DEPARTMENT OF LIFE SCIENCES

FACULTY OF SCIENCE AND TECHNOLOGY

UNIVERSITY OF COIMBRA

Effects of elevated CO_2 and temperature on litter decomposition in freshwaters: a meta-analysis

Thesis submitted, in partial fulfillment of the requirements for the Master's Degree in Ecology,

By

Amani MABANO

Supervisors: Verónica Ferreira, PhD

Manuel. A. S. Graça

June 2018

Acknowledgments

I would first like to thank my thesis supervisors Verónica Ferreira, PhD, and Professor Manuel A.S. Graça, of the Department of Life Sciences, Faculty of Science and Technology, University of Coimbra. Their doors were always open for me whenever I needed them; I am gratefully indebted to them for their valuable contribution to this thesis.

Secondly, I would like to extend my gratitude to my master's teachers at Université de Poitiers (France), Universidad San Francisco de Quito (Ecuador) and Universidade de Coimbra (Portugal). Many people have provided me with unfailing support throughout my years of study and the process of working on this thesis; I would like to acknowledge them. Specifically, I would like to say thank you to Mercer family for their unconditional love.

I would like to thank Université de Poitiers (UP), Universidad San Francisco de Quito (USFQ) and Universidade de Coimbra (UC) for having given me their best in terms of education. These high learning institutions will always be held near and dear to my heart.

This project was financially supported by the European Commission through the program "Erasmus Mundus Master Course - International Master in Applied Ecology" (EMMC-IMAE) (FPA 532524-1-FR-2012-ERA MUNDUS-EMMC).

Thank you.

Abstract

Elevated atmospheric [CO_2] can affect litter decomposition by (1) decreasing litter quality and (2) increasing temperature. At elevated [CO_2], plants tend to over-invest in secondary and structural compounds, resulting in low-quality litter (tougher litter, higher lignin concentration, and lower N:C ratio). These compounds decrease litter decomposition rates because of their bitter taste, toxicity and interference with digestion of litter decomposers (microbes and macroinvertebrates). On the other hand, elevated temperature can increase litter decomposition rates by increasing leaching of the recalcitrant compounds and metabolic rates of litter decomposers. However, it is not understood how litter decomposition responds to increases in both [CO_2] and temperature. This study tested the hypothesis that the overall effect size of elevated [CO_2] and temperature is significant and positive. The findings of 43 published and unpublished studies conducted worldwide, between 1993 and 2017, on the effects of elevated [CO_2], elevated temperature or both on litter decomposition in freshwaters are synthesized by meta-analysis. After estimating the standardized mean difference between litter decomposition rates reported in impacted (increases in CO_2, temperature or both) and control conditions, the overall effect size of elevated atmospheric [CO_2] and temperature on litter decomposition in freshwaters was positive. However, elevated atmospheric [CO_2] decreased litter decomposition, temperature+CO_2 did not affect litter decomposition, while elevated temperature increased litter decomposition. The effect of elevated temperature did not depend on the type of study (laboratory vs. field). Elevated [CO_2] inhibited litter decomposition in lentic, but not lotic systems. The effects of elevated atmospheric [CO_2], temperature and temperature+CO_2 on litter decomposition were species-specific. The type of community did not affect the response of litter decomposition to elevated atmospheric [CO_2] and temperature. Faster decomposition rates might reduce food availability for higher trophic consumers under future global warming scenarios. However, conclusions are geographically limited since most of the primary studies were conducted in Europe, suggesting a need for studies in other parts of the world.

***Keywords**:* Meta-analysis, lignin, climate change, hyphomycetes, shredders

Table of contents

List of Figures

I. Introduction

1.1 Biodiversity response to global warming

The current increase in atmospheric carbon dioxide concentration ([CO_2]) is among the clearest and most studied indicators of how humanity has altered the Earth. Between 1750 and 2011, atmospheric [CO_2] has increased by approximately 40%, from 280 parts per million (ppm) to 391 ppm (IPCC, 2013). Climate models considering 'Representative Concentration Pathways' (RCPs 8.5; van Vuuren et al., 2011) predict that atmospheric [CO_2] will reach 936 ppm by the end of the 21st century (IPCC, 2013). CO_2 is a greenhouse gas; i.e., it absorbs long wave level radiation (heat). In this way, air temperature is expected to rise by up to 4.8 ^{o}C until the end of the century (IPCC, 2013).

Global warming will likely lead to changes in (1) species distribution (species are expected to displace poleward or higher in altitudes) (Hufnagel & Garamvölgyi, 2014) and (2) phenology (shifts in the timing of seasonal activities, such as flowering, breeding, and migration) (Parmesan, 2006; Miller-Rushing & Primack, 2008), and (3) reduction in body size (Gardner et al., 2011). The relationship between temperature and body size is described in what are known as the Bergmann's rule (interspecific latitudinal clines: species have larger body size in colder climatic conditions) and the James' rule (intraspecific latitudinal clines: individuals have larger body size in colder conditions) (Teplitsky & Millien, 2014; Horne et al., 2017; Shelomi & Zeuss, 2017).

Since the surface-area-to-volume ratio is inversely proportional to body size, large body size helps organisms to minimize heat generation (heat that is needed to regulate body temperature) and heat dissipation in cold environments (Shelomi & Zeuss, 2017). Although the Bergmann's rule was originally described for endotherms, it is also valid for ectotherms, which tend to grow faster at higher temperatures but attain smaller size at maturity (Sibly & Atkinson, 1994; Atkinson, 1995; Shelomi & Zeuss, 2017). Body size is an important trait that affects individual fitness (reproduction, growth and survival) and ecological processes, such as food web dynamics (Horne et al., 2017). For instance, fitness of ectotherms (which comprise over 99% of all species; Forster et al., 2012) increases with body size.

Large size ectotherms tend to have faster growth rates and larger reproductive outputs when compared with smaller specimens (Kingsolver & Huey, 2008). Elevated temperatures also increase metabolic rates and oxygen consumption by aquatic ectotherms. Oxygen is less bioavailable in water than on land (Horne et al., 2017), and for this reason natural selection should favour reduced body size to minimize oxygen demand under warmer temperatures. Therefore, the reduction in body size with increases in global temperature should be greater in aquatic than in terrestrial species (Forster et al.,

2012). Given the importance of body size in species interactions (Horne et al., 2017), reduction in this trait is expected to affect ecosystem-level processes, such as litter decomposition in freshwaters.

1.2 Litter decomposition in freshwaters

Small woodland streams have reduced incoming sunlight and therefore instream primary productivity is significantly limited (Vannote et al., 1980). Thus, these streams depend on allochthonous plant litter from riverine ecosystems as a source of energy and carbon (Vannote et al., 1980; Minshall et al., 1985; Kominoski & Rosemond, 2011). Allochthonous plant litter, mainly in the form of leaves, is the major source of energy for woodland stream food webs (Tuchman et al., 2002; Tank et al., 2010). Plant litter is incorporated into aquatic food webs by the activities of microbes and macroinvertebrates, leading to litter decomposition. Therefore, litter decomposition is the catabolism of organic matter taking place over three timely co-occurring and interdependent phases: (1) leaching, (2) microbial colonization and conditioning, and (3) fragmentation by macroinvertebrates and physical abrasion (Abelho, 2001; Graça, 2001; Hieber & Gessner, 2002).

Most of the leaching occurs mainly in the first 24 to 48 hours, but it can last for several days (Canhoto & Graça, 1996). It results in the release of soluble compounds (i.e., carbohydrates, amino acids, and phenolics), which give rise to dissolved organic matter (DOM). Leaching may account for the loss of up to 42% of the initial mass of plant litter (Maloney et al., 1995; France et al., 1997). Leaching is faster at elevated temperature and also depend on the litter structural or secondary compounds and nutrients (Abelho, 2001). After compounds with antimicrobial activity (e.g., polyphenolics) are leached, the microbial colonization of plant litter intensifies (Webster & Benfield, 1986; Gessner et al., 1999).

Among microbial decomposers, aquatic hyphomycetes and bacteria are the key drivers of litter decomposition in freshwaters (Baldy et al., 2007). They are responsible for ~27 – 100% of litter mass loss (Hieber & Gessner, 2002; Ferreira et al., 2015; Mas-Martí et al., 2015). Aquatic hyphomycetes are polyphyletic fungi mainly represented by ascomycetes and, to a lesser extent, basidiomycetes (Sridhar, 2009). These hyphomycetes dominate early stages of litter decomposition (Gessner & Chauvet, 1994), while bacterial biomass increases along the process of litter decomposition (Baldy et al., 1995; Hieber & Gessner, 2002).

Although aquatic hyphomycetes have higher biomass than bacteria during decomposition (Flury & Gessner, 2011; Tant et al., 2015; Duarte, et al., 2016), bacteria exhibit higher turnover rates (Baldy et al., 2002). The relative importance of fungi and bacteria is also habitat dependent: aquatic hyphomycetes are diverse and dominate litter decomposition in lotic systems whereas bacteria are

more important in lentic systems (Baldy et al., 2002). Fungi and bacteria enhance litter degradation directly by macerating leaves due to activities of exoenzymes (e.g., pectinases, hemicellulases, and cellulases, which hydrolyse polysaccharides), incorporating plant carbon and nutrients into their biomass, and mineralizing it (Hieber & Gessner, 2002; Gulis & Suberkropp, 2003; Cornut et al., 2010).

Microbial assemblages affect litter decomposition indirectly by enhancing litter palatability to detritivores, which incorporate litter carbon and nutrients into secondary production (Golladay et al., 1983; Graça et al., 1993; Chung & Suberkropp, 2009b). Microbial conditioning results from the incorporation of nutrients (from leaves and water) into microbial biomass and the conversion of indigestible (to invertebrates) to digestible plant compounds by, chiefly, aquatic hyphomycetes (Bärlocher, 1985). Thus, when it comes to feeding, macroinvertebrates prefer conditioned over unconditioned litter (Friberg & Jacobsen, 1994; Graça et al., 2001; Chung & Suberkropp, 2009b).

Macroinvertebrates contribute to litter decomposition by consuming and incorporating the organic matter into secondary production, and promoting the release of fine particulate organic matter (FPOM) (Graça, 2001; Wantzen & Wagner, 2006; Chauvet et al., 2016). Invertebrate feeding may account for up to 64% of litter mass loss (Hieber & Gessner, 2002). Indirectly, macroinvertebrates can also contribute to litter decomposition by reducing organic matter into small particles and increasing the active surface area of litter for colonization by microorganisms (Wantzen & Wagner, 2006). On the other hand, litter decomposition is affected by (1) intrinsic (i.e., litter quality) and (2) extrinsic factors (i.e., identity and diversity of microbial decomposers and macroinvertebrates consumers present in a system).

1.3 Effects of elevated [CO_2] on litter decomposition

Litter quality, which varies across plant species, is among the most important intrinsic factors that affect litter decomposition. Litter quality can be defined by chemical (e.g., nitrogen concentration, lignin concentration) and physical (toughness, resistance or recalcitrance) properties. High-quality litter (i.e., soft litter, with low lignin concentration and C:N ratio) supports higher microbial activity and consequently decompose faster than low-quality litter (Fernandes, et al., 2014; Ferreira et al., 2015; Martínez et al., 2016). Litter decomposers, especially invertebrates, prefer to feed on high-quality and try to avoid poor-quality litter (Motomori et al., 2001; Graça & Cressa, 2010). Elevated atmospheric [CO_2] has been documented to decrease litter quality (Rier et al., 2002; Tuchman et al., 2003).

When the carbon source is higher than its sink, plants tend to over-synthesize non-structural carbohydrates (starch, fructan, and sucrose), and carbon-based secondary and structural compounds (phenolics, terpenes, cellulose, hemicellulose, and pectin) (Poorter et al., 1997; Peñuelas & Estiarte, 1998; Stiling & Cornelissen, 2007), which results in tough, nutrient-poor litter. These compounds can impair litter decomposition because of their toxicity and interference with invertebrate digestion (Graça, 2001). Therefore, one way elevated atmospheric [CO_2] decreases litter decomposition is by decreasing litter quality. For instance, *Populus tremuloides* leaves grown at 720 ppm CO_2 contained higher levels of phenolics, lignin, C:N ratio, and lower levels of nitrogen, and consequently decomposed more slowly than *P. tremuloides* leaves grown at 360 ppm CO_2 (Tuchman et al., 2003). However, the impact of elevated atmospheric [CO_2] on litter quality seems to be species-specific (Monroy et al., 2016). Nitrogen concentration of *Agrostis capillaris* remained similar at 400 and 700 ppm of CO_2 whereas it decreased in *Trifolium pratense* at 700 ppm of CO_2 (Monroy et al., 2016).

It is unclear how changes in litter quality induced by elevated atmospheric [CO_2] effect litter decomposition rates. Some researchers have reported no effects. For instance, leaves of *Trifolium pratense* grown at 700 ppm CO_2 had lower nitrogen concentrations than leaves grown at 400 ppm CO_2, but decomposition rates were similar at ambient and elevated [CO_2] (Monroy et al., 2016). *Alnus glutinosa* litter produced at 580 ppm CO_2 had 41% less phosphorus than conspecific litter produced at 380 ppm CO_2, but litter decomposition rates did not significantly differ (Ferreira & Chauvet, 2011a). *Hevea spruceana* leaves grown at 1637 ppm CO_2 had nearly 50% less phosphorus than leaves grown at 538 ppm CO_2, but litter decomposition was similar (Martins et al., 2017).

However, other researchers reported faster litter decomposition rates for leaves grown at elevated than ambient [CO_2]. *Quercus petraea* leaves grown at elevated atmospheric [CO_2] (520 ppm of CO_2) decomposed faster than conspecific leaves grown under ambient CO_2 conditions (380 ppm of CO_2) due, probably, to increases in litter quality (lower lignin and higher phosphorus concentrations) in the former (Hammrich, 2008). Litter quality in *Betula pendula* leaves decreased more (lower nitrogen concentration) when grown at 956 than at 407 ppm of CO_2, but litter decomposition was faster for leaves grown at elevated [CO_2] (Dray, 2014). Moreover, species can also differ in carbon-based compounds they over-invest in at elevated [CO_2]. Leaves of *P. tremuloides*, *Salix alba* and *Acer saccharum* grown at 720 ppm CO_2 contained, respectively, higher concentrations of lignin, carbohydrates-bound condensed tannins and soluble phenolics than leaves grown at 360 ppm CO_2 (Rier et al., 2005).

1.4 Effects of elevated temperature on litter decomposition

Elevated atmospheric [CO_2] can indirectly affect litter decomposition by increasing temperature (IPCC, 2013) and its effect on metabolism / fungal activity (Weyers & Suberkropp, 1996). High temperatures are also known to promote leaching (Batista, et sal., 2012). Another extrinsic factor affecting litter decomposition is the quantity, the identity and diversity of microbes and macroinvertebrates involved in litter decomposition; which in turn are also affected by temperature. High temperatures increase fungal biomass accumulation (and therefore litter conditioning by fungi), growth and reproduction of fungi (Rajashekhar & Kaveriappa, 2000; Chung & Suberkropp, 2009b; Moghadam & Zimmer, 2016).

Additionally, growth, development and respiration rates of invertebrates increase with temperature (Harper, 2006; Mas-Martí et al., 2015), when this temperature does not exceed optimal thermal limits (Brown et al., 2004). Litter decomposition increases with invertebrate density, and total invertebrate density was found to be higher at warmer than cooler temperatures, at the stream level (Griffiths & Tiegs, 2016). However, it was also found that bacterial diversity and fungal biomass can decrease with increases in temperature (Flury & Gessner, 2011). Elevated temperature also increases litter decomposition by increasing litter consumption rates by macroinvertebrates (González & Graça, 2003; Azevedo-Pereira et al., 2006).

Elevated temperature may increase litter decomposition rates by increasing litter quality. *Quercus robur* leaves incubated in a channel at elevated temperature had less phenols concentration, lower toughness and C:N ratios than leaves incubated under ambient thermal conditions (Mas-Martí et al., 2015). In this regard, several studies reported that litter decomposition rates increase with temperature in freshwaters. Field studies have found a positive correlation between plant litter decomposition rates and water temperature over altitudinal (Fabre & Chauvet, 1998; Martínez et al., 2014; Taylor & Chauvet, 2014; Martínez et al., 2016), latitudinal (Irons et al., 1994; Boyero et al., 2011), geothermal (Friberg et al., 2009; Griffiths & Tiegs, 2016) and seasonal (Ferreira et al., 2006; Pereira et al., 2017) gradients. This positive relationship between litter decomposition rates and temperature has been corroborated by laboratory studies (Dang et al., 2009; Ferreira & Chauvet, 2011a; Martínez et al., 2014).

The effect of increases in temperature may, however, depend on ambient temperature. For instance, litter decomposition rates were higher during experimental warming in colder than in warmer months (Ferreira & Canhoto, 2014, 2015). Also, it is frequent to find faster decomposition rates at lower than at higher temperatures (Taylor & Andrushchenko, 2014; Correa-Araneda et al., 2015). This may be

due to the fact that elevated temperatures decrease bacterial diversity, fungal biomass, and invertebrate abundance and species richness (Flury & Gessner, 2011).

1.5 Objectives

Studies addressing the effects of elevated [CO_2] and of elevated temperature on litter decomposition in freshwaters have reported contrasting results. Nevertheless, elevated atmospheric [CO_2] is expected to decrease litter decomposition while elevated temperature is expected to stimulate litter decomposition.

Even though elevated atmospheric [CO_2] and temperature have antagonistic effects on litter decomposition, the overall response of litter decomposition to elevated atmospheric [CO_2] and temperature should be a stimulation since temperature is expected to have a stronger effect on decomposition than a slight decrease in litter quality promoted by elevated atmospheric [CO_2] (Ferreira & Chauvet, 2011b). Contrasting results among primary studies could result from small sample size and relatively small CO_2 or temperature changes between elevated and ambient treatments. Further, the above conflicting findings indicate that the response of litter decomposition to elevated atmospheric [CO_2] and temperature may depend on experimental settings and/or confounding environmental variables.

Different experimental approaches have been used to address the effects of elevated temperature on litter decomposition. The response of litter decomposition to elevated temperature might be stronger when more controlled approaches are used (e.g. laboratory vs. field experiments) (Ferreira et al., 2015; Ferreira & Canhoto, 2015).

Specifically, the objectives of this study are: (1) to summarize data of other studies that have addressed the effects of elevated [CO_2] and temperature on litter decomposition in freshwaters and (2) to test the effects of study characteristics on litter decomposition.

Meta-analysis achieves greater statistical robustness by combining the results of several primary studies and weighting individual effects by their sampling variances (Borenstein et al., 2009). Moreover, primary studies synthesized by this study were faced by temporal and spatial limitations, which requires a quantitative review to achieve a better understanding of the effects of elevated [CO_2] and temperature on litter decomposition. Meta-analysis can also be used to find out crucial litter decomposition drivers that could be tested in primary studies.

In this systematic review, I performed a meta-analysis of 43 studies, published between 1993 and 2017, to determine the magnitude and direction of the overall effect of elevated atmospheric [CO_2] and temperature on litter decomposition in freshwaters. I further assessed the moderators of this

effect. Specifically, this study investigated whether the type of stressor (elevated atmospheric [CO_2] alone *versus* elevated temperature alone *versus* both), study type (laboratory *versus* correlative field studies *versus* manipulative field studies), type of aquatic decomposer community involved in litter decomposition (microbes alone *versus* microbes and invertebrates), litter genus, and system type (lotic *versus* lentic) (Fig. 1) affect the response of litter decomposition to elevated [CO_2] and temperature. The main questions and hypotheses addressed by this meta-analysis are detailed in Table 1.

1.6 Questions and hypotheses of the study

Table 1. Questions and hypotheses addressed, and datasets used by the present systematic review

Questions	Hypotheses	Dataset	Results
1. Do atmospheric changes affect the decomposition of litter in freshwaters, i.e. is the overall response significantly different from zero?	*H_1:* Even though both elevated atmospheric [CO_2] and temperature have antagonistic effects on litter decomposition in freshwaters, the overall response of litter decomposition to atmospheric changes should be a stimulation since temperature is expected to have a stronger effect on decomposition than a slight decrease in litter quality due to elevated CO_2 (review generated evidence).	All	Fig. 2
Does any characteristic of the studies influence the magnitude and direction of the response, i.e. are study characteristics sources of heterogeneity between studies?			
2. Does the response of litter decomposition to atmospheric changes depend on the type of change (elevated temperature, elevated CO_2 or both)?	*H_{2a}*: Elevated atmospheric CO_2 concentrations are expected to slow down litter decomposition because plants should invest more in structural and secondary compounds under elevated atmospheric CO_2 and litter rich in such compounds is known to be of low quality and to be colonized and decomposed slower compared with litter with lower concentration of such compounds.	CO_2	Fig. 2

	H_{2b}: Elevated temperature is expected to stimulate plant litter decomposition by stimulating metabolic activities of microbes and shredders involved in litter decomposition.	Temp	Fig. 2
	H_{2c}: Since both elevated atmospheric [CO_2] and temperature have antagonistic effects on litter decomposition in freshwaters, the overall response of litter decomposition to atmospheric changes should be a stimulation since temperature is expected to have a stronger effect on decomposition than a slight decrease in litter quality due to elevated CO_2 (study generated evidence).	Temp+CO_2	Fig. 2
3. Does the response of litter decomposition to elevated temperature depend on the type of study (laboratory vs. field; type of field study) in lotic systems?	*H_3:* Litter decomposition in laboratory studies may be more strongly affected by increases in temperature or changes in litter quality 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.	Temp	Fig. 3A
4. Does the response of litter decomposition to atmospheric changes depend on litter quality (genus, type)?	*H_4*: The decomposition of high-quality (i.e., soft with high nutrient concentration) litter may be more responsive to atmospheric changes than that of low-quality litter since the potentially stimulatory effect of elevated temperature could be limited in the latter. Still high-quality litter will be more responsive to elevated CO_2 since if litter is already bad quality it should not matter much if it becomes worse, while for good	Temp, Laboratory studies Temp, Correlative altitudinal field studies Temp+CO_2 CO_2, Lentic studies	Fig. 3B Fig. 4A Fig. 5A Fig. 5B

	quality litter a slight decrease can be noticeable.		
5. Does the response of litter decomposition to atmospheric changes depend on the type of decomposers involved (microbial in fine mesh bags and microbes plus invertebrates in coarse mesh bags)?	H_5*:* Litter decomposition mediated by both macroinvertebrates and microorganisms may be more sensitive to atmospheric changes than microbial-driven litter decomposition as the effect of atmospheric changes on microbes might be amplified by invertebrates, which are strongly affected by the conditioning level of the detritus.	Temp, Manipulative field studies	Fig. 4B
6. Does the response of litter decomposition to elevated atmospheric CO_2 depend on the type of freshwater system (lotic or lentic)?	H_6: Microbial litter decomposition in lentic and lotic systems is predominantly carried out by distinct communities (aquatic hyphomycetes dominate in lotic systems and bacteria dominate in lentic systems), so distinct effects of elevated CO_2 changes are expected.	CO_2	Fig. 5B
7. Does the response of litter decomposition to elevated atmospheric CO_2 or temperature depend on the magnitude of increase?	H_7: The higher the increase in atmospheric [CO_2] or temperature the stronger effects on litter decomposition.	Temp Temp+CO_2	Table 3 Table 3

II. Methods

2.1 Literature search and primary studies inclusion criteria

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 (Hedges & Gurevitch, 1999; Borenstein et al., 2009; van Rhee & Hak, 2017). The present meta-analysis summarizes the findings of primary studies that addressed the effects of elevated atmospheric CO_2 concentration and/or elevated temperature on allochthonous plant litter decomposition in freshwater ecosystems (both lotic and lentic). Primary studies were produced over the last 47 years, between January 1970 and November 2017, in English or French, and they were published in international and national journals or they were grey literature (theses and scientific reports). Studies were located using personal databases, electronic journal indices, and electronic reference databases (Google Scholar and Web of Science).

For the literature search online, 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 (example: *processing AND leaves AND temperature AND freshwater*). The equivalents of these keywords in French were equally used. In Google Scholar, names of researchers known to work on litter decomposition were also used and their publication record was screened. Reference lists in primary papers were also screened for additional studies.

Only primary studies that fulfilled the following criteria were selected:

Studies aimed at addressing the effect of elevated water temperature (by at least 1ºC) and/or elevated atmospheric CO_2 concentration (directly or mediated by changes in litter quality) on any aquatic variable; if this was a goal of the primary study, the probability that the effects are confounded by changes in other variables decreases as the authors would likely have chosen ambient and 'elevated' conditions that are comparable. Only increases in temperature by at least 1ºC were considered since climatic models predict that the smallest temperature increases by the end of the 21st century will be by 1ºC (IPCC, 2013).

Different experimental approaches were used across studies and thus data were shown (i) as the comparison of two groups in terms of continuous variables (e.g., litter decomposition in ambient and 'elevated' conditions) or (ii) as the relationship between two continuous variables (e.g., litter

decomposition rates across a gradient of temperature). In the first case (i) 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 (ii), studies had to report Pearson *r* (or enough information to allow its estimation) and sample size.

The application of these criteria resulted in the selection of 43 studies with data reported as comparison of two groups in terms of continuous variables, which contributed with 189 ambient – elevated comparisons to the database. Additional 6 studies reported data as the relationship between two continuous variables and contributed with 10 Pearson *r* to the database. Many studies contributed with multiple effects sizes to the database, which might affect the results if the non-independency of effect sizes is a problem. However, not considering them would have restricted the analysis by reducing sample size (i.e., number of available effect sizes) and moderators. I have therefore considered multiple effect sizes per study but assessed their impact on the results in a sensitivity analysis (see below).

2.2 Data extraction

Data were obtained from graphs, tables, text and directly from authors. When the means and measurements of dispersion (generally SE) were available on graphs, these were extracted using WebPlotDigitizer (Version 4.0), available online at https://automeris.io/WebPlotDigitizer/. When decomposition data were reported at multiple dates, I considered data of the latest date only. For studies that did not report Pearson *r*, I estimated it if those studies reported multiple decomposition data by making a correlation between decomposition rates and the explanatory variable (i.e., temperature). When available, SE values were converted into SD ($SD = SE \times \sqrt{n}$). In the few cases where 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):

$$SDm = X_m \times \left(\frac{\sum SDr}{\sum X_r}\right)$$

Where, X_m: mean litter decomposition rate of the study with missing SD; X_r: mean litter decomposition rate of studies that reported SD; SDr: reported SDs.

Extracting, estimating and imputing data might introduce errors and bias the results, but excluding studies with missing information would limit the analyses. Thus, an effort was made to include the maximum number of ambient – elevated comparisons. The potential for bias due to inclusion of 'estimated' cases was assessed in sensitivity analyses (see below).

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 et al., 2009). The effect size can be computed based on means, binary data or correlations, depending on the type of data in primary studies (Borenstein et al., 2009).

Where primary studies reported data as the comparison of two groups in terms of continuous variables, I calculated the effect sizes 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):

$$g = J \times d,$$

with,

$$J = 1 - \frac{3}{4df-1}\,,\ df = n_{elevated} + n_{ambient} - 2,$$

and

$$d = \frac{X_{elevated} - X_{ambient}}{SD_{within}},\quad SD_{within} = \sqrt{\frac{(n_{elevated}-1)SD_{elevated}^2 + (n_{ambient}-1)SD_{ambient}^2}{n_{elevated}+n_{ambient}-2}}.$$

The variance associated with Hedges' *g* (*Vg*) was calculated to allow weighting the effect size by its precision in the analysis (see below);

$$Vg = J^2 \times Vd$$

with,

$$Vd = \frac{n_{elevated}+n_{ambient}}{n_{elevated} \times n_{ambient}} + \frac{d^2}{2(n_{elevated}+n_{ambient})}.$$

For studies that reported data as the correlation between litter decomposition and continuous variables, Pearson *r* was taken (or estimated) as the effect size. Pearson *r* was then converted into Hedges' *g* as follows:

$$d = \frac{2r}{\sqrt{1-r^2}} \quad \text{and} \quad g = J \times d \text{ (as above),}$$

and the variance associated with Pearson *r* was calculated as

$$Vr = \frac{(1-r^2)^2}{n-1}.$$

Then Pearson *r* was converted into *Vg* as follows:

$$Vg = J^2 \times Vd,$$

with

$$Vd = \frac{4Vr}{(1-r^2)^3}.$$

2.4 Moderators

Variables that might affect the magnitude and direction of the response of plant litter decomposition to elevated CO_2 and temperature are called moderators (Borenstein et al., 2009; Ferreira et al., 2015). These can be environmental or methodological factors that vary across studies. In the present meta-analysis, I considered the moderators mentioned in the hypotheses regarding factors that are likely to affect the impact of elevated temperature and atmospheric CO_2 on litter decomposition. Moderators included 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), study system (lotic or lentic), type of aquatic decomposer community (microbial or total: microbes plus invertebrates) and litter genus (Table 2). Not included in the hypotheses but used in sensitivity analyses was the origin of data (reported or estimated) (Table 2).

Table 2. Identity, levels and description of moderator variables used in this meta-analysis

Moderator variables	**Levels**	**Description**
Study	Several	Primary studies included in the analyses.
Type of change	Elevated temperature	Increase in water temperature during incubation by at least 1ºC.
	Elevated CO_2	Increase in atmospheric [CO_2] from 360 ppm (the lowest concentration) to 1300 ppm (the highest concentration).
	Both	Combination of both elevated atmospheric [CO_2] and temperature.
Study type	Laboratory	Studies conducted in the laboratory (in microcosms).
	Field	Studies conducted in the field (freshwater systems).
Field Study	Manipulative	Studies manipulating freshwater ecosystems by increasing the temperature.
	Correlative	Correlative studies along a gradient of temperature existing naturally in the ecosystem.
Correlative study	Altitudinal	Study whose incubation sites took place at different altitudes.
	Latitudinal	Study whose incubation sites ranged over different latitudes.
	Seasonal	Study whose incubation periods were repeated over several seasons.
	Geothermal	Study whose incubation sites were differently influenced by geothermal heating.
Litter genus	Several	Leaves from different plant genera with assumingly different litter quality.
Community type	Total	Litter decomposition driven by both invertebrates and microorganisms, assessed in the field using

		coarse mesh size (10 mm mesh) or in the laboratory in the presence of macroinvertebrates.
	Microbial	Microbial-driven litter decomposition assessed in the field using fine mesh size (0.5 mm mesh) or in the laboratory in the absence of macroinvertebrates.
System	Lotic	Running freshwaters (i.e., streams, rivers, and laboratory microcosms with agitation).
	Lentic	Still freshwaters (e.g., lakes).
Origin of data	Reported	Both mean litter decomposition and standard deviation were reported in studies or provided by authors.
	Estimated	Mean litter decomposition and standard deviation were extracted from graphs, or estimated, or imputed.

2.5 Statistical analyses

All statistical analyses were performed with OpenMEE software (Wallace et al., 2017), available online at http://www.cebm.brown.edu/openmee/.

2.5.1 Overall effect size

I used the random-effects model of meta-analysis, with between-study variance estimated by the restricted maximum likelihood (REML) method, to calculate the overall effect size of elevated atmospheric CO_2 and temperature on litter decomposition in freshwaters. The summary effect size or the overall weighted mean effect size, *M*, was computed as (Borenstein et al., 2009):

$$M = \frac{\sum_{i=1}^{k} WiEi}{\sum_{i=1}^{k} Wi}$$

Wi is the weight assigned to each effect size (E) as

$$Wi = \frac{1}{VEi},$$

with VE_i being the variance for effect size (i).

In the random-effects model of meta-analysis it is assumed that there are two sources of variation: within-study variation (i.e., sampling error; *Vi*) and between-studies variation due to real differences among studies (T^2) (DerSimonian & Kacker, 2007; Borenstein et al., 2009). Thus, $VEi = Vi + T^2$,

with

$$T^2 = \frac{Q-df}{C},\ df = n - 1 \text{ (n, number of effect sizes),}$$

and

$$C = \sum Wi - \frac{\sum Wi^2}{\sum Wi}.$$

The variance of the summary effect (V_M) is computed as

$$VM = \frac{1}{\sum_{i=1}^{k} Wi}.$$

The overall effect size, which is the weighted mean of individual effect sizes, Hedges' g was significant if the 95% CL did not include zero (non-effect line), and the effect was considered weak if Hedges' $g \sim |0.2|$, moderate if Hedges' $g \sim |0.5|$, and strong if Hedges' $g \geq |0.8|$ (Borenstein et al., 2009). The central goal of meta-analysis is not simply to compute a summary effect, but also to quantify the heterogeneity among effect sizes. Heterogeneity can be quantified using Q_M and I^2 Q_M quantifies the observed dispersion among effect sizes or total heterogeneity:

$$Q = \sum_{i=1}^{k} Wi(Yi - M)^2.$$

Q_M and the degree of freedom (*df*, expected dispersion in the absence of between-studies variation) allow to test the null hypothesis that all studies share a common effect size and variance among studies is due to chance (i.e., sampling error), i.e., $Q = df$. If $P < 0.05$ ($Q > df$), the H_0 is rejected because dispersion exists among effect sizes and it is not due to chance only. This rejection indicates also that there is real variation among studies. If $P \geq 0.05$ ($Q = df$), the null hypothesis is not rejected, but it cannot also be accepted. A non-significant *p*-value might mean that all studies are similar (i.e., there is no between-studies variation; $Q = df$) but may also mean that dispersion within effect sizes is high (e.g., high sampling error) or that the sample size is low (i.e., low number of effect sizes).

I^2 indicates the dispersion among effect sizes and the percentage of observed variation that is due to real variation (heterogeneity) across effect sizes (i.e., between-studies variation) (Simon, 2006), and $0 \leq I^2 \leq 100$. Heterogeneity is considered low if $I^2 \sim 25\%$, moderate if $I^2 \sim 50\%$ and high if $I^2 \geq 75\%$.

$$I^2 = \left(\frac{Q-df}{Q}\right) \times 100\%, \text{ or } I^2 = \left(\frac{Variance_{between}}{Variance_{total}}\right) \times 100\%.$$

2.5.2 Analyses of moderators

2.5.2.1 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) and available sample size (only levels with $n \geq 3$ were tested within a given moderator). Mean effect sizes (Hedges' *g*) for 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 (Fig. 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. Then, within each stressor subset (elevated temperature or elevated CO_2 or elevated temperature+CO_2) I tested subsequent moderators.

For the temperature dataset, I first tested for differences in the overall effect size between laboratory and field studies. Thereafter analyses were performed separately for both laboratory and field studies. For field studies, I tested the difference between manipulative and correlative studies. Further analyses were done separately for both manipulative and correlative studies (Fig.1).

For the CO_2 dataset, I first tested for differences in effect size between lotic and lentic systems. Then an analysis for other moderators (community type and litter genus) was done for studies conducted in lentic systems (Fig. 1). For the temp+CO_2 subset I tested only the effect of litter genus on the response of litter decomposition to elevated atmospheric CO_2+temperature, since all studies were conducted in the laboratory replicating lotic systems (Fig. 1).

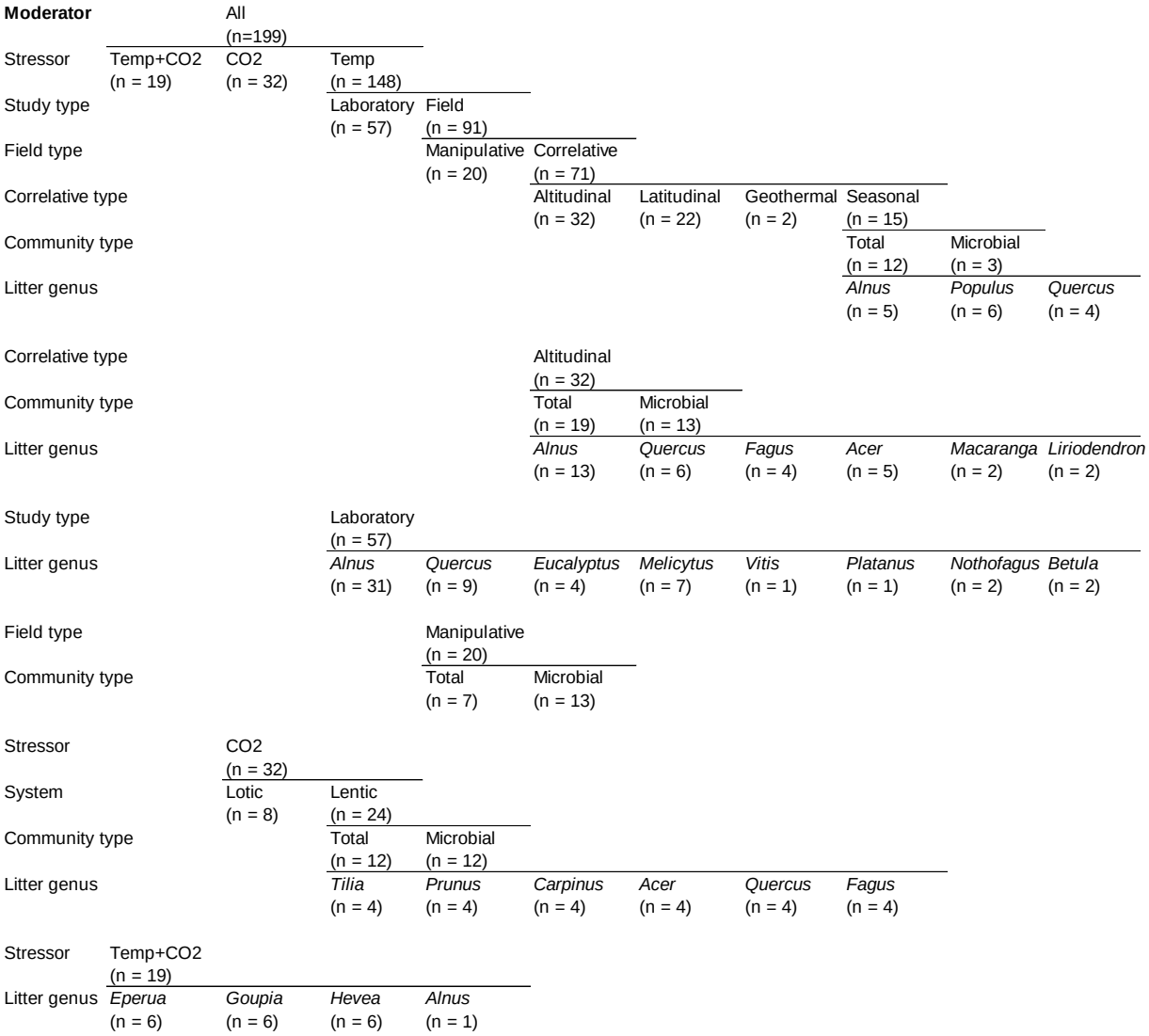

Fig. 1. Schematic design of the database indicating the number of cases per moderator variable (n). Refer to Table 2 for descriptions of moderator variables.

2.5.2.2 Meta-regression

Weighted meta-regressions were used to investigate the correlation between effect sizes (Hedges' *g*) and continuous variables: temperature increase ($Temperature_{elevated} - Temperature_{ambient,}$ in ^{o}C) and CO_2 increase ($[CO_2]_{elevated} - [CO_2]_{ambient}$, in ppm). For temperature increase, meta-regressions were performed for laboratory and field studies (both correlative and manipulative) of the temperature and temp+CO_2 datasets. For CO_2 increase, meta-regression was performed for laboratory studies of the temperature+CO_2 dataset.

2.5.2.3 Sensitivity analysis

Sensitivity analyses allow to assess how decisions undertaken during the main analyses may have affected the results (Borenstein et al., 2009). In the dataset, there are studies that contributed multiple effect sizes, which are non-independent and could affect the estimation of the mean effect size. Thus, a sensitivity analysis was performed to account for the non-independence of effect sizes. Using subgroup analysis (with Study as the categorical moderator) I estimated a single effect size per study, which I used to create a new dataset with sample size (i.e., available effect sizes) equal to the number of studies. I then repeated the analyses to the extent possible using this new dataset and compared the significance and direction of the results with those obtained using the main dataset.

Also, in several cases I had to estimate decomposition based on information reported in the studies or impute SD when they were missing, which might introduce a bias in the matrix. To assess for potential bias in mean effect sizes due to including studies for which decomposition or SD were estimated, the analyses were repeated, and results based on reported and estimated effect sizes were compared.

III. Results

3.1 Data description

The matrix used in analyses is provided as Appendix 1. Thirty-two (75%) out of 43 studies included in this meta-analysis were conducted in Europe, 3 studies (7%) in the USA, 2 (5%) in Brazil, 1 (2%) was conducted in each of Canada, Chile, Malaysia, New Zealand and USA-Costa Rica. Another study (2%) covered latitudes ranging from 0.37^{o} to 47.80^{o} in both hemispheres of all inhabited continents. Most studies (88%) were conducted in temperate, 7% in tropical and 5% simultaneously in temperate and tropical regions. Thirty-five (78%), 7 (15%) and 3 (7%) studies addressed, respectively, the effects of elevated temperature, elevated CO_2 and elevated temperature+CO_2 on litter decomposition in freshwaters.

Out of 43 studies, 42 (98%) and 1(2%) were conducted in lotic and lentic systems, respectively. Twenty-six (61%), 16 (37%) and 1 (2%) studies were carried out in the field, laboratory and both laboratory and field, respectively. Within the field studies, 15 were correlative and 6 were manipulative. Litter decomposition driven by both microbes and invertebrates was studied most (57%), whereas microbial-driven decomposition was studied in 43% of the studies. Four of the 43 studies included in this review were conducted between 1990 and 1999, 7 studies were conducted between 2000 and 2009 and 32 studies were conducted between 2010 and 2017.

3.2 Overall effect of elevated CO_2 and temperature on litter decomposition

The overall effect size was strongly positive (Hedges' *g*: 0.79; 95% CL: 0.56 to 1.02) (Fig. 2) and significant (Q_M = 1424.09, df = 196, $P < 0.001$). Real differences between studies explain 92.6% (I^2) of the observed variation in the overall effect size.

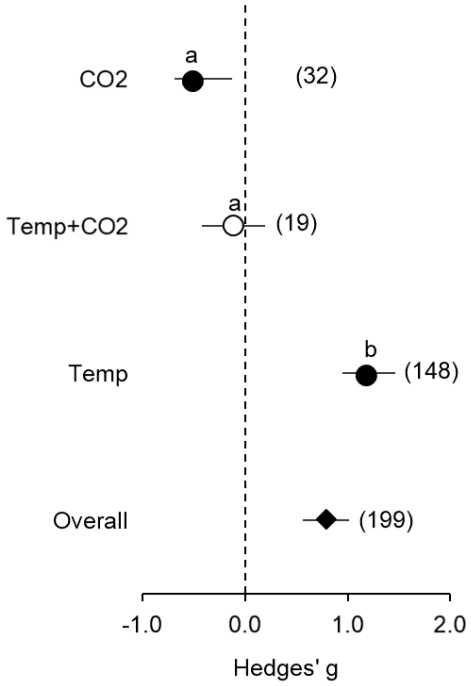

Fig. 2. Effect (Hedges' $g \pm 95\%$ CL) of elevated CO_2, elevated temperature+CO_2 and elevated temperature on leaf litter decomposition in freshwater ecosystems. The dashed line (mean effect size = 0) indicates no effect; mean effect size > 0 indicates stimulation whereas mean effect size < 0 indicates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

3.3 Effects of moderators on the response of litter decomposition to elevated CO_2 and temperature

The effect of elevated atmospheric CO_2 significantly inhibited litter decomposition (Hedges' g = –0.48, P = 0.003), the effect of temperature+CO_2 did not affect litter decomposition (Hedges' g = –0.11, P = 0.485), whereas elevated temperature significantly and strongly stimulated litter decomposition (Hedges' g = 1.21, $P < 0.001$) (Fig. 2; Appendix 2).

Several experimental and environmental characteristics of the primary studies included in this meta-analysis affected the response of litter decomposition to environmental change. The effect of elevated temperature on leaf litter decomposition did not depend on the type of study (Q_B = 1.380, df = 1, P = 0.240), with a significant strong stimulation for both laboratory and field studies (Fig. 3A, Appendix 2). The type of field study also did not affect the response of litter decomposition to elevated temperature (Q_B = 0.383, df = 1, P = 0.536), with a significant strong stimulation for both manipulative and correlative studies (Fig. 3A). The type of correlative study (altitudinal, seasonal and latitudinal), however, significantly affected the response of litter decomposition to elevated temperature (Q_B = 14.195, df = 2, P < 0.001), with stronger stimulation over latitudinal than over altitudinal gradients (Fig. 3A).

The response of litter decomposition to elevated temperature for laboratory studies did not depend on litter genus (Q_B = 3.262, df = 3, P = 0.353), although the decomposition of *Eucalyptus*, *Alnus* and *Quercus* leaves was significantly stimulated, while that of *Melicytus* was not significantly affected (Fig. 3B, Appendix 2). The response of leaf litter decomposition to elevated temperature in manipulative studies did not depend on the type of aquatic community involved in litter decomposition (Q_B = 2.319, df = 1, P = 0.128), although microbial-driven litter decomposition was strongly stimulated while no significant effect was found for total litter decomposition (Fig. 3B).

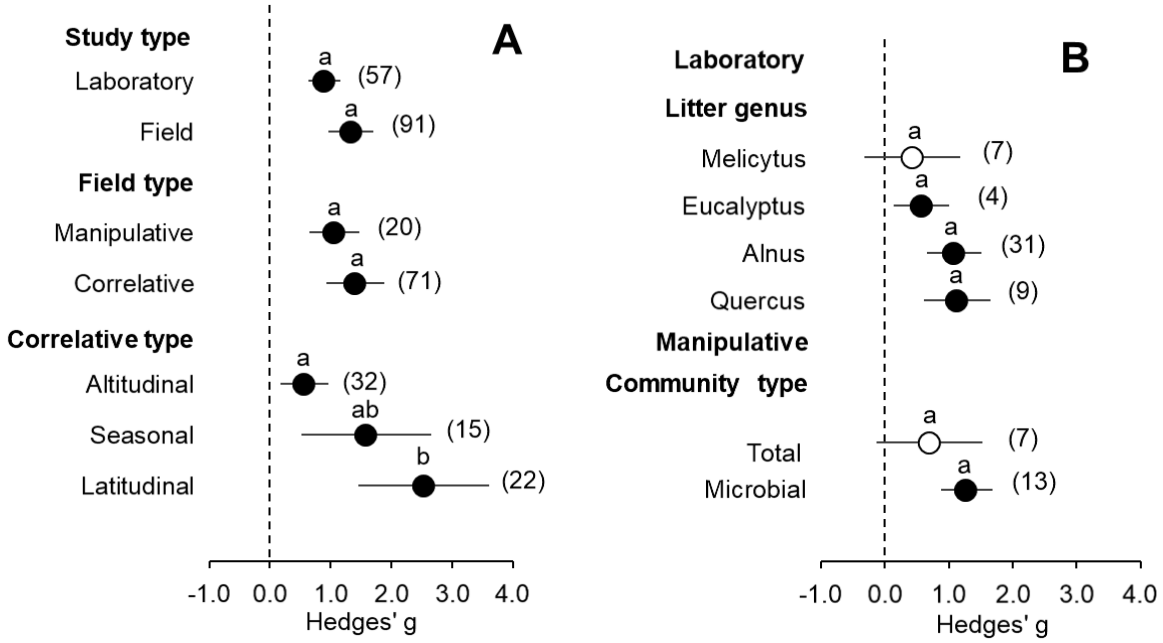

Fig. 3. Effect (Hedges' *g* ± 95% CL) of elevated temperature on leaf litter decomposition as a function of study type (A) and for laboratory studies as a function of litter genus and for manipulative studies as a function of decomposer community type (B). The dashed line (mean effect size = 0) indicates 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 non-effect line (black circles). Levels with overlapping 95% CL within a given moderator do not statistically differ. Values in brackets are sample sizes.

Neither litter genus nor the type of aquatic community involved in litter decomposition affected the response of litter decomposition to elevated temperature in studies conducted along altitudinal or seasonal gradients (Fig. 4, Table 3). However, elevated temperature had a significant effect on total litter decomposition and decomposition of *Fagus* leaves along altitudinal gradients. Also, microbial-driven and total litter decomposition, and decomposition of *Populus* and *Quercus* leaves along seasonal gradients were significantly stimulated under elevated temperature (Fig. 4).

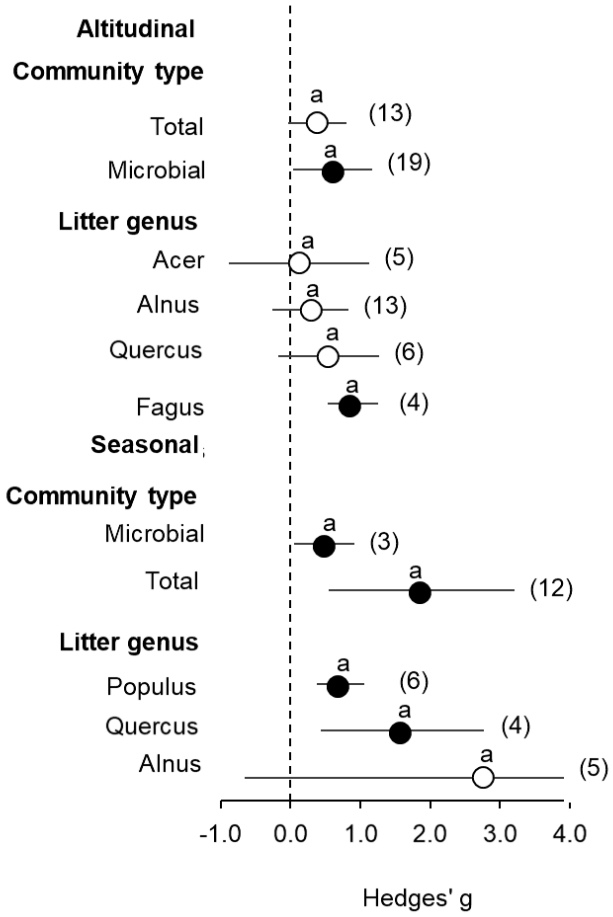

Fig. 4. Effect (Hedges' $g \pm 95\%$ CL) of elevated temperature on litter decomposition as a function of leaf genus and decomposer community type in field altitudinal and seasonal studies in freshwater ecosystems. The dashed line (mean effect size = 0) indicates no effect; mean effect size > 0 indicates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

The effect of elevated temperature+CO_2 on decomposition depended on leaf genus (Q_B = 15.713, df = 2, P < 0.001), with a significant inhibition of leaf decomposition for *Goupia* and *Eperua* while the decomposition of *Hevea* leaves was significantly stimulated (Fig. 5A, Appendix 2). The effect of elevated CO_2 on leaf litter decomposition depended on study system (Q_B = 10.684, df = 1, P = 0.001), with a strong significant inhibition for lentic systems while no significant effect for lotic systems (Fig. 5B; Appendix 2). Within lentic systems, community type did not significantly affect the response of leaf litter decomposition to elevated CO_2 (Q_B = 0.709, df = 1, P = 0.400), although there was a strong significant inhibition of microbial-driven litter decomposition, while the inhibition of total litter decomposition was marginally non-significant (Fig. 5B). The response of leaf litter decomposition to elevated CO_2 in lentic systems depended, however, on leaf genus (Q_B = 33.087, df = 5, P < 0.001),

with *Quercus* and *Tilia* litter decomposition being strongly and significantly inhibited, while that of *Carpinus*, *Prunus*, *Acer* and *Fagus* was not significantly affected (Fig. 5B).

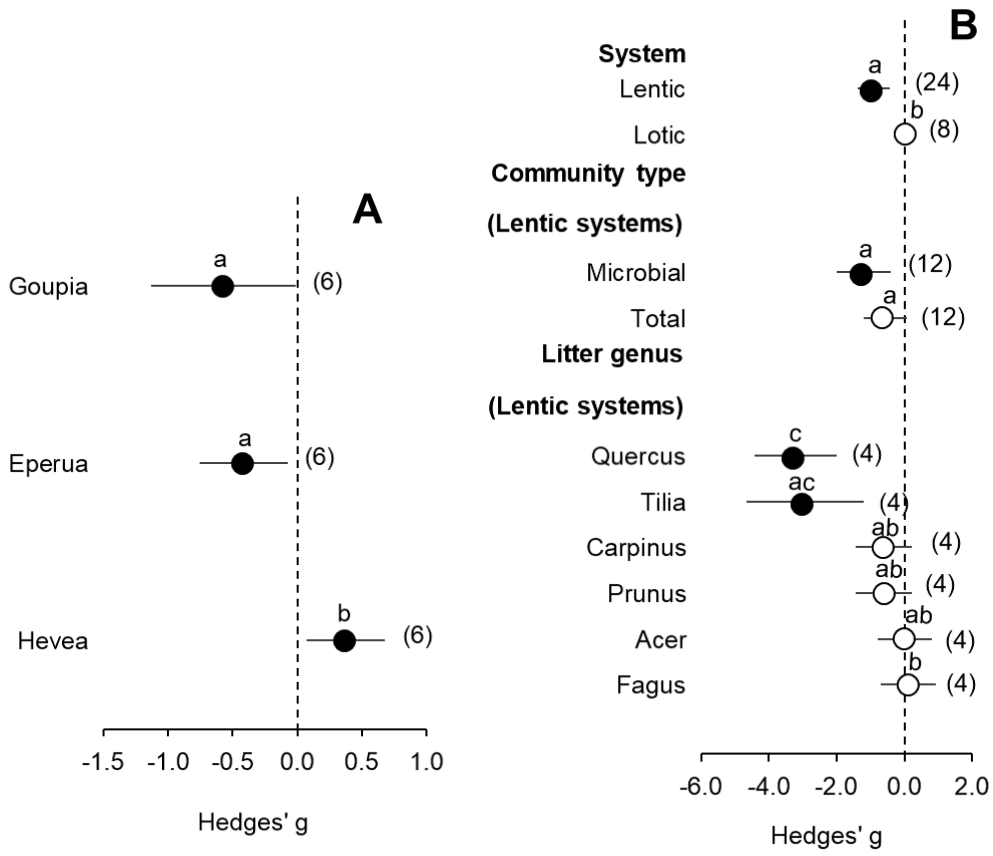

Fig. 5. Effect (Hedge's $g \pm 95\%$ CL) of elevated temperature+CO_2 on litter decomposition of leaves from different genus (A) and of elevated CO_2 on litter decomposition as a function of system, decomposer community type and genus (B). The dashed line (mean effect size = 0) indicates no effect; mean effect size > 0 indicates stimulation whereas mean effect size < 0 indicates inhibition. The effect is significant when the 95% CL does not overlap the non-effect line (black circles). Levels with overlapping 95% CL within a given moderator do not statistically differ. Values in parentheses are sample sizes.

There was no relationship between the response of litter decomposition and the magnitude of CO_2 increase for studies that, simultaneously, evaluated the effects of elevated temperature and CO_2 (temperature+CO_2 dataset) ($P = 0.284$, Table 3). Also, there was no correlation between the response of litter decomposition and the magnitude of temperature increase for studies in the temperature+CO_2 dataset ($P = 0.603$), laboratory studies (temperature dataset; $P = 0.123$) and manipulatives studies only (temperature dataset; $P = 0.245$). There was a positive relationship between the response of litter decomposition and the magnitude of temperature increase for correlative studies in the temperature dataset (slope = 0.13, $P < 0.001$) (Table 3).

Table 3. Correlations between effect sizes and mean atmospheric [CO_2] and water temperature. Meta-regression was assessed using the Temp+CO_2 dataset (temperature and CO_2 increases) and the temperature dataset (temperature increase, for laboratory, manipulative and correlative studies). Slopes and intercepts, associated 95% CL and *P*-values are given for the meta-regressions. The slope > 0 indicates positive correlation or stimulation while the slope < 0 indicates negative correlation or inhibition. The significant correlation is highlighted in bold (*P*-values < 0.050).

Meta-regression	Hedges' *g*	95% CL	*P*
Temperature dataset – Temperature increase			
Laboratory studies			
Intercept	0.40	– 0.28 to 1.09	0.246
Slope	0.07	– 0.02 to 0.17	0.123
Manipulative studies			
Intercept	0.66	0.19 to 1.13	0.005
Slope	0.04	– 0.03 to 0.12	0.245
Correlative studies			
Intercept	0.21	– 0.49 to 0.89	0.560
Slope	**0.13**	0.08 to 0.19	**< 0.001**
Temperature+CO_2 dataset			
CO_2 increase			
Intercept	0.19	– 0.43 to 0.81	0.557
Slope	< 0.01	< 0.01 to 0.00	0.284
Temperature increase			
Intercept	0.09	– 0.72 to 0.89	0.831
Slope	– 0.07	– 0.31 to 0.18	0.603

3.3 Sensitivity analysis

When I repeated the analysis using a single effect size per study, the overall effect size changed from 0.79 (95% CL: 0.56 to 1.01) to 0.59 (95% CL: 0.26 to 0.92) (Table 4). Although the overall magnitude of the effect size, as well as the magnitude of effect sizes for subgroup analyses, generally became smaller when compared with those found using the overall larger matrix. However, 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 non-independency of effect sizes.

Table 4. Summary table of subgroup analyses using a mean effect size per study. Mean effect size, 95% CL, sample size (n), test for heterogeneity between levels of moderators (Q_M), degree of freedom (df), *P*-values are provided (levels with a common letter do not significantly differ). Mean effect size > 0 indicates stimulation whereas mean effect size < 0 indicates inhibition.

Level	Hedges' *g*	95% CL	n	Sign diff
Overall	0.63	0.30 to 0.90	45	
Q_M = 212.34, df = 42, P < 0.001, I^2 = 90.96%				
Type of change				
CO_2	– 0.01	– 0.31 to 0.30	7	a
Temp+CO_2	0.04	– 0.52 to 0.60	3	ab
Temp	0.82	0.41 to 1.23	35	b
Q_M = 0.010, df = 1, P = 0.921				
Temperature dataset				
Study type				
Laboratory	0.85	0.20 to 1.50	14	a
Field	0.80	0.26 to 1.34	21	a
Q_M = 0.010, df = 1, P = 0.921				
Type of field study				
Manipulative	0.96	0.09 to 1.84	6	a
Correlative	0.74	0.02 to 1.45	15	a
Q_M = 0.151, df = 1, P = 0.697				
Type of correlative study				
Seasonal	0.84	– 1.63 to 3.32	4	a
Altitudinal	0.23	– 0.45 to 0.91	8	a
Q_M = 0.405, df = 1, P = 0.525				

When I estimated mean effect sizes based on reported and estimated data, trends and interpretations remained generally the same, although stronger mean effect sizes were generally found based on reported data. The smaller mean effects sizes based on estimated data suggest that the results based on the original database are conservative (Table 5).

Table 5. Summary table of subgroup analyses comparing effect sizes of reported and estimated data. Mean effect size, associated 95% CL, sample size (n), test for heterogeneity between levels of moderators (Q_M), degree of freedom (df) and *P*-values are provided (levels with a common letter do not significantly differ). Mean effect size > 0 indicates stimulation whereas mean effect size < 0 indicates inhibition.

Level	Hedges' *g*	95% CL	n	Sign Diff
Temperature dataset				
Reported	1.53	1.09 to 1.98	70	a
Estimated	0.89	0.63 to 1.15	78	b
Q_M = 5.247, df = 1, P = 0.022				
Study type – Laboratory (Temperature dataset)				
Reported	0.84	0.52 to 1.17	18	a
Estimated	0.96	0.57 to 1.35	39	a
Q_M = 0.010, df = 1, P = 0.922				
Study type – Field (Temperature dataset)				
Reported	1.75	1.16 to 2.34	52	a
Estimated	0.83	0.47 to 1.19	39	b
Q_M = 6.016, df = 1, P = 0.014				
Field type – Correlative, Altitudinal (Temperature dataset)				
Reported	0.74	0.34 to 1.14	14	a
Estimated	0.34	0.32 to 1.01	18	a
Q_M = 0.853, df = 1, P = 0.356				
Field type – Correlative, Seasonal (Temperature dataset)				
Reported	2.76	– 0.66 to 6.19	5	a
Estimated	0.98	0.52 to 1.44	10	a
Q_M = 2.209, df = 1, P = 0.137				
Field type – Manipulative (Temperature dataset)				
Reported	1.03	0.43 to 1.63	11	a
Estimated	1.10	0.55 to 1.65	9	a
Q_M = 0.061, df = 1, P = 0.805				
Community type – Microbial (Temperature, Manipulative dataset)				
Reported	1.63	1.14 to 2.12	5	a

Estimated	1.00	0.45 to 1.56	8	a
Q_M = 2.981, df = 1, P = 0.084				

IV. Discussion

4. 1 Do atmospheric changes affect the decomposition of litter in freshwaters, i.e. is the overall response significantly different from zero?

To the best of my knowledge, this is the first meta-analytic study to address the effects of elevated atmospheric [CO_2] and temperature on litter decomposition in freshwater ecosystems. Many studies have separately studied the effects of increasing atmospheric CO_2 (Rier et al., 2002; Tuchman et al., 2003; Ferreira et al., 2010) and temperature (Martínez et al., 2014; Mora-Gómez et al., 2015; Pereira et al., 2017) on litter decomposition. However, the effects of multiple global changing factors on litter decomposition should not be predicted from their individual effects (Ferreira & Chauvet, 2011), because the effects of those changes may not be additive (Williams et al., 2003; Kashian et al., 2007).

In this regard, there is a need to integrate all previous results of primary studies conducted on the effects of elevated CO_2 and temperature on litter decomposition in freshwaters, to arrive to general conclusions. The results of the present meta-analysis support the hypothesis that the overall effect size of elevated atmospheric [CO_2], through effects on litter quality, and elevated temperature on litter decomposition in freshwaters is significant. Elevated CO_2 and temperature have opposing effects on litter decomposition, inhibitory and stimulatory, respectively, but the effect of temperature proved to be stronger than the effect of elevated CO_2.

4. 2 Does the response of litter decomposition to atmospheric changes depend on the type of change (elevated temperature, elevated CO_2 or both)?

Elevated atmospheric [CO_2] is expected to affect litter decomposition in many ways, including increases in water temperatures (IPCC, 2013) and decreases in litter quality (increases in structural and secondary compounds and decreases in the quantity of nutrients) (Norby et al., 2001; Tuchman et al., 2003; Adams et al., 2005). The present study found that the type of change affected the response of litter decomposition. Elevated atmospheric [CO_2] inhibited, while elevated temperature stimulated litter decomposition. Simultaneous increase in temperature+CO_2 had no significant effect on litter decomposition.

Regarding CO_2, inhibition of litter decomposition rates at elevated CO_2 was also reported in a meta-analysis of 31 studies carried out in terrestrial ecosystems (Yue et al., 2015). In consistency with the present study hypothesis, elevated atmospheric [CO_2] can decrease litter decomposition rates, likely due to a reduction of litter quality. This decrease in litter quality results from the over-investment in structural and secondary compounds and decreases in nutrient concentration (Norby et al., 2001;

Adams et al., 2003, 2005). These compounds normally decrease litter decomposition rates because they are toxic, they taste bitter, and they interfere with the digestion of litter decomposers (microorganisms and macroinvertebrates).

Regarding temperature, the synthesis of 33 studies that have addressed the effects of elevated temperature on litter decomposition in lotic freshwaters indicated that temperature stimulates litter decomposition rates. This stimulation was expected since temperature normally increases leaching (Batista et al., 2012), litter consumption by invertebrates (González & Graça, 2003; Brown et al., 2004), fungal fitness (Dang et al., 2009), litter quality (Mas-Martí et al., 2015), and total density of aquatic insects (Griffiths & Tiegs, 2016). For instance, leaching and microbial degradation of recalcitrant compounds have been documented to critically decrease the levels of phenolics and other non-labile compounds such as lignin (Tuchman et al., 2002; Adams et al., 2003; Tuchman et al., 2003).

Also, total density of invertebrates was found to be higher at warmer than cooler reaches in Walker Branch stream (Griffiths & Tiegs, 2016). Invertebrate detritivores accelerate litter decomposition through consumption or stimulation of litter colonization by microbes (Wantzen & Wagner, 2006). According to the metabolic theory of ecology (Brown et al., 2004), temperature can also increase detritivore-driven litter decomposition by increasing their metabolic rates. However, detritivores (such as Trichoptera and Plecoptera) involved in litter decomposition have evolved and still are mainly found in cold waters (Wiggins & Mackay, 1978). Therefore, these stenothermal organisms might be negatively affected by increases in temperature, with negative effects on litter decomposition.

Opposing to what was anticipated, the simultaneous increases in temperature and CO_2 (temperature+CO_2) did not significantly affect litter decomposition. I expected that elevated temperature would have a stronger effect on litter decomposition than elevated [CO_2] (Ferreira & Chauvet, 2011a). Elevated atmospheric [CO_2] might inhibit litter decomposition by limiting O_2 bioavailability (Monroy et al., 2016), by reducing the performance of litter decomposers, and increasing aquatic acidity (Feely et al., 2009). Low pH can, for instance, delay litter decay by denaturing extracellular enzymes that are required to improve litter-nutritional quality by mainly aquatic hyphomycetes (Jinggut & Yule, 2015).

However, this meta-analysis included only three studies that simultaneously investigated the effects of elevated temperature+CO_2 on litter decomposition, and results need to be interpreted with caution. All of these primary studies reported litter decomposition rates to be similar at both ambient and elevated CO_2 and temperature (Ferreira & Chauvet, 2011b; Martins et al., 2017a; 2017b). The effects

of elevated temperature were not stronger than the effects of elevated CO_2 maybe because of larger average CO_2 increase (896 ppm), while there was a small average temperature increase (3 ºC).

4. 3 Does the response of litter decomposition to elevated temperature depend on the type of study in lotic systems (laboratory or field; type of field: altitudinal, latitudinal or seasonal)?

The response of litter decomposition to elevated temperature did not depend on the type of study in lotic freshwaters, i.e. whether the study was done in the field or laboratory. I anticipated that the effects of elevated temperature would be stronger in laboratory than in field studies due to the better control of confounding factors in laboratory than in field experiments, as found previously (Woodward et al., 2010; Ferreira et al., 2015). However, effect sizes were not significantly different between field and laboratory studies. This may be due, partly, to higher temperature ranges considered in field studies. For example, Irons et al. (1994) in a latitudinal study that contributed 21 cases to the dataset considered a temperature range of 25 ºC and Boyero et al. (2011) considered a temperature range of 24 ºC. The largest temperature range reported in laboratory studies was 13 ºC (Batista et al., 2017).

Additionally, confounding factors could have interacted synergistically with temperature in field studies. Field studies allow the investigation of the effects of temperature under realistic conditions. However, they do not allow discrimination between the effects temperature *per se* and other environmental variables that might exacerbate these 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 is increased alone (Ferreira & Chauvet, 2011b; Martínez et al., 2014; Moghadam & Zimmer, 2016). Another confounding factor that could stimulate litter decomposition in the field is fine sediments. Fine sediments in flowing waters can accelerate litter decomposition by promoting physical fractionation and/or smothering of detritus (Matthaei et al., 2010; Piggott et al., 2012).

Within field studies, manipulative studies allow to manage, to some extent, some confounding factors, thus, the effect of temperature on litter decomposition was expected to be stronger in manipulative than correlative field studies (Ferreira et al., 2015). However, this was not the case due to two main factors; litter quality and temperature ranges. Most of manipulative studies included in this meta-analysis were conducted in near-pristine streams (i.e., with low human activities). Since nutrients might limit microbial activity in those oligotrophic streams, the effects of rises in temperature should be stronger for high-quality than low-quality litter (Thormann et al., 2004; Ferreira et al., 2015). However, low-quality *Quercus* was the most used genus in manipulative studies while correlative

studies included high-quality (e.g., *Alnus*), intermediate (e.g., *Acer*) and low-quality (e.g., *Quercus*) litter genera (Ostrofsky, 1997). Furthermore, average temperature ranges were higher for correlative (9.1 ºC) than manipulative (2.8 ºC) studies (Appendix 1).

For correlative studies, the magnitude of the effect size was higher for studies along latitudinal than altitudinal gradients, while the effect size for seasonal gradients was not different from the two others. The fact that the response of litter decomposition to elevated temperature was higher for latitudinal than altitudinal experiments can be explained by, among others, two factors. Firstly, high-quality litter is known to be colonized and decomposed faster than poor-quality litter. Litter quality increases with latitude (Boyero et al., 2017) and correlative latitudinal studies used mainly high quality leaves from temperate systems. However, there is no clear relationship between litter quality and elevation. For instance, Jinggut and Yule (2015) found higher lignin concentration but lower polyphenolics at low elevations in *Macaranga tanarius* leaves while higher phenolics and lower lignin concentrations were revealed at high elevations.

Secondly, average temperature ranges in latitudinal studies were higher (18.4 ºC) than in altitudinal studies (3.1 ºC) (Appendix 1). The average temperature range for seasonal gradient was intermediate (7.9 ºC), which can explain why the effect size for these studies was not different from the effect sizes of latitudinal and altitudinal studies.

4. 4 Does the response of litter decomposition to atmospheric changes depend on litter quality?

Different plant species are characterized by different physical (e.g., toughness or resistance) and chemical (e.g., nitrogen, lignin, and phenolic concentrations) properties. High-quality litter (soft and with low concentration of secondary and structural compounds) was expected to be more responsive to elevated [CO_2] and temperature, but this was not always observed. Temperature stimulated litter processing of poor-quality litter (e.g., *Eucalyptus*), it did not have any effect on litter processing of intermediate quality litter (*Acer*) and stimulated or did not have any effect on litter processing of high-quality litter (*Alnus*). Under elevated CO_2, litter decomposition rates of poor-quality litter (*Quercus*) were inhibited while intermediate quality litter quality (*Acer*) was not affected. Another meta-analysis showed that phytochemical discrepancies resulting from increases in [CO_2] do not necessarily translate into decreases in litter decomposition rates (Norby et al., 2001), and effects can be species specific (Monroy et al., 2016).

For studies that simultaneously addressed the effects of elevated CO_2 and temperature, litter decomposition of *Goupia* and *Eperua* leaves was inhibited while the decomposition of *Hevea* leaves was stimulated. Litter quality of *Goupia* and *Hevea* leaves is relatively higher than *Eperua* (Martins

et al., 2017a; 2017b). As expected, for the high quality *Hevea*, the effects of temperature were stronger than effects of elevated [CO_2]. Despite phytochemical discrepancies, the effects of temperature+CO_2 were the same for *Goupia* and *Eperua*. From this observation, it seems that the response of litter decomposition to elevated [CO_2] and temperature is species-specific, as also suggested by Monroy et al. (2016). Moreover, intraspecific variations can be expected due to genotype variation and environmental conditions in which individual plants were grown (LeRoy et al., 2007; Lecerf & Chauvet, 2008).

4. 5 Does the response of litter decomposition to atmospheric changes depend on the type of decomposers involved (microbial in fine mesh bags and microbes plus invertebrates in coarse mesh bags)?

The response of total (microorganisms plus invertebrates) and microbial-driven litter decomposition to elevated [CO_2] and temperature was similar. Nevertheless, microbial-driven litter decomposition was stimulated with increases in temperature and inhibited with increases in atmospheric [CO_2] although microbial-driven litter decomposition generally responded to atmospheric changes according to expectations. It was stimulated with increases in temperature and inhibited with increases in atmospheric CO_2, while total litter decomposition was generally not affected. Total litter decomposition rates are not normally increased by rises in temperature because higher temperatures decrease invertebrate-driven decomposition while they simultaneously increase microbial-driven litter decomposition (Boyero et al., 2011). Moreover, at higher latitudes (cooler temperatures), microbial activity is reduced, but shredder density and species richness increase (Boyero et al., 2011), which generally increase invertebrate-driven litter decomposition rates.

This unresponsiveness of total litter decomposition to elevated temperature may be a result of the stenothermic (i.e. tolerance for a narrow range of temperatures) nature of invertebrates involved in litter decomposition. Most of macroinvertebrates involved in litter decomposition (such as Trichoptera and Plecoptera) have evolved and are still mainly restricted to cooler waters (Wiggins & Mackay, 1978). They are consequently sensitive to temperatures variabilities, i.e. small increases in temperature can be stressful enough to negatively affect litter decomposition mediated by macroinvertebrates.

Freshwater systems substantially contribute to carbon cycle by transforming a big amount of plant litter originating in terrestrial ecosystems (Battin et al., 2008, 2009). Since the main output of microbial-driven litter decomposition is CO_2 while invertebrates produce FPOM (Baldy et al., 2007), microbial-dominated litter decomposition, under global warming, might lead to a positive feedback

between CO_2 emissions from freshwaters, global warming and the production of recalcitrant carbon-based compounds.

4. 6 Does the response of litter decomposition to elevated atmospheric [CO_2] depend on the type of freshwater system (lotic or lentic)?

As hypothesized, the response of litter decomposition to elevated [CO_2] was affected by the type of freshwater system. The effect size of elevated [CO_2] on litter decomposition was negative in lentic systems, while it was not significant in lotic systems. In lentic waters, when recalcitrant compounds are leached, they are not carried downstream, as they are in lotic wasters. They remain in water around detritus, potentially inhibiting litter decomposition by complexation of invertebrate digestive enzymes and microbial exoenzymes (Zucker, 1983). Since litter grown under elevated atmospheric [CO_2] may have higher concentration of phenols, this inhibitory effect by dissolved phenols should be higher than leaves grown under ambient [CO_2].

Moreover, studies that addressed the effects of elevated [CO_2] on litter decomposition in lotic waters are a mixture of field and laboratory studies. These laboratory studies can overestimate the effects of elevated [CO_2], because of the ability to better discriminate confounding variables that might decrease the effects elevated [CO_2]. These factors are, among others, increasing acidity and less oxygen availability that might realistically help decipher the effects of [CO_2] in field conditions.

Another distinguishing factor can be water current, which is expected to be higher in lotic than in lentic waters, and high decomposition rates were reported under high current (Canton & Martinson, 1990; Rader et al., 1994). Then, microbial-driven litter decomposition is known to be dominated by bacteria and aquatic hyphomycetes in lentic and lotic systems, respectively (Baldy et al., 2002). However, it was shown that bacterial productivity and biomass were negatively affected by litter produced under enriched CO_2, while fungal biomass was not affected (Tuchman et al., 2002). This negative effect of CO_2 enrichment on bacteria can decrease litter decomposition by both bacteria and invertebrates in lentic systems.

4. 7 Ecological implications and research gaps to address in future studies

From the effect sizes found in this meta-analysis, increases in decomposition rates under elevated atmospheric [CO_2] and temperature would lead to serious ecological implications in aquatic ecosystems. Faster decomposition rates under warmer conditions would result in the depletion of food for higher trophic consumers (Ferreira & Chauvet, 2011a). On the other hand, it has been documented that elevated atmospheric [CO_2] concentrations increase plant biomass and net primary production

(NPP) (Finzi et al., 2002; Hamilton et al., 2002). However, a long-term study is still required to know whether high primary productivity under elevated [CO_2] will replenish the void in aquatic food resources that should be left by faster litter decomposition rates in freshwaters under future global warming scenarios.

Primary studies of the present meta-analysis were geographically limited, all of the 7 primary studies that addressed the effects of elevated [CO_2] have been conducted in temperate regions. However, plants have normally good litter quality, because litter has been proven to increase with latitude (Boyero et al., 2017). Plants species naturally differ in the levels of recalcitrant compounds, such as phenolics and tannins. Species that have less recalcitrant phytochemical compounds increase the production of these compounds under elevated [CO_2] more rapidly than poor-quality plant species (Hemming & Lindroth, 1995; Kinney et al., 1997). A slight decrease in litter quality of high-quality litter has more negative effects on litter decomposition than decreases in litter quality of already low-quality litter (Hieber & Gessner, 2002).

Furthermore, at medium latitudes (temperate regions where primary studies of this meta-analysis were conducted), litter decomposition is mainly carried out by macroinvertebrates (Boyero et al., 2016) due to detritivore high abundance and diversity (Boyero et al., 2012), high body size (*see* body size-temperature relationship theory in Horne et al. 2017 and Shelomi & Zeuss 2017), and high plant litter consumption capacity (Boyero et al., 2011). Additionally, Hieber and Gessner (2002) reported that the contribution of detritivore macroinvertebrates to low-quality litter is small.

Studies are required in other parts of the world, such as tropical regions where litter quality is low (supposedly less sensitive to increases in [CO_2]) and litter decomposition is carried out by microbes. This can allow making predictions of how decreases in litter quality due to future rises in atmospheric [CO_2] will globally affect litter decomposition in freshwaters. Increases in atmospheric [CO_2] can have less effect on litter decomposition rates in other parts of the world. Consequently, findings of the effects of elevated [CO_2] on litter decomposition in temperate regions should not be extrapolated to other regions.

Most of the primary studies included in this meta-analysis have reported decreases in litter quality under elevated [CO_2]. However, crayfish fed elevated litter were diagnosed to have lower percentages in proteins and lipids than crayfish that were fed ambient litter (Adams et al., 2005). Furthermore, grasshoppers that were reared on N-poor plants manifested smaller adult size than their counterparts reared on fertilized plants (Berner et al., 2005). If this is true for detritivores, this can lead to bottom-up and top-down cascading effects in trophic food webs in aquatic ecosystems and other ecosystems interacting with them.

Insectivorous will be subjected to less nutritious detritivores resulting from poor-quality litter and detritivores might have a small body size (bottom-up effect). Through the compensatory feeding theory (Lee et al., 2004; Berner et al., 2005), detritivores can be expected to over-consume poor-quality litter. This will result in high mortality of detritivores from two main reasons: (1) increased ingestion of secondary compounds (Stiling et al., 2003) and (2) over-consumption by their predators. The over-killing of detritivores by insectivorous might be due to two reasons: (i) high exposure to the enemies and (ii) compensatory feeding (once detritivores have less nutritional values or small-body size). The over-consumption and high mortality of detritivore insects might lead to reduction in carbon sequestration in freshwaters (top-down effect), since litter decomposition will be carried out by microbes. In this regard, studies are needed to get an insight into whether feeding on low-quality litter reduces nutritional values and body size of detritivore insects.

The leaching of soluble phenolic compounds can inhibit litter decomposition by binding exoenzymes (Zucker, 1983). When all plants will be subjected to high CO_2, the concentrations of soluble phenolics in streams might be stressful to the level that can impair litter decomposition. However, it is not known how litter decomposers will respond to the concentration of phenolics and other metabolites when all plants, at an ecosystem level, will be subjected to increased [CO_2]. Previous studies have investigated how phenolics and other secondary metabolites, in litter, affect litter decomposition. But, no study has studied how high concentrations of these compounds, in the stream, will affect litter decomposition. A study, simulating what will happen when all ecosystem-level vegetation will experience higher [CO_2] should give an insight into how litter decomposition will be affected in the future, vis-à-vis higher concentrations of secondary metabolites in the stream, under elevated atmospheric [CO_2].

V. References

Abelho, M. (2001). From litterfall to breakdown in streams : a review. *The Scientific World*, *1*, 656–680. https://doi.org/10.1100/tsw.2001.103

Adams, J. A., Tuchman, N. C., & Moore, P. A. (2003). Atmospheric CO_2 enrichment alters leaf detritus: impacts on foraging decisions of crayfish (*Orconectes virilis*). *Journal of the North American Benthological Society*, *22*, 410–422.

Adams, J. A., Tuchman, N. C., & Moore, P. A. (2005). Effects of CO_2-altered detritus on growth and chemically mediated decisions in crayfish (*Procambarus clarkii*). *Journal of the North American Benthological Society*, *24*, 330–345. https://doi.org/10.1899/04-042.1

Atkinson, D. (1995). Effects of temperature on the size of aquatic ectotherms: Exceptions to the general rule. *Journal of Thermal Biology*, *20*, 61–74. https://doi.org/10.1016/0306-4565(94)00028-H

Azevedo-Pereira, H. V. S., Graça, M. A. S., & González, J. M. (2006). Life history of *Lepidostoma hirtum* in an Iberian stream and its role in organic matter processing. *Hydrobiologia*, *559*, 183–192. https://doi.org/10.1007/s10750-005-1267-1

Baldy, V., Chauvet, E., Charcosset, J.-Y., & Gessner, M. O. (2002). Microbial dynamics associated with leaves decomposing in the mainstream and floodplain pond of a large river. *Aquatic Microbial Ecology*, *28*, 25–36. https://doi.org/10.3354/ame028025

Baldy, V., Gessner, M. O., & Chauvet, E. (1995). Bacteria, fungi and the breakdown of leaf litter in a large river. *Oikos*, *74*, 93. https://doi.org/10.2307/3545678

Baldy, V., Gobert, V., Guerold, F., Chauvet, E., Lambrigot, D., & Charcosset, J. Y. (2007). Leaf litter breakdown budgets in streams of various trophic status: effects of dissolved inorganic nutrients on microorganisms and invertebrates. *Freshwater Biology*, *52*, 1322–1335. https://doi.org/10.1111/j.1365-2427.2007.01768.x

Bärlocher, F. (1985). The role of fungi in the nutrition of stream invertebrates. *Botanical Journal of the Linnean Society*, *91*, 83–94. https://doi.org/10.1111/j.1095-8339.1985.tb01137.x

Batista, D., Pascoal, C., & Cássio, F. (2012). Impacts of warming on aquatic decomposers along a gradient of cadmium stress. *Environmental Pollution*, *169*, 35–41. https://doi.org/10.1016/j.envpol.2012.05.021

Batista, D., Pascoal, C., & Cássio, F. (2017). Temperature modulates AgNP impacts on microbial decomposer activity. *Science of the Total Environment, 601–602*, 1324–1332. https://doi.org/10.1016/j.scitotenv.2017.05.229

Battin, T.J., Kaplan, L.A., Findlay, S., Hopkinson, C.S., Marti, E., Pack- man, A.I. et al. (2008). Biophysical controls on organic carbon fluxes in fluvial networks. *Nature Geosciences, 1*, 95–100.

Battin, T.J., Luyssaert, S., Kaplan, L.A., Aufdenkampe, A.K., Richter, A. & Tranvik, L.J. (2009). The boundless carbon cycle. *Nature Geosciences, 2*, 598–600

Berner, D., Blanckenhorn, W. U., & Körner, C. (2005). Grasshoppers cope with low host plant quality by compensatory feeding and food selection: N limitation challenged. *Oikos, 111*, 525–533. https://doi.org/10.1111/j.1600-0706.2005.14144.x

Boyero, L., Graça, M. A. S., Tonin, A. M., Pérez, J., Swafford, J. A., Ferreira, V., Landeira-Dabarca. A., Alexandrou, A. M., Gessner, O. M., Mckie, G. B., Albariño, J. R., Barmuta, A. L., Castillo, M., Chará, J., Chauvet, E., Colón-Gaud, C., Dudgeon, D., Encalda, C. A., Figueroa, R., Flecker, S. A., Fleituch, T., Frainer, A., Gonçalves F. J. Jr., Helson, E. J., Iwata, T., Mathooko, J., M'Erimba, C., Pringle, M. C., Ramírez, A., Swan, M. C., Yule, M. C., & Pearson, R. G. (2017). Riparian plant litter quality increases with latitude. *Scientific Reports*, *7*, 10562. https://doi.org/10.1038/s41598-017-10640-3

Boyero, L., Pearson, R. G., Dudgeon, D., Ferreira, V., Graça, A. S., Gessner, M. O., Boulton, J. A., Chauvet, E., Yule, M. C., Albariño, J. R., Ramírez, A., Helson, E. J., Castillo, M., Arunachalam, M., Chará, J., Figueroa, R., Mathooko, M. J., Gonçalves F. J. Jr., Moretti, S. M., Chará-Serna, M. A., Davies, N. J., Encalda, A., Lamothe, S., Buria, M. L., Castela, J., Cornejo, A., Li, O. Y. A., M'Erimba, C., Villanueva, D. V., Zuñiga, María del Carmen, Swan., M. C., Barmuta, A. L., & Graça, M. A. S. (2012). Global patterns of distribution in stream detritivores: implications for biodiversity loss in changing climates. *Global Ecology and Biogeography, 21*, 134–141. https://doi.org/10.1111/j.1466-8238.2011.00673.x

Boyero, L., Pearson, R. G., Gessner, M. O., Barmuta, L. A., Ferreira, V., Graça, M. A. S., Dudgeon, D., Boulton, J. A., Castillo, M., Chauvet, E., Helson, E. J., Bruder, A., Albariño, J. R., Yule, M. C., Arunachalam, M., Davies, N. J., Figueroa, R., Flecker, S. A., Ramírez, A., Death, G. R., Iwata, T., Mathooko, M. J., Mathuriau, C., Gonçalves, F. J. Jr., Moretti, S. M., Jinggut, T., Lamothe, S., M'Erimba, C., Ratnarajah, L., Schindler, H. M., Castela, J., Buria, M. L., Cornejo, A., Villanueva, D. V., & West, D. C. (2011). A global experiment suggests climate warming will not accelerate litter

decomposition in streams but might reduce carbon sequestration. *Ecology Letters*, *14*, 289–294. https://doi.org/10.1111/j.1461-0248.2010.01578.x

Boyero, L., Pearson, R. G., Hui, C., Gessner, M. O., Alexandrou, M. A., Graça, M. A. S., Cardninale, J. B., Albariño, J. R., Arunachalam, M., Barmuta, A. L., Boulton, J. A., Bruder, A., Castillo, M., Chauvet, E., Death, G. R., Dudgeon, D., Encalada, E. A., Ferreira, V., Figueroa, V., Figueroa, R., Flecker, S. A., Gonçalves, F. J. Jr., Helson, J., Iwata, T., Mathooko, J., Mathuriau, C., M'Erimba, C., Moretti, S. M., Pringle, M. C., Ramírez, A., Ratnarajah, L., Rincon, J., Yule, M. C., & Jinggut, T. (2016). Biotic and abiotic variables influencing plant litter breakdown in streams : a global study. *The Royal Society, 283*, 20152664. https://doi.org/10.1098/rspb.2015.2664.

Brown, J. H., Gillooly, J. F., Allen, A. P., Savage, V. M., & West, G. B. (2004). Toward a metabolic theory of ecology. *Ecology*, *85*, 1771–1789. https://doi.org/Doi 10.1890/03-9000

Canhoto, C., & Graça, M. A. S. (1996). Decomposition of *Eucalyptus globulus* leaves and three native leaf species (*Alnus glutinosa*, *Castanea sativa* and *Quercus faginea*) in a Portuguese low order stream. *Hydrobiologia*, *333*, 79–85. https://doi.org/10.1007/BF00017570

Canton, S. P., & Martinson, R. J. (1990). The effects of varying current on weight loss from willow leaf packs. *Freshwater Biology*, *5*, 413–415. https://doi.org/10.1080/02705060.1990.9665257

Chauvet, E., Ferreira, V., Giller, P. S., McKie, B. G., Tiegs, S. D., Woodward, G., Elosegi, A., Dobson, M., Fleituch, T., Graça, M. A. S., Gulis, V., Hladyz, S., Lacoursière, J. O., Lecerf, A., Pozo, J., Preda, E., Riipinen, M., Rîşnoveanu, G., Vadineanu, A., Vought, L. B.-M., & Gessner, M. O. (2016). Litter decomposition as an indicator of stream ecosystem functioning at local-to-continental scales: insights from the European RivFunction Project. *Advances in Ecological Research*, *55*, 99–182. https://doi.org/10.1016/bs.aecr.2016.08.006

Chung, N., & Suberkropp, K. (2009). Effects of aquatic fungi on feeding preferences and bioenergetics of *Pycnopsyche gentilis* (Trichoptera: Limnephilidae). *Hydrobiologia*, *630*, 257–269. https://doi.org/10.1007/s10750-009-9820-y

Clements, W. H., & Cherry, D. S. (1988). Impact of heavy metals on insect communities in streams: a comparison of observational and experimental results. *Canadian Journal of Fisheries and Aquatic Sciences*, *45*, 2017–2025. https://*doi*.org/10.1139/f88-235

Cornut, J., Elger, A., Lambrigot, D., Marmonier, P., & Chauvet, E. (2010). Early stages of leaf decomposition are mediated by aquatic fungi in the hyporheic zone of woodland streams. *Freshwater Biology*, *55*, 2541–2556. https://doi.org/10.1111/j.1365-2427.2010.02483.x

Dang, C. K., Schindler, M., Chauvet, E., & Gessner, M. O. (2009). Temperature oscillation coupled with fungal community shifts can modulate warming effects on litter decomposition. *Ecology*, *90*, 122–131. https://doi.org/10.1890/07-1974.1

Dray, M. W. (2014). *Effects of multiple environmental stressors on litter chemical composition and decomposition.* Unpublished PhD thesis. University of Cardiff. https://doi.org/http://dx.doi.org/10.1016/j.soilbio.2013.12.013

Duarte, S., Cássio, F., Ferreira, V., Canhoto, C., & Pascoal, C. (2016). Seasonal variability may affect microbial decomposers and leaf decomposition more than warming in streams. *Microbial Ecology*, *72*, 263–276. https://doi.org/10.1007/s00248-016-0780-2

Duarte, S., Pascoal, C., Alves, A., Correia, A., & Cássio, F. (2008). Copper and zinc mixtures induce shifts in microbial communities and reduce leaf litter decomposition in streams. *Freshwater Biology*, *53*, 91–101. https://doi.org/10.1111/j.1365-2427.2007.01869.x

Fabre, E., & Chauvet, E. (1998). Leaf breakdown along an altitudinal stream gradient. *Archiv Für Hydrobiologie*, *141*, 167-179.

Farver, J. R. (1994). Oxygen self-diffusion in calcite: dependence on temperature and water fugacity. *Earth and Planetary Science Letters*, *121*, 575–587. https://doi.org/10.1016/0012-821X(94)90092-2

Feely, R., Doney, S., & Cooley, S. (2009). Ocean acidification: present conditions and future changes in a high-CO_2 world. *Oceanography*, *22*, 36–47. https://doi.org/10.5670/oceanog.2009.95

Fernandes, I., Seena, S., Pascoal, C., & Cássio, F. (2014). Elevated temperature may intensify the positive effects of nutrients on microbial decomposition in streams. *Freshwater Biology*, *59*, 2390–2399. https://doi.org/10.1111/fwb.12445

Ferreira, V., & Canhoto, C. (2014). Effect of experimental and seasonal warming on litter decomposition in a temperate stream. *Aquatic Sciences*, *76*, 155–163. https://doi.org/10.1007/s00027-013-0322-7

Ferreira, V., & Canhoto, C. (2015). Future increase in temperature may stimulate litter decomposition in temperate mountain streams: evidence from a stream manipulation experiment. *Freshwater Biology*, *60*, 881–892. https://doi.org/10.1111/fwb.12539

Ferreira, V., Castagneyrol, B., Koricheva, J., Gulis, V., Chauvet, E., & Graça, M. A. S. (2015). A meta-analysis of the effects of nutrient enrichment on litter decomposition in streams. *Biological Reviews*, *90*, 669–688. https://doi.org/10.1111/brv.12125

Ferreira, V., & Chauvet, E. (2011a). Future increase in temperature more than decrease in litter quality can affect microbial litter decomposition in streams. *Oecologia*, *167*, 279–291. https://doi.org/10.1007/s00442-011-1976-2

Ferreira, V., & Chauvet, E. (2011b). Synergistic effects of water temperature and dissolved nutrients on litter decomposition and associated fungi. *Global Change Biology*, *17*, 551–564. https://doi.org/10.1111/j.1365-2486.2010.02185.x

Ferreira, V., Chauvet, E., & Canhoto, C. (2015). Effects of experimental warming, litter species, and presence of macroinvertebrates on litter decomposition and associated decomposers in a temperate mountain stream. *Canadian Journal of Fisheries and Aquatic Sciences*, *72*, 206–216. https://doi.org/10.1139/cjfas-2014-0119

Ferreira, V., Gonçalves, A. L., Godbold, D. L., & Canhoto, C. (2010). Effect of increased atmospheric CO_2 on the performance of an aquatic detritivore through changes in water temperature and litter quality. *Global Change Biology*, *16*, 3284–3296. https://doi.org/10.1111/j.1365-2486.2009.02153.x

Finzi, A. C., Delucia, E. H., Hamilton, J. G., Richter, D. D., & Schlesinger, W. H. (2002). The nitrogen budget of a pine forest under free air CO_2 enrichment. *Oecologia*, *132*, 567–578. https://doi.org/10.1007/s00442-002-0996-3

Flury, S., & Gessner, M. O. (2011). Experimentally simulated global warming and nitrogen enrichment effects on microbial litter decomposers in a marsh. *Applied and Environmental Microbiology*, *77*, 803–809. https://doi.org/10.1128/AEM.01527-10

Forster, J., Hirst, A. G., & Atkinson, D. (2012). Warming-induced reductions in body size are greater in aquatic than terrestrial species. *Proceedings of the National Academy of Sciences*, *109*, 19310–19314. https://doi.org/10.1073/pnas.1210460109

France, R., Culbert, H., Freeborough, C., & Peters, R. (1997). Leaching and early mass loss of boreal leaves and wood in oligotrophic water. *Hydrobiologia*, *345*, 209–214.

Friberg, N., DybkjÆr, J. B., Olafsson, J. S., Gislason, G. M., Larsen, Sø. E., & Lauridsen, T. L. (2009). Relationships between structure and function in streams contrasting in temperature. *Freshwater Biology*, *54*, 2051–2068. https://doi.org/10.1111/j.1365-2427.2009.02234.x

Friberg, N., & Jacobsen, D. (1994). Feeding plasticity of 2 detritivore-shredders. *Freshwater Biology*, *32*, 133–142. https://doi.org/10.1111/j.1365-2427.1994.tb00873.x

Gardner, J. L., Peters, A., Kearney, M. R., Joseph, L., & Heinsohn, R. (2011). Declining body size: A third universal response to warming? *Trends in Ecology and Evolution*, *26*, 285–291. https://doi.org/10.1016/j.tree.2011.03.005

Gessner, M., & Chauvet, Eric, Dobson, M. (1999). A perspective on leaf litter breakdown in streams. *Oikos*, *85*, 377–384.

Golladay, S. W., Webster, J. R. and Benfield, E. F. 1983. (1983). Factors affecting food utilization by a leaf shredding aquatic insect: leaf species and conditioning time. *Holarctic Ecology 6: 157-162.*

González, J. M., & Graça, M. A. S. (2003). Conversion of leaf litter to secondary production by a shredding caddis-fly. *Freshwater Biology*, *48*, 1578–1592. https://doi.org/10.1046/j.1365-2427.2003.01110.x

Graça, M. A. S. (2001). The role of invertebrates on leaf litter decomposition in streams – a review. *International Review of Hydrobiology*, *86*, 383–394.

Graça, M. A. S., & Cressa, C. (2010). Leaf quality of some tropical and temperate tree species as food resource for stream shredders. *International Review of Hydrobiology*, *95*, 27–41. https://doi.org/10.1002/iroh.200911173

Graça, M. A. S., Cressa, C., Gessner, M. O., Feio, M. J., Callies, K. A., Barrios, C., & Gessner, T. (2001). Food quality, feeding preferences, survival and growth of shredders from temperate and tropical streams. *Freshwater Biology*, *46*, 947–957. https://doi.org/10.1046/j.1365-2427.2001.00729.x

Graça, M. A. S., Maltby, L., & Calow, P. (1993). Importance of fungi in the diet of *Gammarus pulex* (L.) and *Asellus aquaticus* (L.): II effects on growth, reproduction and physiology. *Oecologia*, *96*, 304–309. https://doi.org/10.1007/BF00317498

Griffiths, N. A., & Tiegs, S. D. (2016). Organic-matter decomposition along a temperature gradient in a forested headwater stream. *Freshwater Science*, *35*, 518–533. https://doi.org/10.1086/685657.

Gulis, V., & Suberkropp, K. (2003). Interaction between stream fungi and bacteria associated with decomposing leaf litter at different levels of nutrient availability. *Aquatic Microbial Ecology*, *30*, 149–157. https://doi.org/10.3354/ame030149

Hamilton, J. G., Delucia, E. H., George, K., Naidu, S. L., Finzi, A. C., & Schlesinger, W. H. (2002). Forest carbon balance under elevated CO_2, *2*, 250–260. https://doi.org/10.1007/s00442-002-0884-x

Hammrich, A. (2008). *Effects of warming and nitrogen enrichment on carbon turnover in a littoral wetland*. Unpublished PhD thesis. Universität Hamburg.

Han, P., & Bartels, D. M. (1996). Temperature dependence of oxygen diffusion in H_2O and D_2O. *The Journal of Physical Chemistry*, *100*, 5597–5602. https://doi.org/10.1021/jp952903y

Harper, M Atthew, Peckarsky, L. B. (2006). Emergence cues of a mayfly in a high-altitude stream ecosystem : potential response to climate change. *Ecological Applications*, *16*, 612–621. https://doi.org/10.1890/1051-0761(2006)016[0612:ECOAMI]2.0.CO;2

Hemming, J. D. C., & Lindroth, R. L. (1995). Intraspecific variation in aspen phytochemistry: effects on performance of gypsy moths and forest tent caterpillars. *Oecologia*, *103*, 79–88. https://doi.org/10.1007/BF00328428

Hieber, M., & Gessner, M. O. (2002). Contribution of stream detritivores, fungi and bacteria to lead breakdown based on biomass estimates. *Ecology*, *83*, 1026–1038. https://doi.org/10.1890/0012-9658(2002)083[1026:COSDFA]2.0.CO;2

Horne, C. R., Hirst, A. G., & Atkinson, D. (2017). Seasonal body size reductions with warming covary with major body size gradients in arthropod species. *Proceedings of the Royal Society B: Biological Sciences*, *284*, 20170238. https://doi.org/10.1098/rspb.2017.0238

Hufnagel, L Garamvölgyi, Á. (2014). Impacts of climate change on vegetation distribution No. 1: Climate change induced vegetation shifts in the palearctic region. *Applied Ecology and Environmental Research*, *12*, 355–422. https://doi.org/10.15666/aeer/1101_079122

IPCC. (2013). *Climate Change 2013*. *the Fifth Assessment Report* (Vol. 5).

IPCC, 2013: Summary for policymakers. In: climate change 2013: the physical science basis. Contribution of working group I to the fifth assessment report of the intergovernmental panel on climate change [Stocker, T.F., D. Qin, G.-K. Plattner, M. Tignor, S. K. Allen, J. Boschung, A. Nauels, Y. Xia, V. Bex and P.M. Midgley (eds.)]. Cambridge University Press, Cambridge, United Kingdom and New York, NY, USA.

Irons III, J. G., Oswood, M. W., Stout, R. J., & Pringle, C. M. (1994). Latitudinal patterns in leaf litter breakdown: is temperature really important? *Freshwater Biology*, *32*, 401–411. https://doi.org/10.1111/j.1365-2427.1994.tb01135.x

Jinggut, T., & Yule, C. M. (2015). Leaf-litter breakdown in streams of East Malaysia (Borneo) along an altitudinal gradient: initial nitrogen content of litter limits shredder feeding. *Freshwater Science*, *34*, 691–701. https://doi.org/10.1086/681256

Kashian, D. R., Zuellig, R. E., Mitchell, K. A., & Clements, W. H. (2007). The cost of tolerance : sensitivity of stream benthic communities to UV-B and metals. *Ecological Society of America*, *17*, 365–375. https://doi.org/10.1890/06-0396

Kingsolver, J. G., & Huey, R. B. (2008). Size, temperature, and fitness: three rules. *Evolutionary Ecology Research*, *10*, 251–268. https://doi.org/10.1111/j.1525-142X.2006.00090.x

Kinney, K. K., Lindroth, L. R., Jung. M. S., & Nordheim, V. E. (1997) (1997). Effects of CO_2 and NO_3- availability on deciduous trees: phytochemistry and insect performance. *Ecological Society of America*, *78*, 215–230. https://doi.org/10.1890/00129658(1997)078[0215:EOCANA]2.0.CO;2

Kominoski, J. S., & Rosemond, A. D. (2011). Conservation from the bottom up: forecasting effects of global change on dynamics of organic matter and management needs for river networks. *Freshwater Science*, *31*, 51–68. https://doi.org/10.1899/10-160.1

Lajeunesse, M. (2013). Recovering missing data or partial data from studies: A survey of conversions and imputation for meta-analysis. In J. Koricheva, J. Gurevitch, and K. Mengersen, editors. Handbook of meta-analysis in ecology and evolution (pp. 195–206). Princeton University, New Jersey, USA.

Larry V. Hedges, Jessica Gurevitch, and P. S. C. (1999). The meta-analysis of response ratios in experimental ecology. *Ecological Society of America*, *80*, 1150–1156. http://dx.doi.org/10.2307/177062

Lecerf, A., & Chauvet, E. (2008). Intraspecific variability in leaf traits strongly affects alder leaf decomposition in a stream. *Basic and Applied Ecology*, *9*, 598–605. https://doi.org/10.1016/j.baae.2007.11.003

Lee, K. P., Raubenheimer, D., & Simpson, S. J. (2004). The effects of nutritional imbalance on compensatory feeding for cellulose-mediated dietary dilution in a generalist caterpillar. *Physiological Entomology*, *29*, 108–117. https://doi.org/10.1111/j.0307-6962.2004.00371.x

LeRoy, C. J., Whitham, T. G., Wooley, S. C., & Marks, J. C. (2007). Within-species variation in foliar chemistry influences leaf-litter decomposition in a Utah river. *Journal of the North American Benthological Society*, *26*, 426–438. https://doi.org/10.1899/06-113.1

Maloney, C. D., & Lamberti, A. G. (1995). Rapid decomposition of summer-input leaves in a northern michigan stream. *American Midland Naturalist*, *133*, 184–195. https://doi.org/10.2307/2426360

Martínez, A., Larrañaga, A., Pérez, J., Descals, E., & Pozo, J. (2014). Temperature affects leaf litter decomposition in low-order forest streams: field and microcosm approaches. *FEMS Microbiology Ecology*, *87*, 257–267. https://doi.org/10.1111/1574-6941.12221

Martínez, A., Monroy, S., Pérez, J., Larrañaga, A., Basaguren, A., Molinero, J., & Pozo, J. (2016). In-stream litter decomposition along an altitudinal gradient: does substrate quality matter? *Hydrobiologia*, *766*, 17–28. https://doi.org/10.1007/s10750-015-2432-9

Martins, T. R., Rezende, RdS., Gonçalves, J. F. Jr., Lopes, A., Piedade, M. T. F., Cavalcante, HdL., & Hamada, N. (2017). Effects of increasing temperature and CO_2 on quality of litter, shredders , and microorganisms in amazonian aquatic systems. *PLoS ONE*, *12*, e0188191. https://doi.org/10.1371/journal.pone.0188791

Martins, R. T., Melo, A. S., Gonçalves, J. F.Jr., Campos, C. M., & Hamada, N. (2017). Effects of climate change on leaf breakdown by microorganisms and the shredder *Phylloicus elektoros* (Trichoptera: Calamoceratidae). *Hydrobiologia*, *789*, 31–44. https://doi.org/10.1007/s10750-016-2689-7

Mas-Martí, E., Muñoz, I., Oliva, F., & Canhoto, C. (2015). Effects of increased water temperature on leaf litter quality and detritivore performance: A whole-reach manipulative experiment. *Freshwater Biology*, *60*, 184–197. https://doi.org/10.1111/fwb.12485

Matthaei, C. D., Piggott, J. J., & Townsend, C. R. (2010). Multiple stressors in agricultural streams : interactions among sediment addition , nutrient enrichment and water abstraction. *Journal of Applied Ecology*, *52*, 639–649. https://doi.org/10.1111/j.1365-2664.2010.01809.x

Miller-Rushing, A. J., & Primack, R. B. (2008). Global warming and flowering times in Thoreau's Concord: a community perspective. *Ecology*, *89*, 332–341. https://doi.org/10.1890/07-0068.1

Minshall, W. G., Cummins, W. K., Petersen, C. R., Cushing, E. C., Bruns, A. D., Sedell, R. J., & Vannote, L. R. (1985). Developments in stream ecosystem theory. *Canadian Journal of Fisheries and Aquatic Sciences*, *42*, 1045–1055. https://doi.org/http://dx.doi.org/10.1139/f85-130

Moghadam, F. S., & Zimmer, M. (2016). Effects of warming, nutrient enrichment and detritivore presence on litter breakdown and associated microbial decomposers in a simulated temperate woodland creek. *Hydrobiologia*, *770*, 243–256. https://doi.org/10.1007/s10750-015-2596-3

Monroy, S., Miranda-apodaca, J., Pérez-lópez, U., Mena-petite, A., Elosegi, A., Muñoz-rueda, A., & Pozo, J. (2016). Elevated atmospheric CO_2 interacts with drought and competition to produce complex results in plant quality and subsequent microbial aquatic decomposition. *Canadian Journal of Fisheries and Aquatic Sciences*, *73*, 1770–1776. https://doi.org/10.1139/cjfas-2016-0034

Mora-Gómez, J., Elosegi, A., Mas-Martí, E., & Romaní, A. M. (2015). Factors controlling seasonality in leaf-litter breakdown in a Mediterranean stream. *Freshwater Science*, *34*, 1245–1258. https://doi.org/10.1086/683120

Motomori, K., Mitsuhashi, H., & Nakano, S. (2001). Influence of leaf litter quality on the colonization and consumptionof stream invertebrate shredders. *Ecological Research*, *16*, 173–182. https://doi.org/10.1046/j.1440-1703.2001.00384.x

Niyogi, D. K., Simon, K. S., & Townsend, C. R. (2003). Breakdown of tussock grass in streams along a gradient of agricultural development in New Zealand. *Freshwater Biology*, *48*, 1698–1708. https://doi.org/10.1046/j.1365-2427.2003.01104.x

Norby, R. J., Cotrufo, M. F., Ineson, P., O'Neill, E. G., & Canadell, J. G. (2001). Elevated CO_2, litter chemistry, and decomposition: a synthesis. *Oecologia*, *127*, 153–165. https://doi.org/10.1007/s004420000615

Ostrofsky, M. L. (1993). Effect of tannins on leaf processing and conditioning rates in aquatic ecosystems: an empirical approach. *Canadian Journal of Fisheries and Aquatic Sciences*, *50*, 1176–1180. https://doi.org/https://doi.org/10.1139/f93-134

Ostrofsky, M. L. (1997). Relationship between chemical characteristics of autumn-shed leaves and aquatic processing rates. *Journal of the North American Benthological Society*, *16*, 750–759. https://doi.org/10.2307/1468168

Parmesan, C. (2006). Ecological and evolutionary responses to recent climate change. *Annual Review of Ecology, Evolution, and Systematics*, *37*, 637–669. https://doi.org/10.1146/annurev.ecolsys.37.091305.110100

Pascoal, C., & Cássio, F. (2004). Contribution of fungi and bacteria to leaf litter decomposition in a polluted river. *Applied and Environmental Microbiology*, *7*, 5266–5273. https://doi.org/10.1128/AEM.70.9.5266

Peñuelas, J., & Estiarte, M. (1998). Can elevated CO_2 affect secondary metabolism and ecosystem function? *Trends in Ecology and Evolution*, *13*, 20–24. https://doi.org/10.1016/S0169-5347(97)01235-4

Pereira, A., Trabulo, J., Fernandes, I., Pascoal, C., Cássio, F., & Duarte, S. (2017). Spring stimulates leaf decomposition in moderately eutrophic streams. *Aquatic Sciences*, *79*, 197–207. https://doi.org/10.1007/s00027-016-0490-3

Piggott, J. J., Lange, K., Townsend, C. R., & Matthaei, C. D. (2012). Multiple stressors in agricultural streams: a mesocosm study of interactions among raised water temperature, sediment addition and nutrient enrichment. *Plos One*, *7*, e49873. https://doi.org/10.1371/journal.pone.0049873

Poorter, H., Van Berkel, Y., Baxter, R., Den Hertog, J., Dijkstra, P., Gifford, R. M., … & Wong, S. C. (1997). The effect of elevated CO_2 on the chemical composition and construction costs of leaves of 27 C_3 species. *Plant Cell and Environment*, *20*, 472–482. https://doi.org/10.1046/j.1365-3040.1997.d01-84.x

Rader, R. B., Mcarthur, J. V, Aho, J. M., Rader, R. B., & Aho, J. M. (1994). Relative importance of mechanisms determining decomposition in a Southeastern Blackwater stream. *American Midland Naturalist*, *132*, 19–31. http://dx.doi.org/10.2307/2426197

Rajashekhar, M., & Kaveriappa, K. M. (2000). Effects of temperature and light on growth and sporulation of aquatic hyphomycetes. *Hydrobiologia*, *441*, 149–153.

Rier, S. T., Tuchman, N. C., & Wetzel, R. G. (2005). Chemical changes to leaf litter from trees grown under elevated CO_2 and the implications for microbial utilization in a stream ecosystem. *Canadian Journal of Fisheries and Aquatic Sciences*, *62*, 185–194. https://doi.org/10.1139/f04-148

Shelomi, M., & Zeuss, D. (2017). Bergmann's and Allen's rules in aative European and Mediterranean phasmatodea. *Frontiers in Ecology and Evolution*, *5*, 1–13. https://doi.org/10.3389/fevo.2017.00025

Sibly, R. M., & Atkinson, D. (1994). How rearing temperature affects optimal adult size in ectotherms. *Functional Ecology*, *8*, 486. https://doi.org/10.2307/2390073

Simon, G. (2006). Collaborative care for depression. *Archives of Internal Medicine*, *166*, 2314–2321. https://doi.org/10.1136/bmj.332.7536.249

Sridhar, K. R. (2009). Freshwater hyphomycetes. *Frontiers in Fungal Ecology, Diversity and Metabolites*, 1–16. https://doi.org/10.13140/RG.2.1.1563.3045

Stiling P., & Cornelissen, T. (2007). How does elevated carbon dioxide (CO_2) affect plant – herbivore interactions? A field experiment and meta-analysis of CO_2-mediated changes on plant chemistry and herbivore performance. *Global Change Biology*, *13*, 1823–1842. https://doi.org/10.1111/j.1365-2486.2007.01392.x

Stiling, P., Moon, D. C., Hunter, M. D., Colson, J., Rossi, A. M., Hymus, G. J., & Drake, B. G. (2003). Elevated CO_2 lowers relative and absolute herbivore density across all species of a scrub-oak forest. *Oecologia*, *134*, 82–87. https://doi.org/10.1007/s00442-002-1075-5

Suurmond, R., van Rhee, H., & Hak, T. (2017). Introduction, comparison, and validation of Meta-Essentials: a free and simple tool for meta-analysis. *Research Synthesis Methods*, *8*, 537–553. https://doi.org/10.1002/jrsm.1260

Tank, J. L., Rosi-marshall, E. J., Griffiths, N. A., Entrekin, S. A., & Stephen, M. L. (2010). A review of allochthonous organic matter dynamics and metabolism in streams, *29*, 118–146. https://doi.org/10.1899/08-170.1

Tank, J. L., Rosi-Marshall, E. J., Griffiths, N. A., Entrekin, S. A., & Stephen, M. L. (2010). A review of allochthonous organic matter dynamics and metabolism in streams. *The Society of Freshwater Science*, *29*, 118–146. https://doi.org/10.1899/08-170.1

Tant, C. J., Rosemond, A. D., Helton, A. M., & First, M. R. (2015). Nutrient enrichment alters the magnitude and timing of fungal, bacterial, and detritivore contributions to litter breakdown. *Freshwater Science*, *34*, 1259–1271. https://doi.org/10.1086/683255

Taylor, B. R., & Andrushchenko, I. V. (2014). Interaction of water temperature and shredders on leaf litter breakdown: a comparison of streams in Canada and Norway. *Hydrobiologia*, *721*, 77–88. https://doi.org/10.1007/s10750-013-1650-2

Taylor, B. R., & Chauvet, E. E. (2014). Relative influence of shredders and fungi on leaf litter decomposition along a river altitudinal gradient. *Hydrobiologia*, *72*, 239–250. https://doi.org/10.1007/s10750-013-1666-7

Teplitsky, C., & Millien, V. (2014). Climate warming and Bergmann's rule through time: is there any evidence? *Evolutionary Applications*, *7*, 156–168. https://doi.org/10.1111/eva.12129

Thormann, M. N., Bayley, S. E., & Currah, R. S. (2004). Microcosm tests of the effects of temperature and microbial species number on the decomposition of *Carex aquatilis* and *Sphagnum fuscum* litter from southern boreal peatlands. *Canadian Journal of Microbiology*, *50*, 793–802. https://doi.org/10.1139/w04-064

Tuchman, N. C., Wetzel, R. G., Rier, S. T., Wahtera, K. A., &Teeri, J. A. (2002). Elevated atmospheric CO_2 lowers leaf litter nutritional quality for stream ecosystem food webs. *Global Change Biology*, *8*, 163–170. https://doi.org/10.1046/j.1365-2486.2002.00460.x

Tuchman, N. C., Wahtera, K. A., Wahtera, K. A., Wetzel, R. G., & Teeri, J. A. (2003). Elevated atmospheric CO_2 alters leaf litter quality for stream ecosystems: an *in situ* leaf decompositon study. *Hydrobilogia*, *495*, 203–21. https://doi.org/10.1890/1051-0761(2006)016[0612:ECOAMI]2.0.CO;2

Tuchman, N. C., Wahtera, K. A., Wetzel, R. G., Russo, N. M., Kilbane, G. M., Sasso, L. M., & Teeri, J. A. (2003). Nutritional quality of leaf detritus altered by elevated atmospheric CO_2: effects on development of mosquito larvae. *Freshwater Biology, 48,* 1432–1439. https://doi.org/10.1046/j.1365-2427.2003.01102.x

van Vuuren, D. P., Edmonds, J., Kainuma, M., Riahi, K., Thomson, A., Hibbard, K., Hurtt, G. C., Kram, T., Krey, V., Lamarque, J. F., Masui, T., Meinshausen, M., Nakicenovic, N., Smith, S. T., & Rose, S. K. (2011). The representative concentration pathways: An overview. *Climatic Change, 109,* 5–31. https://doi.org/10.1007/s10584-011-0148-z

Vannote, R. L., Cummins, K. W., & Sedell, J. R. (1980). The river continuum concept. *Canadian Journal of Fisheries and Aquatic Sciences, 37,* 130–137. https://doi.org/10.1139/f80-017

Wagner, R., & Wantzen, M. K. (2006). Detritus processing by shredders: a tropical-temperate comparison. *Journal of the North American Benthological Society, 25,* 99–107. https://doi.org/10.1899/0887-3593(2006)25

Webster, J. R., & Benfield, E. F. (1986). Vascular plant breakdown in freshwater ecosystems. *Annual Review of Ecology and Systematics, 17,* 567–594.

Weyers, H. S., & Suberkropp, K. (1996). Fungal and bacterial production during the breakdown of yellow poplar leaves in 2 streams. *Journal of the North American Benthological Society, 15,* 408–420. https://doi.org/10.2307/1467795

Wiggins, G. B., & Mackay, R. J. (1978). Some relationships between systematics and trophic ecology in nearctic aquatic insects, with special reference to Trichoptera. *Ecological Society of America, 59,* 1211-1220. https://doi.org/https://doi.org/10.2307/1938234

Williams, R. S., Lincoln, D. E., & Norby, R. J. (2003). Development of gypsy moth larvae feeding on red maple saplings at elevated CO_2 and temperature. *Oecologia, 137,* 114–122. https://doi.org/10.1007/s00442-003-1327-z

Woodward, G., Perkins, D. M., & Brown, L. E. (2010). Climate change and freshwater ecosystems: impacts across multiple levels of organization. *Philosophical Transactions of the Royal Society B: Biological Sciences, 365,* 2093–2106. https://doi.org/10.1098/rstb.2010.0055

Young, R. G., Matthaei, C. D., & Townsend, C. R. (2008). Organic matter breakdown and ecosystem metabolism: functional indicators for assessing river ecosystem health. *Journal of the North American Benthological Society, 27,* 605–625. https://doi.org/10.1899/07-121.1

Yue, K., Peng, C., Yang, W., Peng, Y., Fang, J., & Wu, F. (2015). Study type and plant litter identity modulating the response of litter decomposition to warming, elevated CO_2, and elevated O_3: a meta-analysis, *Journal of Geophysical Research: Biogeosciences*, *120*, 1–11. https://doi.org/10.1002/2014JG002885

Zucker, W. V. (1983). Tannins: does structure determine function? An ecological perspective. *The American Naturalist*, *121*, 335–365. https://doi.org/10.1086/284065

VI. Appendices

Appendix 1. Matrix used in the analyses showing studies, effect size (Hedges' *g*) and its variance (*Vg*) and moderators. For definition of moderators and levels, see Table 2.

Study	*g*	*Vg*	Type of change	System	Study type	Field study	Correlative study	Community type	Litter genus	Temp increase	CO_2 increase	Origin of Data
Batista&al2012	0.76	0.72	Temp	Lotic	Laboratory				*Alnus*	6		Estimated
Batista&al2017	4.73	2.53	Temp	Lotic	Laboratory				*Alnus*	6		Estimated
Batista&al2017	3.65	1.77	Temp	Lotic	Laboratory				*Alnus*	13		Estimated
Batista&al2017	3.82	1.89	Temp	Lotic	Laboratory				*Alnus*	6		Estimated
Batista&al2017	3.05	1.44	Temp	Lotic	Laboratory				*Alnus*	13		Estimated
Boyero&al2011	0.23	0.08	Temp	Lotic	Field	Correlative	Latitudinal	Microbial	*Alnus*			Reported
Boyero&al2011	1.68	0.07	Temp	Lotic	Field	Correlative	Latitudinal	Total	*Alnus*			Reported
Correa-Araneda&al2015	-1.16	0.13	Temp	Lotic	Laboratory			Total	*Nothofagus*	7		Estimated
Correa-Araneda&al2015	1.25	0.13	Temp	Lotic	Laboratory			Total	*Nothofagus*	7		Estimated
Correa-Araneda&al2015	0.96	0.12	Temp	Lotic	Laboratory			Total	*Eucalyptus*	7		Estimated
Correa-Araneda&al2015	0.31	0.11	Temp	Lotic	Laboratory			Total	*Eucalyptus*	7		Estimated
Correa-Araneda&al2015	0.20	0.11	Temp	Lotic	Laboratory			Total	*Alnus*	5		Estimated
Correa-Araneda&al2015	-0.22	0.11	Temp	Lotic	Laboratory			Total	*Alnus*	5		Estimated
Correa-Araneda&al2015	0.11	0.11	Temp	Lotic	Laboratory			Total	*Eucalyptus*	5		Estimated
Correa-Araneda&al2015	0.97	0.12	Temp	Lotic	Laboratory			Total	*Eucalyptus*	5		Estimated
Dang&al2009	-3.66	0.89	Temp	Lotic	Laboratory				*Alnus*	5		Estimated
Domingos&al2015	-0.90	0.18	Temp	Lotic	Field	Manipulative		Total	*Quercus*	2.7		Reported
Duarte&al2016	0.94	0.15	Temp	Lotic	Field	Manipulative		Microbial	*Quercus*	3		Estimated
Duarte&al2016	0.31	0.14	Temp	Lotic	Field	Manipulative		Microbial	*Quercus*	2.3		Estimated
Fabre&Chauvet1998	-1.65	0.53	Temp	Lotic	Field	Correlative	Altitudinal	Total	*Alnus*			Estimated
Fernandes&al2009	1.23	0.10	Temp	Lotic	Laboratory				*Alnus*	7		Reported
Fernandes&al2012	0.94	0.74	Temp	Lotic	Laboratory				*Alnus*	8		Estimated
Fernandes&al2012	0.41	0.68	Temp	Lotic	Laboratory				*Vitis*	8		Estimated
Fernandes&al2012	0.88	0.73	Temp	Lotic	Laboratory				*Quercus*	8		Estimated
Fernandes&al2012	1.43	0.84	Temp	Lotic	Laboratory				*Platanus*	8		Estimated

Fernandes&al2014	1.57	0.44	Temp	Lotic	Laboratory				*Alnus*	6			Estimated
Fernandes&al2014	2.43	0.58	Temp	Lotic	Laboratory				*Alnus*	6			Estimated
Fernandes&al2014	1.39	0.41	Temp	Lotic	Laboratory				*Alnus*	6			Estimated
Fernandes&al2014	0.45	0.34	Temp	Lotic	Laboratory				*Alnus*	6			Estimated
Fernandes&al2014	0.47	0.34	Temp	Lotic	Laboratory				*Alnus*	6			Estimated
Fernandes&al2014	1.79	0.47	Temp	Lotic	Laboratory				*Quercus*	6			Estimated
Fernandes&al2014	1.45	0.42	Temp	Lotic	Laboratory				*Quercus*	6			Estimated
Fernandes&al2014	1.82	0.47	Temp	Lotic	Laboratory				*Quercus*	6			Estimated
Fernandes&al2014	1.90	0.48	Temp	Lotic	Laboratory				*Quercus*	6			Estimated
Fernandes&al2014	2.13	0.52	Temp	Lotic	Laboratory				*Quercus*	6			Estimated
Ferreira&al2006	6.32	0.80	Temp	Lotic	Field	Correlative	Seasonal	Total	*Alnus*	8.2			Reported
Ferreira&al2006	7.00	1.12	Temp	Lotic	Field	Correlative	Seasonal	Total	*Alnus*	8.2			Reported
Ferreira&al2006	1.08	0.22	Temp	Lotic	Field	Correlative	Seasonal	Total	*Alnus*	8.2			Reported
Ferreira&al2006	2.17	0.25	Temp	Lotic	Field	Correlative	Seasonal	Total	*Alnus*	8.2			Reported
Ferreira&al2015	1.80	0.31	Temp	Lotic	Field	Manipulative		Microbial	*Quercus*	2.8			Reported
Ferreira&al2015	1.79	0.31	Temp	Lotic	Field	Manipulative		Microbial	*Castanea*	2.8			Reported
Ferreira&al2015	1.73	0.31	Temp	Lotic	Field	Manipulative		Total	*Quercus*	2.8			Reported
Ferreira&al2015	0.53	0.23	Temp	Lotic	Field	Manipulative		Total	*Castanea*	2.8			Reported
Ferreira&Canhoto2014	2.19	0.69	Temp	Lotic	Field	Manipulative		Total	*Quercus*				Estimated
Ferreira&Canhoto2014	289%	44%	Temp	Lotic	Field	Manipulative		Microbial	*Quercus*				Estimated
Ferreira&Canhoto2015	-0.39	0.14	Temp	Lotic	Field	Manipulative		Total	*Quercus*	3			Reported
Ferreira&Canhoto2015	0.65	0.14	Temp	Lotic	Field	Manipulative		Total	*Quercus*	2.4			Reported
Ferreira&Canhoto2015	1.65	0.18	Temp	Lotic	Field	Manipulative		Total	*Quercus*	2.8			Reported
Ferreira&Canhoto2015	1.99	0.20	Temp	Lotic	Field	Manipulative		Microbial	*Quercus*	3			Reported
Ferreira&Canhoto2015	0.88	0.15	Temp	Lotic	Field	Manipulative		Microbial	*Quercus*	2.3			Reported
Ferreira&Canhoto2015	1.93	0.20	Temp	Lotic	Field	Manipulative		Microbial	*Quercus*	2.8			Reported
Ferreira&Chauvet2011a	2.09	0.77	Temp	Lotic	Laboratory				*Alnus*	5	0		Reported
Ferreira &Chauvet2011b	1.24	0.20	Temp	Lotic	Laboratory				*Alnus*	5			Reported
Ferreira &Chauvet2011b	1.69	0.23	Temp	Lotic	Laboratory				*Alnus*	10			Reported
Friberg&al2009	2.34	0.15	Temp	Lotic	Field	Correlative	Geothermal	Microbial	*Betula*				Estimated
Friberg&al2009	1.63	0.14	Temp	Lotic	Field	Correlative	Geothermal	Total	*Betula*				Estimated
Geraldes&al2012	0.66	0.53	Temp	Lotic	Laboratory				*Alnus*	8			Estimated

Geraldes&al2012	6.39	3.05	Temp	Lotic	Laboratory				*Alnus*	8	Estimated
Geraldes&al2012	1.61	0.66	Temp	Lotic	Laboratory				*Alnus*	8	Estimated
Geraldes&al2012	1.89	0.72	Temp	Lotic	Laboratory				*Alnus*	8	Estimated
Gessner&al1993	-2.74	1.29	Temp	Lotic	Field	Correlative	Seasonal	Total	*Alnus*	7.35	Reported
Gonçalves&al2013	0.22	0.08	Temp	Lotic	Laboratory				*Alnus*	5	Reported
Gonçalves&al2013	0.56	0.09	Temp	Lotic	Laboratory				*Alnus*	10	Reported
Gonçalves&al2013	0.06	0.08	Temp	Lotic	Laboratory				*Alnus*	15	Reported
Gonçalves&al2013	0.04	0.08	Temp	Lotic	Laboratory				*Quercus*	5	Reported
Gonçalves&al2013	0.59	0.09	Temp	Lotic	Laboratory				*Quercus*	10	Reported
Gonçalves&al2013	1.11	0.10	Temp	Lotic	Laboratory				*Quercus*	15	Reported
Irons&al1994	2.05	0.12	Temp	Lotic	Field	Correlative	Latitudinal	Total	*Pithecellobium*	9.45	Reported
Irons&al1994	6.13	0.46	Temp	Lotic	Field	Correlative	Latitudinal	Total	*Trema*	11.30	Reported
Irons&al1994	2.67	0.15	Temp	Lotic	Field	Correlative	Latitudinal	Total	*Cornus*	11.33	Reported
Irons&al1994	3.73	0.22	Temp	Lotic	Field	Correlative	Latitudinal	Total	*Quercus*	11.10	Reported
Irons&al1994	-1.27	0.10	Temp	Lotic	Field	Correlative	Latitudinal	Total	*Acer*	12.66	Reported
Irons&al1994	4.96	0.33	Temp	Lotic	Field	Correlative	Latitudinal	Total	*Fagus*	16.66	Reported
Irons&al1994	0.81	0.09	Temp	Lotic	Field	Correlative	Latitudinal	Total	*Alnus*	12.88	Reported
Irons&al1994	1.89	0.12	Temp	Lotic	Field	Correlative	Latitudinal	Total	*Quercus*	12.82	Reported
Irons&al1994	-2.61	0.15	Temp	Lotic	Field	Correlative	Latitudinal	Total	*Alnus*	12.09	Reported
Irons&al1994	-1.32	0.10	Temp	Lotic	Field	Correlative	Latitudinal	Total	*Salix*	12.97	Reported
Irons&al1994	7.99	0.72	Temp	Lotic	Field	Correlative	Latitudinal	Total	*Pithecellobium*	25.73	Reported
Irons&al1994	7.68	0.67	Temp	Lotic	Field	Correlative	Latitudinal	Total	*Trema*	25.51	Reported
Irons&al1994	4.62	0.29	Temp	Lotic	Field	Correlative	Latitudinal	Total	*Cornus*	25.05	Reported
Irons&al1994	3.45	0.20	Temp	Lotic	Field	Correlative	Latitudinal	Total	*Quercus*	25.21	Reported
Irons&al1994	2.35	0.14	Temp	Lotic	Field	Correlative	Latitudinal	Total	*Acer*	25.42	Reported
Irons&al1994	2.38	0.14	Temp	Lotic	Field	Correlative	Latitudinal	Total	*Fagus*	19.64	Reported
Irons&al1994	2.71	0.15	Temp	Lotic	Field	Correlative	Latitudinal	Total	*Alnus*	24.71	Reported
Irons&al1994	2.23	0.13	Temp	Lotic	Field	Correlative	Latitudinal	Total	*Quercus*	24.80	Reported
Irons&al1994	2.16	0.13	Temp	Lotic	Field	Correlative	Latitudinal	Total	*Alnus*	24.72	Reported
Irons&al1994	2.43	0.14	Temp	Lotic	Field	Correlative	Latitudinal	Total	*Salix*	24.70	Reported
Jiggut&Yule2015	4.56	0.19	Temp	Lotic	Field	Correlative	Altitudinal	Total	*Macaranga*		Estimated
Jiggut&Yule2015	0.49	0.17	Temp	Lotic	Field	Correlative	Altitudinal	Microbial	*Macaranga*		Estimated

Martinez&al2014	1.26	0.24	Temp	Lotic	Field	Correlative	Altitudinal	Microbial	*Alnus*	2.44	Reported
Martinez&al2014	2.66	0.38	Temp	Lotic	Field	Correlative	Altitudinal	Microbial	*Alnus*	3.51	Reported
Martinez&al2014	1.19	0.59	Temp	Lotic	Laboratory				*Alnus*	5	Reported
Martinez&al2014	1.02	0.57	Temp	Lotic	Laboratory				*Alnus*	10	Reported
Martinez&al2014	0.11	0.50	Temp	Lotic	Laboratory				*Alnus*	5	Reported
Martinez&al2014	1.49	0.64	Temp	Lotic	Laboratory				*Alnus*	10	Reported
Martinez&al2014	2.26	0.82	Temp	Lotic	Laboratory				*Alnus*	5	Reported
Martinez&al2014	0.54	0.52	Temp	Lotic	Laboratory				*Alnus*	10	Reported
Martinez&al2016	0.19	0.13	Temp	Lotic	Field	Correlative	Altitudinal	Microbial	*Alnus*	2.5	Reported
Martinez&al2016	-0.69	0.13	Temp	Lotic	Field	Correlative	Altitudinal	Microbial	*Quercus*	2.5	Reported
Martinez&al2016	0.73	0.13	Temp	Lotic	Field	Correlative	Altitudinal	Microbial	*Fagus*	2.5	Reported
Martinez&al2016	0.78	0.14	Temp	Lotic	Field	Correlative	Altitudinal	Total	*Alnus*	2.5	Reported
Martinez&al2016	1.09	0.14	Temp	Lotic	Field	Correlative	Altitudinal	Total	*Quercus*	2.5	Reported
Martinez&al2016	0.96	0.14	Temp	Lotic	Field	Correlative	Altitudinal	Total	*Fagus*	2.5	Reported
Martinez&al2016	0.08	0.13	Temp	Lotic	Field	Correlative	Altitudinal	Microbial	*Alnus*	4.5	Reported
Martinez&al2016	-0.41	0.13	Temp	Lotic	Field	Correlative	Altitudinal	Microbial	*Quercus*	4.5	Reported
Martinez&al2016	0.81	0.14	Temp	Lotic	Field	Correlative	Altitudinal	Microbial	*Fagus*	4.5	Reported
Martinez&al2016	1.26	0.15	Temp	Lotic	Field	Correlative	Altitudinal	Total	*Alnus*	4.5	Reported
Martinez&al2016	1.29	0.15	Temp	Lotic	Field	Correlative	Altitudinal	Total	*Quercus*	4.5	Reported
Martinez&al2016	1.07	0.14	Temp	Lotic	Field	Correlative	Altitudinal	Total	*Fagus*	4.5	Reported
Mas-Marti&al2015	1.22	0.47	Temp	Lotic	Field	Manipulative		Microbial	*Quercus*	2.8	Estimated
Mas-Marti&al2015	0.08	0.40	Temp	Lotic	Field	Manipulative		Microbial	*Quercus*	2.8	Estimated
Mas-Marti&al2015	1.04	0.45	Temp	Lotic	Field	Manipulative		Microbial	*Quercus*	2.8	Estimated
Mas-Marti&al2015	1.07	0.46	Temp	Lotic	Field	Manipulative		Microbial	*Quercus*	2.8	Estimated
Mas-Marti&al2015	1.05	0.46	Temp	Lotic	Field	Manipulative		Microbial	*Quercus*	2.8	Estimated
Mogadham&Zimmer2016	0.21	0.05	Temp	Lotic	Laboratory				*Betula*	5	Reported
Mogadham&Zimmer2016	1.80	0.07	Temp	Lotic	Laboratory				*Betula*	5	Reported
Mora-Gomez&al2015	0.04	0.03	Temp	Lotic	Field	Correlative	Seasonal	Microbial	*Populus*	12.85	Estimated
Mora-Gomez&al2015	0.55	0.03	Temp	Lotic	Field	Correlative	Seasonal	Total	*Populus*	9.63	Estimated
Mora-Gomez&al2015	0.71	0.03	Temp	Lotic	Field	Correlative	Seasonal	Microbial	*Populus*	12.85	Estimated
Mora-Gomez&al2015	1.36	0.04	Temp	Lotic	Field	Correlative	Seasonal	Total	*Populus*	9.63	Estimated
Mora-Gomez&al2015	0.80	0.03	Temp	Lotic	Field	Correlative	Seasonal	Microbial	*Populus*	12.85	Estimated

Mora-Gomez&al2015	0.87	0.03	Temp	Lotic	Field	Correlative	Seasonal	Total	*Populus*	9.63		Estimated
Pereira&al2017	2.54	0.30	Temp	Lotic	Field	Correlative	Seasonal	Total	*Quercus*	1.88		Estimated
Pereira&al2017	2.82	0.33	Temp	Lotic	Field	Correlative	Seasonal	Total	*Quercus*	3.07		Estimated
Pereira&al2017	0.59	0.17	Temp	Lotic	Field	Correlative	Seasonal	Total	*Quercus*	3.86		Estimated
Pereira&al2017	0.66	0.18	Temp	Lotic	Field	Correlative	Seasonal	Total	*Quercus*	2.44		Estimated
Piggott&al2015	-1.46	0.63	Temp	Lotic	Laboratory				*Melicytus*	0.7		Estimated
Piggott&al2015	-0.60	0.52	Temp	Lotic	Laboratory				*Melicytus*	1.8		Estimated
Piggott&al2015	0.98	0.56	Temp	Lotic	Laboratory				*Melicytus*	2.6		Estimated
Piggott&al2015	1.30	0.61	Temp	Lotic	Laboratory				*Melicytus*	3.6		Estimated
Piggott&al2015	0.65	0.53	Temp	Lotic	Laboratory				*Melicytus*	4.2		Estimated
Piggott&al2015	0.80	0.54	Temp	Lotic	Laboratory				*Melicytus*	5.1		Estimated
Piggott&al2015	1.25	0.60	Temp	Lotic	Laboratory				*Melicytus*	6		Estimated
Pozo&al2011	-0.23	0.11	Temp	Lotic	Field	Correlative	Altitudinal	Total	*Alnus*			Estimated
Rowe&al1996	1.02	0.15	Temp	Lotic	Field	Correlative	Altitudinal	Total	*Liriodendron*	1.6		Estimated
Rowe&al1996	1.23	0.16	Temp	Lotic	Field	Correlative	Altitudinal	Total	*Acer*	1.6		Estimated
Rowe&al1996	1.39	0.17	Temp	Lotic	Field	Correlative	Altitudinal	Total	*Quercus*	1.6		Estimated
Rowe&al1996	0.21	0.13	Temp	Lotic	Field	Correlative	Altitudinal	Total	*Liriodendron*	2.1		Estimated
Rowe&al1996	0.75	0.14	Temp	Lotic	Field	Correlative	Altitudinal	Total	*Acer*	2.1		Estimated
Rowe&al1996	0.65	0.14	Temp	Lotic	Field	Correlative	Altitudinal	Total	*Quercus*	2.1		Estimated
Taylor&Andrushchenko2014	-1.29	0.81	Temp	Lotic	Field	Correlative	Altitudinal	Total	*Acer*	2.6		Estimated
Taylor&Andrushchenko2014	-1.85	0.95	Temp	Lotic	Field	Correlative	Altitudinal	Total	*Alnus*	2.6		Estimated
Taylor&Andrushchenko2014	0.22	0.67	Temp	Lotic	Field	Correlative	Altitudinal	Microbial	*Acer*	2.6		Estimated
Taylor&Andrushchenko2014	-0.47	0.69	Temp	Lotic	Field	Correlative	Altitudinal	Microbial	*Alnus*	2.6		Estimated
Taylor&Andrushchenko2014	-1.37	0.82	Temp	Lotic	Field	Correlative	Altitudinal	Total	*Acer*	3.2		Estimated
Taylor&Andrushchenko2014	-0.06	0.67	Temp	Lotic	Field	Correlative	Altitudinal	Total	*Alnus*	3.2		Estimated
Taylor&Chauvet2014	0.43	0.17	Temp	Lotic	Field	Correlative	Altitudinal	Microbial	*Alnus*	4.452		Estimated
Taylor&Chauvet2014	0.07	0.17	Temp	Lotic	Field	Correlative	Altitudinal	Microbial	*Alnus*	5.91		Estimated
Dray2014	0.15	0.08	CO_2	Lotic	Field			Total	*Betula*		549	Estimated
Ferreira&al2010	-1.15	0.58	CO_2	Lotic	Field			Microbial	*Betula*		200	Reported
Ferreira&Chauvet 2011	0.30	0.17	CO_2	Lotic	Laboratory				*Alnus*		200	Reported
Ferreira&Chauvet 2011	0.18	0.17	CO_2	Lotic	Laboratory				*Alnus*		200	Reported
Hammrich2008	-4.98	2.73	CO_2	Lentic	Field			Microbial	*Tilia*		140	Reported

Hammrich2008	-0.90	0.73	CO_2	Lentic	Field	Microbial	*Prunus*		140	Reported
Hammrich2008	-1.37	0.82	CO_2	Lentic	Field	Microbial	*Carpinus*		140	Reported
Hammrich2008	-0.32	0.68	CO_2	Lentic	Field	Microbial	*Acer*		140	Reported
Hammrich2008	-2.85	1.34	CO_2	Lentic	Field	Microbial	*Quercus*		140	Reported
Hammrich2008	0.61	0.70	CO_2	Lentic	Field	Microbial	*Fagus*		140	Reported
Hammrich2008	-2.43	1.16	CO_2	Lentic	Field	Total	*Tilia*		140	Reported
Hammrich2008	-0.37	0.68	CO_2	Lentic	Field	Total	*Prunus*		140	Reported
Hammrich2008	-0.38	0.68	CO_2	Lentic	Field	Total	*Carpinus*		140	Reported
Hammrich2008	-0.06	0.67	CO_2	Lentic	Field	Total	*Acer*		140	Reported
Hammrich2008	-4.66	2.48	CO_2	Lentic	Field	Total	*Quercus*		140	Reported
Hammrich2008	-0.41	0.68	CO_2	Lentic	Field	Total	*Fagus*		140	Reported
Hammrich2008	-4.61	2.44	CO_2	Lentic	Field	Microbial	*Tilia*		140	Reported
Hammrich2008	-0.81	0.72	CO_2	Lentic	Field	Microbial	*Prunus*		140	Reported
Hammrich2008	-0.92	0.74	CO_2	Lentic	Field	Microbial	*Carpinus*		140	Reported
Hammrich2008	-0.20	0.67	CO_2	Lentic	Field	Microbial	*Acer*		140	Reported
Hammrich2008	-2.92	1.38	CO_2	Lentic	Field	Microbial	*Quercus*		140	Reported
Hammrich2008	0.15	0.67	CO_2	Lentic	Field	Microbial	*Fagus*		140	Reported
Hammrich2008	-1.27	0.80	CO_2	Lentic	Field	Total	*Tilia*		140	Reported
Hammrich2008	-0.36	0.68	CO_2	Lentic	Field	Total	*Prunus*		140	Reported
Hammrich2008	0.05	0.67	CO_2	Lentic	Field	Total	*Carpinus*		140	Reported
Hammrich2008	0.66	0.70	CO_2	Lentic	Field	Total	*Acer*		140	Reported
Hammrich2008	-3.08	1.46	CO_2	Lentic	Field	Total	*Quercus*		140	Reported
Hammrich2008	0.12	0.67	CO_2	Lentic	Field	Total	*Fagus*		140	Reported
Monroy&al2016	0.08	0.50	CO_2	Lotic	Field	Microbial	*Trifolium*		300	Reported
Monroy&al2016	-0.43	0.51	CO_2	Lotic	Field	Microbial	*Agrostis*		300	Reported
Rier&al2002	-0.24	0.40	CO_2	Lotic	Field	Total	*Populus*		360	Reported
Tuchman&al2003	0.00	0.10	CO_2	Lotic	Field	Total	*Populus*		350	Estimated
Ferreira&Chauvet 2011	1.03	0.19	Temp+CO_2	Lotic	Laboratory		*Alnus*	5	200	Reported
Martins&al2017a	-0.15	0.13	Temp+CO_2	Lotic	Laboratory		*Eperua*	1.9	201.44	Reported
Martins&al2017a	-0.76	0.14	Temp+CO_2	Lotic	Laboratory		*Eperua*	2.92	424.59	Reported
Martins&al2017a	-0.71	0.14	Temp+CO2	Lotic	Laboratory		*Eperua*	4.46	863.11	Reported
Martins&al2017a	-0.69	0.14	Temp+CO_2	Lotic	Laboratory		*Goupia*	1.9	201.44	Reported

Martins&al2017a	-1.20	0.16	Temp+CO_2	Lotic	Laboratory	*Goupia*	2.92	424.59	Reported
Martins&al2017a	-1.47	0.17	Temp+CO_2	Lotic	Laboratory	*Goupia*	4.46	863.11	Reported
Martins&al2017a	-0.08	0.25	Temp+CO_2	Lotic	Laboratory	*Eperua*	1.9	201.44	Reported
Martins&al2017a	-0.28	0.25	Temp+CO_2	Lotic	Laboratory	*Eperua*	2.92	424.59	Reported
Martins&al2017a	-0.27	0.25	Temp+CO2	Lotic	Laboratory	*Eperua*	4.46	863.11	Reported
Martins&al2017a	0.02	0.25	Temp+CO_2	Lotic	Laboratory	*Goupia*	1.9	201.44	Reported
Martins&al2017a	0.14	0.25	Temp+CO_2	Lotic	Laboratory	*Goupia*	2.92	424.59	Reported
Martins&al2017a	0.08	0.25	Temp+CO_2	Lotic	Laboratory	*Goupia*	4.46	863.11	Reported
Martins&al2017b	0.51	0.14	Temp+CO_2	Lotic	Laboratory	*Hevea*	1.23	213.12	Reported
Martins&al2017b	0.76	0.14	Temp+CO_2	Lotic	Laboratory	*Hevea*	2.04	415.27	Reported
Martins&al2017b	0.40	0.14	Temp+CO_2	Lotic	Laboratory	*Hevea*	4.3	825.92	Reported
Martins&al2017b	-0.18	0.13	Temp+CO_2	Lotic	Laboratory	*Hevea*	1.23	213.12	Reported
Martins&al2017b	0.75	0.14	Temp+CO_2	Lotic	Laboratory	*Hevea*	2.04	415.27	Reported
Martins&al2017b	0.07	0.13	Temp+CO_2	Lotic	Laboratory	*Hevea*	4.3	825.92	Reported

Appendix 2. Table summarizing subgroup analyses using the whole dataset. Mean effect size, 95% CL, sample size (n), test for heterogeneity between levels of moderators (Q_M), degree of freedom (df) and *P*-values are provided (levels with a common letter do not significantly differ). Mean effect size > 0 indicates stimulation whereas mean effect size < 0 indicates inhibition.

Level	Hedges' *g*	95% CL	n	Sign Diff
Whole dataset	0.79	0.56 to 1.02	199	
Q_M = 1424.086, df = 196, P < 0.001				
Stressor (whole dataset)				
CO_2	– 0.48	– 0.79 to –0.17	32	a
Temp+CO_2	– 0.11	– 0.42 to 0.20	19	a
Temp	1.21	0.95 to 1.47	148	b
Q_M = 49.554, df = 2, P < 0.001				
Study type (Temperature dataset)				
Laboratory	0.90	0.64 to 1.16	57	a
Field	1.33	0.96 to 1.71	91	a
Q_B = 1.380, df = 1, P = 0.240				
Field type (Temperature dataset)				
Manipulative	1.06	0.65 to 1.48	20	a
Correlative	1.40	0.93 to 1.88	71	a
Q_B = 0.383, df = 1, P = 0.536				
Correlative (Temperature dataset)				
Altitudinal	0.57	0.17 to 0.96	32	a
Seasonal	1.59	0.52 to 2.66	15	ab
Latitudinal	2.53	1.45 to 3.62	22	b
Q_B = 14.195, df = 2, P < 0.001				
Litter genus (Temperature dataset, Laboratory)				
Melicytus	0.42	– 0.32 to 1.17	7	a
Eucalyptus	0.58	0.14 to 1.01	4	a
Alnus	1.09	0.66 to 1.51	31	a
Quercus	1.13	0.61 to 1.65	9	a
Q_B = 3.262, df = 3, P = 0.353				
Community type (Temperature dataset, Manipulative)				
Total	0.70	– 0.13 to 1.53	7	a
Microbial	1.28	0.87 to 1.69	13	a

Q_B = 2.319, df = 1, P = 0.128				
Community type (Temperature dataset, Altitudinal)				
Microbial	0.39	–0.04 to 0.81	13	a
Total	0.64	0.03 to 1.25	19	a
Q_B = 0.442, df = 1, P = 0.506				
Litter genus (Temperature dataset, Altitudinal)				
Acer	0.13	– 0.88 to 1.14	5	a
Alnus	0.30	– 0.26 to 0.85	13	a
Quercus	0.54	– 0.18 to 1.26	6	a
Fagus	0.89	0.53 to 1.25	4	a
Q_B = 1.769, df = 3, P = 0.622				
Decomposer community (Temperature dataset, Seasonal)				
Microbial	0.51	0.05 to 0.98	3	a
Total	1.89	0.54 to 3.23	12	a
Q_B = 1.039, df = 1, P = 0.308				
Litter genus (Temperature dataset, Seasonal)				
Populus	0.72	0.38 to 1.06	6	a
Quercus	1.60	0.44 to 2.77	4	a
Alnus	2.76	– 0.67 to 6.19	5	a
Q_B = 2.575, df = 2, P = 0.276				
System (CO_2 dataset)				
Lentic	– 0.89	– 1.37 to – 0.42	24	b
Lotic	0.03	– 0.27 to 0.33	8	a
Q_B = 10.684, df = 1, P = 0.011				
Community type (CO_2 dataset)				
Microbial	– 1.20	– 1.99 to – 0.40	12	a
Total	– 0.64	– 1.21 to 0.07	12	a
Q_B = 0.709, df = 1, P = 0.400				
Litter genus (CO_2 dataset, Lentic)				
Quercus	– 3.21	– 4.44 to – 1.99	4	c
Tilia	– 2.94	– 4.67 to – 1.20	4	ac
Carpinus	– 0.61	– 1.45 to 0.22	4	ab
Prunus	– 0.60	– 1.42 to 0.22	4	ab
Acer	0.01	– 0.79 to 0.82	4	ab

Fagus	0.11	– 0.69 to 0.92	4	b
Q_B = 33.087, df = 5, P < 0.001				
Litter genus (Tem+CO_2 dataset)				
Goupia	– 0.57	– 1.13 to 0.01	6	a
Eperua	– 0.42	– 0.75 to – 0.08	6	a
Hevea	0.37	0.07 to 0.68	6	b
Q_B = 15.713, df = 2, P < 0.001				