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RESEARCH ARTICLE

Positive Feedback on Climate Warming by Stream Microbial Decomposers Indicated by a Global Space-For-Time Substitution Study

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ABSTRACT

Decomposition of plant litter is a key ecological process in streams, whose contribution to the global carbon cycle is large relative to their extent on Earth. We examined the mechanisms underlying the temperature sensitivity (TS) of instream decomposition and forecast effects of climate warming on this process. Comparing data from 41 globally distributed sites, we assessed the TS of microbial and total decomposition using litter of nine plant species combined in six mixtures. Microbial decomposition conformed to the metabolic theory of ecology and its TS was consistently higher than that of total decomposition, which was higher than found previously. Litter quality influenced the difference between microbial and total decomposition, with total decomposition of more recalcitrant litter being more sensitive to temperature. Our projections suggest that (i) warming will enhance the microbial contribution to decomposition, increasing CO_2 outgassing and intensifying the warming trend, especially in colder regions; and (ii) riparian species composition will have a major influence on this process.

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1 | Introduction

It is imperative to identify the mechanisms that control the temperature sensitivity (TS; Demars et al. 2016; Follstad Shah 2021) of ecological processes (Tiegs et al. 2019) and biogeochemical cycles (Mahecha et al. 2010) across ecosystems, given the gradual rise in temperature worldwide. In this context, it is important to understand inland aquatic ecosystems, whose contribution to the global carbon (C) cycle is disproportionately large in relation to their spatial extent on Earth (Battin et al. 2009; Hotchkiss et al. 2015; Friedlingstein et al. 2022; van Hoek et al. 2022). In particular, running waters transport C from land to the ocean and thus link terrestrial and aquatic realms, which are usually regarded separately in C budgets (Regnier et al. 2022). Moreover, far from being passive conduits, streams and rivers are active biogeochemical reactors (Larned et al. 2010; Harvey and Gooseff 2015; Krause et al. 2017) transforming C, which supports food webs, ecosystem processes, and services to humans (Marks 2019; Cole et al. 2020; Ferreira et al. 2022).

A major source of C in headwater streams (which typically constitute 60%–80% of stream length in catchments, Lowe and Likens 2005; Allan et al. 2021) is terrestrial plant litter, which may be transported downstream, incorporated into aquatic food webs, or decomposed into inorganic components, including carbon dioxide (CO_2), which can outgas to the atmosphere (Gessner et al. 1999; Marks 2019). The amount of C that goes into the different compartments depends on the relative action of agents such as water flow, microorganisms (mostly aquatic hyphomycetes, Bärlocher 2012), and litter-consuming detritivores (Boyero et al. 2020). It ultimately supports multiple trophic levels, from detritivores to predatory invertebrates, fish, amphibians, reptiles, birds, and mammals (Marks 2019).

Globally, C fluxes in streams and rivers account for a net efflux of 1.8 Pg C year^{-1} to the atmosphere (Raymond et al. 2013), which is equivalent to more than half of the ocean and land sinks (estimated at 2.9 and 3.5 Pg C year^{-1}, respectively) and 18% of global fossil CO_2 emissions in 2022 (Friedlingstein et al. 2022). Although an important part of the contribution of riverine systems comes from terrestrial dissolved C (i.e., lateral inputs; Regnier et al. 2022), this fraction often corresponds to decomposition of young organic matter (Mayorga et al. 2005) coming from nearby areas (Jones Jr and Smock 1991; Zhou et al. 2020). Decomposition in the riparian area resembles instream decomposition due to the high humidity conditions (Naiman et al. 2010), and both are tightly related (Abelho and Descals 2019). Understanding the environmental and biotic drivers of plant litter decomposition in streams and rivers is thus a central question in ecology (Swan et al. 2021), which includes comprehending the TS of the process in the face of global climate change (Tiegs et al. 2019; Boyero, Gessner, et al. 2021; Follstad Shah 2021; Tonin et al. 2021).

1.1 | The TS of Ecosystem Processes

The term TS used in the context of ecosystem functioning (as here) refers to the change in the rate of a given ecological process with respect to temperature (Sierra 2012). Traditionally, the most common metrics for measuring TS (especially under laboratory conditions) have been the Arrhenius model and the Q_{10} temperature coefficient (Alster et al. 2020), which were originally intended to describe physicochemical rather than biological reactions, using an exponential temperature relationship according to empirical observations (Gessner and Peeters 2020). However, although these models are still commonly used (e.g., Vaughn and Torn 2019; Pérez et al. 2021; Wang et al. 2021; Yu et al. 2023), other approaches have gained popularity in ecological field studies (e.g., Davidson et al. 2006; Tang and Riley 2015; Alster et al. 2020). For example, the use of degree-days to standardize measures of temperature effects on decomposition rates (Irons et al. 1994; Boyero et al. 2011; Gessner and Peeters 2020) is especially useful to account for seasonality or differences among regions (Pérez et al. 2011; Woodward et al. 2012). However, this approach has shortcomings (Irons et al. 1994; Lecerf 2021; Follstad Shah 2021), as it assumes a linear relationship (Gessner and Peeters 2020). Instead, some relevant studies have turned to the metabolic theory of ecology (MTE; Brown et al. 2004) to assess the influence of temperature on decomposition rates (e.g., Boyero et al. 2011; Follstad Shah et al. 2017; Wilmot et al. 2021; Cummins et al. 2024).

The MTE describes the TS of an ecological process as the slope (activation energy, in eV) of the natural logarithm of biological activity versus the inverse of the product of absolute temperature (*T*, in K) and the Boltzmann constant ($k = 8.617 \times 10^{-5}$ eV K^{-1}) (Gillooly et al. 2001; Brown et al. 2004; Allen et al. 2005). The resulting temperature is thus the inverse of the temperature scale in °C (Figure 1, compare *y*-axes). Thus, like the Q_{10} and Arrhenius models (Gessner and Peeters 2020), the TS measured as activation energy assumes an exponential relationship, although it uses a different function. Importantly, these different approaches render similar values of TS at temperature ranges that are relevant for litter decomposition in natural environments (Gessner and Peeters 2020). The MTE has been used to describe the TS of instream plant litter decomposition in several studies, including an empirical study conducted at 22 sites distributed worldwide (Boyero et al. 2011) and a synthesis based on 169 published studies (Follstad Shah et al. 2017), which is the approach that we use here.

1.2 | Global-Scale Decomposition Studies Have Produced Contrasting Results

A recurring question is whether TS differs for both microbial and total decomposition, the latter involving both microbes and detritivores (e.g., Ferreira and Canhoto 2015; Follstad Shah et al. 2017; Amani et al. 2019; Landeira-Dabarca et al. 2019; Tiegs et al. 2019; Wilmot et al. 2021; Monroy et al. 2023). This question has important repercussions for the global C cycle (Canadell et al. 2023), as increased microbial decomposition can boost climate warming through greater outgassing of CO_2 to the atmosphere (Boyero et al. 2016; Marks 2019), whereas detritivore-mediated decomposition favors C sequestration (Raymond et al. 2013; Marks 2019). In this context, Boyero et al. (2011) used space-for-time substitution (Pickett 1989) in a coordinated distributed experiment (sensu Fraser et al. 2013), conducted through the GLoBE network (www.globenetwork.es) to assess large-scale variation in plant litter decomposition in streams and infer future trends in the C cycle (Boyero et al. 2011; Tiegs et al. 2019; Rubio-Ríos et al. 2022). Boyero et al. (2011) determined that the TS of decomposition was higher for microbially mediated than for total decomposition (averaging 0.58 vs. 0.06 eV, respectively).

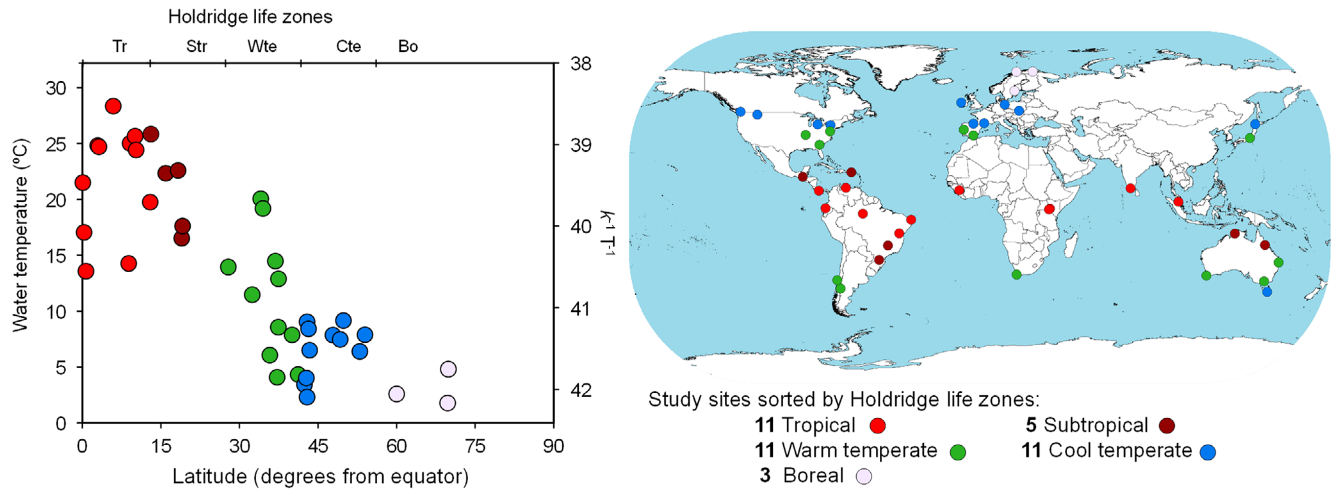

FIGURE 1 | Relationship between mean water temperature during the DecoDiv experiment (left *y*-axis, °C; and right *y*-axis, the inverse of absolute temperature [*T*, in K] and the Boltzmann constant [*k*]) and absolute latitude degrees (left panel) and map showing the global distribution of study sites (right panel) sorted by life zones (Holdridge 1967). Map lines delineate study areas and do not necessarily depict accepted national boundaries.

In contrast, Follstad Shah et al. (2017), in a synthesis including data from plant litter of multiple species, concluded that TS was similar for microbial and total decomposition (average of 0.37 vs. 0.33 eV, respectively). In this case, the rates were negatively correlated with litter quality, and TS was solely driven by the presence of a single genus (*Alnus*). This result was striking given (i) the well-known, strong influence of litter quality on decomposition rate whereby litter with higher concentrations of nutrients and lower concentrations of structural (lignin) and secondary compounds (tannins) decomposes faster (Casas et al. 2013; Rubio-Rios et al. 2021); and (ii) the negative relationship between litter quality and TS of decomposition rate in terrestrial ecosystems (Fierer et al. 2005).

Although results are variable across studies, litter quality effects on decomposition are often more pronounced than effects of warming in both terrestrial (Coûteaux et al. 1995; Bosatta and Ågren 1999; Aerts 2006) and freshwater ecosystems (Fernandes et al. 2012; Pérez et al. 2021; Monroy et al. 2023; Fenoy et al. 2024), particularly when detritivores are involved (Landeira-Dabarca et al. 2019; Zhang et al. 2019). However, most of the relevant studies have been conducted at the local scale, and many have used a low number of litter types, generally single species (Ostrofsky 1997; Martínez et al. 2016; Follstad Shah et al. 2017), in contrast to field conditions where litter is typically found in mixtures of a few to many species (Swan et al. 2009; Gessner et al. 2010). To examine the interaction between climate and litter quality, global-scale studies encompassing large climatic variation and a wide variety of litter types are desirable (De Frenne et al. 2013).

1.3 | A Global Study Focusing on Litter Diversity Sheds Light on TS Patterns

The present study arose from the coordinated distributed DecoDiv experiment, which found important roles of plant litter and detritivore diversity on instream litter decomposition (Boyero, López-Rojo, et al. 2021; Boyero, Pérez, et al. 2021). Taking advantage of the broad temperature range of the network's 41 sites (1.8°C–28.3°C average temperature; Figure 1, Table S1) and the inclusion of nine litter types combined in six different mixtures (Figure S1), we aimed to disentangle the mechanisms underlying the TS of decomposition and, ultimately, to forecast effects of climate warming on this ecosystem process.

We predicted that (i) the TS of microbial decomposition would conform to the MTE (Brown et al. 2004), with values of 0.60–0.70 eV, which are within the range typically observed for metabolic reactions (Gillooly et al. 2001). Conversely, we expected (ii) a reported reduction in TS in the presence of detritivores (Boyero et al. 2011; Follstad Shah et al. 2017). Additionally, we expected (iii) TS to vary with the diversity (Boyero, Pérez, et al. 2021; López-Rojo et al. 2021) and quality (Fierer et al. 2005; Follstad Shah et al. 2017) of plant litter, particularly for total decomposition, since detritivore abundance, identities, and activity show greater variation at the global scale than those of microbial decomposers (Boyero et al. 2015; Follstad Shah et al. 2017; Boyero, Gessner, et al. 2021; Boyero, López-Rojo, et al. 2021). Finally, by combining a space-for-time substitution approach and current climate change models (De Frenne et al. 2013), we assessed (iv) the magnitude of the anticipated differences in TS between microbial decomposers and detritivores across latitudes.

2 | Materials and Methods

2.1 | Study Sites

We conducted our study in 41 headwater streams located in 26 countries across a latitudinal gradient of over 110°, from Tasmania to the northernmost Finnish Lapland (Figure 1, Table S1). According to the Holdridge life zone classification, our study included 11 tropical, 5 subtropical, 11 warm temperate, 11 cool temperate, and 3 boreal sites (Holdridge 1967). As a random distribution of sites was unfeasible, some regions (e.g., Africa and northern Asia) and biomes (e.g., colder regions) were underrepresented, as is typically the case for coordinated globally distributed experiments (Tiegs et al. 2009; Borer et al. 2014; Ferreira et al. 2018). Streams were similar in size (1st–3rd order) and geomorphology, characterized by alternating riffles and pools. Most had rocky substrate and were shaded by a dense riparian vegetation representative of the region. Sites covered a range of water temperature of 26.6°C (Table S1), which was directly related to their distance from the equator (Figure 1; $R^2=0.69$, $p<0.0001$), with most within-zone variability (standardized residuals) explained by altitude ($R^2=0.37$, $p<0.0001$). We conducted the decomposition experiment by deploying the litterbags within 5 consecutive pools along ca. 100 m reaches in each stream (Bärlocher 2020). All litterbags in each site were collected after the same incubation period, but the timespan differed across sites (35.1 ± 6.6 days) to accommodate the wide climatic variation or, more specifically, differences in stream temperature (Table S1; Boyero, Pérez, et al. 2021).

2.2 | Experimental Procedure

To maximize the generality of our results, we used several plant litter mixtures representing a variety of species and litter traits (Boyero, López-Rojo, et al. 2021), in contrast to prior large-scale decomposition studies that used one or two species (Boyero et al. 2011; Woodward et al. 2012; Tiegs et al. 2019). Six distinct three-species litter mixtures (I–VI), which included nine species in total (Figure S1) were deployed at each site. Litter mixtures were enclosed within paired fine-mesh (0.4 mm) and coarse-mesh (5 mm) litterbags containing the same amount and type of litter, respectively, allowing us to quantify microbial and total decomposition (microorganisms plus detritivores). Upon retrieval of the litterbags and return to the laboratory, we sorted the remaining litter of each species within the mixture, which allowed us to assess the decomposition rate of both the litter mixtures and the individual species (Boyero, López-Rojo, et al. 2021; Boyero, Pérez, et al. 2021).

2.3 | Data Analyses

Data are deposited in the Dryad repository (https://doi.org/10.5061/dryad.mw6m9067k). We explored our predictions (i) and (ii) by quantifying microbial and total decomposition in fine-mesh and coarse-mesh litterbags, respectively. We expressed the litter decomposition rate in each litter bag based on the negative exponential decay model, using both the decomposition rate per day (k, d^{-1}) and per degree day (dd^{-1}), the latter to account for differences in temperature across sites (Gessner and Peeters 2020). Following the approach of Boyero et al. (2011), we first examined variation in decomposition rate (k, d^{-1}) with mean water temperature during the experiment, using linear regression analysis. Second, we explored our results in terms of the MTE (Brown et al. 2004; Allen et al. 2005), with the natural logarithm of the decomposition rate ($\log_e$ (k, d^{-1})) regressed against the inverse of absolute temperature (T) and the Boltzmann constant (k). The slope of this regression is a direct estimate of TS, representing the activation energy of microbial (TS_F, fine-mesh litterbags) or total decomposition (TS_C, coarse-mesh litterbags) in eV. Finally, we regressed the average decomposition rate in terms of thermal sums (k, dd^{-1}) versus the absolute latitude (degrees from the equator) of the study site (Gessner and Peeters 2020).

To explore our prediction (iii) and further identify the mechanisms underlying the TS of decomposition, we followed a top-down approach from more general to more specific patterns. Thus, we first examined TS for the average decomposition rate across all litter mixtures, then for each individual mixture (I–VI), and, finally, for each of the nine species within each of the two mixtures in which a given species was present. This approach rendered a total of 25 combinations for which TS_F and TS_C were assessed (Tables S2 and S3). We explored the relationship between TS and two common indices of litter quality and functional diversity (Lopez-Rojo et al. 2020; Rubio-Rios et al. 2021): the litter quality index (LQI) and Rao's quadratic distance (RaoQ; dbFD function) in the "FD" R package (Laliberté et al. 2014). Both were based on five litter traits (Petchey and Gaston 2006) potentially influencing microbial and detritivore-mediated decomposition (Hladyz et al. 2009; Fernandes et al. 2012; López-Rojo et al. 2021; Fenoy et al. 2024): toughness, the inverse of SLA (specific leaf area), C:N and C:P molar ratios, and NSC (non-structural carbohydrates). The LQI was originally proposed to facilitate comparisons among species by considering a limited set of relevant litter traits (Solagaistua et al. 2019) and to assess the quality of litter mixtures (Rubio-Rios et al. 2021) weighted by proportions of species in terms of initial dry mass (Figure S1, Table S4). It follows the equation $LQI = 1 - [(T_1/(n \times T_{1(\max)})) + \ldots + (T_n/(n \times T_{n(\max)}))]$, where T is the average of the measured value for the trait and n is the number of measured traits. (Note that the use of elemental ratios, e.g., C:N, instead of nutrient concentrations, e.g., N, %DM, and the inverse of SLA instead of SLA, is necessary because of the way the LQI is calculated, by subtracting trait values from 1.) The RaoQ is the sum of pairwise functional distances of measured traits between species in a mixture weighted by their relative abundances (Rao 1982; Roscher et al. 2012). Mean values of litter traits for each species and the weighted estimate of both indices for litter mixtures are given in the Supporting Information (Table S4, Figure S1).

Finally, for our objective (iv) of projecting future trends in the TS of decomposition, we used the CCM3 scenario for the year 2100, which assumes a doubling of current greenhouse gas emissions (Govindasamy et al. 2003). This model is similar to the average of several IPCC scenario families (Arribas et al. 2012) and, therefore, represents a baseline for conservative evaluations of the ecological effects of climate change.

3 | Results and Discussion

3.1 | Microbial Decomposition is Particularly Sensitive to Warming

We observed a clear increase in microbial decomposition rate across the temperature gradient covered by our study (Figure 2a). Furthermore, when temperature was expressed in terms of MTE (Figure 2b), a negative slope resulted with a coefficient of 0.60 ± 0.09 eV (mean ± SE, Table S1), equivalent to a mean Q_{10} coefficient of 2.3 (Table S2). These findings support our first hypothesis and corroborate the results obtained in a coordinated experiment across 22 globally distributed sites with a single species, *Alnus glutinosa* (Boyero et al. 2011). Also, following that study, the latitudinal pattern disappeared when applying a simple water temperature normalization to microbial decomposition, expressing decomposition rates as a function of degree-days instead of elapsed time (Figure 2c, Figure S2).

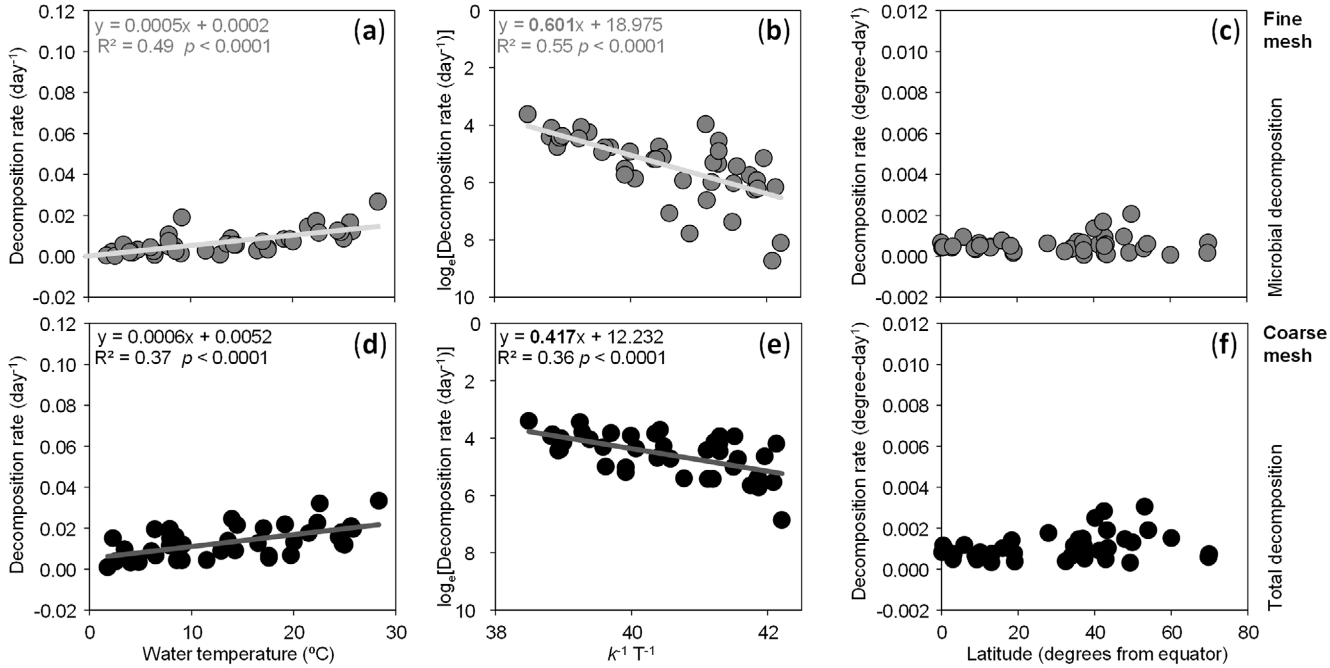

FIGURE 2 | Mean decomposition rates of the six studied litter mixtures in fine-mesh (a–c) and coarse-mesh litterbags (d–f) across 41 globally distributed study sites. Relationships are between decomposition rate per day and stream temperature in °C (a, d); between the natural logarithm of decomposition rate per day and stream temperature expressed in terms of the metabolic theory of ecology as the inverse of absolute temperature (*T*, in K) and the Boltzmann constant (*k*), being the slopes equal to the TS in eV (b, e); and between temperature-normalized decomposition rate (i.e., per degree day) and absolute latitude (c, f). This figure revisits Boyero et al. (2011)—figure 2, using the same layout for the panels.

Our new analysis based on multiple species mixtures underscores the distinct latitudinal pattern found by Boyero et al. (2011) for total decomposition, but finds a lower difference between the mean TS of decomposition by microbes and detritivores (second hypothesis), also contrasting a conclusion drawn from the analysis of a large body of published data (Follstad Shah et al. 2017). Specifically, although total decomposition increased with temperature (Figure 2d), unlike the absence of pattern in Boyero et al. (2011), the apparent TS of the total decomposition rate (Figure 2e) was lower than predicted by the MTE (0.42 ± 0.08 eV, Table S1; mean Q_{10} coefficient of 1.8, Table S2), and considerably higher than that found in previous studies (Boyero et al. 2011; Follstad Shah et al. 2017). Although some of the reported differences in mean TS could be obscured due to the high variability of the data (i.e., overlapping confidence intervals), which is inherent to spatially extensive datasets like ours, the existence of significant slopes is particularly relevant at such a large scale (De Frenne et al. 2013). When temperature-normalized (degree-days) total and microbial decomposition rates were plotted against latitude (Figure 2c,f), slopes of the regression lines were not significant, with total decomposition varying more strongly both among and within distinct latitudinal zones than microbial decomposition (Figure S2).

3.2 | Litter-Quality Influence on the TS of Total Decomposition for Diverse Litter Mixtures and Different Species

To test whether the observed TS patterns were influenced by the litter mixtures or only governed by the individual species included in our study, we explored the data separately from both perspectives. Despite considerable variation in the mean TS of microbial decomposition across the six tested litter mixtures (0.47–0.65 eV), the mean TS of total decomposition was invariably lower (0.32–0.47 eV), but the observed reductions between total and microbial TS were not always equivalent (Figure 3, Table S2). Plots of decomposition rates projected from these models at different temperatures (Table S2, Figure S3) indicated differences in decomposability and temperature effects among litter mixtures. As suggested by Follstad Shah et al. (2017), mixtures undergoing faster total decomposition (I and VI) (Boyero, Pérez, et al. 2021) were those showing greater differences between the mean TS of microbial and total decomposition. This suggests a key role of a single species (*Alnus incana*) in these two mixtures for average litter quality in the mixtures (López-Rojo et al. 2021), which were the only ones to include litter from this species.

For individual species in litter mixtures (Figures S4 and S5), our results show that, in most cases (15 out of 18; Table S3), the mean TS was lower for total (0.230–0.630 eV) than for microbial decomposition (0.350–0.783 eV). The average reduction was 0.12 eV, but it varied considerably among species and depended on the composition of the mixture. For example, the reduction for *A. incana* was greater (0.39 eV) when the leaves decomposed with other *Alnus* species and lower (0.19 eV) when decomposing with species from other families. Conversely, *Ficus dulciaria*, the species with the highest TS in our study (Table S3), showed a similar reduction in TS independent of the presence of litter from other families (0.15 eV; Figure S5f) or other *Ficus* species (0.13 eV; Figure S4f). Although the patterns for mixtures were largely consistent, some species were exceptions, indicating that the response to increasing

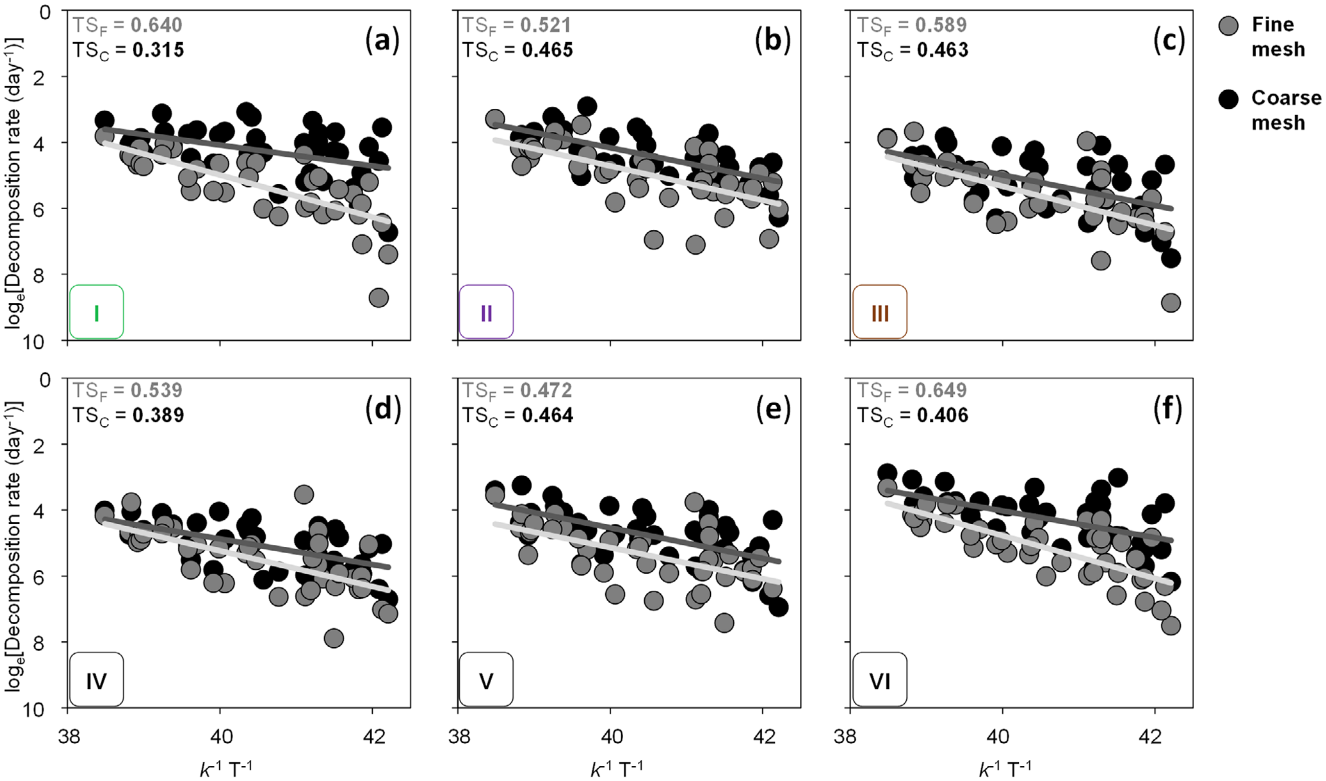

FIGURE 3 | Relationship between the natural logarithm of decomposition rate per day and stream temperature expressed in terms of the metabolic theory of ecology, for the six studied litter mixtures (a-f) in fine-mesh (light grey) and coarse-mesh litterbags (dark grey), across 41 globally distributed study sites. The slopes equal the TS in eV. See further information in Table S2.

temperature may not be general. For example, *Quercus prinus*, typically a slow decomposer, and *Ficus insipida*, a medium to high decomposer (Boyero, Pérez, et al. 2021), each presented very similar mean TS for microbial and total decomposition (Table S4, Figures S4d and S5d).

To test whether the observed variation in the TS of decomposition was determined by quality or functional diversity of the litter mixtures, we examined the correlation between the TS of decomposition and two indices—the litter quality index, LQI, and Rao's quadratic diversity, RaoQ (López-Rojo et al. 2021; Rubio-Rios et al. 2021). Although previous studies have explored the effect of litter traits and their variability on decomposition (e.g., Lecerf et al. 2011; Zhang et al. 2019), this is the first empirical study to test their effects on the TS of total and microbial decomposition in streams. While there was no relationship with LQI or RaoQ for microbial decomposition (Figure 4a,b) nor with RaoQ for total decomposition (Figure 4d), there was a negative relationship between the TS of total decomposition and LQI, indicating that TS tended to decrease as litter quality increased (Figure 4c).

3.3 | Projections of Litter Decomposition in the Face of Climate Warming

Our study reveals different patterns in microbial and total decomposition (Figure 2, Figures S2 and S3) and their TS (Figure 3) and different mechanisms underlying the TS of decomposition driven by microbes and detritivores (Figure 4). Given the relationship between water temperatures and decomposition rates (Figure 2a,d), and the observed 1:1 ratio between water and air temperature (Fick and Hijmans 2017) (Figure S6a), we estimated current and future ratios of total to microbial decomposition (C/F ratios hereafter), derived from coarse- and fine-mesh litterbags as an indicator of the relative contribution of microorganisms and detritivores to decomposition (Gessner and Chauvet 2002). The underlying assumption was that an increase in water temperature is equivalent to the increase in air temperature projected by the CCM3 (Govindasamy et al. 2003) climatic model (Figure S6b) for each of our 41 study sites (0.9°C–2.9°C).

The current C/F ratio for the mean of all litter mixtures increased exponentially with latitude, from values of 1–2 in the equator—indicating a minor role of detritivores at lower latitudes, and microbes accounting for 63% of total decomposition—to >4 at higher latitudes, where microbes contributed <25% to total decomposition at some sites (Figure S6a). The mean value of this ratio across Holdridge life zones demonstrates this exponential trend (Figure 5).

According to the scenario of future temperature rises and the accelerated pace of life zone changes (e.g., Elsen et al. 2022), this latitudinal trend would be reduced considerably, enhancing the role of microbes in colder regions, whose average contribution would increase from 35% to 44% in cool temperate sites and from 23% to 36% at higher latitudes (Figure 5). The implications of these changes for the fate of litter entering inland waters (Marks 2019) could be substantial, as an increment in the role of

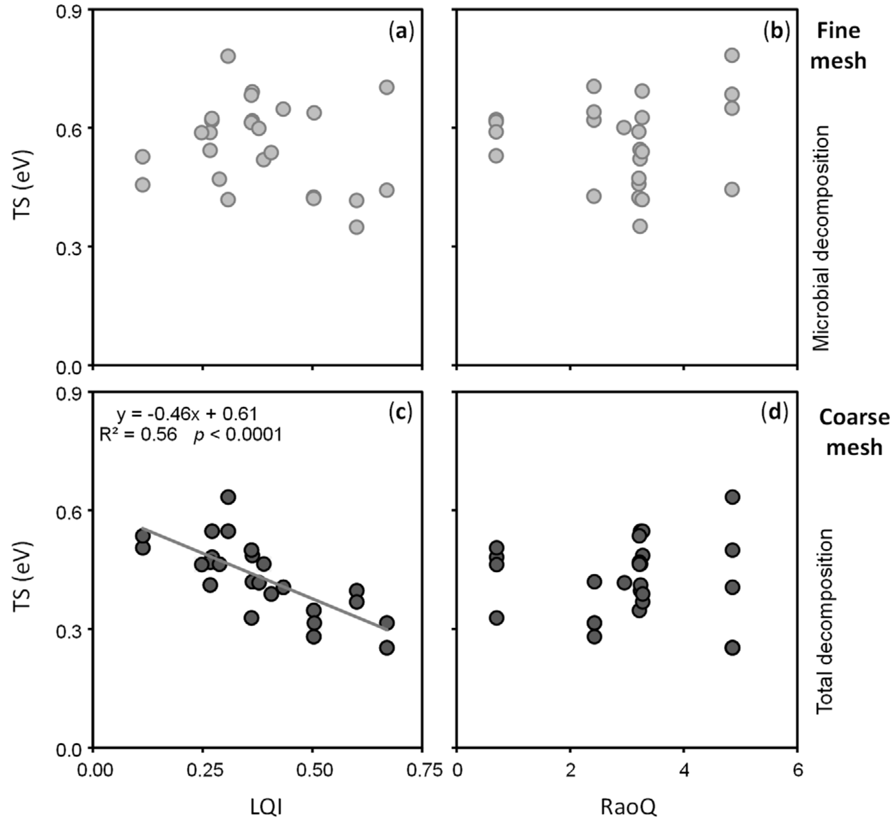

FIGURE 4 | Relationships between the TS of microbial (a and b) and total decomposition (c and d) and the litter quality index (LQI) and litter trait diversity measured by the RaoQ index.

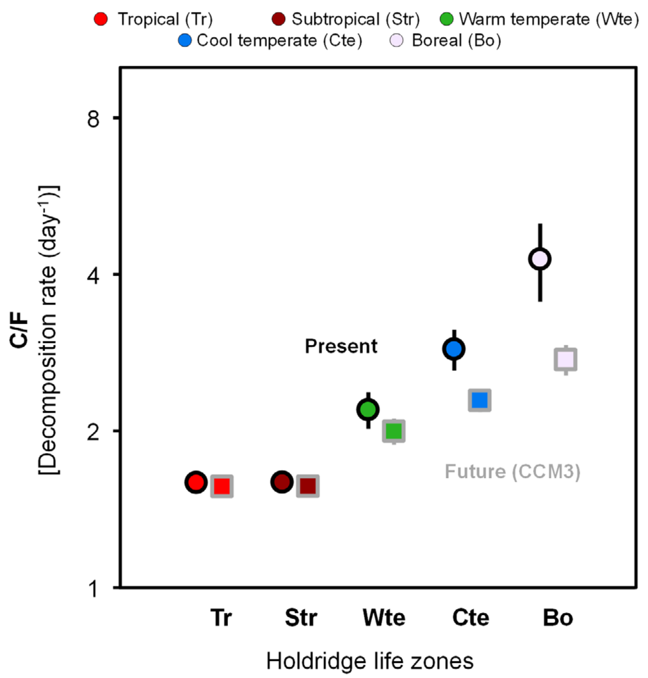

FIGURE 5 | Relative contribution of microbial decomposers and detritivores to decomposition by means of the total to microbial decomposition ratio (C/F). Note that *y*-axis is presented in log-scale, considering experimental data (Present, black circles) and projections under the global warming scenario (Future CCM3, grey squares). Means ± SE are presented for Holdridge life zones (Holdridge 1967) (see C/F ratios for each site in Figure S7).

microbes in colder zones of the planet would promote an overall increase of CO_2 outgassing, thus shifting the C cycle and producing a positive feedback on climate warming (Boyero et al. 2011). However, this shift might not entail an increase in microbial carbon use efficiency (Fenoy et al. 2022) despite the increase in microbial respiration.

As the TS of decomposition can vary depending on litter characteristics, individual species or genera, such as *Alnus* (Follstad Shah et al. 2017) may drive some of the patterns observed here. Given that *Alnus* was included in four out of the six litter mixtures used, we calculated the C/F ratio and examined current and future patterns for each of the six mixtures (Figure S8). The two mixtures showing the greatest differences between the TS of microbial and total decomposition (I and VI) also presented the most pronounced latitudinal variation in the C/F ratio and a projected greater future increase in the role of microbes at higher latitudes (Figure S8a,f). However, the two mixtures without *Alnus* (II and III) showed a pattern similar to the average (Figure S8b,c), suggesting that our results were not entirely dependent on the presence of *Alnus* and, hence, could apply to a wider range of litter types.

4 | Conclusions

Our study predicts an increase in the proportional contribution of microorganisms to the total decomposition of plant litter in streams as a result of climate warming. This finding is consistent across a variety of plant litter types and matches the pattern previously demonstrated for *A. glutinosa* (Boyero et al. 2011). Although the shift from detritivores to microbes is expected to be clearer for colder regions, changes are also expected in tropical areas given their higher rates of deforestation (Vancutsem et al. 2021) and eutrophication (Bridhikitti et al. 2022), which impair invertebrate communities (Peralta et al. 2020) and are thus detrimental to detritivore-mediated processes (Cornejo et al. 2020). The pattern observed here was partly controlled by the quality of plant litter, which suggests a major role of riparian species composition in determining future shifts in decomposition rates. Therefore, we anticipate further consequences associated with the widespread afforestation with exotic tree species such as pine and eucalyptus (Larrañaga et al. 2021), which render low-quality litter with known adverse effects on detritivore-mediated decomposition (Martínez et al. 2013; Ferreira et al. 2018). This may be particularly relevant in temperate areas, where natural riparian vegetation tends to shed higher-quality litter (Boyero et al. 2017), but may also be important at lower latitudes if the forecast decrease of leaf quality of riparian species (Rubio-Ríos et al. 2022) or the substitution of deciduous by evergreen species (Kominoski et al. 2013; Salinas et al. 2018) occurs. Therefore, riparian forest conservation and restoration measures using species of high litter quality may favor decomposition by detritivores and partly mitigate the predicted shift toward a primarily microbial process.

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Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

The data that support the findings of this study are available from the corresponding author upon reasonable request.

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Supporting Information

Additional supporting information can be found online in the Supporting Information section.