effect (Hedges' g ± 95% confidence limit [*CL*]) of elevated temperature + [CO_2], elevated [CO_2] and elevated temperature on leaf litter decomposition in freshwater ecosystems. The dashed line (mean effect size = 0) indicates no effect; mean effect size > 0 indicates stimulation whereas mean effect size < 0 indicates inhibition. The effect is significant when the 95% CL does not overlap the no-effect line (black symbols). Levels with overlapping 95% CL do not statistically differ (same letter). Values in brackets are sample sizes

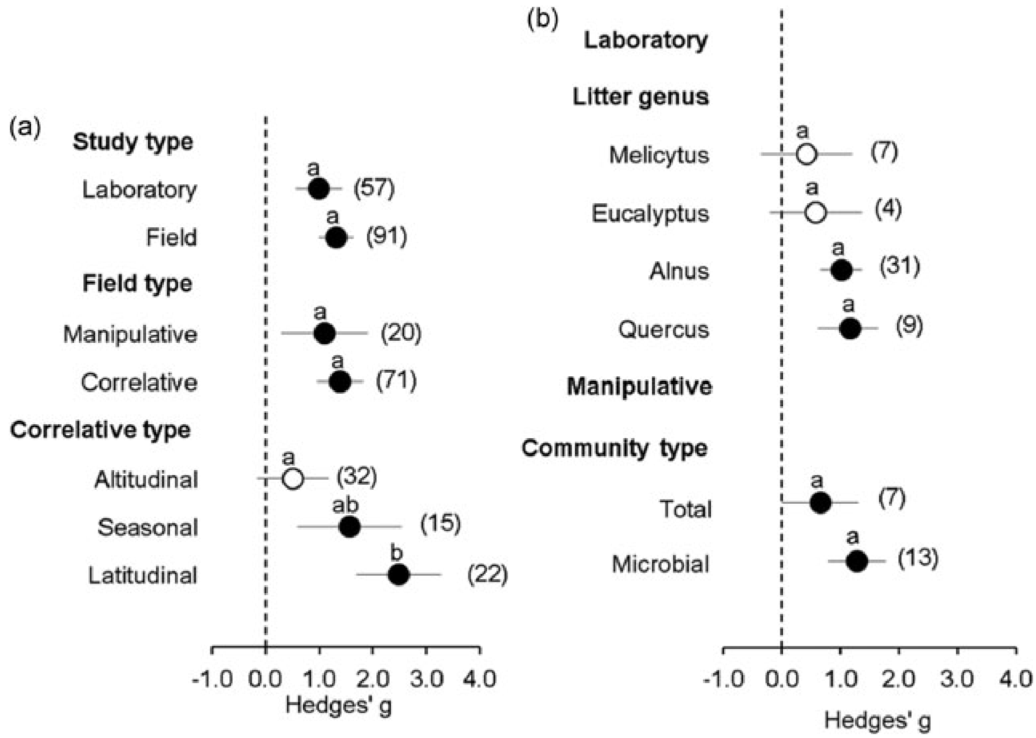

FIGURE 3 Effect (Hedges' $g \pm 95\%$ confidence limit [*CL*]) of elevated temperature on leaf litter decomposition as a function of study type (a) and for laboratory studies as a function of litter genus and for manipulative studies as a function of decomposer community type (b). The dashed line (mean effect size = 0) indicates no effect; mean effect size > 0 indicates stimulation whereas mean effect size < 0 indicates inhibition. The effect is significant when the 95% CL does not overlap the no-effect line (black circles). Levels with overlapping 95% CL within a given moderator do not statistically differ (same letter). Values in brackets are sample/effect sizes

combined effect of elevated temperature and [CO_2] did not significantly affect litter decomposition but the sample size was reduced in these two latter data sets and, therefore, these results need to be interpreted with caution.

4.1 | Do atmospheric changes (elevated temperature, elevated [CO_2] or both) affect the decomposition of litter in streams, and do the effects depend on the type of change?

Elevated temperature significantly increased litter decomposition rates, whereas elevated atmospheric [CO_2] and simultaneous increases in temperature and [CO_2] (temperature + [CO_2]) did not significantly affect litter decomposition.

Elevated temperature increases litter decomposition by increasing metabolic rates of microbial and macroinvertebrate decomposers (Azevedo-Pereira, et al., 2006; Flury & Gessner, 2011; González & Graça, 2003). Higher temperatures also promote leaching (Batista, Pascoal, & Cássio, 2012), which can result in fast litter decomposition by removing the recalcitrant compounds. Elevated temperatures, within species tolerance limits, can also increase fungal biomass, growth, and reproduction, which lead to higher litter decomposition rates (Chung & Suberkropp 2009; Moghadam & Zimmer 2016; Rajashekhar & Kaveriappa, 2000).

Elevated [CO_2] can decrease litter decomposition rates by producing slow-decomposing litter (Tuchman et al., 2003). When atmospheric [CO_2] is high, plants change their physiology and biochemistry by producing more carbon-based secondary and structural compounds (Stiling & Cornelissen, 2007). Among secondary compounds, polyphenols are known to delay litter decomposition through the complexation of digestive enzymes and exoenzymes produced by detritivores and microbes, respectively (Zucker, 1983). Therefore, our study hypothesized elevated [CO_2] to delay litter decomposition but small sample size may have prevented us from detecting an effect.

The effect of simultaneous increases in temperature and [CO_2] (temperature + [CO_2]) did not significantly affect litter decomposition but small sample size suggested that caution was needed when addressing this result. Under field conditions, it is difficult to distinguish between the effects of elevated [CO_2] and those of elevated temperature on litter decomposition, especially because they may have opposite individual effects. The literature also does not allow to clearly distinguish between both effects because studies addressing the effects of elevated temperature use litter grown under ambient [CO_2] (Fernandes et al., 2014; Ferreira, Castagneyrol, et al., 2015; Ferreira, Chauvet, et al., 2015) and studies addressing the effects of increases in atmospheric [CO_2] performed analyses either at ambient temperature (stream

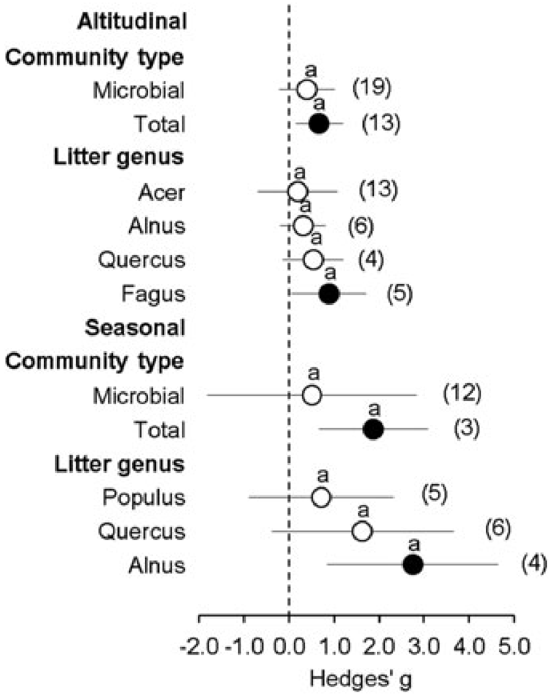

FIGURE 4 Effect (Hedges' $g \pm 95\%$ confidence limit [*CL*]) of elevated temperature on litter decomposition as a function of litter genus and decomposer community type in field altitudinal and seasonal studies. The dashed line (mean effect size = 0) indicates no effect; mean effect size > 0 indicates stimulation whereas mean effect size < 0 indicates inhibition. The effect is significant when the 95% CL does not overlap the no-effect line (black circles). Levels with overlapping 95% CL within a given moderator do not statistically differ (same letter). Values in brackets are sample sizes

incubations; Rier et al., 2002; Tuchman et al., 2003) or at different temperatures but without considering other changes associated with atmospheric increases in [CO_2] (laboratory trials; Ferreira & Chauvet, 2011a; Ferreira, Gonçalves, Godbold & Canhoto, 2010). Only the studies by Martins, Melo, et al. (2017) have addressed the combined effect of elevated temperature and [CO_2] on litter decomposition in chambers in which temperature and [CO_2] increased simultaneously and litter grown in each chamber was used in microcosms trials in the corresponding chamber, thereby simulating future scenarios in which [CO_2] and temperature will increase simultaneously. In these studies, it was also not possible to distinguish individual effects.

In studies that synthesized the effects of elevated temperature and [CO_2] in terrestrial ecosystems, the elevated temperature increased litter decomposition whereas elevated [CO_2] decreased litter decomposition (Yue et al., 2015). This meta-analysis of terrestrial ecosystems used 92 case studies for elevated [CO_2] whereas there were only eight case studies available for streams in our study. Therefore, the comparison of the effects of elevated [CO_2] on litter decomposition between terrestrial and stream systems should be done with caution.

TABLE 2 Correlations between effect sizes and increase in water temperature

Metaregressions	Hedges' *g*	95% CL	*p*
Laboratory studies			
Intercept	0.40	−0.28–1.09	0.246
Slope	0.07	−0.02–0.17	0.123
Manipulative studies			
Intercept	0.66	0.19–1.13	0.005
Slope	0.04	−0.03–0.12	0.245
Correlative studies			
Intercept	0.21	−0.49–0.89	0.560
Slope	**0.13**	0.08–0.19	**<0.001**

Note. Meta-regression was assessed using the laboratory, manipulative, and correlative studies data sets. Slopes and intercepts, associated 95% CL and *p*-values are given for the metaregressions. The slope > 0 indicates positive correlation or stimulation, whereas the slope < 0 indicates negative correlation or inhibition. Bold values indicate the significant correlation ($p < 0.050$).
CL: confidence limit.

4.2 | Does the response of litter decomposition to elevated temperature depend on the type of study (laboratory or field; type of field study: manipulative or correlative; type of correlative study: altitudinal, latitudinal or seasonal)?

We hypothesized the effects of elevated temperature to be stronger in more controlled conditions (i.e., in laboratory than in field studies and in field manipulative than in field correlative studies) due to the better control of confounding factors in the laboratory and manipulative experiments (Ferreira, Castagneyrol, et al., 2015; Ferreira, Chauvet, et al., 2015; Woodward, Perkins, & Brown, 2010). This was not the case in our meta-analysis and may be, partly, due to higher temperature ranges considered in field correlative studies. For example, Irons, Oswood, Stout, and Pringle (1994) considered a temperature range of 25°C in a latitudinal study that contributed 21 cases to the data set and Boyero, Pearson, Dudgeon, et al. (2011) considered a temperature range of 24°C, whereas the largest temperature range reported in laboratory studies was only 13°C (Batista, Pascoal, & Cássio, 2017).

In addition, confounding factors could have interacted synergistically with temperature in field correlative studies. Field studies allow the investigation of the effects of temperature under realistic conditions but they do not allow discrimination between the effects of temperature per se and other environmental variables that might exacerbate the effects of temperature on litter decomposition. For instance, litter decomposition rates are generally higher under increases in both temperature and dissolved nutrients than when temperature increases alone (Ferreira & Chauvet, 2011b; Martínez et al., 2014; Moghadam & Zimmer, 2016). Fine sediments in flowing waters can also accelerate litter decomposition by promoting physical fractionation and/or smothering of detritus (Matthaei, Piggott, & Townsend, 2010; Piggott, Lange, Townsend, & Matthaei, 2012).

Finally, the manipulative studies included in this meta-analysis were conducted in an oligotrophic stream (Candal, Central Portugal; Domingos, Ferreira, Canhoto, & Swan, 2014; Duarte et al., 2016; Ferreira & Canhoto, 2014, 2015; Ferreira et al. 2014; Mas-Martí et al., 2015), in which microbial activity was likely limited by low nutrient concentration and thus less responsive to warming (Ferreira, Castagneyrol, et al., 2015; Ferreira, Chauvet, et al., 2015; Thormann, Bayley, & Currah, 2004). Moreover, these manipulative studies used slow-decomposing *Quercus* litter whereas correlative studies (e.g., Ferreira et al., 2006; Martínez et al., 2016; Pozo et al., 2011) included fast-decomposing litter (e. g., *Alnus*; Boyero, Pearson, Gessner, et al., 2011; Fernandes et al., 2014). This difference in litter decomposability derived from differences in phytochemical composition might have interacted with the temperature effect (see Section 4.3.). Furthermore, average temperature increase was higher for correlative (9.1°C) than manipulative studies (2.8°C; Table S1).

For correlative studies, the magnitude of the effect size was higher for studies along latitudinal than altitudinal gradients due to higher temperature ranges in the former studies (Table S1) and fast-decomposing litter types generally found at high latitude (Boyero et al., 2017) but not at high elevation (Jinggut & Yule, 2015).

4.3 | Does the response of litter decomposition to elevated temperature depend on litter type?

We found that the effects of elevated temperature on litter decomposition did not depend on litter type (fast vs. slow-decomposing litter), despite a significant stimulation of decomposition by elevated temperature in some litter genera but not in others. Previous meta-analyses showed that phytochemical discrepancies often lead to differences in litter decomposition rates (Kennedy & El-Sabaawi, 2017; Norby, Cotrufo, Ineson, O'Neill, & Canadell, 2001). Follstad Shah et al. (2017) also expected fast-decomposing litter types to be more sensitive to temperature than slow-decomposing litter types but found mixed support for this prediction.

4.4 | Does the response of litter decomposition to elevated temperature depend on the type of decomposers involved (microbes only or microbes plus invertebrates)?

The response of litter decomposition to elevated temperature did not depend on the type of decomposers involved. However, temperature effects were always significant for total litter decomposition (i.e., driven by both microbes and invertebrates) whereas for microbial-driven litter decomposition they were significant only for manipulative studies. Nevertheless, results suggest that both macroinvertebrate detritivores and microbial decomposers respond to elevated temperature in a consistent manner (both tend to show positives responses).

4.5 | Ecological implications and research gaps

It is difficult to distinguish between the effects of elevated [CO_2] and those of elevated temperature on litter decomposition because they may have opposite effects that are mediated through changes in decomposer communities and activities, litter input characteristics, environmental conditions, and their interactions. Moreover, it is difficult to extrapolate results of litter decomposition under laboratory conditions or at the litter bag scale to the whole ecosystem.

Faster decomposition rates under warmer conditions could result in the depletion of food for detritivores. However, elevated atmospheric [CO_2] may increase plant biomass and net primary production (Finzi, Delucia, Hamilton, Richter, & Schlesinger, 2002; Hamilton et al., 2002). Therefore, long-term and large-scale studies are still required to know whether higher primary productivity under elevated [CO_2], possibly of more recalcitrant nature (Stiling & Cornelissen, 2007), will replenish the void in aquatic food resources that should be left by faster litter decomposition rates in streams under future global change scenarios.

In temperate regions, litter decomposition is mainly carried out by macroinvertebrates (Boyero et al., 2016) as they are abundant and diverse (Boyero, Pearson, Gessner, et al., 2011) and have large body size (Horne, Hirst, & Atkinson, 2017; Shelomi & Zeuss, 2017) allowing for high consumption capacity (Boyero, Pearson, Gessner, et al., 2011). Increases in temperature may stimulate metabolic activities (Ferreira, Castagneyrol, et al., 2015; Ferreira, Chauvet, et al., 2015) while restricting the distribution of detritivore macroinvertebrates (Boyero, Pearson, Gessner, et al., 2011). The combined effects of individual-level and community-level effects of warming on litter decomposition need further consideration. As the contribution of detritivore macroinvertebrates to the decomposition of slow-decomposing litter is smaller than to that of fast-decomposing litter (Hieber & Gessner, 2002) and litter may become more recalcitrant under elevated [CO_2], the relative role of detritivores on litter decomposition under future global change is uncertain.

The primary studies used in the present meta-analysis were geographically limited and most studies that addressed the effects of elevated [CO_2] were conducted in temperate regions (mainly Europe; but see Martins, Melo, et al., 2017; Martins, Rezende, et al., 2017 for studies conducted in the neotropics) and used fast-decomposing litter types. Studies are required in other parts of the world, such as tropical regions where slow-decomposing litter types are common and litter decomposition is mainly carried out by microbes.

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SUPPORTING INFORMATION

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

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