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RESEARCH PAPER

Litter decomposition of exotic and native plant species of agricultural importance in Amazonian streams

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Abstract
The conversion of riparian vegetation into monocultures alters the input of allochthonous energy and the heterotrophy of streams. Here, we aimed to assess the implication of leaf litter inputs from plant species of agricultural importance on decomposition in Amazonian streams. We hypothesized that decomposition is low in litter with high concentrations of lignin and cellulose, regardless of the origin of plant species (exotic or native). We incubated leaf litter from plant species of agricultural importance, such as cocoa (native) and oil palm (exotic), as a control, leaf litter of *Hymenaea courbaril* (native) in four streams for 60 days. Contrary to our initial expectations, the leaf litter from oil palm, which was of higher quality and had lower concentrations of structuring compounds (lignin and cellulose), did not differ in decomposition rates from the lower quality leaf litter of the control species, which presented higher concentrations of structuring compounds. We recorded higher decomposition rate in cocoa, which had intermediate concentrations of structural compounds. Our results indicate a negative effect of the conversion of riparian vegetation into oil palm monocultures (*Elaeis guineensis*) for the processing of organic matter in Amazonian streams, due to the slower decomposition rate of the leaf litter of this species.

Keywords Litter quality · Oil palm · Cocoa · Litter processing · Amazon

Introduction

Agriculture is one of the human activities that most threaten freshwater ecosystems worldwide, causing biodiversity loss and impacts on ecosystem processes (Carpenter et al. 2011). Removal of riparian vegetation is an agricultural practice that also involves deforestation and plantations of exotic species. This can alter the spatial and temporal distribution of organic matter entering into streams, changing the quality and quantity of suitable inputs for ecosystem functioning (Graça et al. 2002; Leite-Rossi and Trivinho-Strixino 2012; Boyero et al. 2012, 2014).

Leaf litter from riparian vegetation is the main energy resource that enters into the stream (Wallace et al. 1997; Tank et al. 2010; Benfield et al. 2017). When leaf litter enters the stream, decomposition begins as a process usually driven by aquatic microbial communities (bacteria and fungi) and shredder invertebrates (Gonçalves et al. 2013; Graça et al. 2015). Nevertheless, shredders are generally scarce in tropical streams, and microbial decomposition becomes predominant on leaf litter (Rezende et al. 2015, 2018; Boyero et al. 2017). Bacterial communities act in the early stages of decomposition because of their high capacity to degrade soluble compounds, such as carbohydrates and phenols (Gonçalves et al. 2006; Alvim et al. 2015a). On the other hand, aquatic hyphomycetes contribute to the final decomposition stages by degrading structural compounds, such as lignin and cellulose (Graça et al. 2015, 2016).

The quality of leaf litter is a controlling factor of decomposition due to its direct effects on decomposers

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(Tank et al. 2010). Leaf litter quality can be defined as a set of physical and chemical characteristics that give nutritive and energetic value to microorganisms and invertebrates, leading to enhanced decomposition (Ardón and Pringle 2008; Wantzen et al. 2008). In tropical streams, leaf litter with higher concentrations of nutrients (e.g., nitrogen and phosphorus) and labile compounds tend to decompose more rapidly compared to leaf litter with higher concentrations of structural compounds, such as lignin and cellulose (Rezende et al. 2014; Gonçalves et al. 2017; Kiffer et al. 2018).

In the Amazon region, the exotic African species *Elaies guineensis* Jacq. (oil palm tree) and the native Amazonian species *Theobroma cacao* L. (cacao tree) are ostensibly cultivated, and the state of Pará is among the largest producers of palm oil and cocoa beans in Brazil (Fapespa 2017; Benami et al. 2018; Montag et al. 2021). Only in 2014, were planted in Pará state 256,000 ha of the oil palm tree, and it is estimated that ~ 30 million ha are suitable for cultivation in this region (Brandão and Schoneveld 2015). Also, the Pará state currently has a total area of 175,000 ha of cocoa cultivation (Melo et al. 2017).

Oil palm plantations often provide smaller quantity, less diverse and lower quality leaf litter and in consequence, result in slower decomposition (Chellaiah and Yule 2018). In lowland humid Ghana, forests recently converted to cocoa crops (3 years old) have a reduction in the supply of organic matter and slowed decomposition compared to secondary forests (Dawoe et al. 2010). Some studies have shown that oil palm monocultures negatively affect the diversity and taxonomic composition of aquatic insects in the Amazon streams (Cunha and Juen 2017; Paiva et al. 2017; Mendes et al. 2019), but no study has evaluated how palm oil leaf litter decomposes in Amazonian streams. Besides, one study performed in the Indian subcontinent evaluated colonization by aquatic hyphomycetes and cocoa leaves decomposition. In this study, cocoa leaves were rapidly colonized by aquatic hyphomycetes and decomposed rapidly compared to other crop leaf litter, such as coffee and cashew (Sridhar et al. 1992).

Considering the expansion of cultivation of *E. guineensis* and *T. cacao* in the Amazon region (Fapespa 2017; Benami et al. 2018; Montag et al. 2021), and due to the lack of information on the decomposition of leaf litter from both species in Amazonian streams, we aimed to evaluate the decomposition of leaf litter from exotic and native plant species used in economic exploitation in Amazon. We hypothesized that litter with high lignin and cellulose concentrations have reduced decomposition, due to a higher concentration of refractory compounds which decompose slowly, regardless of plant species origin (exotic or native species).

Material and methods

Study area

The study was conducted in streams inserted in forest remnants with predominant dense ombrophile forest. We conducted the experiments in forested streams to simulate possible ecological implications of the input of agricultural plant species on the leaf litter decomposition. We selected four streams in two micro basins of the Acará river drainage network, two streams in each micro basin, located in the municipality of Tailândia, northeast Pará State (Fig. 1). We used a hierarchical design to control for possible spatial autocorrelation effects on leaf litter decomposition. The region's climate is classified as tropical humid (Af), according to the Köopen-Geiger classification (Peel et al. 2007), with an average annual temperature of 26 °C, relative air humidity around 85% and an average annual rainfall of 2344 mm. The streams had an average of water temperature of 25.5 °C (± 0.5, standard deviation), pH of 4.9 (± 0.4), electrical conductivity of 0.16 μS/cm (± 0.002), and dissolved oxygen of 6.8 mg/L (± 2.8). The average stream width was 2.9 m (± 0.5) and depth was 38.2 cm (± 11.5).

Sampling design

The decomposition experiment was conducted from September to November 2018 (60 days), during the dry season. We evaluated the leaf litter of two native species (*Hymenaea courbaril* and *Theobroma cacao*) and one exotic species (*Elaeis guineensis*). Both *T. cacao* and *E. guineensis* are of agricultural importance, while *H. courbaril* (Control) is found widely distributed in both dryland forests and riparian vegetation (Leite 2001, 2007). We collected senescent leaves of all species that recently fallen to the ground. Due to their high humidity, they were all dried for 72 h at 60 °C.

We used litter bags (26 × 16 cm) with coarse (10 mm) and fine (0.5 mm) mesh sizes. We selected four stream segments from first to third order (Strahler 1957), located at two micro basins, and in each segment, we selected three pool sites of similar physical conditions (see Fig. 2). The distance between pools was approximately 40 m and, in each one, one litter bags of each mesh size (coarse and fine) were incubated for each plant species studied. Thus, 24 litter bags containing 4.00 ± 0.05 g were installed for each species, totalling 72 litter bags. At the occasion of installation (incubation), the following physical–chemical parameters of the water were measured in each pool: pH, conductivity, width, depth, temperature, dissolved oxygen (Horiba model U-50, Japan) (see Supplementary material—Table S1).

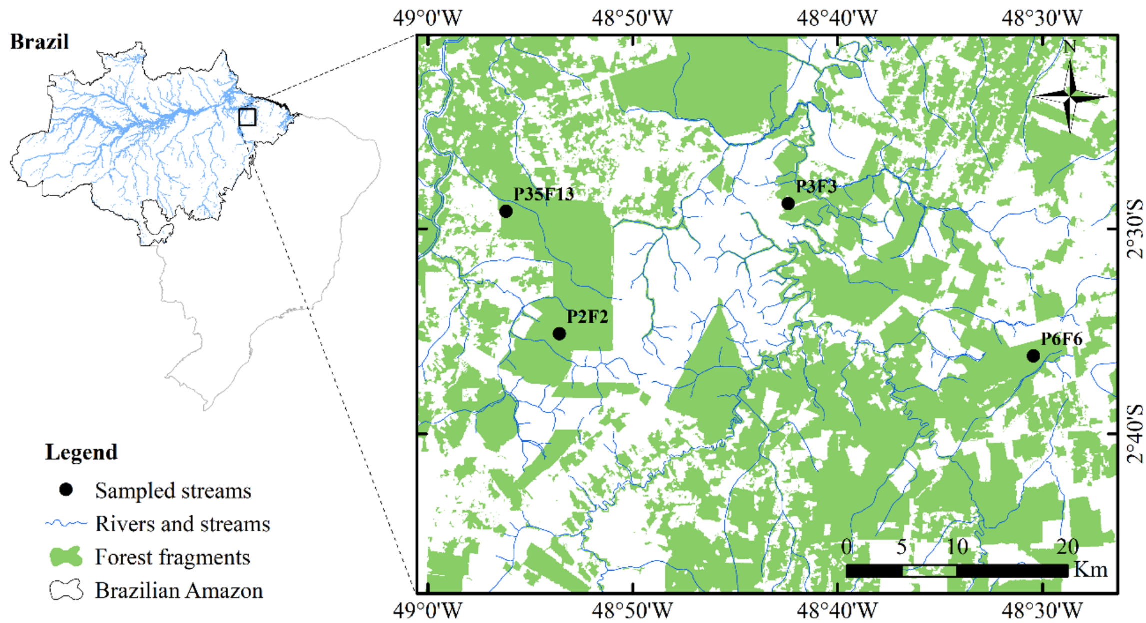

Fig. 1 Streams sampled in protected areas in the Acará river basin, municipality of Tailândia, Pará, Brazil

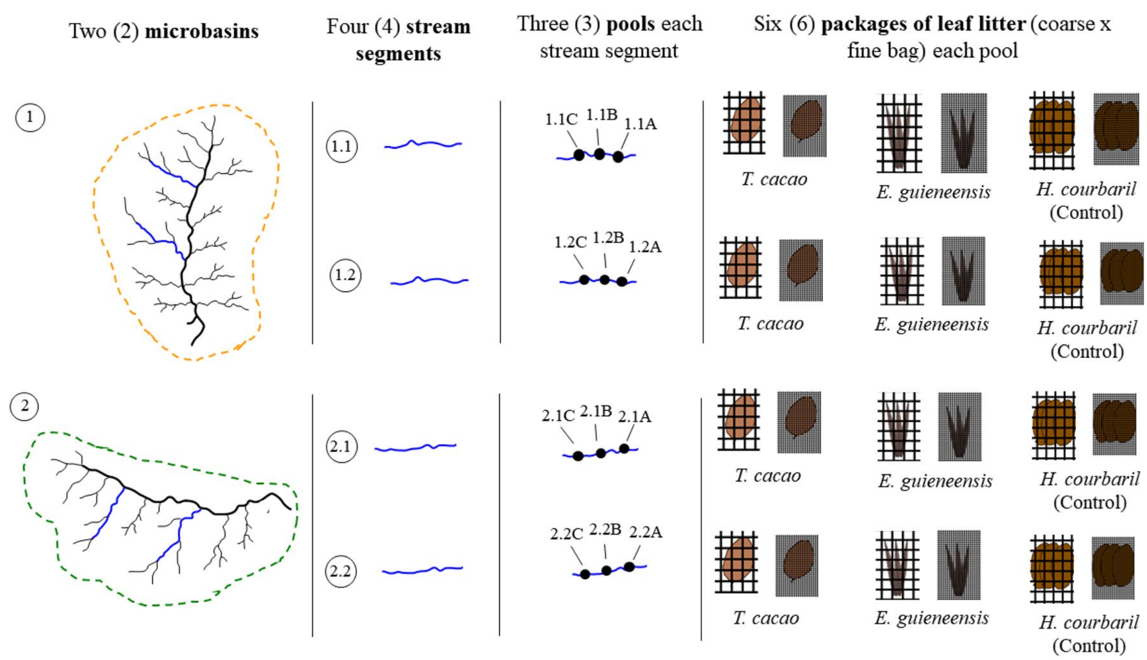

Fig. 2 Experimental design representing the three spatial levels considered: micro basins, streams segments and pools

After 60 days of incubation, litter bags were retrieved from the streams. In the laboratory, leaf litter were cleaned with running water using a 0.045 mm mesh sieve. The invertebrates retained in the sieve were preserved in 90% ethyl alcohol and identified at the lowest possible taxonomic level, according to the taxonomic key for the Amazonian region (Hamada et al. 2014). Later, invertebrates were classified into five functional trophic groups (filters, collectors, shredders, predators, and scrapers) according to specific literature for tropical environments (e.g., Cummins et al. 2005; Hamada et al. 2014) (see Table S2). We tested difference of abundance between leaf species only of the shredders and scrapers functional feeding groups, as they act more directly in litter decomposition (Gonçalves et al. 2017). However, we used the entire aquatic invertebrate assemblage to verify the colonization of decomposing leaf litter. The remaining leaf litter was dried for 72 h at 60 °C and weighed.

We estimated litter decomposition for each plant species (k day^{-1}) using the negative exponential model, where mass was expressed in grams and time in days (e.g., Petersen and Cummins 1974), considering the following equation: $k = -$ (ln [final mass/initial mass]/time). The rates of total and microbial decomposition (k total and k microbial) were determined from the coarse and fine mesh size bags, respectively. The contribution of invertebrates to the decomposition of leaf litter was estimated by the difference between the remaining mass in fine mesh and coarse mesh bags for each leaf litter type and then a new value of k was calculated (k invertebrates; Tonin et al. 2018).

Chemical analysis of leaf litter

To determine lignin and cellulose concentrations, leaf litter samples from each species were blade milled and then in a ball mill until obtaining a homogeneous and fine powder. All analyses were performed in triplicates. The concentrations of lignin and cellulose were obtained by gravimetric determination using the acid fibre detergent procedure (Gessner 2020).

Leaf litter from *E. guineensis* showed the lowest concentrations of lignin (32.5 ± 0.49%) and cellulose (33.5 ± 0.15%), followed by *T. cacao* (lignin = 36.1 ± 0.53% and cellulose = 35.6 ± 0.68%). Leaf litter of *H. courbaril* had the highest concentrations of these compounds (lignin = 40.5 ± 0.56% and cellulose = 35.9 ± 1.35%).

Data analysis

To test our hypothesis, we used Linear Mixed Effects models (LME), considering the decomposition rates of the total (k total), microbial (k microbial) and invertebrate-mediated (k invertebrates) as response variables. Species were used as a fixed effect and the spatial levels were replicated and nested hierarchically (micro basins: stream segments: pool sites) as a random effect. Litter bags were considered as the sample unit. The assumptions of normality and homogeneity of residuals were checked for all models. The adjusted models were subjected to an analysis of variance (ANOVA), and then we performed pairwise comparisons using Tukey's test. Finally, we performed a direct ordination of the relative abundance of aquatic invertebrates according to the decomposition rate of each leaf litter (k day^{-1}). All analyses were performed in R, version 3.6.2 using the 'lme4' and 'multcomp' packages (R Core Team 2019; Bates et al. 2015; Hothorn et al. 2008).

Results

We recorded lower percentage of remaining mass in leaf litter of *T. cacao* (62 ± 5%; mean ± standard deviation), followed by *E. guineensis* (74 ± 5%) and *H. courbaril* (74 ± 3%) (Fig. 3). Higher decomposition rates were recorded in *T. cacao* (total and microbial $k = 0.008 \pm 0.001$ day^{-1}). Total and microbial decomposition rates were similar in *E. guineensis* (total $k = 0.006 \pm 0.001$; k Microbial = 0.005 ± 0.001 day^{-1}) and *H. courbaril* (total $k = 0.005 \pm 0.001$; k Microbial = 0.004 ± 0.004 day^{-1}).

There was no effect of leaf litter species on invertebrate decomposition rates. Fixed effects explained 63% of the variance (marginal R^2) of total k model. The marginal R^2 for k microbial and k invertebrate models were 68% and 9%, respectively (Table 1, Fig. 4). Random effects had little influence on the response variables (see Table S3).

A total of 59 individuals belonging to 18 genera of aquatic invertebrates colonized the leaf litter bags (Fig. 5). There was no difference in the mean abundance of invertebrates in the leaf litter of all species (*T. cacao* = 3 ± 3; *E. guineensis* = 2 ± 2; *H. courbaril* = 2 ± 1) individuals/ bag. The shredders and scrapers were recorded in the detritus of all plant species, with relative abundances of 4 ± 4% (mean ± standard deviation) and 6 ± 7%, respectively.

Discussion

The total and microbial decomposition rates of native (*T. cacao* and *H. courbaril*) and exotic (*E. guineensis*) species can be classified as intermediate (k = 0.0041–0.0173),

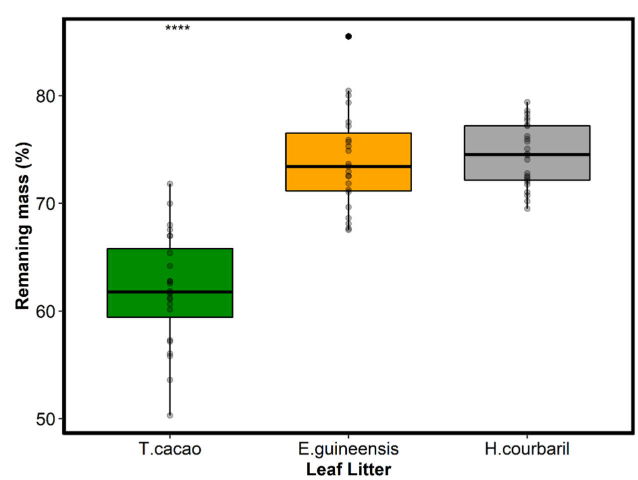

Fig. 3 Remaining mass (%) per species of leaf litter. H. courbaril = *Hymenaea courbaril*; E. guineensis = *Elaeis guineensis*; T. cacao = *Theobroma cacao*. Asterisks indicate statistical differences ($P < 0.05$)

Table 1 Results of analysis of variance for the adjusted models, with leaf litter species as a fixed effect, analysing the variation in: *k* total, *k* microbial and *k* invertebrates, as well as the pairwise comparison of the means.

Source of variation	Sum of sqrs	*df*	*F*	*p*	R^2 (%)*
k total					
Leaf litter	0.0001	2	32.13	**< 0.05**	63
k microbial					
Leaf litter	0.0001	2	47.59	**< 0.05**	68
k invertebrates					
Leaf litter	< 0.0001	2	2.17	0.14	9

Tukey's contrast	Mean diff	SE	Z	*p*
k total				
H. courbaril vs. *E. guineensis*	− 0.0005	0.0004	− 1.20	0.45
T. cacao vs. *H. courbaril*	0.0029	0.0004	7.47	**< 0.05**
T. cacao vs. *E. guineensis*	0.0024	0.0004	6.26	**< 0.05**
k microbial				
H. courbaril vs. *E. guineensis*	0.0001	0.0004	0.35	0.94
T. cacao vs. *H. courbaril*	0.0033	0.0004	8.27	**< 0.05**
T. cacao vs. *E. guineensis*	0.0035	0.0004	8.62	**< 0.05**

The values in bold represent the *p* value (< 0.05)

*R^2 (%)** Marginal R-squared (only fixed effects), *SE* Standardized error, *H. courbaril* = *Hymenaea courbaril* (Control), *E. guineensis* = *Elaeis guineensis*; *T. cacao* = *Theobroma cacao*

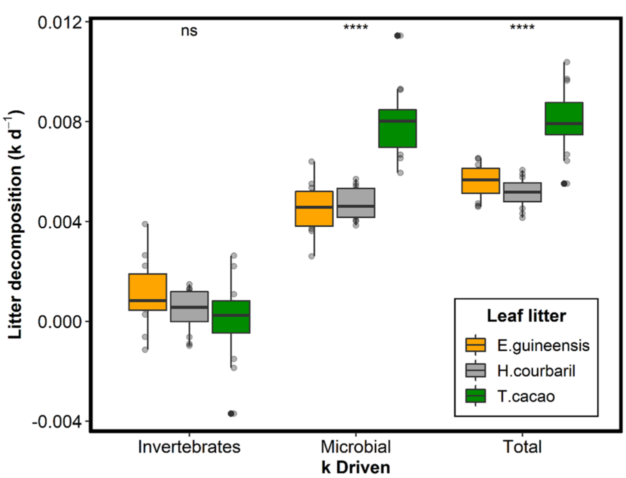

Fig. 4 Decomposition rates: *k* total, *k* microbial and *k* invertebrates for each species of leaf litter. H. courbaril = *Hymenaea courbaril*; E. guineensis = *Elaeis guineensis*; T. cacao = *Theobroma cacao*. Asterisks indicate statistical differences ($p < 0.05$); *ns* not significant ($p > 0.005$)

based on the classification for tropical species (Gonçalves et al. 2013). The chemical composition of leaf litter affected total and microbial decomposition, giving a better explanation microbial decomposition variance. For this reason, our results corroborate that the species of leaf litter influence the microbial community and the litter decomposition in tropical streams (Irons et al. 1994; Gonçalves et al. 2006; Boyero et al. 2015, 2017).

Although the litter from *T. cacao* showed intermediate concentrations of lignin and higher concentrations of cellulose than *H. courbaril* leaf litter, microbial communities were already recorded as able to efficiently process the cellulose of detritus in tropical rivers and streams (Gonçalves et al. 2017; Tiegs et al. 2019). Also, leaf litter characteristics may change over the time immersed in the streams (Graça et al. 2001). For example, Alvim et al. (2015b) observed that cellulose and lignin concentrations might increase or decrease over time depending on the species evaluated. Thus, the entry of *T. cacao* leaf litter into Amazonian streams will increase the availability of fine particulate organic matter, as this litter decomposes faster. Sridhar et al. (1992) observed that the rapid decomposition of cocoa leaves in streams is due to the non-use of pesticides in crops, enabling colonization by aquatic hyphomycetes. In addition, a rapid rate of decomposition of *T. cacao* leaves was observed in a river under the influence of cocoa cultivation associated with other plant species (that is, in agroforestry systems (Rojas et al. 2017).

Contrary to our initial expectations, the leaf litter from *E. guineensis*, which was of higher quality and had lower concentrations of structuring compounds, did not differ in total and microbial decomposition rates from the lower quality leaf litter of the control species *H. courbaril*, which presented higher concentrations of lignin and cellulose. This result contrasts with previous studies that found a positive relationship between litter quality and decomposition rates, regardless of the origin of leaf litter (Rezende et al. 2010;

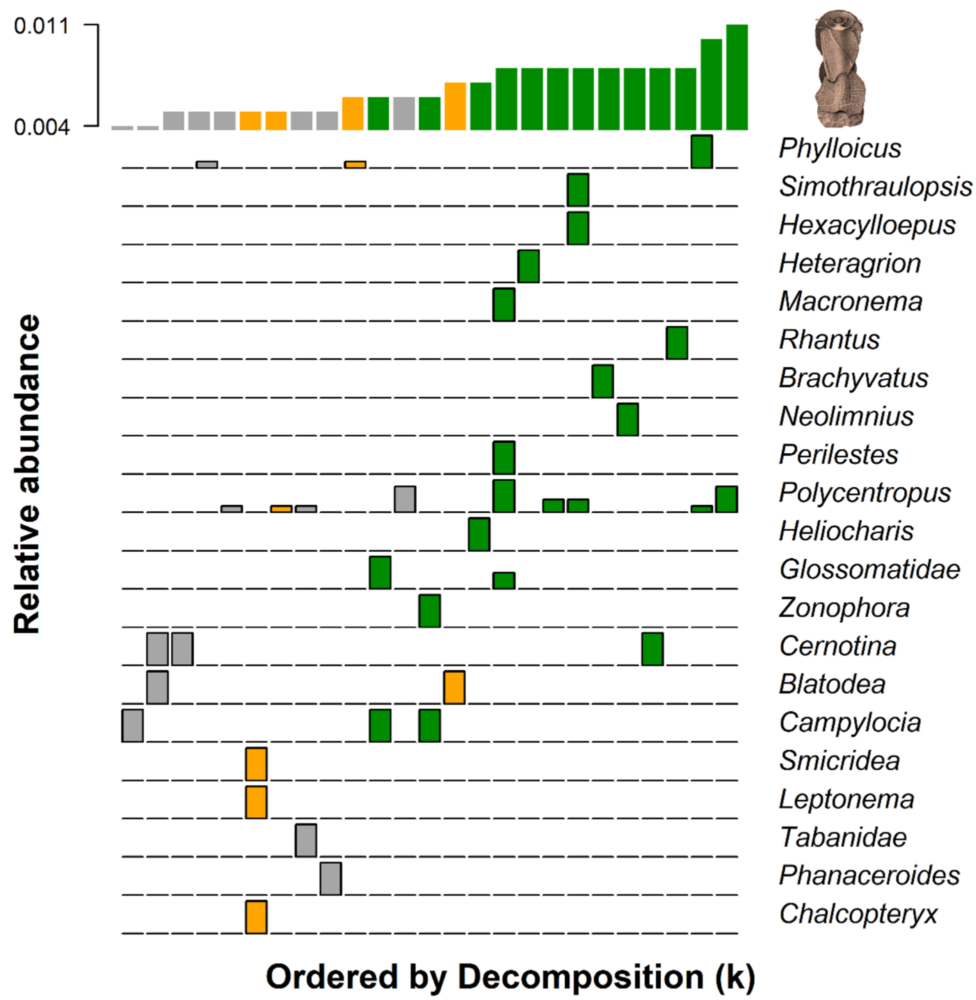

Fig. 5 Direct ordination of relative abundances for taxa associated with each leaf litter, based on the decomposition rate (k day^{-1}). The bar colours represent the species of leaf litter: *Hymenaea courbaril* (gray), *Elaeis guineensis* (orange) and *Theobroma cacao* (green)

Gonçalves et al. 2017), indicating that litter quality is a controlling factor for organic matter decomposition in streams. Therefore, our results indicate a potential negative effect of leaf litter from the exotic species *E. guineensis* on the processing of organic matter and the functioning of Amazonian streams. Chellaiah and Yule (2018), in a study performed in Malaysia, found that the native leaves of *Macaranga* sp. decomposed five times faster than the leaf litter of *E. guineensis*, both in streams with natural riparian vegetation and in streams with direct and indirect effect from palm monocultures.

Unlike *T. cacao* leaf litter, the higher concentration of lignin in *H. courbaril* indicates that this compound could be a controlling factor for decomposition because it is a polymer with high resistance to enzymatic degradation by microorganisms (Kirk and Farrell 1987; Jabiol et al. 2019). Thus, leaf litter rich in lignin and cellulose tends to be intractable and tends to decompose slowly (Gessner 2020), corroborating our hypothesis that detritus with higher concentrations of lignin and cellulose decompose more slowly. Similarly, Gonçalves et al. (2017) found a negative correlation between lignin concentrations and the decomposition rates of native and exotic species.

Invertebrate-mediated decomposition did not differ between leaf litter sources. This can be explained by the low frequency of shredders and scrapers in our study, on average 4 and 6%, respectively. Our results are in line with Gonçalves et al. (2017), who found low frequencies of shredders (on average 6%) and scrapers (on average 5%) colonizing the leaf litter in Amazonian streams. Besides, some studies have shown that shredders are scarce and not remarkably diverse in tropical streams, suggesting that they have little influence on the decomposition process (Boyero et al. 2012, 2017; Gonçalves et al. 2012; Rezende et al. 2018).

The low abundance of invertebrates colonising the litter bags may reflect the low quality of leaf litter used in this study. Janke and Trivinho-Strixino (2007) observed that litter with high concentrations of structural compounds (e.g., lignin and cellulose) and secondary compounds might result in low colonization by aquatic invertebrates. This is exacerbated by the fact that low abundances of macroinvertebrates are usually found in many Amazonian streams (Montag et al.

2019). Also, high densities of invertebrates colonizing high-quality leaf litter, i.e., with high concentrations of nitrogen and phosphorus, had already been reported in previous studies (Rezende et al. 2010; Gonçalves et al. 2012, 2017).

Conclusions

Our hypothesis was partially corroborated, and the leaf litter from *H. courbaril*, with lower leaf quality, had decomposition values like those found in *E. guineensis*, a best quality leaf litter, both with high remaining mass. The leaf litter from *T. cacao* had intermediate lignin concentrations and high cellulose concentrations, and a lower remaining mass, suggesting that high cellulose concentrations can compensate for a high lignin content. Our results indicate that streams dominated by *E. guineensis* monocultures and *T. cacao* crop may potentially have their energy dynamics altered due to the low decomposition values to *E. guineensis* and high for *T.cacao*, which may impact the ecosystem functioning of streams in the Amazon region. Considering the constant conversion of native Amazonian forests to other types of land use, in addition to the palm oil and cocoa investigated here, it is important to continuously assess the impacts of land use changes on the processing of organic matter at Amazonian streams, since the input of leaf litter from exotic crops with low-quality leaves can compromise essential ecosystem processes.

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