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META-ANALYSIS

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Leaf litter traits predominantly control litter decomposition in streams worldwide

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Abstract

Aim: Leaf litter decomposition in freshwater ecosystems is a vital process linking ecosystem nutrient cycling, energy transfer and trophic interactions. In comparison to terrestrial ecosystems, in which researchers find that litter traits predominantly regulate litter decomposition worldwide, the dominant factors controlling its decomposition in aquatic ecosystems are still debated, with global patterns not well documented. Here, we aimed to explore general patterns and key drivers (e.g., litter traits, climate and water characteristics) of leaf litter decomposition in streams worldwide.

Location: Global.

Time period: 1977–2018.

Major taxa studied: Leaf litter.

Methods: We synthesized 1,707 records of litter decomposition in streams from 275 studies. We explored variations in decomposition rates among climate zones and tree functional types and between mesh size groups. Regressions were performed to identify the factors that played dominant roles in litter decomposition globally.

Results: Litter decomposition rates did not differ among tropical, temperate and cold climate zones. Decomposition rates of litter from evergreen conifer trees were much lower than those of deciduous and evergreen broadleaf trees, attributed to the low quality of litter from evergreen conifers. No significant differences were found between decomposition rates of litter from deciduous and evergreen broadleaf trees. Additionally, litter decomposition rates were much higher in coarse- than in fine-mesh bags, which controled the entrance of decomposers of different body sizes. Multiple regressions showed that litter traits (including lignin, C:N ratio) and elevation were the most important factors in regulating leaf litter decomposition.

Main conclusions: Litter traits predominantly control leaf litter decomposition in streams worldwide. Although further analyses are necessary to explore whether commonalities of the predominant role of litter traits in decomposition exist in both aquatic and terrestrial ecosystems, our findings could contribute to the use of trait-based approaches in modelling the decomposition of litter in streams globally and exploring mechanisms of land–water–atmosphere carbon fluxes.

KEYWORDS
C:N ratio, climate zones, leaf litter traits, lignin content, litter decomposition, streams and rivers, tree functional types

1 | INTRODUCTION

Leaf litter is a major allochthonous input to streams and a common source of energy and nutrients for heterotrophic aquatic communities (e.g., Graça, Ferreira, & Coimbra, 2001). Its decomposition in streams and rivers (hereafter, streams) is a vital process linking ecosystem processes such as nutrient cycling, energy transfer and trophic interactions (Ardón, Stallcup, & Pringle, 2006; Kominoski, Marczak, & Richardson, 2011; Leite-Rossi, Saito, Cunha-Santino, & Trivinho-Strixino, 2016; Lidman, Jonsson, Burrows, Bundschuh, & Sponseller, 2017; Powers et al., 2009; Zhang, Luo, Chen, & Ruan, 2018). Studies on the decomposition of leaf litter in aquatic ecosystems have attracted extensive attention worldwide since the 1960s, aiming to explore the mechanisms of land–water–atmosphere carbon (C) fluxes (Abelho, 2001; Tank, Rosi-Marshall, Griffiths, Entrekin, & Stephen, 2010; Webster & Benfield, 1986). Massive amounts of organic carbon are processed in freshwater ecosystems, constituting an indispensable component of the global C cycle (Boyero et al., 2016). Raymond et al. (2013) estimated that the global CO_2 respired from streams is 1.8 Pg C/year, accounting for 86% of the total CO_2 respired from inland waters. So far, however, global-scale studies are less common, and we still do not know how litter decomposition rates in streams vary at a global scale or which factors predominately control litter decomposition in streams (Boyero et al., 2016; Kennedy & El-Sabaawi, 2017).

Empirical studies have undoubtedly improved our understanding of leaf litter decomposition in streams (e.g., Boyero, Pearson, & Camacho, 2006; Boyero et al., 2011; Irons, Oswood, Stout, & Pringle, 1994; Kominoski et al., 2011; Schlesinger & Hasey, 1981). Generally, the decomposition of leaf litter in streams is mainly driven by both extrinsic (e.g., environmental factors and water characteristics of streams; Rosemond et al., 2015; Woodward et al., 2012) and intrinsic factors (e.g., litter traits; Gonçalves et al., 2017; Jinggut & Yule, 2015; Lecerf & Chauvet, 2008; Leite-Rossi et al., 2016). Of the dozens of extrinsic factors that can influence litter decomposition in streams, such as temperature, dissolved nutrients, pH and dissolved oxygen (O_2), temperature has undoubtedly captured more than its fair share of attention (Ferreira & Canhoto, 2015; Ferreira, Chauvet, & Canhoto, 2015; Follstad Shah et al., 2017). For example, many studies have found a positive temperature–decomposition relationship, with faster decomposition in tropical compared with temperate streams, mainly attributable to higher water temperatures favouring increased biological activity (e.g., Ardón, Pringle, & Eggert, 2009; Ferreira & Canhoto, 2015; Ferreira & Chauvet, 2011). Conversely, other studies have found higher litter decomposition rates in temperate compared with tropical streams (Ferreira, Encalada, & Graça, 2012; Gonçalves, Graça, & Callisto, 2006, 2007), largely attributable to favourable conditions, such as cool, well-aerated, flowing water preferred by aquatic hyphomycetes. Despite much research, however, no consistent patterns have emerged regarding litter decomposition in streams among different temperature zones (i.e., tropical, temperate and cold) at a global scale.

Besides being affected by extrinsic factors, litter decomposition rates also depend greatly on the nature of leaf litter, such as the carbon : nitrogen (C:N) ratio and lignin content (Gessner & Chauvet, 1994; Ostrofsky, 1997; Wang, Ruan, & Wang, 2009). Previous studies show that leaf litter with low C:N ratio are preferentially colonized and degraded by aquatic hyphomycetes and invertebrate detritivores (Ferreira et al., 2012; Richardson, Shaughnessy, & Harrison, 2004; Shieh, Wang, Hsu, & Yang, 2008; Swan & Palmer, 2004). Lignin content, on the contrary, is generally found to regulate litter decomposition negatively, because specialized enzymes are required to process this recalcitrant form of C (Alvim, Medeiros, Rezende, & Gonçalves, 2015; Ardón et al., 2009; König, Hepp, & Santos, 2014; Li, Ng, & Dudgeon, 2009). A good example is the decomposition patterns among different tree functional types. Litter derived from deciduous plant species generally decomposes more rapidly than that from evergreen species (López, Pardo, & Felpeto, 2001; Pozo et al., 1998). Broadleaf litter is usually broken down much more easily than conifer needles (Albariño & Balseiro, 2002; Ferreira, Faustino, Raposeiro, & Gonçalves, 2017; Hisabae, Sone, & Inoue, 2011; Imbert & Pozo, 1989; Kominoski et al., 2011; Whiles & Wallace, 1997). These differences among functional types are principally on account of intrinsic factors, the nutritional qualities of leaf litter, which are widely recognized as "litter quality", such as nutrient contents [e.g., N and phosphorus (P)], litter stoichiometry (e.g., C:N and C:P ratios), structural compounds (e.g., lignin and cellulose), secondary compounds (e.g., tannins and polyphenols) (Ferreira et al., 2012; García-Palacios, Mckie, Handa, Frainer, & Hättenschwiler, 2016; Lecerf & Chauvet, 2008; Ostrofsky, 1997). This biochemical composition of leaf litter affects its availability for invertebrate feeding and microbial growth (Enriquez, Duarte, & Sand-Jensen, 1993). In comparison to terrestrial ecosystems, in which researchers find that litter traits predominantly regulate its decomposition globally (e.g., Cornwell et al., 2008; Zhang, Hui, Luo, & Zhou, 2008), debate is ongoing over the dominant factors controlling litter decomposition across the global aquatic ecosystems (Boyero et al., 2016).

Understanding the relative contribution of these extrinsic and intrinsic factors, and their interactions, at both the site level and the global scale, will undoubtedly contribute to elucidating the main factors affecting litter decomposition in aquatic ecosystems (LeRoy & Marks, 2006). These factors regulate leaf litter decomposition simultaneously; therefore, it is challenging but essential to identify the predominant controlling factors worldwide to aid our understanding of nutrient cycling, energy transfer and trophic interactions in streams. In this systematic review, our aims were as follows: (a) to explore the global patterns of leaf litter decomposition in streams among climate zones and tree functional types and between coarse- and fine-mesh size groups; and (b) to identify the key drivers of litter decomposition worldwide. We hypothesize that litter traits, such as lignin and C:N ratio, might play dominant roles in litter decomposition at the global scale.

2 | METHODS

2.1 | Datasets

In this study, we compiled 1,707 independent data points based on 275 published studies (Figure 1, Supporting Information Figure

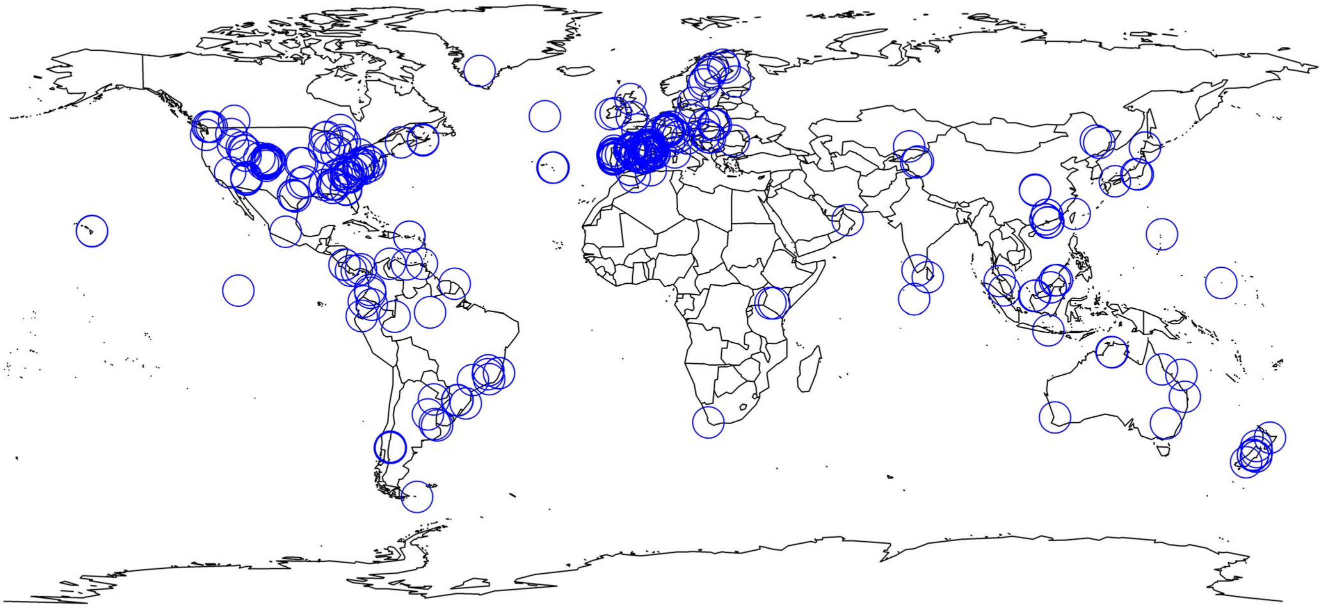

FIGURE 1 The global distribution of leaf litter decomposition records in streams/rivers (n = 1,591). There were 1,707 cases in total, with 116 cases having no latitude reported

S1). A list of the data sources can be found in Appendix 1. Datasets were extracted by conducting a systematic literature search using ISI Web of Science, Google Scholar and China National Knowledge Infrastructure (CNKI, for papers published in Chinese). We used the following keywords in our literature review: (litter OR leaf OR leaves) AND (decomposition OR breakdown OR processing OR decay) AND (stream OR river OR watercourse). Studies that met the following criteria were included in this analysis: (a) the decomposition of leaf litter (not wood, bark or artificial substrates, such as cotton strips) was measured in natural freshwater ecosystems (i.e., streams or rivers) rather than in experimental or manipulative stream channels; (b) the streams or rivers where decomposition studies were carried out were not affected by pollution or artificial nutrient enrichment experiments; (c) the leaf litter substrate used in the study was composed of a single species (i.e., not litter mixtures) collected from the dominant riparian trees of the study site; and (d) either the decomposition rates or litter mass loss over a known decomposition period was reported.

We extracted four categories of factors that might have an impact on leaf litter decomposition: environmental factors (including latitude and elevation); water characteristics (including pH, temperature, dissolved O_2, alkalinity, conductivity, PO_4-P, NO_3-N, NH_4 + N, width, depth, discharge, velocity, NO_2-N, NO_3-N + NO_2-N, O_2, Ca^{2+}, total P, dissolved inorganic N, Cl^-, total N, dissolved organic C, $SO_4^{\,2-}$, turbidity, Mg, Al, Fe, Na, acid-neutralizing capacity, hardness, Zn, Cd, Cu, Pb, Mn, salinity and As); litter traits (including initial N, initial P, N:P, C:N, initial lignin, lignin:N, C:P, tannins, leaf polyphenols, toughness, cellulose, hemicellulose, specific leaf area, fibre:N and total fibre); and experimental factors (including mesh size, duration of litter decomposition and initial litter mass per bag). When data were reported in graphs, they were extracted using GetData Graph Digitizer v.2.24 (http://getdata-graph-digitizer.com/).

We either collected the decomposition coefficients directly when they were reported or estimated the coefficient indirectly based on the mass of leaf litter remaining after the decomposition period. Negative exponential models were used in our coefficient estimation (Follstad Shah et al., 2017; Olson, 1963):

$$\frac{m_t}{m_0} = e^{-kt} \tag{1}$$

where m_t is the remaining mass of leaf litter at time t in days, m_0 is the initial litter mass at the beginning of the experiment, and k is the decomposition coefficient (k, per day). When temperature-adjusted decomposition coefficients (k_{dd}, per degree day) were reported to represent the breakdown rates (Bastias et al., 2018; Boyero et al., 2015; Ferreira, Larrañaga, et al., 2015; Monroy et al., 2016; Pereira et al., 2017), we estimated k (per day) by multiplying the k_{dd} by the mean water temperature of the decomposition study (Follstad Shah et al., 2017).

Study sites were divided into three climate zones based on latitude (0° < Tropical ≤ 23°26′, 23°26′ < Temperate ≤ 60° and Cold > 60°; Ferreira, Castagneyrol, et al., 2015). Information on leaf litter identity (tree functional type) was retrieved, and tree functional types were categorized into deciduous broadleaf, evergreen broadleaf and evergreen conifer trees. We focused solely on trees in this study owing to the limited number of records found for the other plant growth forms (Supporting Information Figure S2). Additionally, the data were divided into two groups based on litter bag mesh sizes (fine mesh ≤ 1 mm versus coarse mesh > 1 mm; Follstad Shah et al., 2017).

2.2 | Statistical analysis

Linear modelling was used to analyse the impacts of climate zones, tree functional types, mesh size of the litter bags, and their interactions, on leaf litter decomposition in streams worldwide. We used linear and stepwise multiple regression analyses to explore the relationships of leaf litter decomposition rates in streams with the four categories of influencing factors mentioned above. Only factors that were correlatee significantly with *k* (for details, see Supporting Information Table S1) and with a number of observations >170 are included in the multi-regression analysis. The regression analysis had two steps: (a) the factors of each category with >170 observations were included in the analysis (model A); and (b) we ran the analysis with all the variables entering model A (model B). All statistical analyses were conducted using SPSS v.22.0 for Windows (SPSS Inc., Chicago, IL, USA).

3 | RESULTS

The rates of leaf litter decomposition did not differ among climate zones ($p > .05$; Table 1; Figure 2; Supporting Information Figure S3). In terms of tree functional types, the decomposition rates of leaf litter from evergreen conifer trees were much lower than those of leaf litter from deciduous broadleaf and evergreen broadleaf trees ($p < .05$; Table 1; Figure 3). No significant differences were found in the leaf litter decomposition rates between deciduous and evergreen broadleaf trees ($p > .05$; Figure 3). Although climate zones and tree functional types affected the decomposition interactively ($p < .05$; Table 1), the statistical difference might result from the missing values of evergreen broadleaf trees in the cold climate zone (Supporting Information Figure S4). The mesh size of the litter bags, which controls the entrance of decomposers of different body sizes, had a positive impact on decomposition rates ($p < .001$; Table 1; Figure 4). We found no interactive impacts of mesh size with climate zones or tree functional types on the decomposition (all $p > .05$; Table 1; Supporting Information Figures S5 and S6).

Leaf litter decomposition in streams was influenced by all four categories of factors: environmental factors, water characteristics of streams or rivers, litter traits and experimental factors (Supporting Information Table S1). Multiple regressions within each factor category showed that decomposition of leaf litter in streams was negatively affected by elevation, initial lignin content, C:P ratio and decomposition duration and positively affected by water dissolved O_2 and temperature, C:N ratio and mesh size (all $p < .001$; Table 2). However, further multiple regression analyses indicated that litter traits (including lignin and C:N ratio) and elevation were the most important factors in regulating litter decomposition in streams (all $p < .01$; Table 2). Litter traits and elevation explained 58 and 9% of the variation, respectively (Table 2).

TABLE 1 Results of linear models for responses of litter decomposition rate in streams (*k*, per day) to climate zone, tree functional type, mesh size group and their interactions

	d.f.	*F*, *p*
Climate zones (Climate)	2	3.03
Tree functional types (TFY)	2	11.09***
Mesh size groups (Mesh)	1	39.15***
Climate × TFY	3	6.06***
Climate × Mesh	2	0.49
TFY × Mesh	2	0.04
Climate × TFY × Mesh	1	4.58

***$p < .001$.

4 | DISCUSSION

4.1 | The pattern of leaf litter decomposition among climate zones

Our results suggest that extrinsic factors (e.g., latitude and water temperature) are not necessarily the dominant factors in regulating

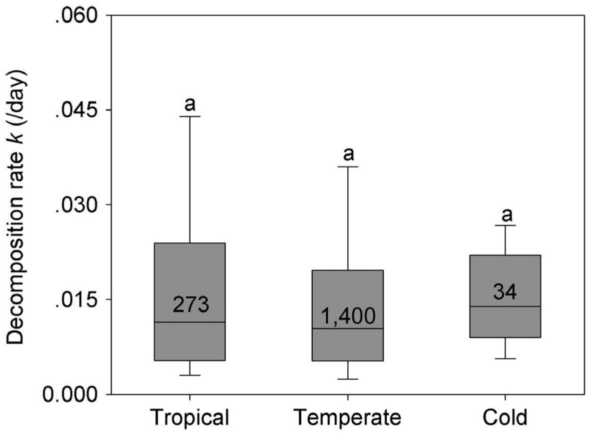

FIGURE 2 Comparison of leaf litter decomposition rate in streams (*k*, per day) among different climate zones. Sample size is indicated by the number inside of each column. Different lowercase letters on error bars indicate significant differences at $p < .05$

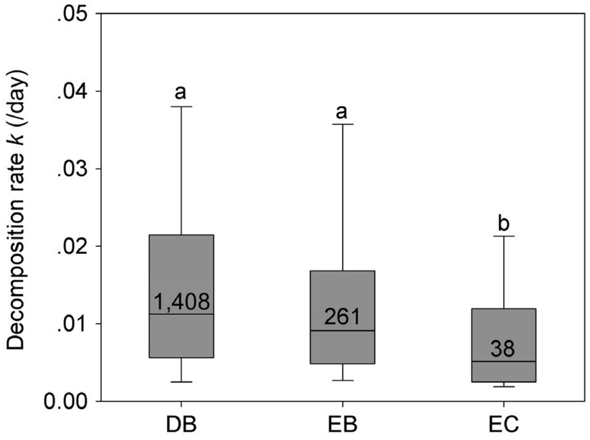

FIGURE 3 Comparison of leaf litter decomposition rate in streams (*k*, per day) among different tree functional types. DB = deciduous broadleaf; EB = evergreen broadleaf; EC = evergreen conifer. Sample size is indicated by the number inside of each column. Different lowercase letters on error bars indicate significant differences at $p < .05$

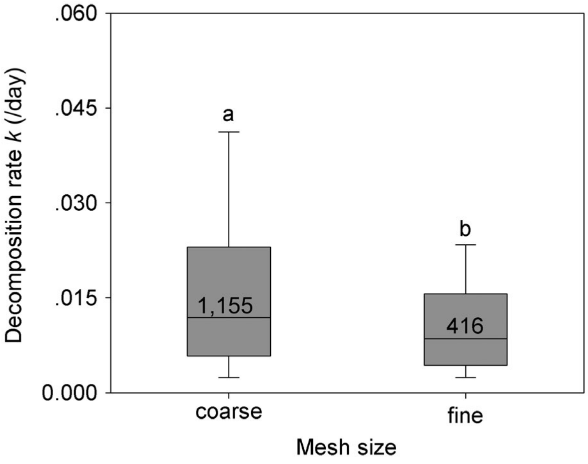

FIGURE 4 Comparison of the litter decomposition rate in streams (*k*, per day) between coarse- and fine-mesh size litter bags. Sample size is indicated by the number inside of each column. Different lowercase letters on error bars indicate significant differences at $p < .05$

litter decomposition in streams at the global scale. We found no significant differences in litter decomposition rates among tropical, temperate and cold climates, although both temperature and the inherent capacity of ecosystems to decompose organic matter decrease with latitude (Tiegs et al., 2019). No differences in decomposition rates across climate zones might result from the following reasons. First, the positive impacts of high stream water temperature are counteracted by low water dissolved O_2 at low latitudes (Iñiguez-Armijos et al., 2016; Lopes, Martins, Silveira, & Alves, 2015). High temperature usually stimulates litter decomposition (Ferreira & Canhoto, 2015; Ferreira, Chauvet, et al., 2015). However, water dissolved O_2 in streams usually decreases significantly with increasing water temperatures (Gonçalves et al., 2006; Iñiguez-Armijos et al., 2016; Pettit et al., 2012). Low dissolved O_2 could lead to anaerobic conditions and significantly decrease decomposition by inhibiting decomposer activities (Lopes et al., 2015; Medeiros, Pascoal, & Graça, 2009; Pérez, Menéndez, Larrañaga, & Pozo, 2011; Pettit et al., 2012; Schlief & Mutz, 2009; Webster & Benfield, 1986). Second, high microbial activities at low latitudes are counteracted by low invertebrate activities (Haapala, Muotka, & Markkola, 2001; Walpola, Leichtfried, Amarasinghe, & Füreder, 2011). Irons et al. (1994) explored litter decomposition processes in streams across a latitudinal gradient and concluded that the contribution of the invertebrates to litter decomposition increases with latitude, whereas the proportion attributable to microbes concomitantly decreases with increasing latitude (Haapala et al., 2001; Leite-Rossi et al., 2016; Mathuriau & Chauvet, 2002; Tonin, Hepp, Restello, & Gonçalves, 2014; Walpola et al., 2011). Consistent with our results, for example, Boyero et al. (2011) reported unchanged decomposition rates driven by both microbes and invertebrates in an experiment across 22 sites along a latitudinal gradient (0.37–47.8°). Third, although high temperature could accelerate decomposition, leaf litter originating from the tropics might be resistant and tenacious to stream decomposers and thus inhibit litter decomposition (Chara, Baird, Telfer, & Giraldo, 2007; Makkonen et al., 2012). This might result from the low quality of tropical litter (high structural and recalcitrant compounds, secondary metabolites and N:P ratio) associated with the high pressure from terrestrial herbivores (Boyero et al., 2017; Gonçalves et al., 2017; Jinggut & Yule, 2015). Reich and Oleksyn (2004) summarized the global patterns of leaf N and P and concluded that the closer to the tropics, the higher the temperature and the longer the growing season length become, hence leaf N and P decline. These elements show remarkable afterlife effects of green leaf traits (Pietsch et al., 2014), strongly associated with leaf litter decomposability and litter decomposition rates (Ardón et al., 2009; Fernández et al., 2016; Ferreira et al., 2012; Lecerf & Chauvet, 2008; Richardson et al., 2004; Shaftel, King, & Back, 2012).

4.2 | Variation of the decomposition rates among tree functional types

Overall, our results indicate that litter traits, such as nutrient contents and structural compounds, could play an important role in the variation of the decomposition rates among different tree functional types. We found that the decomposition of litter from evergreen conifer trees was much slower than that of litter from deciduous broadleaf and evergreen broadleaf trees. Our results were in line with previous findings that decomposition rates of broadleaf species are significantly higher than those of conifer species (e.g., Albariño & Balseiro, 2002; Hisabae et al., 2011; Lidman et al., 2017; Richardson et al., 2004). This difference is mostly a result of the intrinsic physicochemical variables of substrate quality from different tree functional types (Albariño & Balseiro, 2002; Ferreira et al., 2017; Richardson et al., 2004). Conifer needles generally decompose slowly because they have lower nutrient contents (e.g., N and P) and higher structural (e.g., lignin and cellulose) and refractory compounds (e.g., tannins and polyphenols) than broadleaf litter (Ardón et al., 2009; Lidman et al., 2017). These characteristics of coniferous litter would delay microbial colonization and macroinvertebrate feeding activities (Albariño & Balseiro, 2002), leading to slow decomposition processes (Collen, Keay, & Brs, 2004).

4.3 | The predominant roles of litter traits in decomposition

Our results showed that litter traits (C:N and lignin) played dominant roles in leaf litter decomposition in streams. This is consistent with small-scale findings that litter decomposition rates are negatively correlated with the C:N ratio (König et al., 2014; Menéndez, Martinez, Hernández, & Comín, 2001; Richardson et al., 2004; Roberts, Strauch, Wiegner, & Mackenzie, 2016; Shieh et al., 2008). High N content and corresponding low C:N ratio increase the palatability and attractiveness of litter to microbes, resulting in greater microbial colonization that leads to higher decomposition rates (Gonçalves, Rezende, Martins, & Gregório, 2012; Hamid & Che, 2017; Rier, Tuchman, Wetzel, & Teeri, 2002; Roberts et al., 2016; Swan & Palmer, 2006). The N facilitates

TABLE 2 Results of multi-regression analyses of litter decomposition rate in streams (k, per day) with environmental factors, water characteristics of streams, litter traits and experimental factors

Factors	Model	Variables	Regression	n	r^2	Excluded variables
Environmental factors	A	elevation	$k = -2.95 \times 10^{-6}$ elevation + 0.02	1,218	0.01^{***}	n/a
Water characteristics	A	dissolO_2, temp	$k = 0.005$ dissolO_2 + 0.002 temp − 0.04	193	0.20^{***}	discharge, pH
Litter traits	A	lignin, C:N, C:P	$k = -0.001$ lignin − 1.10×10^{-5} C:P + 0.001 C:N + 0.05	120	0.19^{***}	N, lignin:N
Others	A	mesh size, duration	$k = 0.001$ mesh size − 5.93×10^{-5} duration + 0.02	1,257	0.10^{***}	initial litter mass
All	B-1	lignin	$k = -0.001$ lignin + 0.05	17	0.42^{**}	elevation, dissolO_2, temp, C:P, C:N, mesh size, duration
	B-2	lignin, C:N	$k = -0.003$ lignin − 0.001 C:N + 0.13	17	0.58^{***}	elevation, dissolO_2, temp, C:P, mesh size, duration
	B-3	lignin, C:N, elevation	$k = -0.003$ lignin − 0.001 C:N − 2.81×10^{-5} elevation + 0.15	17	0.67^{***}	dissolO_2, temp, C:P, mesh size, duration

Note: There were four categories of factors, and the number of observations collected for each specific factor is indicated in parentheses. The total number of data points was 1,707. The factors are as follows. Environmental factors: latitude (1,590) and elevation (1,219). Water characteristics: pH (1,270), temperature (temp, in degrees Celsius; 1,384), dissolved O_2 (dissolO_2 in milligrams per litre; 543), alkalinity (in milligrams $CaCO_3$ per litre; 457), conductivity (in microsiemens per centimetre; 1,123), PO_4-P (in micrograms per litre; 708), NO_3-N (in micrograms per litre; 754), NH_4 + N (in micrograms per litre; 432), width (in metres; 820), depth (in centimetres; 499), discharge (in cubic metres per second; 555), velocity (in metres per second; 401), NO_2-N (in micrograms per litre; 212), NO_3-N + NO_2-N (in micrograms per litre; 321), water O_2 (as a percentage; 170), Ca^{2+} (in milligrams per litre; 150), total P (TP, in micrograms per litre; 103), dissolved inorganic N (in micrograms per litre; 82), Cl^- (in milligrams per litre; 70), total N (TN, in micrograms per litre; 85), dissolved organic carbon (C, in micrograms per litre; 75), SO_4^{2-} (in milligrams per litre; 83), turbidity (in nephelometric turbidity units; 62), Mg (in milligrams per litre; 73), Al (in milligrams per litre; 57), Fe (in milligrams per litre; 32), Na (in milligrams per litre; 30), acid-neutralizing capacity (ANC, in microequivalents per litre; 28), hardness (in milligrams per litre; 19), Zn (in milligrams per litre; 18), Cd (in milligrams per litre; 16), Cu (in milligrams per litre; 16), Pb (in milligrams per litre; 16), Mn (in milligrams per litre; 14), salinity (in milligrams per litre; 6), and As (in micrograms per litre; 4). Litter traits: initial nitrogen (N, as a percentage; 605), initial phosphorus (P, as a percentage; 421), N:P (422), C:N (416), initial lignin (as a percentage; 239), lignin:N (231), C:P (229), tannins (156), leaf polyphenols (as a percentage; 143), toughness (in grams; 148), cellulose (as a percentage; 82), hemi-cellulose (as a percentage; 50), specific leaf area (SLA, in square millimetres per milligram; 18), fibre:N (19) and total fibre (15). Experimental factors: mesh size (1,560), duration of litter decomposition (1,326), and initial litter mass per bag (initial litter mass; 1,578).
$^{**}p < 0.01$; $^{***}p < .001$.

microbial colonization by means of encouraging penetration of fungal hyphae and bacterial enzymes, and lack of structural integrity to resist hostile environment (Jones & Swan, 2016; Pettit et al., 2012). Stimulated microbial colonization and activity further render litter more accessible to invertebrates in the late stages of the decomposition processes (Jinggut & Yule, 2015; Stallcup, Ardón, & Pringle, 2006). On the contrary, lignin content had a negative impact on litter decomposition rates, in line with many researchers who have reported that a high content of this recalcitrant substrate inhibits decomposition in both stream (König et al., 2014; Marano et al., 2013; Tonin et al., 2014) and terrestrial ecosystems (Cornelissen et al., 1999). The presence of this structural defensive compound, which confers toughness on leaf litter, protects the litter from microbial degradation and invertebrate consumption and constitutes waterproofing properties of plant cell walls, slowing down physical abrasion (Gonçalves et al., 2007; Tonin et al., 2014). The lignin content of leaf litter governs decomposition by kinetically controlling C sources for saprotrophic fungi (Gessner & Chauvet, 1994). Only specialized biota, mainly fungi, could be capable of synthesizing specialized extracellular enzymes, making lignin break down metabolically into biologically usable forms for microbes (Austin & Ballare, 2010).

Interestingly, elevation played a negative role in regulating stream litter decomposition. This might result from the finding that low temperatures at high elevations retard litter decomposition indirectly by inhibiting microbial metabolic activity (Couteaux, Sarmiento, Bottner, Acevedo, & Thiery, 2002; Salinas et al., 2011; Schindlbacher et al., 2011; Schlesinger & Hasey, 1981; Zhou, Clark, Su, & Xiao, 2015). In addition to temperature, the nature of leaf litter may also have a substantial influence on decomposition (Salinas et al., 2011; Zhou et al., 2015). With increasing elevation, leaves sacrifice growth efficiency and become low in quality, with low nutrient contents (e.g., N), thick waxy cuticles and high contents of structural and refractory compounds (e.g., lignin and toughness) (e.g., Alvim et al., 2015; Jinggut & Yule, 2015; Tanner, Vitousek, & Cuevas, 1998). As a result, the decomposition of leaf litter originating from high elevation could be inhibited through trait "afterlife" effects (Alvim et al., 2015; Fujii, Cornelissen, Berg, & Mori, 2018; Jinggut & Yule, 2015; Sundqvist, Giesler, & Wardle, 2011). The limitation of this synthesis is that we lack sufficient data points to perform the multiple regression analyses (*n* = 17). However, the results of multiple regressions within each factor category indicated the prominent roles of litter traits played in decomposition in streams. Moreover, the patterns of leaf litter decomposition along the latitudinal gradient and among tree functional types confirmed the dominant impacts of litter traits on decomposition at the global scale. It is likely that litter quality had more impacts than extrinsic factors (e.g., elevation) on deomposition and dominated the decomposition processes.

4.4 | The impact of decomposer community type on decomposition

It is widely reported that litter decomposition is much faster in litter bags with a coarse rather than a fine-mesh size (e.g., Gantes, Marano, & Rigacci, 2011; Ferreira, Chauvet, et al., 2015; Lecerf & Chauvet, 2008). This methodological aspect (mesh size) affects decomposition by means of interfering with decomposition processes, such as physical abrasion and decomposer activity, especially the feeding and maceration by leaf-shredding invertebrates and microbial metabolism (Iñiguez-Armijos et al., 2016; Langhans & Tockner, 2006; Stewart & Davies, 1989). Litter bags with coarse meshes allow large leaf-consuming invertebrates to contact the litter, whereas those with fine meshes exclude a large portion of invertebrates without limiting microbial colonization (Lecerf & Chauvet, 2008). Fine mesh usually eliminates shredding by invertebrates and protects litter from heavy leaching and physical fragmentation, and litter decomposition is thus generally faster in the presence of macroinvertebrates than in their absence (e.g., Langhans & Tockner, 2006; Iñiguez-Armijos et al., 2016; Roberts et al., 2016). Moreover, fungal growth and microbial colonization could be restricted by the protected environment (fine mesh), where exchanges of dissolved O_2 and nutrients are reduced, which consequently retards the decomposition (Fleituch, 2001; LeRoy, Whitham, Keim, & Marks, 2006). A few studies have found no effect of mesh size on decomposition rates, and the authors attributed this to the extremely low litter quality and its associated macroinvertebrates, particularly shredders (Ágoston-Szabó, Schöll, Kiss, & Dinka, 2016; Benfield, Paul, & Webster, 1979). Shredders prefer high-quality litter, and their survivorship is low when fed with low-quality litter (Canhoto & Graça, 1995). Together with the duration of decomposition, decomposers constitute significant factors influencing litter decomposition in streams. As the duration increases, for instance, this would contribute to the building of microbial assemblage composition, especially in the process of decomposition of conifer needles with thick cuticles (Newman, Liles, & Feminella, 2015). Many experiments choose the sampling time to match *c*. 50% litter mass loss, a time at which leaf litter reaches the peak ergosterol concentration (Ferreira, Chauvet, et al., 2015; Haapala et al., 2001). At the 50% breakdown point, leaf litter is most palatable to shredders, and shredder feeding is expected to be maximal (Cummins, Wilzbach, Gates, Perry, & Taliaferro, 1989; Richardson et al., 2004). Given the differences in the contents of nutrient elements and recalcitrant compounds of specific litter species, serious consideration should be given when choosing a suitable mesh size for litter bags and designing a rational sampling time.

In conclusion, our results showed that leaf litter traits predominantly controlled litter decomposition in streams worldwide, paralleling the findings for terrestrial ecosystems (Cornwell et al., 2008; Zhang et al., 2008). Our findings could contribute to the use of trait-based approaches in modelling the decomposition of leaf litter in streams at the global scale and exploring mechanisms of land–water–atmosphere C fluxes. Further comprehensive analysis is required, however, to uncover whether commonalities of the predominant role of litter traits in decomposition exist in aquatic and terrestrial ecosystems, aimed at promoting the development of common global models.

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AUTHOR CONTRIBUTIONS

All authors contributed intellectual input and assistance to this study and manuscript preparation. X.X. conceived the idea and designed the study. M.Z. collected and analysed the data with help from X.X., X.C. and Z.S. M.Z. and X.X. wrote the paper with input from all authors.

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BIOSKETCH

Menghua Zhang is a Master student interested in leaf litter decomposition in both terrestrial and stream ecosystems. She uses a combination of field experiments and data synthesis to examine the patterns and mechanisms of litter decomposition at the site level and at the global scale.

SUPPORTING INFORMATION

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

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APPENDIX 1: DATA SOURCES

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