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Traits or habitat? Disentangling predictors of leaf-litter decomposition in Amazonian soils and streams

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Abstract. Quantifying the relative contributions of plant physicochemical traits and environmental conditions to leaf decomposition is essential to increase our understanding of ecosystem processes in forested terrestrial and aquatic habitats. This is particularly crucial in tropical rainforests that display high levels of tree diversity and environmental heterogeneity over relatively small spatial scales. For example, in Amazonia, detritus from hundreds of tree species fuels carbon cycling in watersheds, but much remains to be learned about how species traits interact with environmental conditions to mediate decomposition. We investigated the leaf-litter decomposition of 17 tree species with contrasting traits in soil and stream habitats in Yasuní National Park, Ecuador. We hypothesized that (1) habitat type would be the major determinant of leaf decomposition (faster in stream than soil systems), (2) species would be ranked similarly in terms of leaf decomposition rates, according to decomposability traits (i.e., litter quality), within each habitat, and (3) the variability of leaf decomposition within habitats would be greater for soil than for stream systems. Contrary to our first hypothesis, we found that leaf-litter decomposition rates for any given tree species were similar in stream and soil systems. However, we found that the relative importance of litter traits for decomposition such as concentrations of micronutrients (Mn and Cu, in particular) was consistent across habitats. Finally, we found that decomposition was equally highly variable in both terrestrial and aquatic systems. This variability was explained by differences in microhabitat within soils, but appeared to be more stochastic in streams. Overall, we found that plant traits had an overwhelming effect on the decomposition process in the intertwined aquatic and terrestrial matrices of the Yasuní rainforest, with significant effects of microhabitat features. This study sheds light on the fate of the pool of dead organic matter in tropical rainforests and highlights the need for further studies of the mechanisms underlying microhabitat variability.

Key words: hyperdiverse ecosystem; litter decay; nutrient cycling; tropical rainforest; tropical soil; tropical stream.

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INTRODUCTION

More than 90% of the ~120 billion tons of organic carbon annually produced by terrestrial

plants return to soils as litter and constitute the major pool of fresh dead organic matter (OM; Cebrian 1999, Beer et al. 2010). This OM represents a central source of energy and nutrients for

heterotrophic communities in forested terrestrial and aquatic ecosystems (e.g., Chapin et al. 2002, Tank et al. 2010). Decomposition of plant litter is therefore a key belowground function in both environments (e.g., Gessner et al. 1999, Battin et al. 2009, García-Palacios et al. 2015), which transforms dead OM into inorganic nutrients in forested ecosystems (Millenium Ecosystem Assessment 2005, Cotrufo et al. 2015). Feedback between above- and belowground strata plays a crucial role in regulating community structure and the functioning of terrestrial and aquatic environments (Chapin et al. 2002, Bardgett and Wardle 2010).

Terrestrial decomposition of dead OM produces large amount of finer materials, soluble compounds, and nutrients that potentially enter into aquatic environments (e.g., Kutsch et al. 2009), which plays a key role in the transportation and redistribution of OM and nutrients across the landscape (Gessner et al. 1999, Wallace et al. 1999). Moreover, the inter- and intraspecific phenological variability of plants results in differences in both the quantity and quality of resources returned to soils (e.g., Hättenschwiler et al. 2008, Kattge et al. 2011, Cárdenas et al. 2014). Since individual plant species may have major effects on the components of the belowground biota, and, consequently, on the processes and functions they regulate (Wardle 2004, Cárdenas et al. 2015, García-Palacios et al. 2015), energy and nutrients fluxes, but also the factors regulating them (e.g., communities), may vary at (micro)habitat, and local and regional scales (e.g., Ritter et al. 2019). While terrestrial and aquatic systems are functionally linked in terms of energy transfers and nutrient cycle, the driver of OM decomposition has rarely been investigated simultaneously in these two environments (see review in Appendix S1).

The relative importance of key drivers of OM decomposition—the environment (e.g., temperature and humidity), plant traits (e.g., nutrients, lignin, and tannin concentrations), or the presence of particular micro- and macro-organisms—has long been a matter of debate for both terrestrial and aquatic ecologists (Gessner et al. 2010, Frouz et al. 2015).

This process is generally constrained by the same extrinsic factors (e.g., temperature, water availability, nutrients) in streams and soils (Graça

2001, Lecerf et al. 2005, Kaspari et al. 2008, Schindler and Gessner 2009, Graça et al. 2015), but these two types of habitats differ fundamentally in a number of ways, precluding generalization. The principal differences between these two types of habitat are (1) temperature range, which is buffered in streams; (2) water availability, which may be limited in terrestrial habitats; (3) oxygen levels, which may be limited in Amazonian headwater streams (especially when current is very low and/or litter is buried by sediment) but not in the superficial soil layer of terrestrial systems; (4) resource availability, which is more homogeneous in streams, as water flow favors nutrient dilution and food transportation, and more patchy in soils, with a distribution dependent on winds and rainfall, topography, the underlying parental rock, and nearby plants (e.g., John et al. 2007); (5) abrasion by water flow may increase stream litter breakdown rates (Hubai et al. 2017); and (6) the upstream-to-downstream transport of processed OM and nutrients, which may favor litter species decay in streams (e.g., Graça et al. 2015).

Leaf-litter traits, such as N, P, Mg, Mn, Ca, Cu, lignin, and tannin concentrations in particular, are intrinsic factors that have been shown to control leaf-litter decomposition in both environments (e.g., Coq et al. 2010, Capps et al. 2011, Cárdenas et al. 2015, García-Palacios et al. 2015, Monroy et al. 2016). These chemical and mechanical leaf traits influence feeding preferences and consumption rates (Pérez-Harguindeguy et al. 2000), but their relative importance remains unclear and the predictors of decomposition rates seem to be highly context-dependent (Handa et al. 2014, Boyero et al. 2016).

Leaves are the most important component of dead OM in Amazonian forests (Chave et al. 2010). Therefore, their decomposition is a central process to recycle nutrients in these forests. A study comparing leaf-litter decomposition in soils and streams is an ideal approach for exploring the trait vs. habitat hypothesis to better understand nutrient cycle in forested systems. We studied leaf-litter decomposition in both soil and stream habitats, using 17 tree species with a wide range of physicochemical traits (Cárdenas et al. 2015) and using a large number of replicates per species, in the highly diversified forest of the Yasuní National Park, Ecuador. In the

context of trait vs. habitat hypothesis, we expected (1) leaf-litter decomposition rates to be higher in streams than in soils due to favorable environmental conditions for this process (e.g., higher levels of leaching and of physical and biological breakdown), (2) more palatable species to decompose faster than recalcitrant ones but at higher rates in streams than in soil habitats, and (3) the variability of leaf decomposition within habitats would be greater for soil than for stream systems (e.g., due to higher resource homogeneity in streams).

METHODS

Study area

The Yasuní National Park (YNP) covers 1.6 million ha of forest, constituting the largest protected area in Amazonian Ecuador, which harbors one of the world's most diverse tropical forests (Bass et al. 2010, Pérez et al. 2014). In this area, there is no definite seasonal pattern of rainfall and temperature. Mean annual rainfall is about 3000 mm (Valencia et al. 2004). Mean air

temperature is $24.9^{\circ} \pm 3.9^{\circ}\text{C}$, and the mean relative humidity of the air is $88.4\% \pm 13.9\%$ (data obtained from the Yasuní Research Station [YRS] meteorological station). The YNP is an evergreen lowland rainforest located 200–300 m above sea level. Our study area was located in the vicinity of the YRS ($00^{\circ}40'16.7''$ S, $07^{\circ}24'1.8''$ W), within an area of $\sim 150,000$ m² of terra firme. This study area consisted of a multitude of slope-, upper-ridge-, and valley-type habitats (see Valencia et al. 2004 for a detailed description of these habitats). The area is drained by a dense network of small streams (0.4–4 m wide, 0–0.9 cm deep, with a flow rate of 0–2 m/s). In the 25-ha plot studied, Valencia et al. (2004) found more than 1100 morphospecies of trees (1.3 m dbh > 10 mm), with a mean of 655 (SD: 32) morphospecies/ha. Most tree species are angiosperms.

Properties of stream and soil environments

Various abiotic and biotic characteristics of the soil and stream environments are recorded in Table 1. While daily mean temperature was very similar in soils and streams (24.7°C in soil and

Table 1. Abiotic and biotic characteristics of soil and stream habitats of the surrounding area of the biological research station of the Catholic University of Ecuador in the Yasuní National Park.

Factors included in the analyses	Soil	Streams
Abiotic characteristics		
pH	4.6 (3.8–5.5) [†]	6.6 (6.2–6.9) [‡]
Temperature (°C)	24.7 (21.6–30.7) [§]	24.2 (23.1–26.1) [‡]
Flow rate (m/s)	–	0.4 (<0.1–0.7) [¶]
Humidity (%)	97.4 (73.2–100) [§]	100
Water depth (m)	– (<0.05) [#]	0.4 (0.2–0.6) [¶]
Width (m)	–	1.1 (0.6–3.2) [¶]
Dissolved oxygen (mg/L)	–	3.9 (2.1–5.6) [‡]
Biotic characteristics		
Invertebrate total richness (number of morphospecies)	339	73
Invertebrate community composition similarity (Sorensen index)	0.35 (0.1–0.56)	0.85 (0.58–1)
Invertebrate community abundances (ind/m ²)	86.5 (14–218)	4800 (1700–9360)
Invertebrate community biovolume (mm ³ /m ²)	115.8 (1.5–452.7)	32100.6 (4062.6–65710.7)
Detritivore community abundances (ind/m ²)	35.1 (3–142)	3625.3 (1500–6660)
Detritivore community biovolume (mm ³ /m ²)	51.9 (0.5–222.6)	27213.5 (2530.6–64628.4)
Detritivore biovolume per species (mm ³ /sp)	3.0 (0.01–73.9)	29.2 (0.05–766.1)
Detritivore abundances per species (ind·sp ⁻¹ ·mm ⁻²)	0.2 (0.03–2.8)	65.8 (0.7–1928.7)
Detritivore total biovolume per species (mm ³ ·sp ⁻¹ ·mm ⁻²)	0.3 (<0.01–7.0)	439.7 (0.03–23494.5)

Note: En dash indicates no measurements or data available.

[†] Values from Baldeck et al. (2013).

[‡] Values from the three streams studied and from five other comparable streams in the area (in August 2017, 6 dates and times for pH, 2 dates and times for O₂, and continuous temperature recording over 18 d).

[§] Values at the soil litter level (continuous recording for 18 d in August 2017).

[¶] Values from the three streams studied.

[#] After the temporal accumulation of rainwater due to local soil values from the three streams studied depressions.

^{||} Data from 30 Winkler and 30 Surber samples; B. Four and R. E. Cárdenas, unpublished data.

24.2°C at 23 ± 16.9 cm depth in streams), other physicochemical characteristics differed considerably between these two types of environment. For example, mean pH was found to be much lower in soils (4.4) than in streams (6.6). The concentration of oxygen in the air over leaf litter lying on the soil ensures that this is an oxic environment. By contrast, mean oxygen concentrations are low in streams (about 3.9 mg/L), and some of microhabitats are almost anoxic. The structure and composition of the invertebrate community also differs considerably between these two habitats. Indeed, in this area total invertebrate species richness is five times higher in soil than in stream environments (B. Four and R. E. Cárdenas, *unpublished data*). However, invertebrates are generally scattered in soil environments (i.e., small number of individuals \times m⁻²) in comparison with streams. In addition, the invertebrate communities of streams are dominated by generalist taxa, with the Chironomidae as the most abundant in terms of numbers (mean abundance of 1929 individuals \times m⁻²), and in the biovolume, they are mostly filled by rare (less than 30 individuals \times m⁻²) but large shrimps (*Macrobrachium* sp.).

Selection of leaf-litter species

We selected 17 angiosperm tree species common at our study site (Valencia et al. 2004, Cárdenas et al. 2015). The species chosen were not only common at this site, but were also selected to represent a wide range of taxa, covering 11 different families and nine orders (Appendix S2: Table S1). Finally, these species were also chosen for study because they encompassed a wide range of leaf-litter traits (Appendix S6: Table S1 for the complete data set for traits, taken from Cárdenas et al. 2015) previously shown to be correlated with decomposition (e.g., Coûteaux et al. 1995, Cornwell et al. 2008, García-Palacios et al. 2015).

Leaf-litter decay

In April 2011, freshly fallen senescent leaves were collected by shaking the trunk or individual branches from three to five individuals of subadult and adult trees of the 17 species studied. Falling leaves were intercepted in nets attached 1 m above the forest floor. Leaves that were too young (typically bright green in color), too old

(i.e., rotten or with a large necrotic area), or presenting obvious fungal infection, insect galleries, galls, or >60% damage were discarded. The leaves retained were dried by heating at 40°C for up to 72 h and weighed. The leaves were then mixed, wetted with rainwater, and placed in litterbags, which were folded up and sewn closed. The upper surface of the litterbags had 900-mm² holes, to allow micro- to megafauna access to their contents. By contrast, the lower surface of the litterbags consisted of a mesh with holes of 100 mm², to limit the gravimetric loss of litter material while allowing the micro- to macrofauna to enter the bags as well (Cárdenas et al. 2017). Each litterbag was filled with two to seven leaves (petioles removed) of the same species, depending on leaf size. Each bag contained 2.78 ± 1.25 g (mean \pm SD) of leaf-litter material depending on tree species and respective leaf size. We set up 1020 litterbags, for comparisons within and between environments (17 species \times 2 treatments: soil and stream environments \times 30 replicates; see Appendix S3: Fig. S1 for an overview of the experimental design used). In the soil environments, the litterbags were assigned to 85 batches (3 replicates \times 2 of the 17 species chosen at random; Hurlbert 1984). They were placed directly on the soil surface, in the same area in which the leaves were collected. In this environment, the distance between batches was about 5 m (on a 17 \times 5 grid; Cárdenas et al. 2015). For studies of decomposition in streams, we chose three representative second-order clear water streams (i.e., 1.3–2.9 m wide and 0.2–0.6 m deep; Table 1). Streams were located within the study area and distant from about 300 m. In this habitat, random blocks of three, six, or nine litterbags (3 replicates \times 1, 2, or 3 of the 17 species; Hurlbert 1984) were attached to 1-m, 2-m, or 3-m polyvinyl chloride (PVC) plastic tubes, respectively. This set-up resulted in 78 batches of litterbags, which were submerged under water and fixed to the bottom of the stream. After 100 d of exposure in the field, all litterbags were collected carefully using a net in streams and wrapped in plastic bags to prevent any loss of material or invertebrates during transportation to the laboratory for analyses. During the field experiment, water flow was low with little sedimentation. However, a couple of litterbags (16 bags) were found out of the water

and were removed from the analysis. In the laboratory, the leaves were gently cleaned to remove adhering debris and invertebrates, dried at 40°C for up to 96 h, and weighed.

Invertebrates from 10 randomly chosen litterbags from each environment and litter species were sorted and analyzed (i.e., invertebrates from ~340 litterbags). They were counted and identified as far as possible with the aid of specialist literature (see Appendix S8: Table S1 for a complete list of all specimens identified). For community comparisons, stream and soil invertebrates were classified by functional feeding group (see Merritt and Cummins 1996, Domínguez and Fernández 2009 for stream invertebrate classification; Cárdenas et al. 2017 for soil invertebrate classification).

Data analyses

Trait vs. environment hypothesis.—We performed nested ANOVA to determine whether site significantly affected litter decomposition in each environment. We also used coefficients of variation to compare the intraspecific variability of leaf-litter decomposition between the two environments (Feltz and Miller 1996). We then compared leaf-litter decomposition between the two environments, by linear regression analysis of the relationships of the 17 leaf-litter decomposition values (aquatic vs. terrestrial). The slope of the regression line obtained was then compared to the theoretical line of the 1:1 relationship along which decomposition rates are identical, by analysis of covariance (ANCOVA). We then searched for litter species-specific patterns of decomposition (i.e., differences in decomposition rates) between environments, by calculating the effect size (ES; log ratio of means; Hedges et al. 1999) for the 17 leaf-litter species. This analysis made it possible to measure and compare litter decomposition between species. Effect sizes were calculated as the ratio of mean decomposition values (and the associated standard deviation) between streams and soil (Hedges et al. 1999).

General drivers of litter decomposition in soil and stream environments.—For the determination and comparison of complex and causal relationships between litter traits, the structure of invertebrate communities, and litter decomposition in the two

environments, we used structural equation modeling (SEM; Sanchez 2013) with the partial least squares (PLS) method. Structural equation modeling is a suitable analytical procedure for disentangling the links between predictors and responses in multivariate data sets through a combination of regression techniques, path analysis, and confirmatory factor analysis based on theoretical models (Grace 2006, Sanchez 2013). Partial least squares methods were used here because they are known to be suitable for exploration purposes and robust with small samples (Chin and Newsted 1999). Because we aimed at identifying the general drivers of litter decay in both habitats and did not have litter trait measurements and the invertebrate communities associated with each litterbag, we chose to work with the mean values for each treatment. We decreased the number of dimensions of the litter trait data set and the invertebrate data set, to make them suitable for SEM, by following the procedure described by García-Palacios et al. (2015). We used principal component analysis (PCA) to extract a smaller number of variables (based on the multivariate axes generated from litter traits and the invertebrate communities found in the litterbags, capturing as much of the variance of the different data sets as possible and reducing redundancy for correlated factors). Before conducting the PCA, we separated the measured litter trait and invertebrate community data into five and two matrices, respectively (see Appendix S7 for a detailed explanation of the categories and PCA methods and results), corresponding to the major litter traits and invertebrate categories known to exert strong direct and indirect control over litter decomposition. We retained only the first axis of each PCA, as this axis explained more than 40% of the total inertia and had eigenvalues greater than 1.5 for normalized litter trait matrices and 0.5 for invertebrate variance-covariance matrices (Appendix S7), to represent the five litter trait categories and the two invertebrate categories in the SEM constructed for litter decomposition. The same a priori SEM path model was proposed for both soil and stream environments (Appendix S4: Fig. S1), according to the hypothetical relationships between predictors (litter traits and invertebrates) and the response (litter decomposition), consistent with the factors studied and current

understanding of the litter decomposition process (see review results in Appendix S1). This made a causal interpretation of the model outputs possible (Grace 2006, Sanchez 2013). As litter traits may have a direct (e.g., physical decomposition of the litter, leaching) or indirect (e.g., modulating consumption by detritivores) effect, they were evaluated with both direct and indirect relationships. The same approach was adopted for predators, which can have direct and indirect top-down effects on litter decomposition (due to their simple presence or their consumption of other invertebrates; Jabiol et al. 2014, Cárdenas et al. 2017). The total effect was then calculated by adding together the direct and indirect effects (see Grace 2006). We progressively removed all non-significant factors with coefficients below 0.1 from the final models, to obtain more parsimonious models increasing their degrees of freedom.

We ensured the unidimensionality of the models by validating both Cronbach's alpha and Dillon-Goldstein's rho values (which must be higher than 0.7) from the latent variable constructs (litter trait and invertebrate categories; Sanchez 2013). We also assessed the quality of the structural model by evaluating the goodness of fit of the model and the r^2 values of the endogenous variables underlying the variation explained by the latent variables.

Finally, as SEMs are dependent on the structure imposed by the modelers (Grace 2006), our models are valid only for the types of relationships we introduced. We cannot exclude the possibility of other types of relationships linked to environmental conditions, and/or the modulating effects of microbial decomposers on the litter decomposition process.

ANOVA, ANCOVA, and PCA were performed using Past software v. 3.04 (Hammer et al. 2001) and PLS-SEM was performed with R software v3.4.1 (R Core Team 2016), with the *plspm* R package (Sanchez 2013).

RESULTS

Leaf-litter species-dependent decomposition rate

Substantial and significant differences in leaf-litter decomposition were observed among species in both habitats (see litter decay results in Table 2; Appendix S2). Mean leaf-litter decay

rate ranged from 25.6% to 88.8% of initial dry mass in streams or from 29.4% to 91.1% of initial dry mass in soils, and the ordination between species was similar in both habitats (Figs. 1, 2). These results underlined species-specific litter decomposition regardless of the environment.

Differences in leaf-litter decomposition between environments

Graphical analyses of the regression between decay in soil and stream habitats for all litter species revealed that all species were significantly near to the theoretical 1:1 line, indicating an overall similar decomposition rate in these two types of environment (Fig. 1, Table 2). However, ANCOVA on soil/stream vs. 1:1 showed that if the whole leaf-litter community decomposed similarly across environments (equal mean test: $F = 1.43$, sum of squares = 42.3, $df = 1$, $P = 0.24$), some species had different rates of decomposition between soil and streams (significant homogeneity of slopes test result for comparison with the 1:1 line: $F = 5.35$, $P = 0.03$). Accordingly, the effect sizes calculated between the two environments were significant and negative for *Neea* "comun," *Inga capitata*, *Mabea* "superbrundu," and *Leonia glycyarpa*, indicating faster decomposition in soil for these species, and they were significant and positive for *Pseudolmedia laevis*, *Miconia* "purpono," *Siparuna cuspidata*,

Table 2. Multiple nested ANOVA results for the leaf-litter decay of the 17 litter species in streams and soil habitats, showing leaf-litter species, site, and/or stream effects.

Variable	numDF	denDF	F-value	P-value
Stream habitat				
Litter decay				
Litter species/stream	16	435	38.92	<0.001
Litter species/block	16	360	38.62	<0.001
Site effect				
Stream/litter species	2	435	0.96	0.39
Block/litter species	77	360	0.95	0.60
Soil habitat				
Litter decay				
Litter species/block	16	404	57.18	<0.001
Site effect				
Block/Litter species	83	404	2.96	<0.001

Notes: Abbreviations are numDF, degrees of freedom of the numerator; denDF, degrees of freedom of the denominator. In italics, significant results with $P < 0.05$.

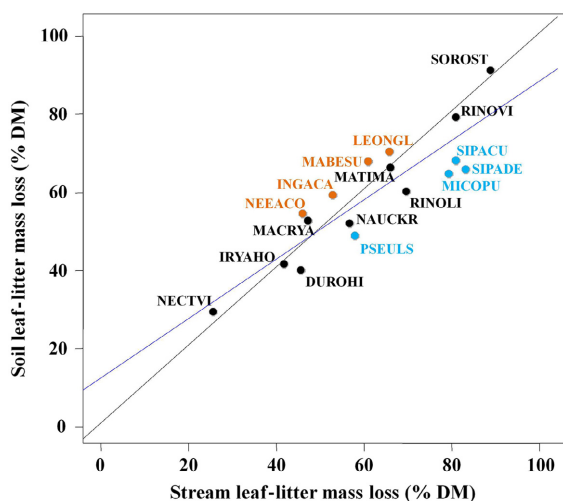


Fig. 1. Leaf-litter mass loss in the soil as a function of leaf-litter mass loss in streams ($n = 24\text{--}30$; dots represent the mean mass loss for the species: Black dots indicate similar mass losses in soils and streams, blue dots indicate significantly greater mass loss in streams, and brown dots indicate significantly greater mass loss in soil habitats; see Appendix S5: Fig. S1 for effect size results). The black diagonal line represents the 1:1 relationship. The blue line represents the linear regression between aquatic and soil leaf-litter mass losses ($r = 0.88$, $P < 0.001$, $y = 0.7517x + 13.128$). DM = dry mass. Please see Appendix S2 for code/leaf-litter species correspondences.

and *Siparuna decipiens* indicating faster decomposition in streams for them (Fig. 1; Appendix S4). The other nine species considered decayed at similar rates in both environments (i.e., no significant effects were found).

Differences in leaf-litter decomposition within environments

Nested ANOVA on leaf-litter decay revealed a significant effect of soil site (block effect: $F = 2.96$, $P < 0.001$) but not of stream site (block/stream effect: $F < 0.96$, $P > 0.39$; Table 2). However, the coefficient of variation showed that leaf-litter decay variability was greater in streams than in soils, for 10 species (Fig. 2). Leaf-litter decay variability was never significantly greater in soils than in streams, for any of the species considered (Fig. 2). There was thus greater between-litter mesh bag but not site/stream-dependent variability in stream environments.

Relative drivers of leaf-litter decay across environments

Both final PLS path models constructed separately for each ecosystem type with the mean data for the 17 leaf-litter species fitted well (0.94 and 0.89 for the stream and soil model, respectively; Fig. 3). They explained about 95% of the variance of leaf-litter decay in streams and about 89% of that in the soil (Fig. 3). Overall, in both ecosystems, litter micronutrient concentrations (mostly a positive effect of Mn and a negative effect of Cu; Appendix S7) accounted for considerable variation in leaf-litter decay rates (the direct path for the stream environment was almost significant, coefficient = 0.33 with $P = 0.08$, and that for the stream environment was significant, coefficient = 0.75 with $P < 0.01$). If direct and indirect effects were considered, this coefficient rose to 0.85 for the stream environment. In streams, litter transformers (LTs; mostly positively associated with the abundance and biovolume of shredders + scrapers + gatherers) and predators (mostly positively associated with the abundance and biovolume of predators) were also associated with leaf-litter decay (path coefficients of 0.62 with $P < 0.01$ for LTs and -0.33 with $P < 0.01$ for predators, respectively). In stream environments, correlation coefficients greater than 0.1 but not significant were also obtained for the relationships between litter decay and macronutrients (mostly positively associated with N, Mg, and Ca concentrations; direct path coefficient = 0.15 and $P = 0.16$, but with a total effect rising to 0.24 when the indirect effect was taken into account). By contrast, invertebrate communities and macronutrients were removed from the final model for soil environments because they explained leaf-litter decay poorly (path coefficients for the primary models less than 0.1 and non-significant). However, weak correlations were found between litter decay and C-quality, physical factors, and stoichiometry in the soil environment (path coefficients >0.17 and $0.18 < P < 0.40$).

DISCUSSION

To our knowledge, this is the first in-depth investigation of the relative contributions of leaf-litter traits and environmental factors to OM decomposition in a megadiverse tropical

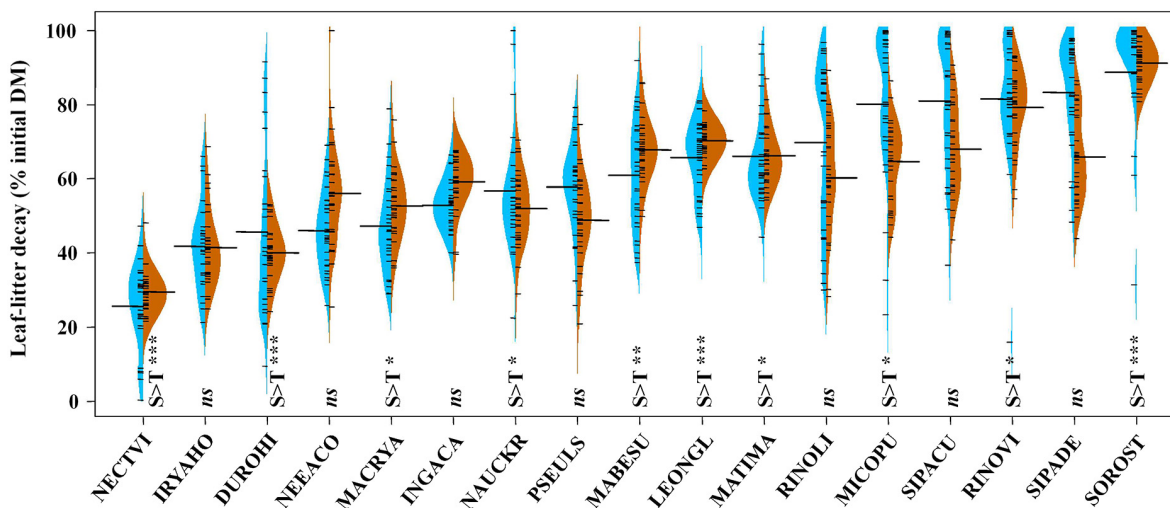


Fig. 2. Beanplots showing the variability of leaf-litter decomposition for 17 tree species, in streams (blue) and soil (brown). The significance in multiple variance coefficient tests of differences between streams and soil data is shown for each tree species. S = Coefficient of variation for streams; T = coefficient of variation for soils; test significance: *** $P < 0.001$, ** $0.001 < P < 0.01$, * $0.01 < P < 0.05$, ns, non-significant; broad horizontal black lines correspond to mean leaf-litter decomposition; narrow horizontal black lines correspond to the experimental values ($n = 24-30$).

rainforest and its relationship to the heterogeneity and particularities of soil and stream habitats (with a large number of replicates). Our study revealed that leaf-litter decomposition rates in 17 tree species were similar between streams and soils and highly influenced by litter traits. Also, we found that decomposition was highly variable in both terrestrial and aquatic systems. This work is hence complementary to the handful of published studies comparing aquatic and terrestrial litter decomposition and/or their drivers in the tropical biome using only a few litter species and/or replicates (e.g., Ribas et al. 2006, Capps et al. 2011, Nakajima et al. 2011).

Leaf-litter decomposition in soil and stream habitats: leaf micronutrients as key drivers

Litter breakdown rates varied widely across species, but their ranking was similar in both habitats. This highlights fundamental intrinsic differences in the decomposability of species regardless of environmental conditions. The high variability in leaf decomposability among species has been commonly observed in a wide range of ecosystems and is often associated with leaf-litter traits (Cornwell et al. 2008, Cárdenas et al. 2015, García-Palacios et al. 2015). In our study, several

litter traits differed largely (up to 140 fold) and significantly among species. In streams and soils, litter decomposition was strongly influenced by micronutrient concentrations (mainly through a positive effect of Mn and a negative effect of Cu). Mn is directly involved in lignin degradation as an essential cofactor of Mn-peroxidase, a lignin-degrading enzyme produced by fungi (e.g., Pérez and Jeffries 1992). Several studies showed that Mn concentrations could favor microbial activities and ultimately litter decomposition (Berg et al. 2007, Keiluweit et al. 2015). By contrast, Cu is known to affect negatively both microbial and invertebrate communities. Cu can limit fungi growth and decomposition activity by inducing an oxidative stress (Azevedo et al. 2007, Duarte et al. 2008, Roussel et al. 2008). As (micro)nutrient availability is low in the Yasuní rainforest (Valencia et al. 2004, John et al. 2007), we assume that the different levels of essential micronutrients in leaf litter may directly stimulate or reduce the biological activity of decomposers and therefore regulate litter breakdown.

Other traits (e.g., N, P, lignin, tannins) are well-known to influence OM decomposition process in both stream and terrestrial habitats (e.g., Cornwell et al. 2008, Capps et al. 2011, Reich 2014,

Cárdenas et al. 2015, 2017, García-Palacios et al. 2015), but surprisingly, they showed either weak or non-significant correlations with measured breakdown rates in both habitats. Yet, we found that eight of the seventeen species had substantial and significant different decomposition rates between both habitats suggesting others and different drivers of litter decay between these two habitats. These results may reflect some limitations of our method for identifying traits involved in litter decomposition. Indeed, while PCA and SEM can identify and compare the relative effects of different factors driving decomposition, we cannot exclude that other traits taken individually may also partially explain litter decomposition rates.

Biological communities associated with decomposition in streams and soil habitats

Even though micronutrients were identified as crucial traits driving decomposition in both habitats, they act concurrently with detritivores. Indeed, SEM revealed that the best correlation between micronutrient concentrations and litter decomposition in streams was reached through an indirect pathway considering detritivore densities. This suggests that, under the oligotrophic conditions of the western Amazon (Graça et al. 2018), detritivores may prefer colonizing leaf litters rich in micronutrients, with higher nutritional values (Graça 2001, Tank et al. 2010, Danger et al. 2013) and higher palatability through increased microbial colonization (Lecerf et al. 2005, Graça et al. 2015).

By contrast, in soil, detritivore densities were correlated neither with litter breakdown rates nor with micronutrient content. Also, in this habitat, detritivores showed much lower abundance and biomass than in streams (Table 1). This suggests that, at this stage of litter decomposition, soil detritivore communities are not very sensitive to litter quality and/or they have a more limited role in litter mass loss than in streams. Indeed, other litter decomposition studies conducted in this area showed that litterbag mesh sizes (fine and coarse mesh bags) did not affect litter decomposition in terra firme (Capps et al. 2011, Cárdenas et al. 2017) underlining the overall minor role of detritivore macrofauna for soil leaf-litter decomposition. However, our field observations moderate this statement at local

scale as we found that the presence of social detritivores (e.g., termites or ants) can locally substantially modify OM decomposition (e.g., Ryder-Wilkie et al. 2010, Dangles et al. 2012). Moreover, the strong correlation between litter micronutrients and litter decomposition in the soil habitat suggests that other communities, probably bacteria and fungi, were crucial for decomposition and that the decomposition activities of these communities were dependent on micronutrient concentrations (positive effect of Mn and negative effect of Cu) according to the mechanisms explained above.

Environmental variables modulate decomposition process in tropical rainforest streams and soil

Studies comparing litter breakdown in aquatic and terrestrial habitats have generally reported lower rates of OM decay in soils in ecosystems across various biomes (e.g., Couëteux et al. 1995, Delon et al. 2015, García-Palacios et al. 2015, Boyero et al. 2016; Appendix S1). Our results from a tropical rainforest disagree with this view. The reasons for this may lie in the characteristics of each environment in this type of biome (Gessner et al. 2010, García-Palacios et al. 2015). For example, the constantly high temperatures and humidity measured at the surface of equatorial rainforest soils may favor microbial decomposition (Gessner et al. 2010, Lee et al. 2014, Delon et al. 2015, Tonin et al. 2017) when compared to colder and drier soils outside the equator. By contrast, in tropical lowland first-order streams of the study area, litter decomposition rates may be decreased by slow water flow (due to the topography of the area; Table 1) limiting physical breakdown and, through low oxygen concentrations, also limiting the biological process of microbial breakdown (Wagener et al. 1998, Grimm et al. 2003).

Interestingly, we also detected a significant block effect in decomposition rates in soils, suggesting that this process strongly depends upon micro-environmental conditions. Given the patchy nature of the tropical forest (e.g., canopy gaps, above- and belowground micro-scale nutrient availabilities, local-scale litter substrate variability, soil moisture variability), there may be “hotspot” microhabitats in which leaf-litter decomposition is enhanced (McClain et al. 2003, Capps et al. 2014). By contrast, litter decomposition

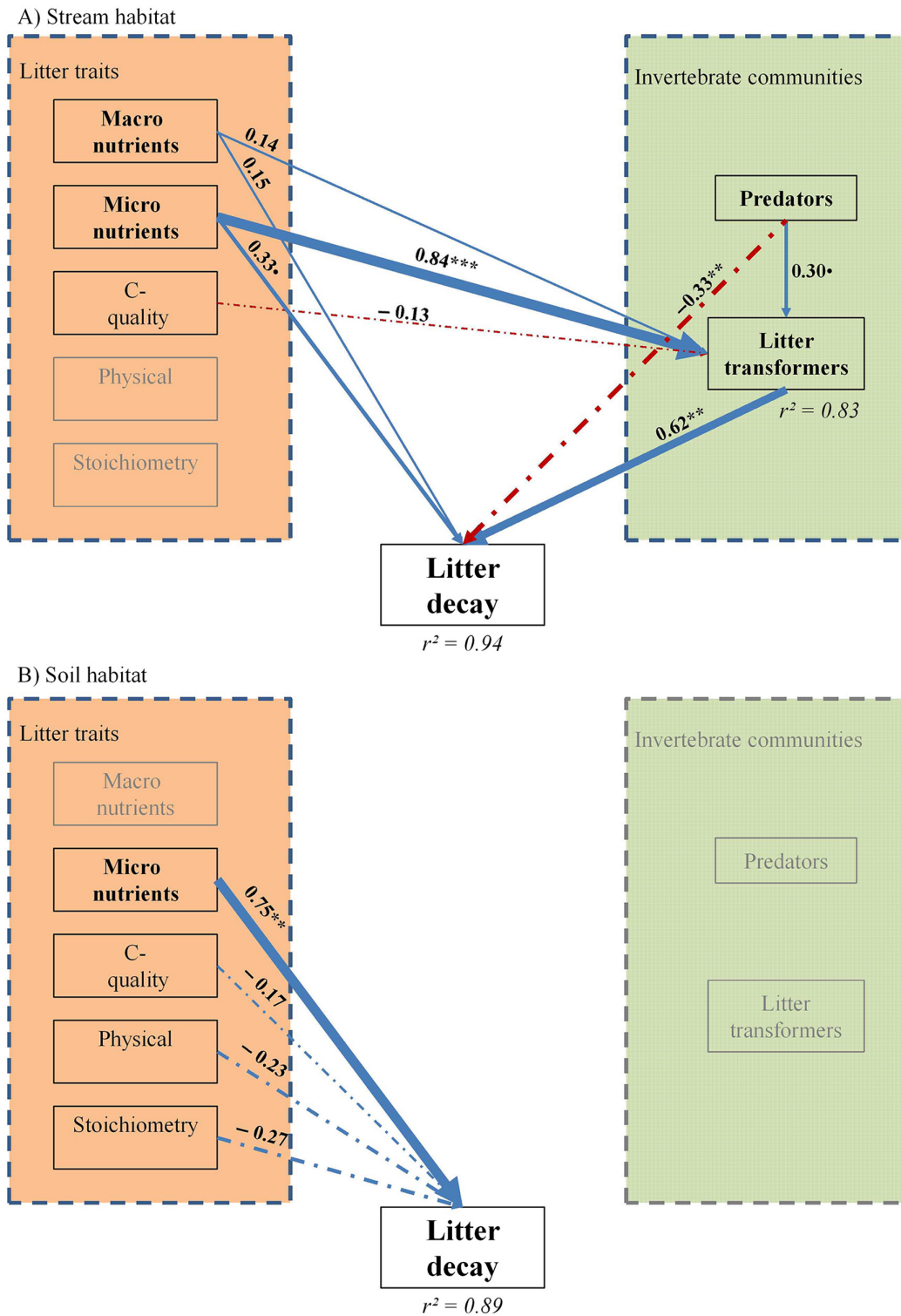


Fig. 3. Partial least squares path models describing the influence of litter traits and fauna communities on litter decay for stream (A) and soil (B) habitats, respectively. Continuous (blue) and dashed (red) arrows represent

(Fig. 3. *Continued*)

positive and negative relationships, respectively. The widths of the arrows are proportional to the size of the path coefficients. Variables significantly influencing litter decay are shown in bold; non-significant variables with path coefficient values greater than 0.10 are indicated in black non-bold font; non-significant variables with path coefficients lower than 0.10 (which were removed from the final model) are shown in gray (without arrow). *** $P < 0.001$, ** $P < 0.01$, * $P < 0.05$, • $0.05 < P < 0.1$. The litter traits and invertebrate community data used in the models were extracted from component 1 of the PCA in Appendix S4, which was positively related to the following variables. Macronutrients: N, Mg, and K; micronutrients: Cu (negative effect) and Mn (positive effect); C-quality: lignin, tannins, and C; Physical: thickness (negative) and SLA; stoichiometry: tannin/N; stream predators: abundance and biovolume of predators and of stream litter transformers (sum of shredders/gatherers/scrapers). Goodness-of-fit values of 0.94 and 0.89 were obtained for the stream and soil models, respectively.

in streams showed no significant block effect and a greater intraspecific variability than in soil (see coefficient variation results). These two results highlight the importance of the variation of litter breakdown rates at the micro-scale (i.e., between two litterbags of the same species in the same block) in streams. This is consistent with the micro-scale patchiness of streams reported in other studies in which streams were described as spatiotemporal mosaics of environments and processes due to various factors, such as local oxygen availabilities, local flow rates and local invertebrate densities, and/or community structures (e.g., Pringle et al. 1988, Townsend and Hildrew 1994, Palmer and Poff 1997, Boyero et al. 2015). Based on the particular features of the aquatic invertebrate community in these streams, that is, the lower densities of large shrimps, we assume this taxon could represent a stochastic factor explaining the intraspecific variability of litter decomposition. Indeed, given to their feeding habits (omnivores) and their nutritional requirements, we may assume that these large but rare invertebrates could mediate high levels of litter breakdown in some litterbags, based on their energy needs (when acting as detritivores), and at the same time, they can also cause low levels of litter breakdown due to top-down effects mediated by predator-prey relations (when acting as predators; Peters 1983, Covich et al. 1999).

CONCLUSION

This study provides evidence of a similar decomposition rate of tree leaf litter between soil and stream habitats in a megadiverse forest. Our results also underlined a predominant effect of micronutrient leaf-litter traits (including Mn and

Cu concentrations in particular), in driving decomposition in both soil and stream environments. The intraspecific variation of litter decomposition seemed to be linked to environmental heterogeneity in soils, but more to stochastic factors (such as macroinvertebrate community structure) in streams. Detritivore invertebrates seemed to be sensitive to litter quality, improving decomposition in streams, but with weaker effects in the soil. Future studies, investigating the relative effects of plant litter trait diversity and environmental heterogeneity on decomposer community structures and functions in particular, will be crucial to improve our understanding of diversity-ecosystem functions in these megadiverse forests.

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