ENVIRONMENTAL STUDIES

Latitude dictates plant diversity effects on instream decomposition

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Running waters contribute substantially to global carbon fluxes through decomposition of terrestrial plant litter by aquatic microorganisms and detritivores. Diversity of this litter may influence instream decomposition globally in ways that are not yet understood. We investigated latitudinal differences in decomposition of litter mixtures of low and high functional diversity in 40 streams on 6 continents and spanning 113° of latitude. Despite important variability in our dataset, we found latitudinal differences in the effect of litter functional diversity on decomposition, which we explained as evolutionary adaptations of litter-consuming detritivores to resource availability. Specifically, a balanced diet effect appears to operate at lower latitudes versus a resource concentration effect at higher latitudes. The latitudinal pattern indicates that loss of plant functional diversity will have different consequences on carbon fluxes across the globe, with greater repercussions likely at low latitudes.

INTRODUCTION

The relationship between plant diversity and key ecosystem functions such as litter decomposition has been a focal point of ecological research since the late 1990s, prompted by rapidly ongoing biodiversity losses worldwide (*1*). Riparian forests are greatly altered by human practices such as deforestation and monoculture plantations, as well as various aspects of global environmental change (e.g., microbial infections, plant invasions, and climate warming), which lead to the loss of species and functional traits (*2*). Assessing how riparian plant taxonomic and functional diversity (i.e., the number of species and functional traits, respectively), and hence the diversity of litter entering streams, influences decomposition rates and carbon (C) pathways in stream ecosystems is crucial, because streams contribute to global C fluxes the equivalent of one-fifth of human emissions (*3*).

Experimental evidence suggests that litter diversity can accelerate decomposition (*4*). However, effects have been inconsistent and often weak when present, especially compared to effects of plant diversity on primary production (*1*) or effects of detritivore diversity on litter decomposition (*5*). One explanation for this inconsistency could be differences in environmental or biogeographical context that counteract each other. Results of two studies support this contention: One conducted across five climatic zones found a negative effect of functional diversity (quantified as the number of functional types in litter mixtures) on decomposition in subarctic and tropical streams but a positive effect in Mediterranean, temperate, and boreal streams (*4*); the other suggested distinct latitudinal variation in the effect of functional diversity (quantified as phylogenetic distance in litter mixtures) on decomposition across 24 streams distributed globally (*6*).

Here, we report the results of a globally coordinated experiment to test whether the effect of plant litter functional diversity on instream decomposition varies across a wide latitudinal range (40 streams in 6 continents from 70°N to 43°S). We predicted that latitudinal variation would influence this effect, mainly as a result of the interplay between plant diversity and detritivore evolutionary adaptations, both of them differing systematically in different regions. Specifically, we envisioned two scenarios for low- and high-latitude streams, approximately corresponding to tropical/subtropical and temperate/cold regions, respectively, as described below.

The first scenario relates to low latitudes, where riparian forests tend to be highly diverse (*7*–*9*). This high diversity, in conjunction with the variable phenology of species (*10*) and lack of pronounced seasonality (*11*) (fig. S1), results in the continuous accumulation in streams of a variety of litter types with diverse functional

traits (*12*, *13*), with instream diversity of litter much greater than at high latitudes (see below). Although average litter quality is often lower than at high latitudes (*14*), the high diversity ensures the availability of multiple resources (i.e., litter with different concentrations of nutrients and micronutrients and different degrees of toughness and palatability). In addition, detritivore diversity in low-latitude streams tends to be lower than at high latitudes (*15*), and detritivores use a broad suite of litter types (*12*) because of their often more generalist strategies (*16*). The characteristics of assemblages at low latitudes suggest that high litter trait diversity might promote decomposition through a "balanced diet" effect in detritivores (Fig. 1). The balanced diet hypothesis states that different resources are complementary in their nutritional composition, so a generalized diet provides a more complete range of nutrients, which translates into higher consumer fitness and activity (*17*, *18*).

The second scenario prevails at high latitudes, where litter is generally of higher quality but is less diverse (*14*) and available only during short periods of the year because the pronounced seasonality restricts leaf fall to a short pulse (fig. S1) (*11*). Detritivore assemblages are richer than at low latitudes (*15*), but species have to obtain resources from the few litter types that are available. We expected that, at these latitudes, decomposition would be greater in lower diversity mixtures, which would reduce search and handling time and thus optimize detritivore energy expenditure (*19*) through a "resource concentration" effect (Fig. 1) (*20*). The resource concentration hypothesis states that consumers are efficient at finding resources that are less diverse because of the higher resource density (*21*).

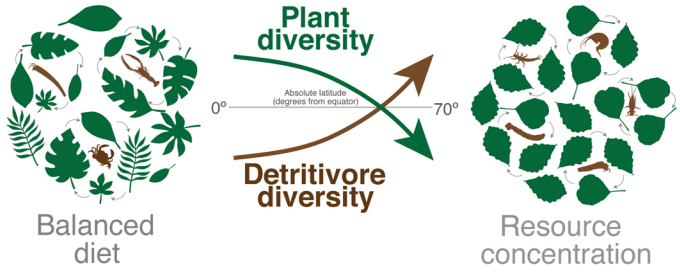

Fig. 1. Predictions about latitudinal variation of the litter diversity effect on decomposition (LDED) resulting from differences in plant and detritivore diversity at low and high latitudes. At low latitudes, the high diversity (and continuous availability, not shown in the figure) of litter provides a wide variety of resources and favors a balanced diet for detritivores. At high latitudes, the low diversity (and seasonal or periodic availability, now shown) of litter favors detritivore specialization in the use of concentrated resources. Gray arrows represent the movement of detritivores (represented by brown drawings) between different types of litter (green drawings).

To investigate these scenarios, we designed an experiment that assessed instream decomposition of litter mixtures differing in species composition and functional diversity. We opted for this approach (instead of manipulating species richness, which is the most common procedure) because it allowed a design that involved multiple species and functional traits, while limiting the number of experimental treatments. We manipulated functional diversity by selecting combinations of species that were similar or different phylogenetically (see Materials and Methods). This approach is particularly useful because phylogenetically closer species often have more

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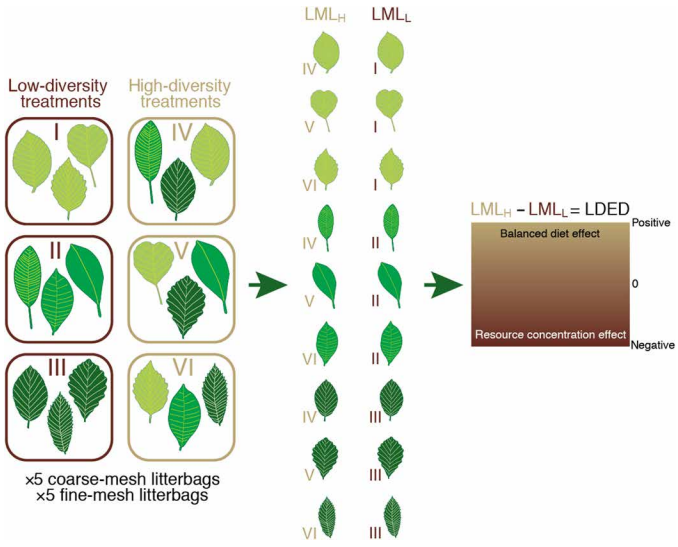

Fig. 2. Graphical summary of our experimental design. We combined litter of nine plant species belonging to three families (represented by different shades of green) in three low-diversity mixtures (each containing three species of the same family) and three high-diversity mixtures (containing three species of different families. Each treatment was incubated in each stream in coarse- and fine-mesh litterbags, replicates of which were placed in five consecutive pool habitats in pairs. After 23 to 46 days of incubation, we quantified decomposition [as litter mass loss (*LML*)] for each species in each mixture. We then calculated the *LDED* (our response variable) as the difference between LML in the high-diversity and the low-diversity mixture from the same pool.

similar trait values than more distantly related species (*22*) and because phylogeny contains more information than an index based on a few selected traits (*23*) and has been shown to be an important predictor of ecosystem functioning (*24*), including litter decomposition (*25*). We created three low-diversity and three high-diversity litter mixtures using different combinations of nine species (Fig. 2) and quantified species-specific decomposition rates in 40 headwater streams of similar basic characteristics but situated across a very wide range of latitudes (Fig. 3A and tables S1 and S2). Each of the nine species was present in one low-diversity and one high-diversity mixture, each replicated five times. The difference in decomposition [i.e., litter mass loss (*LML*)] between the two was used as the response variable, termed "litter diversity effect on decomposition" (*LDED*), the variation of which was explored across latitudes. We separated the effect of microbial decomposers and detritivores through the use of coarse- and fine-mesh litterbags (*26*), which allowed us to test our hypotheses about detritivore-mediated latitudinal patterns (see Materials and Methods).

RESULTS AND DISCUSSION

Resource concentration effect at high latitudes versus balanced diet effect at low latitudes

Our results showed the hypothesized pattern of latitudinal variation in the *LDED* (mean of the nine species), which decreased toward higher latitudes for coarse-mesh litterbags quantifying total decomposition and for the difference between coarse- and fine-mesh litterbags representing detritivore-mediated decomposition (Fig. 3B and table S3). The result was not driven by any particular species

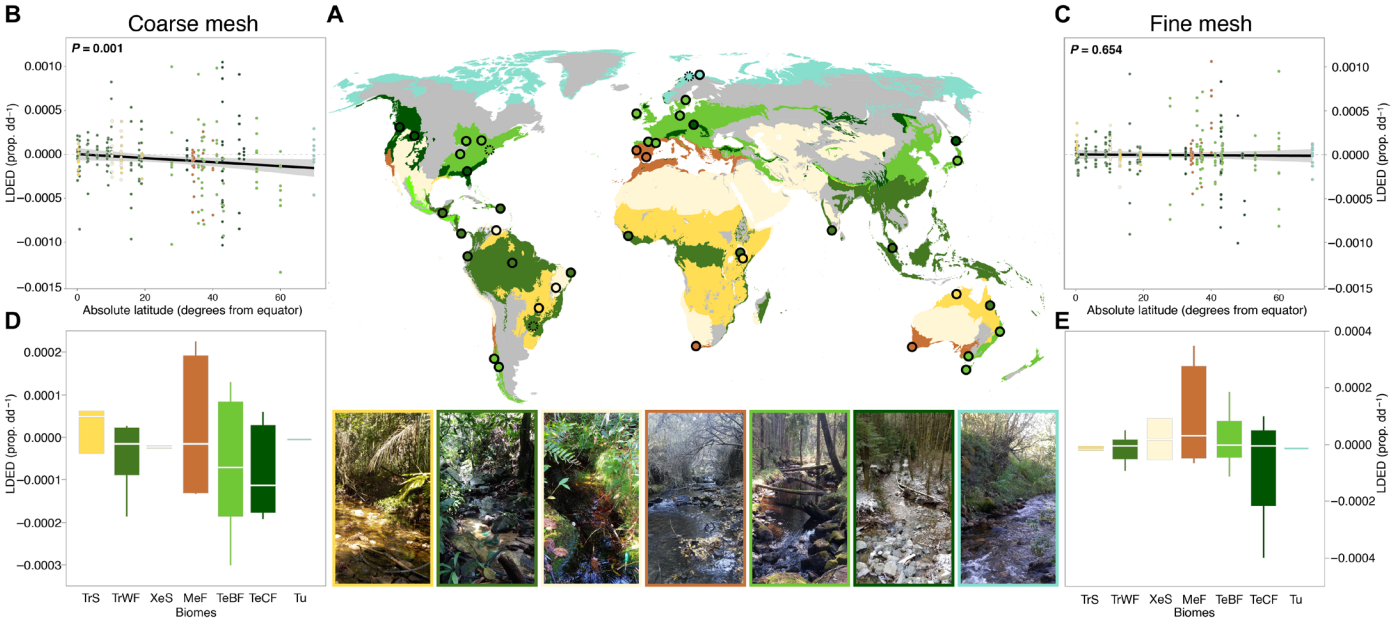

Fig. 3. Global distribution and photos of study sites and variation of the LDED across latitudes and biomes in coarse- and fine-mesh litterbags. Study sites were 43 streams (3 of which were excluded from analyses due to loss of replicates; represented by broken circles) that spanned 113° of latitude and were located in 26 countries in all inhabited continents (**A**). Colors correspond to terrestrial biomes included in the study, with absent biomes represented by gray color. The *LDED* decreased with latitude for coarse-mesh litterbags (**B**) and showed no latitudinal pattern for fine-mesh litterbags (**C**) and no differences among biomes for both types of litterbag (**D** and **E**); see table S3 for whole model results. Photographs show one stream site from each biome (from left to right: tropical savanna, TrS; tropical wet forest, TrWF; xeric shrubland, XeS; Mediterranean forest, MeF; temperate broadleaf forest, TeBF; temperate coniferous forest, TeCF; and tundra, Tu). Photo credit: GLoBE consortium.

(table S4). Nevertheless, *Alnus glutinosa* showed a stronger trend than other species that contributed to the overall latitudinal pattern (Fig. 4 and tables S3 and S4). As expected, the *LDED* was negative at high latitudes, suggesting a resource concentration effect. This effect was greatest when low-diversity mixtures had higher mean nutrient concentrations, as was the case of *Alnus* species, which were characterized by high concentrations of nitrogen (N), a key nutrient for detritivores (table S5) (*27*). Other low-diversity mixtures were less nutrient-rich, but the concentration of resources other than N (e.g., micronutrients) might have favored detritivore feeding compared to high-diversity mixtures; for example, mixture II had more calcium (table S5), which may enhance decomposition (*28*). This pattern may reflect the ability of high-latitude detritivores to feed on single species, even less nutritious ones, when this is the only litter available, providing a long-term resource once the more nutritious litter is gone (*29*, *30*).

At low latitudes, we did not find the expected positive mean *LDED*, possibly because our experimental high-diversity mixtures were considerably less diverse than the natural litter available in these streams (fig. S1). Accordingly, detritivores might not have favored high-diversity over low-diversity mixtures because they could feed on a wider variety of litter types available in the stream. Nevertheless, the lack of an *LDED*, in contrast to the negative *LDED* found at high latitudes, suggests that a balanced diet effect may be operating at low latitudes. In contrast to species-specific patterns, we found no influence of litter functional diversity on the decomposition of the litter mixtures as a whole (table S6), which may be because the stage of decomposition achieved in this experiment (32% for mixtures, on average, compared to 59% for the fastest decomposing species; fig. S2) was insufficient to detect such effects or because diversity effects on decomposition were obscured when multiple species were examined at the same time, as has been shown elsewhere (*31*). Species-specific patterns thus allowed us to remove the effect of intrinsic differences in decomposition rates, separating the influence of other factors (i.e., functional diversity of mixtures and latitude).

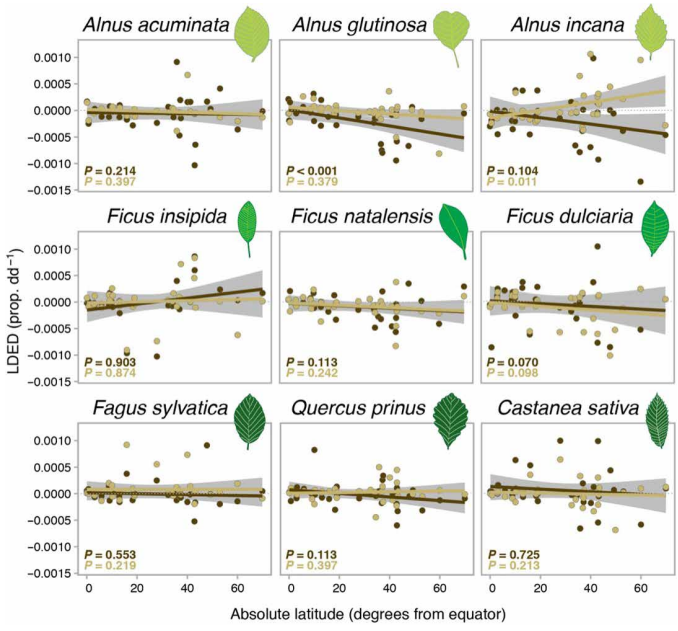

Fig. 4. Results of linear mixed-effects models testing the effect of the interaction between absolute latitude and mesh type on LDED for each species. Mesh types were coarse (dark brown lines) and fine (light brown lines), which allowed or excluded detritivores from litterbags, respectively (see table S3 for whole model results).

Lack of LDED for microbial decomposers

Unlike the decreasing latitudinal trend in *LDED* shown for species-specific patterns in total decomposition and that due solely to detritivores, there was no variation with latitude in fine-mesh litterbags quantifying microbial decomposition, as we expected (Fig. 3C and table S3). There was only one exception to this general pattern when species-specific patterns were examined, with the *LDED* increasing with latitude for *Alnus incana* in fine-mesh litterbags (Fig. 4 and table S3). However, in contrast to coarse-mesh litterbags, we did not find this pattern in other species that collectively caused a significant latitudinal variation in mean *LDED*. It is possible that the very low toughness of *A. incana* (table S5) caused higher physical fragmentation of this species when enclosed with tougher species (i.e., in high-diversity mixtures), although this does not explain the latitudinal gradient. As for coarse-mesh litterbags, total decomposition of mixtures in fine-mesh litterbags was not affected by litter functional diversity (table S6).

Which factors determine the LDED?

We explored whether the *LDED* systematically varied among streams across a variety of biomes (*32*) but found no differences (Fig. 3, D and E). This contrasts with global patterns of microbial decomposition of cotton strips (*33*) and suggests that the likely mechanisms underlying the *LDED* (explained above) vary at a broader scale (i.e., higher versus lower latitudes), as a result of climatic differences, and more specifically by the temperature gradient (fig. S1) (*34*), given that water is constantly available in permanent streams (*6*). It is also noteworthy that, despite the significant latitudinal pattern in the *LDED*, there was substantial variation among regions within latitudes (Figs. 3 and 4), which suggested that local factors also played a role in the *LDED*. However, we found that instream environmental factors were unimportant compared with the key role of temperature seasonality (table S7), supporting our earlier conclusions regarding the latitudinal differences in litter availability. Differences in *LDED* among plant species were most likely driven by litter traits, with N and phosphorus (P) being important in coarse-mesh litterbags and specific leaf area (*SLA*; which is inversely related to toughness) and P in fine-mesh litterbags (table S8). Litter nutrients and toughness are known to play a key role in diversity-decomposition relationships (*35*, *36*), so these differences were to be expected.

How plant diversity loss might affect stream C fluxes globally

Our study revealed differences in the relationship between riparian plant functional diversity and instream decomposition of species within mixtures across a wide range of latitudes. Diversity had similar effects on microbial decomposition across latitudes, so differences may be expected to occur through effects on detritivores. The greatest losses of plant diversity currently occur at low latitudes, where rates of deforestation and conversion of forest to monoculture plantations and agricultural land are high (*37*). Our results suggest that monocultures do not provide the balanced diet that tropical detritivores require and thus are likely to negatively affect them,

reduce their already low diversity (*15*, *38*), and, consequently, enhance the relative contribution of microbial decomposition to C fluxes. At higher latitudes, detritivores may be less affected by plant diversity loss because they efficiently use concentrated resources in low-diversity litter mixtures. However, the traits of lost and remaining species are important, and many plantation species [usually fast-growing trees (*39*) and some genetically modified (*40*)] produce low-quality litter that can deter detritivore feeding in the absence of other nutrient sources (*41*). Our results provide a basis for predicting the consequences of plant diversity loss for instream decomposition based on the biological assemblages and environmental settings present in different parts of the world.

MATERIALS AND METHODS

Study streams

We commenced our study with 43 headwater stream sites located in 43 regions from 26 countries (Fig. 3), but three streams were heavily disturbed by freezing or floods and so were excluded from analysis; the excluded streams were in Norway, Maryland (United States), and Rio Grande do Sul (Brazil). Streams were similar in size (orders 1 to 3) and physical habitat (alternating riffles and pools), mostly with dense canopy cover and rocky substrate, and each was representative of its region in terms of riparian vegetation. Mean water temperature during the experiment (measured with data loggers every 1 hour in most cases, otherwise measured several times during the experiment) varied between 1.8° and 28.3°C; pH varied between 3.9 and 8.3 (being circumneutral in 80% of streams); dissolved oxygen was close to 100% saturation; 70% of streams had low concentrations of nutrients [nitrate ($N\text{-}NO_3$) (<700 μg liter^{-1}), ammonium ($N\text{-}NH_4$) (<65 μg liter^{-1}), and phosphate ($P\text{-}PO_4$) (< 35 μg liter^{-1})]; and riparian plant diversity varied from streams with fewer than 10 species to others with more than 40 species (table S2 and fig. S1).

Litter mixtures

We used three low-diversity and three high-diversity litter mixtures (I to III and IV to VI), which corresponded to species of the same plant family (or genus) or to different families, respectively (Fig. 2). Families were chosen to represent different trait syndromes and worldwide distributions: (i) Betulaceae (*Alnus*), with higher-quality litter and wide distribution; (ii) Moraceae (*Ficus*), with intermediate-quality litter and tropical distribution; and (iii) Fagaceae, with lower-quality litter and northern temperate distribution (Fig. 2) (*29*). The species selected were *Alnus acuminata* Kunth., *A. glutinosa* (L.) Gaertn., *A. incana* (L.) Moench, *Ficus insipida* Willd, *Ficus natalensis* Hochst., *Ficus dulciaria* Dugand, *Fagus sylvatica* L., *Quercus prinus* Willd., and *Castanea sativa* Mill. Given that using all possible high-diversity combinations was unfeasible, we randomly chose one species from each family to be included in each of the three high-diversity mixtures, without replacement (i.e., each species was present in only one high-diversity and one low-diversity mixture). We calculated the phylogenetic distance of each of the six mixtures (and of all other possible high-diversity combinations) using the "leafbud.py" tool in Python 2.7 based on a phylogenetic tree of angiosperms that was constructed for a previous study (*14*). Phylogenetic distance was 237 ± 24 (mean ± SD) in low-diversity mixtures and 357 ± 5 in high-diversity mixtures (table S9).

We collected litter with no visible signs of herbivory or decomposition, from the riparian forest floor or using vertical traps. Different species were collected in different regions (fig. S3), as there was a trade-off between origin and the comprehensiveness of the pool of species and traits. We sacrificed the former despite a possible home-field advantage (HFA) effect (*42*), because there is little evidence that HFA occurs for instream decomposition (*43*, *44*), and HFA generally explains much lower variability in decomposition than litter traits and climate (*42*). In addition, we discarded the use of artificial substrates that would have removed any HFA effect (e.g., cotton strips) because they would not allow the different diversity treatments required to test our hypotheses and because they do not account for detritivore feeding activity (*33*). Litter was air-dried in laboratories and distributed among partners.

Fieldwork

In each region, we selected a permanent stream reach with length approximately 10 times the wetted stream width, within which we chose five consecutive pools in which to conduct the experiment. The experiment was run during stable flow conditions, at the time of the year (2017–2019) with greatest litter inputs to the stream (e.g., autumn in northern temperate regions and dry season in many tropical regions). We enclosed litter of each mixture (I to VI) within coarse-mesh (5 mm) and fine-mesh (0.4 mm) litterbags (approximately 1 g per species, 3 g in total, weighed precisely), with five replicates per treatment (i.e., combination of mixture and mesh type), resulting in 60 litterbags per region and 2580 in total. Despite some potential drawbacks of the litterbag method, it is by far the most widely used method to quantify decomposition in streams, as it resembles the decomposition of litter in depositional zones and allows size-selective exclusion of detritivores (*26*).

We placed one replicate litterbag per treatment in each pool, with coarse- and fine-mesh litterbags paired, and anchored them to the substrate using steel rods and stones. We retrieved the litterbags after 23 to 46 days, depending on the water temperature in each stream (fig. S1), thereby halting the decomposition process at a comparable stage (which was 59 and 27% for coarse- and fine-mesh litterbags, respectively, for the fastest decomposing species, *A. incana*, and 32 and 17% for mixtures; fig. S2). Upon retrieval, litterbags were enclosed individually in ziplock bags, transported to the laboratory on ice, and subsequently rinsed using filtered stream water to remove attached sediment and invertebrates. Litter was sorted into species and oven-dried (70°C, 72 hours), and a subsample was weighed, incinerated (500°C, 4 hours), and reweighed to estimate final ash-free dry mass (AFDM). *LML* due to leaching and drying was estimated for each species in the laboratory, and multiple litter traits were examined for each species as detailed by López-Rojo *et al.* (*36*).

Data analysis

We quantified litter decomposition rate as the proportion of *LML* per degree day for each species within a mixture and in total for each mixture (assuming linear decay), separately for coarse- and fine-mesh litterbags. This measure, which accounted for differences in temperature across regions, was calculated as follows: *LML* = [initial AFDM (g) − final AFDM (g)]/initial AFDM (g), with initial AFDM corrected by leaching, drying, and ash content (i.e., multiplied by the proportion of litter mass remaining after leaching and AFDM calculation, which ranged between 0.59 and 0.85). To assess species-specific patterns, we estimated the litter functional diversity effect on decomposition (*LDED*; for each species and mesh type) as the difference between its *LML* in the high-diversity mixture and the

low-diversity mixture located in the same pool habitat (i.e., there were five replicate values of *LDED* per species and mesh type; Fig. 2).

We could not calculate an LDED to assess whole mixture patterns (i.e., total *LML* of all species in the mixture); therefore, we used different modeling approaches for species-specific and total decomposition in mixtures. We examined the latitudinal variation of species-specific *LDED*s through linear mixed-effects (LME) models (*45*) [lme function and restricted maximum likelihood method, nlme R package (*46*)] in which latitude and mesh were fixed effects (fitted as an interaction), and replicates were a random effect nested within region. We ran one model for each species and an overall model where species was included as a random factor to assess patterns in the mean *LDED*. Data exploration with Cleveland dot plots and boxplots revealed no outliers (*47*), and their absence was confirmed with Cook's distances after fitting the models. Models included the variance function structure varIdent, which allowed different variances for each mesh (for individual species models) or mesh and species (for the overall model); the need for this term was identified in initial data exploration and confirmed by comparison of the Akaike information criterion (AIC) of models with and without this component (*45*). The influence of each species to the overall model was examined with Cook's distances, which indicated that results were not driven by particular species (table S4). For whole mixtures, we used an LME model where total *LML* in mixtures was the response variable, litter functional diversity and latitude were fixed effects (fitted as an interaction), treatment (I to VI) was a random effect, and replicates were nested within treatment.

We explored how the *LDED* varied across biomes (*32*) through LME models, for coarse- and fine-mesh litterbags separately, with biome as a fixed factor and region as a random factor, and using an aggregated dataset (i.e., average values of five replicates per treatment). We used linear models (lm function) and a forward model selection procedure based on AIC (step function) on the aggregated dataset to assess the importance of four climatic variables (extracted from www.worldclim.org) (*48*) and four stream environmental variables measured in situ (table S2), which showed variance inflation factors ranging from 1.27 to 2.40. Last, we examined the influence of multiple litter traits (table S5) on the *LDED* using again linear models and a forward model selection procedure based on AIC.

SUPPLEMENTARY MATERIALS

Supplementary material for this article is available at http://advances.sciencemag.org/cgi/content/full/7/13/eabe7860/DC1

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Latitude dictates plant diversity effects on instream decomposition

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