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Local factors drive leaf breakdown in tropical streams

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A R T I C L E I N F O

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A B S T R A C T

Plants of riparian forests provide abundant dead leaves for freshwater stream ecosystems which support detritus-based food webs. The increased replacement from natural riparian forests to *Eucalyptus* plantations, an exotic species distributed throughout the neotropic landscapes, alters leaf breakdown as a key ecosystem process. We evaluate the breakdown of native and exotic leaf species with distinct physical and chemical characteristics (traits) in two different tropical reference condition streams located in Cerrado and Atlantic Forest biomes. We tested the hypothesis that regardless of the leaves' origin (native or non-native species), leaf litter with higher nutrients and less recalcitrant compounds has higher decay rates. *Eucalyptus camaldulensis* leaf breakdown was faster than the native species *Miconia chartacea* in both streams. Leaf breakdown was driven by local characteristics (context dependent) and the macrodecomposer community, with more intensity to the litter's intrinsic physical and chemical quality. The higher leaf breakdown of *E. camaldulensis* was evidenced in the Atlantic Forest stream, that with the most increased water flow, further accelerating the leaf breakdown. Our findings indicate that due to the innate physical and chemical characteristics of *E. camaldulensis*, its decomposition occurs at a faster rate compared to native tropical species, as evidenced by the stream flows.

1. Introduction

In several regions of the planet, there is a considerable increase in forest monoculture plantations in the landscape due to the demand for wood products and/or the establishment of the carbon sequestration market (Zomer et al., 2008). At the same time, the total natural forest area has decreased worldwide while the area of forest monoculture plantations has increased (Payn et al., 2015). The most planted forest genus in the world is *Eucalyptus*, with ca. 25 million ha planted (Chen and Yong, 1996; Martins et al., 2022). Brazil is one of the largest *Eucalyptus* producers in the world, out of Australia, with about 7.6 million ha planted (Instituto Brasileiro de Geografia e Estatística IBGE, 2019). Meanwhile, transforming natural riparian forests into exotics monoculture plantations may change in freshwater ecosystem processes, which can accelerate decomposition (Fernández et al., 2006; Gonçalves et al., 2014).

Eucalyptus trees have intrinsic characteristics that may affect terrestrial and aquatic ecosystems (Fernández et al., 2006; Lara et al., 2009). *Eucalyptus* can make the soil hydrophobic due to oils released from its leaves, hampering rainwater to penetrate and replenish underground water (Fernández et al., 2006; Lara et al., 2009). Besides, its high-water demand may decrease in runoff and stream water flow

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(Fernández et al., 2006; Amazonas et al., 2018). Furthermore, the presence of *Eucalyptus* in the riparian zone can influence the flow of matter and energy between terrestrial and aquatic ecosystems (Ferreira et al., 2015; 2019). Thus, changes in leaf phenology and litter quantity and quality in streams may occur due to differences in the intrinsic characteristics of native riparian trees (Molinero and Pozo, 2004, 2006). This replacement of native riparian forests by *Eucalyptus* plantations may strongly affect litter breakdown, a fundamental ecosystem process for the energy and matter flow and the maintenance of biodiversity in forested headwater streams (Graça et al., 2015; Gomes et al., 2016; Ferreira et al., 2019).

Forested headwater streams are generally small-order streams in high-altitude regions, with marginal vegetation that often shades the bed, limiting autochthonous primary production (Vannote et al., 1980, Neres-Lima et al., 2017). The contribution of allochthonous organic matter, mainly leaves, is the primary source of energy for the metabolism of these streams (Esteves and Gonçalves, 2011; Bambi et al., 2017), but with high variation in the landscape along the Neotropical gradient from rainforests to dry forests (Tonin et al., 2021), and consequently on the decomposer community (Barreto et al., 2023). Therefore, leaf breakdown is the main energy source for forested streams (Graça, 2001; Graça et al., 2015). In forested streams, leaf breakdown depends on three main factors: (i) leaching of water-soluble compounds facilitated by water flow, which significantly increases litter mass loss; (ii) conditioning by aquatic hyphomycetes and bacteria; and (iii) fragmentation caused by physical abrasion and shredders (Gessner et al., 1999; Graça et al., 2015; Tonin et al., 2021). Although these phases are often analyzed separately, they co-occur and are interdependent (Gessner et al., 1999; Graça et al., 2015).

Previous studies carried out in temperate regions point to a delay in colonization and a reduction in the consumption of *Eucalyptus* leaves by shredders and lower leaf breakdown rates (Gonçalves and Canhoto, 2009; Ferreira et al., 2015; 2019). A recent global assessment found an overall significant inhibition of total litter *Eucalyptus* breakdown (Ferreira et al., 2019). Over time, studies evaluating the influence of *Eucalyptus* litter breakdown as exotic litter on tropical freshwater ecosystems (out of Australia) have increased. Some studies indicate an increase in the colonization of shredders and, consequently, an acceleration of *Eucalyptus* litter breakdown (Gonçalves et al., 2012; 2014; Ferreira et al., 2019). Others found a decrease in the diversity of the microbial community compared to litter from naturally occurring riparian tree species (Gomes et al., 2016; 2018). Such distinct responses in the decomposition of *Eucalyptus* litter may occur because of its higher nutritional quality than other tropical native plant species (Gomes et al., 2018). On the other hand, information on the effects of exotic plant invasion on leaf breakdown is still developing in Neotropical riparian zones (Marks, 2019).

Litter traits refer to a set of intrinsic physical, chemical, and morphological attributes of plant leaves, quantified in terms of palatability, toxicity, and nutritional value for terrestrial and aquatic decomposers (Gessner et al., 1999; Graça et al., 2015). Litter physical characteristics such as toughness (Berg and McClaugherty, 2003; Zhang et al., 2019), concentrations of recalcitrant compounds such as lignin and polyphenols (Moretti et al., 2009; Jabiol et al., 2019), the nutritional concentration of nitrogen (N) and phosphorus (P) (García-Palacios et al., 2016) are important moderators of leaf breakdown. The set of attributes is commonly referred to as *'litter quality'*. The litter of higher quality includes soft leaves with high nutrient concentrations and low structural and secondary compounds, which are generally colonized faster and sustain higher microbial and shredder activity than more recalcitrant leaves (Gessner and Chauvet, 1994; Gulis and Suberkropp, 2003; Ferreira et al., 2012; García-Palacios et al., 2016). Therefore, leaves of high nutritional quality decompose faster than low-quality leaves (Zhang et al., 2019; Sena et al., 2020).

Despite the worldwide importance of *Eucalyptus,* the repercussions of its litter breakdown as an exotic litter on tropical streams have not yet been fully fulfilled. We seek to fill this gap by conducting a field experiment assessing the influence of native and exotic leaf species with distinct physical and chemical characteristics on leaf breakdown in Neotropical headwater streams. We assume the premises that leaf breakdown is the result: (i) of the activity and influence of micro and macro decomposers aided by leaching caused by water flow from streams; (ii) of nutrient restriction for organisms caused by the physical and chemical characteristics of leaf litter.;. We hypothesized that (i) regardless of the leaves' origin, leaf litter with higher nutrients and less recalcitrant compounds have higher litter mass decay; (ii) increased water flow from streams accelerates litter physical fragmentation leading to increased leaf mass decay.

2. Materials and methods

2.1. Study sites

The experiment was performed in two reference condition streams. The Pedras stream is located at the Serra do Cipó National Park (19°12'S, 19°34' and 43°27'W, 43°38') in the Cerrado biome, and the Taboões stream, which is located in The Serra do Rola Moça State Park (20°02'S and 44°0'W) in a semi-deciduous forest at the Atlantic Forest biome, Minas Gerais state, southeastern Brazil.

The climate of the Serra do Cipó National Park is of a high-altitude tropical type Cwb, with cool summers and a pronounced dry season, according to Köppen and Geiger (1930). It fits into the kind of bioclimate called moderately humid sub-tropical, which presents an annual water deficit reaching 60 mm due to the marked dry season. Average annual temperatures range between 17º and 18.5ºC, and average rainfall is between 1450 and 1800 mm, causing yearly potential evapotranspiration of 700–850 mm (Instituto Chico Mendes de Conservação da Biodiversidade ICMBio, 2023). At least three major plant formations can be defined due to geographic positioning, the varied morphology of the rugged soil and the climate variation at different altitudes, which are *Campos de Cerrados*, *Campo Rupestre* and *Matas de Galerias* (Gonçalves et al., 2006).

The Taboões headwater stream is in the Atlantic Forest biome at the Serra do Rola Moça State Park. The climate of the park is high altitude tropical, and the annual average temperature is 15.3°C and 21.4°C (Instituto Estadual de Florestas IEF, 2023). The average altitude of 1300 m. The relief of the park is highly rugged, including some mountains such as Serra do Rola Moça and Serra do Jatobá (Instituto Estadual de Florestas IEF, 2023). The rainfall regime well represents the characteristics of the southeastern region of Brazil, with rainy summers and dry winters (Peixoto, 2004). Although the Park is open to public visitation, the spring areas cannot be used by visitors, which guarantees the maintenance of water quality for human supply as an ecosystem service.

2.2. Field sampling

The experiment was carried out from April to September 2005 in the Pedras stream (3rd order, around 960 m altitude, Serra do Cipó National Park) and in the Taboões stream (2nd order, around 1180 m altitude in the Serra do Rola Moça State Park). Leaves from *Miconia chartacea* Triana were chosen as native litter because of the large occurrence in tropical riparian vegetation zones in Brazil and *Eucalyptus camaldulensis* Dehnh. as a non-native litter. As described by Gomes et al. (2016) and Sena et al. (2022), *Miconia chartacea* has higher concentrations of lignin (mean 25 % dry mass, DM), cellulose (21 % DM), lignin:N ratio (16) and lower N (1.5 % DM) and P (0.2 % DM) than *Eucalyptus camaldulensis* (17 % DM, 17 % DM, 11, 1.6 % DM and 0.5 % DM, respectively).

Leaves from each species were placed separately in litter bags with 10 mm mesh size. The total litter placed in each litter bag was 3 ± 0.1 g air-dry weight. The litter bag removal periods were at time intervals of 3, 7, 15, 30, 60, 90, 120 and 150 days or until the litter had lost more than 70 % of its initial mass (visually estimated value). Four litter bags of

10 mm mesh of each species were removed in each collection period. After each removal period, the litterbags were collected, placed individually in plastic bags and taken to the laboratory in ice boxes. The leaves were cleaned with distilled water in a sieve (250 μm mesh) to retain the associated invertebrates, preserved in 70 % ethanol, dried (60ºC, 72 h) and weighed for estimation of biomass to the nearest 0.001 g. Biomass of shredder detritivores (mg) for each sampling period on each leaf species in both streams. The invertebrates were identified according to Pes et al. (2005), Domínguez and Fernández (2009) and Hamada et al. (2014). Thus, collected detritivores were classified into different functional feeding groups (FFGs), according to Cummins et al. (2005). FFGs were divided into two groups: shredders, those detritivores that feed on coarse organic matter (MOPG) and scrapers, those detritivores that feed on the biofilm that grows on leaves. The density of each FFG was the ratio between the abundance and the remaining mass of leaf litter in each period (individuals/ g leaf dry mass). Chironomidae larvae were not included in the FFG classification due to their generalist-feeding habits (Pes et al., 2005; Domínguez and Fernández, 2009; Hamada et al., 2014).

In the field, the water's physical and chemical characteristics were evaluated at each collection: temperature, pH and electrical conductivity, which were measured in the stream with portable field equipment (DIGIMED brand). Dissolved oxygen concentration (Winkler method) was measured in the laboratory following the methodology proposed in the Standard Methods for the Examination of Water and Wastewater (American Public Health Association (APHA) (APHA), 2001). A flowmeter (model SWOFFER 2100 series) performed the water flow measurement in each stream per sampling.

2.3. Data analyses

To verify the similarity of the physical and chemical characteristics of the streams, the student's t-test was performed using the t-test function from the stats package (R Core Team, 2022). Initial pairwise correlations tests revealed that pH and conductivity are highly correlated ($r = 0.85$), and high correlation between pH and water flow ($r = 0.83$); we thus used shredder detritivores biomass, water dissolved concentration, water flow, water temperature, leaf species and streams to run the models. We performed a multiple linear regression model to analyze the relationship between litter mass loss, detritivores biomass, dissolved oxygen concentration, stream flow, water temperature, pH, conductivity, leaf species, streams and time. The best model was selected using the AICctab function from bbmle package (Bolker and Bolker, 2017). We found the multiple linear regression model without random effects had the best performance. The null model was discarded because of a significant difference ($p < 0.001$) in relation to that the model with the best performance according to the Akaike Information Criterion (AIC). Visual inspection of residual plots with the RVAideMemoire package (Hervé, 2022) revealed no deviations from homoscedasticity or normality.

To test the influence of the two leaf species on the density of different FFG, we performed linear mixed-effects models (LMM) with the lme4 package (Bates et al., 2015) and the AICctab function from the bbmle package (Bolker and Bolker, 2017) to select the best random effect component for the model. Time was included in the models as a random term to account for the influence of time during the leaf breakdown. We used leaf species, streams, and sampling time (without interaction term) as fixed effects in the model. For LMM, the P-values of the models were obtained with the lmerTest package (Kuznetsova et al., 2017) using Satterthwaite's degrees of freedom method. Visual inspection of residual plots with the RVAideMemoire package (Hervé, 2022) revealed no deviations from homoscedasticity or normality. All analyses were performed using R software v. 4.1.3 (R Core Team, 2022). Table 1.

Table 1
Water characterization with mean values and standard deviations for each variable analyzed in the studied stretches of Pedras and Taboões streams. Different letters indicate statistically significant differences between streams.

	Mean ± Standard Deviation
Pedras Stream	
Dissolved oxygen (mg L^{-1})	9.67 ± 1.62^{a}
Water Temperature (ºC)	20.4 ± 2.04^{a}
pH	6.51 ± 0.09^{a}
Conductivity (μS/cm^2)	4.28 ± 0.18^{a}
Water Flow (m/s)	0.084 ± 0.023^{a}
Taboões Stream	
Dissolved oxygen (mg L^{-1})	10.7 ± 1.55^{b}
Water Temperature (ºC)	21.47 ± 1.39^{b}
pH	7.21 ± 0.33^{b}
Conductivity (μS/cm^2)	11.64 ± 0.21^{b}
Water Flow (m/s)	1.09 ± 0.22^{b}

3. Results

3.1. Litter mass loss at streams

We observed that E. camaldulensis had less remaining mass than M. chartacea at the end of the experiments, with much of the initial mass lost within 120 days, while M. chartacea lasted up to 150 days with 24 % more remaining litter mass in the Pedras stream (Table 2; Fig. 1A). A similar pattern was observed in the Taboões stream, where E. camaldulensis had less remaining mass than M. chartacea. Still, much of the initial mass of E. camaldulensis was lost within 30 days, while M. chartacea lasted up to 120 days with 12 % more remaining litter mass (Table 2; Fig. 1B). In general, higher biomass of detritivores, leaf species, local scale/stream, and increase of water flow were correlated to the decrease of litter remaining through time (Table 2; Fig. 2A, B, C, D, E). We have not found a significant relationship between DO and water temperature with litter mass loss (Table 2; Fig. 2F, G).

The densities of shredders and scrapers were not influenced by any leaf species (Table 3; Fig. 3A, D). Shredders had higher density in the Taboões stream (Table 3; Fig. 3B) but without relation to the sampling periods (Table 3; Fig. 3C). The scrapers, otherwise, showed a density increase through the litter breakdown (Table 3; Fig. 3F), but were not influenced by streams (Table 3; Fig. 3E).

4. Discussion

As anticipated, the quality of leaf litter significantly impacted the accelerating of mass loss, regardless of its exotic origin (Rezende et al., 2014). In the Cerrado stream, we noticed a decelerated mass loss rate (Rezende et al., 2021), irrespective of the litter's quality. This can be explained by the decomposers being adapted and accustomed to the decomposition of litter with higher recalcitrance (Rezende et al., 2021; Bacca et al., 2023) or higher shredders biomass (Tonin et al., 2014; Boyero et al., 2015), delay in the decomposition of the toughest leaves

Table 2
Results of linear model exploring temporal patterns of remaining litter mass proportion with detritivores biomass, *Eucalyptus camaldulensis* and *Myconia chartacea* leaves, streams, sample periods, water flow, dissolved oxygen concentration and water temperature.

Source of variation	DF	Sum Sq	Mean Sq	F-value	p-value
Detritivores Biomass	1	0.453	0.453	12.290	**<0.001**
Leaf Species	1	0.901	0.901	24.432	**<0.001**
Streams	1	0.412	0.412	11.187	**0.001**
Sample Periods	1	4.831	4.831	130.963	**<0.001**
Water Flow	1	0.274	0.274	7.434	**0.007**
Dissolved oxygen	1	0.036	0.036	0.974	0.325
Water Temperature	1	0.003	0.003	0.008	0.926
Residuals	123	4.537	0.036		

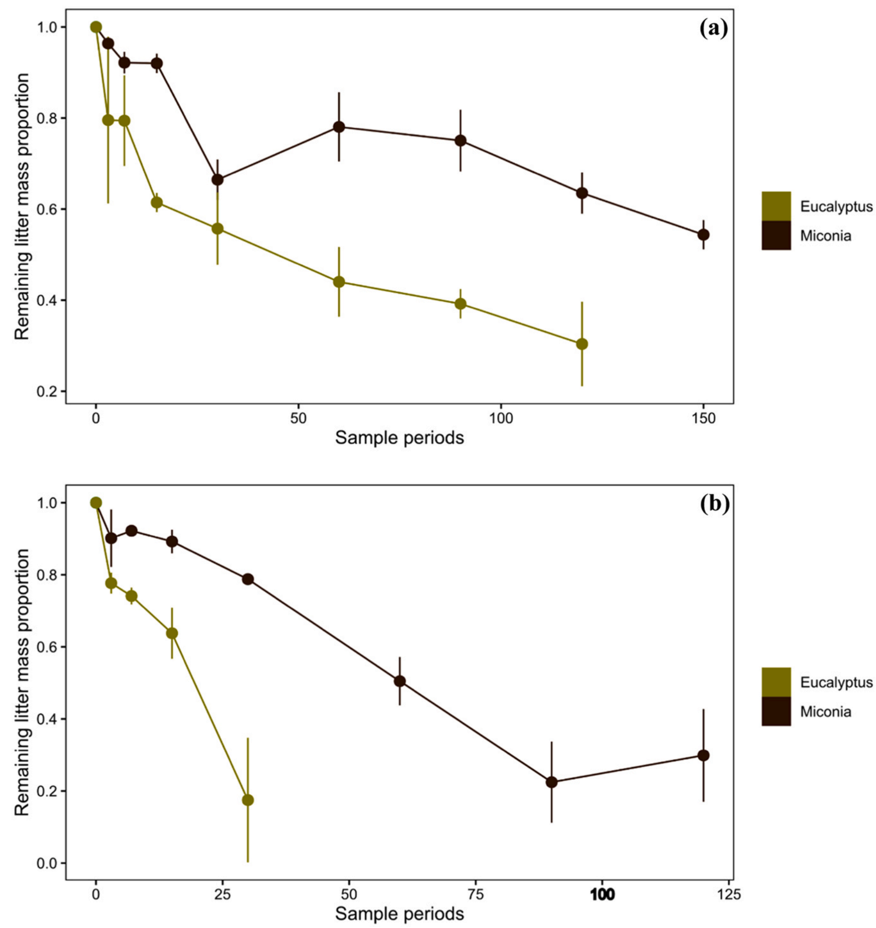

Fig. 1. Remaining litter mass proportion of Eucalyptus camaldulensis and (olive lines) and Myconia chartacea (brown lines) leaves until the end of the experiments in Pedras (A) and Taboões (B) streams.

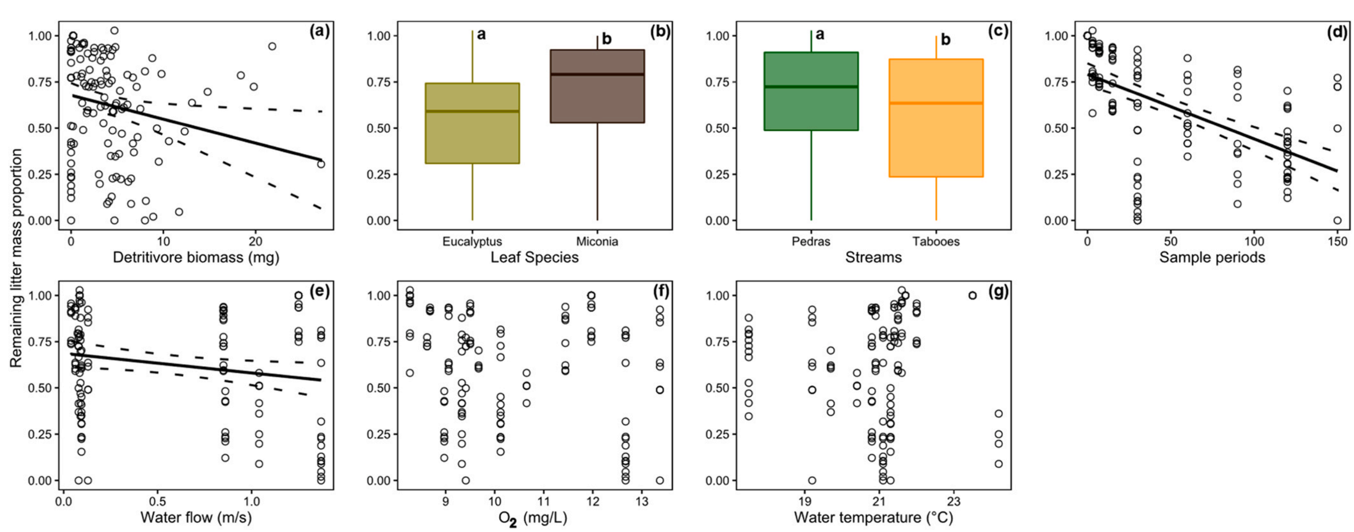

Fig. 2. Relation of remaining mass proportion with detritivores biomass (a), *Eucalyptus camaldulensis* (olive) and *Myconia chartacea* leaves (brown) (b), Pedras stream (green) Taboões stream (orange) (c), sample period (d), water flow (e), dissolved oxygen concentration (f) and water temperature (g). Different letters indicate statistically significant differences between leaf species and streams.

(Foucreau et al., 2013). As a result, when exposed to other types of litter, which might have different chemical compositions and physical structures (Marks, 2019; Sena et al., 2020), the decomposer community may not be as effective (Medeiros et al., 2015; Rezende et al., 2018). As well as the reduction in leaf material leads to a reduction in attractiveness/visibility for shredders and their density decreases over time.

Therefore, the drivers of the leaf processing could change in functions vectorial force of the variable during the time, season or bio-physical phenoms. In this way, the higher-quality *E. camaldulensis* litter

Table 3
Results of linear mixed effects exploring temporal patterns of density of Shredders and Scrapers detritivores with *Eucalyptus camaldulensis* and *Myconia chartacea* leaves; Pedras and Taboões streams and sample periods.

	DF	Sum Sq	Mean Sq	F-value	p-value
shredders					
Leaf Species	1	4.65	4.65	0.07	0.791
Streams	1	2938.76	2938.76	44.39	**<0.001**
Sample Periods	1	29.53	29.53	0.44	0.521
scrapers					
Leaf Species	1	69.32	69.32	3.60	0.059
Streams	1	64.08	64.08	3.33	0.070
Sample Periods	1	207.14	207.14	10.78	**0.025**

decomposed at a rate of approximately 70 % in the Cerrado stream. In comparison, the lower-quality *M. chartacea* litter in the Atlantic Forest stream decomposed at a rate of around 80 %. For instance, it took less than 30 days for *E. camaldulensis* litter to undergo over 90 % mass loss in the Atlantic Forest stream. In contrast, reaching this level in the Cerrado stream required more than 120 days (three times longer). Therefore, external factors such as stream flow (Nuven et al., 2022), plant species diversity in the litter (Rezende et al., 2019), and the structure of the decomposer community (Rezende et al., 2014) may outweigh the differences in litter traits in determining the leaf litter breakdown rate.

Our results showed that exotic leaf litter had higher decay rates than the native, and the leaf decay rates were higher in the Atlantic Forest stream. It was due to the highest water flow value observed in the Atlantic Forest stream and its densities of shredders. This reinforce that the litter's physical and chemical characteristics (see Rezende et al., 2023) and water flow are controlling factors for litter breakdown in tropical streams (Gonçalves et al., 2017; Sena et al., 2020; Nuven et al., 2022), supporting our hypotheses. In this way, the replacement of natural plant species by exotic plant species such as of *Eucalyptus* can modify litter breakdown in tropical streams. Furthermore, any changes in the environmental flows that came from climate change or land use could alter the functioning of streams.

The lower decay rate of *M. chartacea* observed at both streams is probably related to recalcitrant compounds such as lignin and cellulose. High concentrations of recalcitrant compounds may negatively influence litter colonization of decomposers in tropical streams (Medeiros et al., 2015; Rezende et al., 2018). The litter with high refractory compounds and fewer nutrient concentrations tend to hinder microbial colonization (Sales et al., 2015), affecting invertebrate consumption (Graça et al., 2015). *E. camaldulensis* physical and chemical characteristics could make it a preferred litter for consumption by decomposers (Gonçalves et al., 2014; Gomes et al., 2018), mainly due to the higher feeding selectivity of shredders on higher quality litter in tropical streams (Gonçalves et al., 2017; Sena et al., 2020). This directly implicates litter breakdown because, despite the economic benefits of *Eucalyptus* plantations, they alter important ecological processes such as the decomposition of organic matter (Gonçalves et al., 2012; Graça et al., 2015; Gomes et al., 2018).

In addition to variations in the inherent litter characteristics, aquatic decomposers and litter breakdown are sensitive to environmental conditions (Boyero et al., 2016; Yue et al., 2022). Water flow influenced litter mass decay in both streams, reinforcing that physical abrasion of the water is one of the main drivers to litter decay (Nuven et al., 2022; Ferreira et al., 2023). Moreover, must be considered the ability of invertebrates to resist water flow (Smith et al., 2003; Barquín and Death, 2004) and the colonization by microorganisms (Abelho, 2001; Graça et al., 2015; Gomes et al., 2018). The increase in invertebrate biomass and densities are also directly associated with increased microbial biomass, accelerating its leaf breakdown (Gonçalves et al., 2004; Abelho, 2001; Gomes et al., 2016). This reinforces that although the abundance of shredders in tropical streams can varies (Boyero et al.,

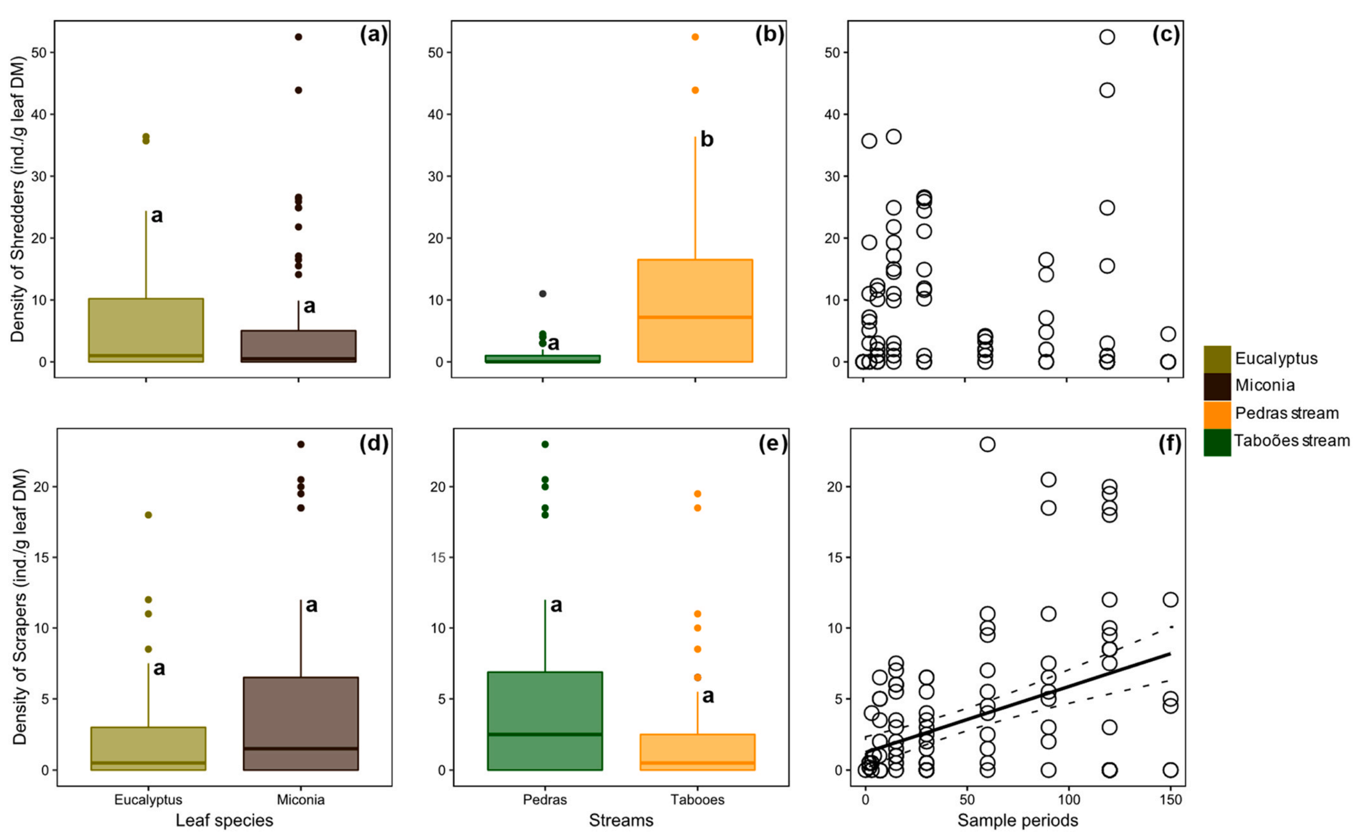

Fig. 3. Relation of densities of shredders (a, b, c) and scrapers (d, e, f) with *Eucalyptus camaldulensis* (olive) and *Myconia chartacea* (brown) leaves; Pedras (green) and Taboões (orange) streams and sample periods, respectively. Different letters indicate statistically significant differences between leaf species and streams.

2011; Prather, 2003), they can be important in the food web due its higher biomass in tropical stream ecosystems (Rezende et al., 2014; Tonin et al., 2014; Martins et al., 2015).

The tropical riparian zones are known for their wide variety of tree species (Bambi et al., 2017; Sena et al., 2022), contributing to a higher functional diversity that may affect litter breakdown rates (Rabelo et al., 2022). Therefore, we shall have the care to interpret the results of this study because it focused solely on one natural tropical plant litter compared to *E. camaldulensis*, potentially disregarding the extensive tree diversity present in tropical riparian forests. A broader exploration of the diverse litter types and their interactions with the decomposer community is warranted to understand litter decomposition dynamics in tropical streams comprehensively.

5. Conclusion

We demonstrate that water flow and decomposer community influence aquatic leaf breakdown in tropical biomes. We reinforce the evidence that regardless of the litter origin, litter characteristics are determinants for litter breakdown in tropical streams. Our findings provide empirical support for the influence of the replacement of native tropical riparian plants by *Eucalyptus* plantations on decomposition and its possible repercussions on the aquatic community on the flow of matter and energy in tropical streams. We believe that understanding the consequences that human activities may cause on the rules that determine organic matter processing in tropical aquatic environments can be helpful in the face of current global social and economic dynamics. Moreover, for the maintenance of riparian forests (Brazilian Forestry Code; Brasil, 2012), forest rehabilitation projects are needed with seedlings of native plant species and never use exotic species. Therefore, we shall guarantee the integrity of riparian forests and ecosystems' functioning.

Authors' contributions

MC conceived the study. MC and JFGJr collected field data and performed laboratorial procedures. GS and RSR managed and analyzed the data. GS wrote the manuscript with feedback from MC, JFGJr and RSR.

Ethics approval

The experimental procedures were conducted following ethical guidelines for invertebrate use in research. The authors have no conflicts of interest to disclose.

Consent to participate

All authors have contributed to the manuscript and approved the submitted version.

Consent for publication

All authors have read and approved the final manuscript and agree with its submission to Limnologica.

CRediT authorship contribution statement

Marcos Callisto: Writing – review & editing, Data curation, Conceptualization. **Guilherme Sena:** Writing – original draft, Formal analysis. **José Francisco Gonçalves Júnior:** Writing – review & editing, Data curation. **Renan Rezende:** Writing – review & editing, Formal analysis.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data Availability

Data will be made available on request.

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