PANAMJAS
Pan-American Journal of Aquatic Sciences

Influence of leaf functional diversity on leaf breakdown in a tropical stream

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Abstract. Leaf breakdown in forest streams depend on the input of allochthonous organic matter (OM). OM input can alter decomposition rates due to several factors, including litter quality. Leaf Functional diversity, in turn, is linked to litter quality, and therefore influences decomposition rates. Here we used a leaf functional trait – the leaf dry matter content (LDMC) – to divide five species of riparian forest trees into two groups: one of high LDMC diversity (HD); and one of low LDMC diversity (LD). We hypothesized that leaves in the HD treatment would be a more diverse resource for the decomposing biota, influencing the breakdown rates. Leaves were conditioned in litter bags and inserted in a first order stream, and were recovered after 4, 7, 17, 32 and 59 days. Decomposition rates (*k*) were significantly higher in HD, although larger LDMC values were found in this group. Therefore, functional diversity may have a greater influence on *k* than the LDMC values themselves. As there are few studies evaluating the effect of LDMC differences on decomposition in aquatic environments, the present study indicates that LDMC has the potential to understand the mechanisms involved in this process.

Key words: decomposition, functional diversity, LDMC, low-order stream

Resumo: Influência da diversidade funcional de folhas na decomposição foliar em um riacho tropical. A decomposição em riachos depende do aporte de matéria orgânica alóctone (OM). A entrada de OM altera as taxas de decomposição por vários motivos, incluindo a qualidade da matéria orgânica. A diversidade funcional, por sua vez, está ligada à qualidade da matéria orgânica e, assim, também influencia as taxas de decomposição. Neste estudo, usamos uma caraterística funcional das folhas, o Conteúdo de Massa Seca de Folhas (LDMC), para dividir cinco espécies de árvores em dois grupos: um com alta (HD) e outro com baixa (LD) diversidade de LDMC. Nós hipotetizamos que HD resultaria em recursos mais diversos para os decompositores, alterando as taxas de decomposição. Foram montados litter bags de cada grupo, que foram inseridos em um riacho de primeira ordem, sendo retirados após 4, 7, 17, 32 e 59 dias. As taxas de decomposição (*k*) foram significativamente maiores em HD, apesar de maiores valores de LDMC serem encontrados neste grupo. Portanto, a diversidade funcional pode ter maior influência sobre as taxas de decomposição do que os valores de LDMC. Como existem poucos trabalhos avaliando o efeito de diferenças de LDMC na decomposição em ambientes aquáticos, o presente estudo indica que o LDMC tem potencial para ajudar na compreensão dos mecanismos envolvidos nesse processo.

Palavras-chave: decomposição, diversidade funcional, LDMC, riachos de baixa ordem

Introduction

According to the River Continuum Concept (Vanotte *et al.* 1980, Franssen *et al.* 2015, Rosi-Marshall *et al.* 2016), energy flow in low-order streams is more dependent on the input of allochthonous organic matter from riparian forests than in larger streams. This happens because riparian trees shade the water surface, reducing primary production. The deposited organic matter is a basal resource for the aquatic food chains, and its decomposition is important to maintain the balance of lotic food webs.

Organic matter (OM) is processed in streams through three major paths: (1) OM input (how and from where OM enters the ecosystem), (2) ecosystem metabolism (how OM is processed after entering the lotic system) and (3) decomposition (Allan & Castillo 2007). The main input of OM comes from coarse particulate organic matter (CPOM = organic particles larger than 1 mm, mostly leaves), and following its entrance and retention in the stream ecosystem, CPOM becomes available for decomposition. After that, leaves are subject to the leaching process, which causes the abiotic removal of soluble substances (e.g. phenolics, carbohydrates and aminoacids) and lasts for approximately 48h, being responsible for a loss of up to 30% of the leaf's original mass, depending on the species (Bärlocher 2005). Subsequently, decomposition processes go on, which were mainly studied regarding leaf litter breakdown in low-order streams. This consists of the reduction of CPOM into fine particles of organic matter or the decomposition to elements that can subsequently be incorporated into the food web (Boyero *et al.* 2016, Sauer *et al.* 2016, Follstad Shah *et al.* 2017).

The rate of leaf litter breakdown can be affected by biotic and abiotic factors such as differences in decomposer communities, temperature, dissolved oxygen concentrations, stream water discharge and stream chemical characteristics as well as by the physical and chemical composition of leaves (Martins *et al*. 2015, Stoler *et al.* 2016, Gonçalves *et al.* 2017). The latter largely influences decomposition rates, because plant litter of different chemical compositions will result in litter of different qualities, affecting the speed at which such litter will decompose (Webster & Benfield 1986, Leroy & Marks 2006, Bruder *et al.* 2014, Cleveland *et al.* 2014, Dale *et al.* 2015, Sales *et al.* 2015, Follstad Shah *et al.* 2017). Some parameters to compare different litter qualities are lignin content and Carbon:Nitrogen (C:N) ratios for example (Aerts, 1997, Boyero *et. al.*, 2016). Both lignin content (Wymore *et al.* 2018) and C and N concentrations (Shumilova *et al.* 2019) can influence leaching from leaf litter in streams. Furthermore, litter quality is also considered a major factor influencing leaf breakdown because litter of different qualities will support distinct microbial (Baldy *et al.* 1995, Hieber & Gessner 2002) and invertebrate communities (Cummins *et al.* 1989, Graça 2001).

A recent approach to evaluate the effects of litter quality on leaf breakdown rates is by using plant functional traits (Schindler & Gessner 2009). Functional traits are related to the distribution and range of effects that the organisms have on communities and ecosystems and can be defined as any element of biodiversity (e.g. genotypic and phenotypic variations) that influences the functioning of a certain ecosystem (Tilman 2001, Schleuter *et al.* 2010). They can be used to classify species into functional groups, which can then be analyzed regarding their effects on a given ecosystem. The influence of biodiversity on ecosystem functioning is more related to functional trait diversity than to species diversity in several systems (McGrady-Steed *et al.* 1997, Emmerson *et al.* 2001, Hooper *et al.* 2005, Vanderwalle *et al.* 2010). Differences in plant functional traits can influence decomposition rates of leaf mixtures within streams (Boyero *et al.* 2016). Therefore, it is expected that, when the same number of leaf species are incubated, breakdown rates are higher when the group has higher functional diversity (species have more dissimilar traits) than when the group has lower functional diversity (more similar traits) (Loreau *et. al.* 2001), but field studies found weak or absent effects (Schindler & Gessner 2009, Frainer *et al*. 2015), although a mesocosm study found a positive relationship when using trait distance calculated on five leaf traits (López-Rojo *et al*. 2018).

Here we investigated whether differences in leaf functional traits influenced decomposition rates in a low-order stream, independently of species diversity. We used the Leaf Dry Matter Content (LDMC) as a functional diversity indicator, a trait that is related to decomposition rates in terrestrial ecosystems (Shipley & Vu 2002, Garnier *et al.* 2004). Plants with higher LDMC values have relatively more dry mass and, therefore, more structural compounds (ex: lignin and cellulose). Thus, it is expected that leaves with higher values of LDMC will decompose more slowly, because structural compounds are harder to break down, resulting in lower-quality leaves (Kazakou *et al.* 2006, Quested *et al.* 2007, De Marco *et al.* 2011, Pakeman *et al.* 2011). However, when incubating mixtures of species, we expected that heterogeneous mixtures (with large differences in LDMC) would present higher breakdown rates than homogeneous mixtures (with similar LDMC values), as suggested by Schindler & Gessner (2009). Possible mechanisms include transfer of nutrients from low- to high-quality leaves, either by leaching or transported within fungal hyphae that connect leaves with distinct qualities (Hoorens *et al*. 2003, Schimel & Hättenschwiler 2007).

Therefore, this study aimed to investigate if differences in riparian vegetation functional diversity influence the leaf breakdown process in a tropical stream. We used leaf litter bags assembled from the same number of tree species, with similar (low functional diversity) or different (high functional diversity) LDMC values. Since low LDMC values were reported to be related with higher decomposition rates, we hypothesized that leaves with higher diversity regarding LDMC would form a more variable resource for the decomposing biota (both microorganisms and macroinvertebrates), resulting in higher leaching and leaf breakdown rates.

Material and Methods

The experiment was carried out in a preserved area within the Federal University of São Carlos *campus*, SE Brazil. The Fazzari stream (21°58'4.00"S; 47°53'18.23"W) is a first order stream with small dimensions that flows into the Monjolinho river, which is part of the Jacaré-Guaçu basin (Siqueira & Trivinho-Strixino 2005). The climate in the region is characterized by wet summers and dry winters, the dry season extending from June to August and the wet season from September to May (Siqueira *et al.* 2008). The riparian vegetation is formed by riparian forests, so that more than 70% of the channel is covered by tree canopies, and the streambed is characterized by the presence of organic matter such as leaves, woods and twigs (Siqueira *et al.* 2008).

The streambed has muddy and sandy soil, largely covered by CPOM deposition. Dissolved oxygen concentrations have been reported to vary between 5.6 and 5.9 mg/L, thermal amplitude from 15 to 23°C, with a stream water velocity of 1.5 m/s (Janke & Trivinho-Strixino 2007, Corbi & Trivinho-Strixino 2008, Siqueira *et al.* 2008). We evaluated stream water conditions weekly throughout the experiment by measuring pH, temperature, and electrical conductivity with a multiprobe (YSI-63 model), and dissolved oxygen concentrations with a YSI ProODO meter.

Experimental design: We used five plant species that naturally occur in riparian forests in the region to assemble the two groups of high and low functional diversity (Table I; data from L. A. D. G. Beltran & A. L. T. Souza, unpublished); species will be treated by their genus names. All species were planted from seeds in a greenhouse and grown in a mixture of organic substrate and manure. After four months, one leaf sample was obtained from ten individuals of each species to determine their LDMC, a measure of the ratio of leaf dry mass to fresh mass, following Garnier *et al.* (2001). Additional leaves for the experiment were collected, air dried and then stored until needed.

Table I. Leaf Dry Matter Content (LDMC) of the five species used in the experiment; values are means ± standard errors (n = 10). Similar letters connect means that do not differ significantly following Tukey´s HSD post-hoc test.

Species	LDMC
Cecropia pachystachya (Trécul)	0.242 ± 0.007^{a}
Colubrina glandulosa (Perkins)	0.282 ± 0.011^{a}
Ceiba speciosa (Ravenna)	0.252 ± 0.005^{a}
Guazuma ulmifolia (Lam.)	0.341 ± 0.012^{b}
Bauhinia variegata (Ducke)	0.414 ± 0.014^{c}

To determine the two groups of functional diversity, we carried out a 1-way ANOVA (Analysis of Variance) on LDMC data from the five species. Differences between species were verified using Tukey´s HSD post-hoc multiple comparisons test (Quinn & Keough 2002). Significant differences were recorded among species (ANOVA: $F_{4,45} = 48.4$, $P < 0.001$). Tukey´s test indicated that no significant differences in LDMC were found among *Cecropia*, *Colubrina* and *Ceiba*, which all presented low values; an intermediate value was obtained for *Guazuma*, and a higher value was obtained for *Bauhinia* (Table I). Therefore, the treatment levels determined for this study were high functional diversity (HD), including *Ceiba*, *Guazuma*, *and*

Bauhinia, and low functional diversity (LD), including *Cecropia*, *Colubrina* and *Ceiba*.

For the leaf breakdown study, we used 15 x 10 cm nylon bags with 10mm mesh size, filled with 1.5g from each plant species, summing 4.5g for each litter bag. A total of 48 litter bags was built, 24 for each treatment level. On 31 March 2017, all litter bags were placed in the Fazzari stream, along four different pools (spatial replicates), distant at least 22m from each other and with distinct depths (mean depth varied from 0.18m to 0.30m). Within each pool, ten litter bags were fixed on the streambed, five from each treatment level (LD or HD). The eight additional litter bags (four from each treatment level) were returned to the lab after the experiment was set up, to determine manipulation losses. After 4, 7, 17, 32 and 59 days, a replicate from each treatment level was carefully retrieved from each of the four pools. In the lab, the leaves were carefully rinsed in tap water, later dried at 40-50ºC for two days in an oven and weighed.

We estimated leaching following Bärlocher (2005) by determining percentage of mass loss after four days in relation to original mass.

Data Analysis: Leaf breakdown rates (*k*) for each treatment level (high and low functional diversity) in each spatial replicate were determined by fitting leaf mass loss to the single-pool negative exponential model using non-linear models (Adair *et al*. 2010):

$$M_t = M_0 e^{-kt}$$

Where M_t is the proportion of mass remaining at the time *t*; M_0 is the initial mass of the litter bag, corrected for manipulation losses; *k* is the coefficient of decay and *t* is the time in days.

We also evaluated if leaching differed between each treatment level. Values were arcsin transformed to obtain normal distributions and variance homogeneity (Quinn & Keough 2002).

The experiment consisted in a randomized blocks design, and dependent variables were analyzed with a 2-factor ANOVA. Data was analyzed using a mixed linear model with two factors: Treatment (fixed: LD or HD) and Blocks (random: each pool). The latter was considered random because different reaches within the same stream can vary in relation to environmental conditions such as stream depth and width, current velocity and luminosity. The interaction was considered the residual, since there were no replicates within blocks (Quinn & Keough 2002). Premises of the linear model were evaluated by graphical analysis of the residuals. The level of significance in this study was $P < 0.05$. All analyses were carried out with Systat 13.0.

Results

The leaf breakdown experiment showed that about 24% of the initial mass remained after 59 days in the HD treatment and 31% in the LD treatment; considering all replicates, the single-pool negative exponential model explained 85% of the variation for HD, and 71% for LD (Fig. 1). Leaching was more variable in the LD treatment (Fig. 2), although the transformation resulted in more similar variances (*F*-test of variances; $P > 0.05$). There were no significant differences in leaching between treatment levels, although a trend for a higher value in the LD treatment was observed ($F_{1,3} = 7.46$, $P = 0.072$). On the other hand, leaf breakdown rates were significantly lower in the LD treatment ($F_{1,3} = 20.43$, $P = 0.020$) compared to the HD treatment (Fig. 2).

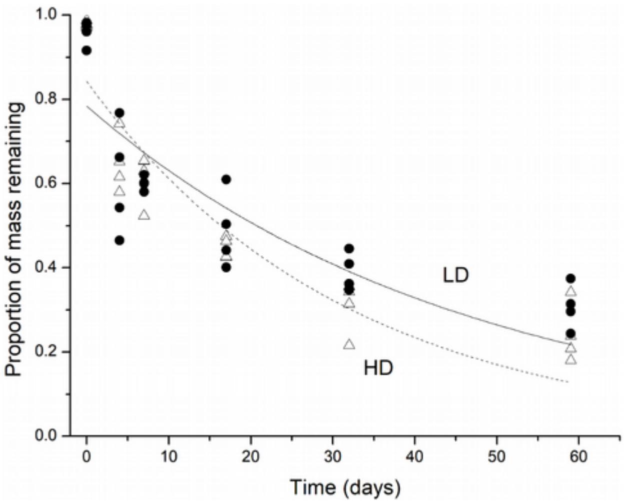

Figure 1. Proportion of mass remaining along time in litter bags with low functional diversity (LD) and high functional diversity (HD), and fitted single-pool negative exponential model for each treatment level considering all spatial replicates.

Discussion

The effects of biological diversity on ecosystem processes are complex, and are found to be more related to functional diversity than to taxonomic diversity (Hooper *et al*. 2005, Gagic *et al*. 2015). Here we evaluated the effect of varying functional diversity while maintaining the same number of leaf species available for decomposers. Although this design is similar to Schindler & Gessner (2009), they used functional groups to assemble the litter bags, based on differences in leaf breakdown rates from single-species experiments.

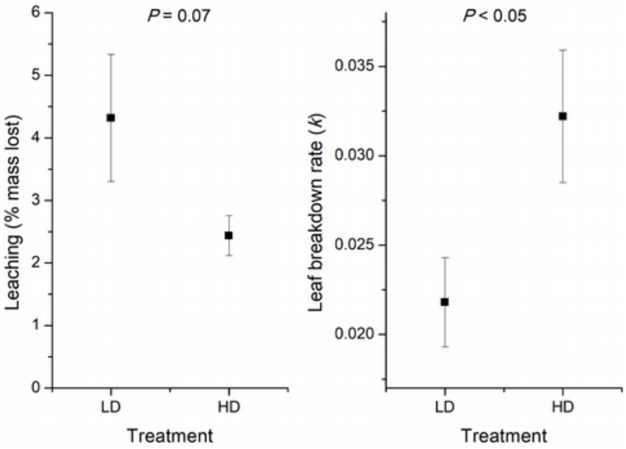

Figure 2. Mean leaching and decomposition rates (*k*) estimated for the low diversity (LD) and high diversity (HD) treatments. Bars indicate the standard error.

On the other hand, we used a leaf functional trait that directly translates the differences in carbon investment on leaves, related to initial litter chemistry (e.g., Hoorens *et al*. 2003).

LDMC is more commonly used to predict differences in breakdown rates in terrestrial systems (e.g., Kazakou *et al*. 2006, Bakker *et al*. 2011), but our study indicates that it may be a strong predictor in aquatic systems as well. Differences in functional diversity in homogeneous (low diversity) and heterogeneous (high diversity) groups of leaves resulted in different decomposition rates as predicted by the model suggested by Schindler & Gessner (2009) and also found by López-Rojo *et al*. (2018) in a mesocosms experiment, although this pattern was not found by Frainer *et al*. (2015). Higher dissimilarity in leaf functional traits related to decomposability could accelerate decomposition rates by leaching of nutrients from more labile (lower LDMC) to more refractory material (higher LDMC), so that the mixed pack would present higher decomposition rates than more homogeneous mixtures. The result would be a synergistic effect, where microbes associated with recalcitrant litter would have access to important nutrients (Frainer *et al*. 2015). Synergistic effects were found by Santschi *et al.* (2018) when combining leaves from species with low C:N ratios with the species with highest C:N ratio in their study, with higher decomposition by microorganisms than expected by additive effects.

In our study, there were no differences in leaching between mixtures (P = 0.072, Fig. 2), with larger variation in the homogeneous (low diversity mixture). Leaching can be highly variable among species (Quinn *et al*. 2000), and lignin content can influence this process (Wymore *et al.* 2018). Therefore, the trend for higher leaching in the low diversity mixture could be related to an average lower LDMC when compared to the high diversity mixture, because lower values of LDMC is related to lower contents of lignin and cellulose (Pakeman *et al.* 2011. The high variability observed in low diversity mixtures suggest, however, that other leaf traits can be important in the leaching process.

Restoration of riparian forests is urgent, but mostly discussed regarding the recovery of the substrate, not considering the recovery of ecosystem functions (Mansourian *et al*. 2017). However, there is accumulating evidence that the composition of riparian forests can influence ecosystem processes (e.g., Seena *et al*. 2017). Our study contributes to this debate, suggesting that functional diversity is an important aspect to consider when restoring riparian forests, since they provide several resources for in-stream communities (Clément *et al*. 2017). Also, more studies should be carried out to understand how leaf traits contribute to dissolved nutrients in the water column, and how leaching influences the decomposition of leaf mixtures in streams. Recovery of ecosystem functions in low-order streams can have important effects on the water quality at watershed levels, and should be considered when planning restoration programs at this spatial scale.

Acknowledgements

We thank the Secretaria de Gestão Ambiental e Sustentabilidade (SGAS-UFSCar) for permitting us to work in the Fazzari stream area. Also, we thank A. L. T. Souza for providing the functional diversity data used in this study, and two anonymous reviewers for their suggestions on an earlier version of the manuscript.

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Received: January 2019
Accepted: May 2019
Published: June 2019