RESEARCH PAPER

Hovenia dulcis Thunb. (Rhamnaceae) invasion in the riparian zone alters the dynamics and decomposition of organic matter in subtropical streams, but not of associated invertebrate assemblages

Lucas Eugenio Fontana[1,2] · Rozane Maria Restello[2] · Luiz Ubiratan Hepp[2,3]

Abstract

Stream functioning is affected by allochthonous and autochthonous energy sources, organic matter decomposition and the structure and composition of the aquatic community. The presence of non-native tree species in the riparian zone may affect stream functioning. Thus, we quantified the allochthonous organic matter input to streams from native tree species and *Hovenia dulcis*, a non-native species, over a year, and we evaluated litter colonization and decomposition by aquatic invertebrates. The input of native organic matter was greater in Winter and Spring. On the other hand, the input of *H. dulcis* was higher in Autumn. The annual contribution of native organic matter was twofold greater than that of *H. dulcis* and was correlated with rainfall. *H. dulcis* leaf litter had decomposition rates that were three- to fourfold greater than those of native leaf litter. The invertebrate abundance and richness, and functional feeding groups did not vary between native and non-native leaf litter. We conclude that the presence of *H. dulcis* in the riparian zone changed the input patterns of allochthonous organic matter into streams. Furthermore, *H. dulcis* litter broke down faster than that of native species and did not directly affect the associated invertebrate community. However, the dominance of this species in riparian zones causes homogenisation of environment, resulting in changes in the composition of other biological communities (e.g., fungi and fish).

✉ Luiz Ubiratan Hepp
luizuhepp@gmail.com

[1] Programa de Pós-Graduação em Ecologia, Departamento de Ecologia e Zoologia, Centro de Ciências Biológicas, Universidade Federal de Santa Catarina (UFSC), Campus Universitário s/n, Trindade, Florianópolis, Santa Catarina CEP 88040-970, Brazil

[2] Programa de Pós-Graduação em Ecologia, Departamento de Ciências Biológicas, Universidade Regional Integrada do Alto Uruguai e das Missões (URI), Avenida Sete de Setembro 1621, Erechim, Rio Grande do Sul CEP 99709-910, Brazil

[3] Universidade Federal de Mato Grosso do Sul (UFMS), Campus de Três Lagoas, Avenida Ranulpho Marques Leal, 3484, Três Lagoas, Mato Grosso do Sul CEP 79613-000, Brazil

Introduction

Stream ecosystem functioning depends on complex process that include (1) allochthonous and/or autochthonous organic matter production (matter and energy source) (Vannote et al. 1980; Rezende et al. 2017), (2) plant litter decomposition (nutrient cycling) (Chauvet et al. 2016) and (3) the structure and composition of aquatic communities, which facilitate the energy incorporation into the trophic web (Wallace and Webster 1996). In forested streams, primary productivity is limited by shading, making the input of allochthonous organic matter essential for the maintenance of aquatic communities (Vannote et al. 1980; Graça 2001; Neres-Lima et al. 2017). Microorganisms and aquatic invertebrates colonize and consume allochthonous organic matter. Microorganisms degrade plant tissue structures, increasing its nutritional richness (e.g., increased nitrogen concentrations) and making it palatable to shredders (Graça 2001; Taylor and Andrushchenko 2014; Biasi et al. 2019). Shredders directly consume leaf litter by converting coarse particulate organic

matter into fine particulate organic matter, which is a food resource for other aquatic invertebrates including collectors and filterers (Graça 1993, 2001; Marks 2019). Therefore, they contribute to decomposition processes, nutrient cycling and the incorporation of matter and energy in the trophic web (Graça 1993; Abelho 2001; Cummins 2002; Graça et al. 2015).

The input of allochthonous organic matter to streams can occur through several pathways. Organic matter can enter vertically (directly from trees), laterally (from the riparian zone) or from upstream (Gonçalves et al. 2006; Gonçalves and Callisto 2013). In the neotropics, allochthonous material comprises leaves (~ 70%), branches (~ 30%) and reproductive materials (i.e., flowers, fruits and seeds) (Gonçalves et al. 2014; Rezende et al. 2017).

The processing of organic matter is directly affected by the chemical and structural characteristics of the matter varying between species (König et al. 2014; Medina-Villar et al. 2015). Thus, leaf litter of high quality (high N concentrations and lowest C:N ratio) (Canhoto and Graça 1996), low concentrations of polyphenols (Tonin et al. 2014a) and low toughness (Biasi et al. 2016) tends to be colonized and consumed more efficiently by detritivores.

Monocultures (e.g., *Eucalyptus* sp. and *Pinus* sp.) (Juvenal and Matos 2002) or the presence of invasive non-native species (e.g., *Hovenia dulcis*) (Dechoum et al. 2015) can negatively affect the dynamics of allochthonous organic matter in streams. For example, the litter fall of *H. dulcis* increases in Autumn and substantially changes the dynamics of stream organic matter (Carvalho 1994). Consequently, riparian zones dominated by such species can have energy deficits in certain periods of the year. Some non-native species may also reduce the rate of the decomposition process (Casas et al. 2013; Martínez et al. 2013a, b). Further, some non-native species can alter the structure and composition of microorganism (Bärlocher and Graça 2002; Menéndez et al. 2013; Ferreira et al. 2017; Biasi et al. 2020) and invertebrate assemblages (Albariño and Balseiro 2002; Gonçalves et al. 2012; Martínez et al. 2013a; Tonin et al. 2014b). The negative effects of non-native species favor functional redundancy (Ferreira et al., 2019) and reduce beta diversity (Biasi et al., 2020) among microbial communities. In addition, non-native species can affect detritivore communities by inducing changes in nutrient availability, solar irradiation or bedding characteristics. The presence of non-native species results in the reduction of the diversity of aquatic invertebrates and influences the activity of shredders (Tonello et al. 2014; Seeney et al. 2019). More specifically, *H. dulcis* has litter with a high nutritional quality and is therefore rapidly decomposed (König et al. 2014; Biasi et al. 2020). However, *H. dulcis* may affect the structure and composition of the aquatic hyphomycete community, also decreasing its reproductive activity (Biasi et al. 2020).

Hovenia dulcis Thunb. (Rhamnaceae) is a deciduous zoochoric tree, originally from Asia, with a high invasive capacity in native forest remnants (Carvalho 1994). In subtropical region of the Atlantic Forest biome, *H. dulcis* is considered extremely aggressive, promoting homogenization of native forests and changes in ecosystems functioning (Padilha et al. 2015; Schmidt et al. 2020). This study was carried out in a remnant of Atlantic Forest biome in southern Brazil, where the biological invasion by *Hovenia dulcis* has become an increasing problem for native forest systems (Padilha et al. 2015) and for aquatic ecosystems (Biasi et al. 2020). The objective of this study was to understand the effects of this on the functioning of small streams ecosystems. We quantified the allochthonous organic matter input to streams from native tree species and *Hovenia dulcis*, over a year, and evaluated leaf litter colonization and decomposition by aquatic invertebrates. Our premises were: (1) the organic matter input in the streams can be influenced by climatic factors (e.g., temperature and rainfall) (Tonin et al. 2017); (2) the most nutritive and less tough leaf litter will be more easily colonized by detritivores (König et al. 2014); and, (3) resource homogeneity reduces the abundance and diversity of organisms (Biasi et al. 2020). Thus, our first hypothesis was that allochthonous organic matter input would be affected by climatic factors. Second, we hypothesized that *H. dulcis* leaf litter would exhibit higher decomposition rates than native plants due to its lower leaf toughness. Our third hypothesis was that there would be higher variability of abundance, richness and feeding functional groups of invertebrates on the litter of native species than that of *H. dulcis*.

Materials and methods

Study area

This study was carried out in a forest remnant (between − 27.4713 and − 27.5161 S; − 51.9208 and − 51.9616 W) located in a conservation unit (Municipal Park Mata do Rio Uruguai Teixeira Soares) in southern Brazil (Fig. 1). Geologically, the region is located around the Serra Geral formation and the climate is classified as subtropical humid (Köppen classification), with an annual mean temperature of 18.7 °C and mean rainfall of 1700 mm (Alvares et al. 2013). This area is located in the Atlantic Forest biome, which consists of a transition zone between the Semideciduous Seasonal Forest and the Araucaria Atlantic Forest (Oliveira-Filho et al. 2015). In addition, the non-native species *Hovenia dulcis* (Thunb.) Rhamnaceae occurs in this region (Padilha et al. 2015; Schmidt et al. 2020).

We selected three morphologically similar streams (2nd order; named PM, SC and BO; Fig. 1) with different densities of *H. dulcis* ((individuals per hectare: 20 in PM; 460 in

Fig. 1 Localization of forest fragment and the three subtropical streams studied in southern Brazil
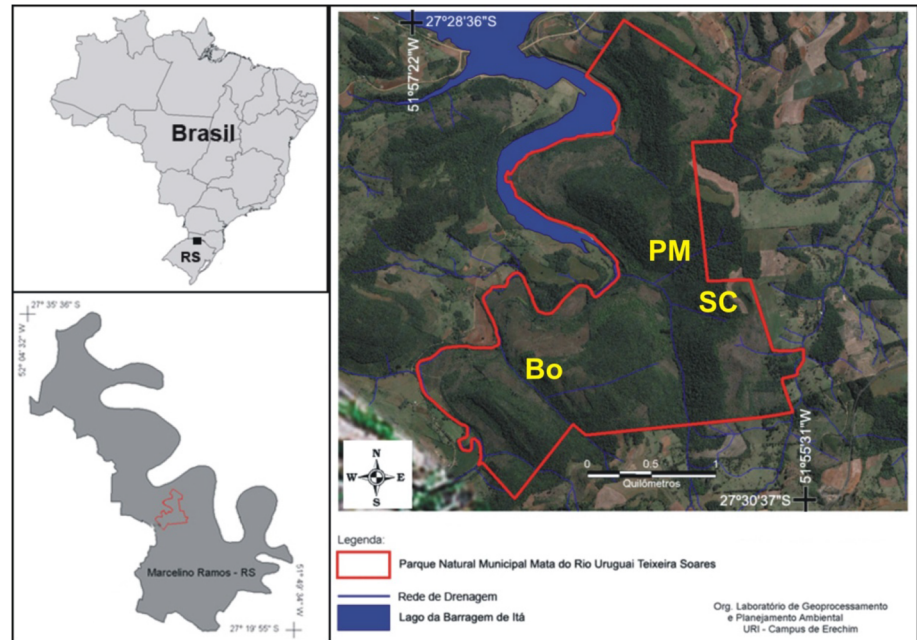
SC; 720 in BO). We measured stream water physical and chemical characteristics during the experimental period. The water from all streams was similar, with good levels of oxygenation (> 11 mg L^{-1}), slightly acidic pH (~ 6.4), and low phosphorus (< 60 µg L^{-1}) and nitrite concentrations (< 6 µg L^{-1}) (Supplementary Material, Table S1). Rainfall data were obtained during the months in which experiments were performed (June 2016–May 2017) from a weather station installed 8 km from the study site (Supplementary Material, Figure S1).

Allochthonous organic matter dynamics

In each stream, we quantified allochthonous organic matter input from plants over the course of 1 year (June 2016–May 2017) using a methodology adapted from Gonçalves and Callisto (2013). We collected allochthonous organic matter with buckets (area 0.04 m^2 per bucket), which were suspended about 1 m from the streambed in three stretches that were about 15–20 m (15 buckets were included in each stretch, and a total of 45 buckets per stream). We drilled holes in the bottoms of the buckets to drain rainfall. Monthly, we collected all allochthonous organic matter retained within the buckets, packed materials in plastic bags and transported them to the laboratory to be dried (40 ± 5 °C for 72 h), identified and weighed. From the plant allochthonous organic matter collected, we included all types of organic matter in our analyses (leaves, branches, fruits and flowers and seeds). We identified non-native *H. dulcis* plant allochthonous organic matter and weighed it separately, while plant material from native species was weighed collectively (called 'native'). We define the seasons in accordance with

the austral system, where Summer months extended from January to March, Autumn from April to June, Winter from July to September and Spring from October to December.

Litter decomposition

We used senescent leaves of non-native *H. dulcis* and native tree species commonly found in the study region. The senescent leaves were previously dried at ambient temperature (~ 20 °C/15 days). We organized two treatments, one composed of *H. dulcis* leaves exclusively and the other composed of a leaf mixture containing *Nectandra megapotamica* (Spreng.) Mez (70% of mixture), *Cryptocarya aschersoniana* Mez, *Luehea divaricata* Mart. & Zucc., *Ilex paraguariensis* A. St.-Hil., *Campomanesia xanthocarpa* O. Berg and *Ocotea puberula* (Rich.) Nees. (30% of mixture). These plant species are common in the forest remnants of the study region, including in the riparian zones of many streams (Leyser et al. 2012; Mélo et al. 2013). We chose to use a large proportion of *N. megapotamica* in the native group because this species was often dominant in the native forest remnants of the study region while the other species occurred less frequently (Leyser et al. 2012; Mélo et al. 2013). We performed a preliminary analysis to characterize the *H. dulcis* and native litter (Supplementary Material, Table S2). Only the toughness of the leaf tissues of treatments differed. It was higher ($t = 5.5$; $df = 5$; $p = 0.01$) in the group comprised of native plants (258.6 ± 41.3 g) than in the non-native treatment (109.5 ± 8.6 g).

We undertook leaf litter decomposition experiments in the Spring of 2016 (November) and Autumn (April) of 2017. In each experiment, we used 54 fine mesh litter

bags (10 × 20 cm; 0.5 mm mesh) and 54 coarse mesh litter bags (10 × 20 cm; 10 mm mesh), with 3.0 ± 0.1 g of leaves each. In each stream, we incubated 36 litter bags (18 of each mesh), which contained a subsample of native mix leaves and 36 litter bags with exclusively *H. dulcis* leaves (total = 108 litter bags). After 3, 15 and 28 immersion days, 6 litter bags of each mesh type (3 litter bags with native and non-native leaves) were randomly removed from each stream for analysis. We packed the litter bags in plastic bags and transported them to the laboratory in an ice box. In the laboratory, we washed leaves to remove sediment and associated invertebrates. We dried the leaf litter in an oven at 40 ± 5 °C/72 h. After this period, we weighed the leaves to determine the remaining mass and decomposition rates.

Associated invertebrates

We washed the leaf litter collected from the coarse mesh litter bags to remove associated invertebrates. We passed water through 250 μm mesh to retain invertebrates. We fixed the invertebrates in 70% ethanol for screening and identification using a stereomicroscope (40× magnification). We identified organisms until the family level according to the taxonomic key proposed by Mugnai et al. (2010). After identification, we classified invertebrates into functional feeding groups (FFG) according to Cummins et al. (2005), Tomanova et al. (2006) and Ramírez and Gutiérrez-Fonseca (2014).

Data analysis

We assessed data normality using the Shapiro–Wilk test and $\ln(x + 1)$ transformed data that were not normally distributed. To assess the differences in allochthonous organic matter input between seasons and organic matter origin types (*H. dulcis* and native), we used a two-way ANOVA. We verified the relationship between monthly rainfall with the native and *H. dulcis* organic matter input using a Pearson linear correlation.

We determined decomposition rates using the negative exponential model $W_t = W_0 \times e^{-kt}$, where W_t is the remaining weight at time t (in days), W_0 is the initial weight and k is the decomposition rate (Webster and Benfield 1986). We evaluated the native and non-native leaf decomposition rates in the fine and coarse mesh separately using a covariance analysis (ANCOVA; time in days as co-variable).

To determine invertebrates associated in leaf litter, we tested data normality using the Shapiro–Wilk test and homoscedasticity was assessed using the Bartlett test. We transformed $(\ln(x + 1))$ the data that were not normally distributed. We used rarefied richness to eliminate the effect of varied abundance of organisms on invertebrate richness (Gotelli and Colwell 2001). We evaluated variation
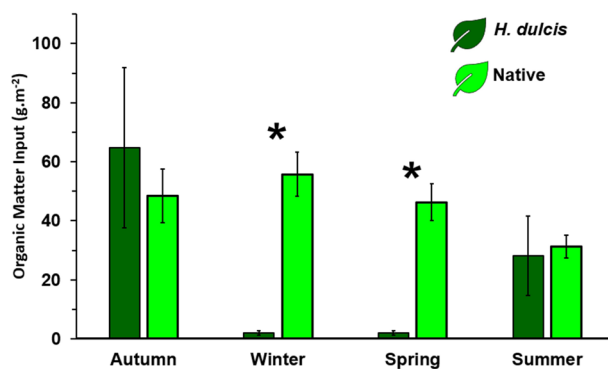

Fig. 2 Native and *H. dulcis* allochthonous organic matter input (mean ± standard error) in the three subtropical streams studied over 1 year. *Significant differences ($p < 0.05$) within seasons

Table 1 Two-way ANOVA of organic matter input between seasons (Autumn, Summer, Spring and Winter) and litter types quantified (native and *Hovenia dulcis*) in subtropical streams

	df	SS	MS	F	p value
Season	3	18.6	6.2	4.6	0.003
Litter type	1	211.0	211.0	157.0	< 0.001
Season:litter type	3	59.9	19.9	14.8	< 0.001
Residuals	208	279.5	1.3		

of abundance, rarefied richness and abundance of each functional feeding group between native and non-native leaf litter using a *t* test. In addition, we used a multivariate permutational variance analysis (PerMANOVA; 999 permutations) to evaluate the invertebrates' taxonomic and functional composition for each leaf litter type and season. We performed statistical analyses using the R statistical software with the "vegan" package (R Core Team 2017).

Results

Stream organic matter dynamics

The annual native organic matter input (181 g m^{-2}) was twofold that of *H. dulcis* (97 g m^{-2}). The highest *H. dulcis* organic matter input was in Autumn (65 g m^{-2}), while for native organic matter the highest input was in Winter (55 g m^{-2}) (Fig. 2). The organic matter input varied between the litter types and throughout the seasons (winter and spring; Fig. 2; Table 1). The native organic matter input was higher than the *H. dulcis* in Winter and Spring (Fig. 2). Only the native organic matter input was positively associated with rainfall ($r = 0.60$; $df = 10$; $p = 0.04$).

Leaf litter decomposition

Hovenia dulcis litter decomposed faster than native litter in fine and coarse mesh in both seasons (Fig. 3). In the
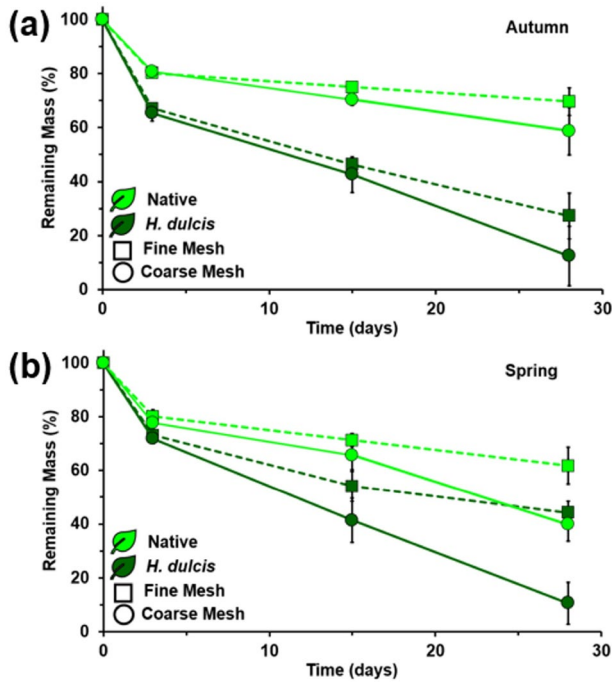

Fig. 3 Remaining mass (%) (mean ± standard error) of the native species (Native treatment) and *Hovenia dulcis* (Hovenia treatment) during Autumn (**a**) and Spring (**b**) in the three subtropical streams studied

fine mesh, the *H. dulcis* leaf decomposition was approximately twofold higher than in the native litter. The accelerated mass loss in the *H. dulcis* litter leaf resulted in higher decomposition rates compared to the native litter (Fig. 3). The *H. dulcis* fine mesh decomposition rates ($k = -0.033 \pm 0.006$ day^{-1}) was twice as high as in the native leaf litter ($k = -0.033 \pm 0.006$ day^{-1}) ($F_{(1;33)} = 73.8$; $p < 0.001$). Likewise, the *H. dulcis* decomposition rates in the coarse mesh ($k = -0.089 \pm 0.023$ day^{-1}) was four times higher than native litter decomposition rates ($k = -0.023 \pm 0.002$ day^{-1}) ($F_{(1;33)} = 68.1$; $p < 0.001$).

Associated invertebrates

We identified a total of 9119 invertebrates associated with native and *H. dulcis* leaf litter in streams throughout the experiments (Supplementary Material, Table S3). Gastropoda and Chironomidae were the most abundant (~ 46 and ~ 44%, respectively), followed by Calamoceratidae (~ 3.6%), Leptoceridae (~ 1.5%), Baetidae (~ 1%) and Leptophlebiidae (~ 1%). Other invertebrate *taxa* made up 5% of the total identified. Invertebrate abundance was similar between native and *H. dulcis* leaf litter in both seasons ($t = 0.2$, $df = 16$, $p = 0.82$ and $t = 0.8$, $df = 16$, $p = 0.40$, Autumn and Spring, respectively) (Fig. 4). In addition, we observed similar pattern for invertebrate richness in both leaf litter ($t = 1.1$, $df = 16$, $p = 0.27$ and $t = 0.6$, $df = 16$, $p = 0.54$, Autumn and Spring, respectively) (Fig. 4).

The most abundant FFG were scrapers (~ 46% of total), collectors (~ 46%) and shredders (~ 5%) (Fig. 4a–d). Gastropoda was the most abundant taxa among scrapers, and

Fig. 4 Mean values (± standard error) of abundance (**a** and **d**) and richness (**b** and **e**) and functional feeding groups (**c** and **f**) associated in the native species (Native treatment) and *Hovenia dulcis* (Hovenia treatments) during Autumn (**a**–**c**) and Spring (**d**–**f**) seasons in the three subtropical streams studied
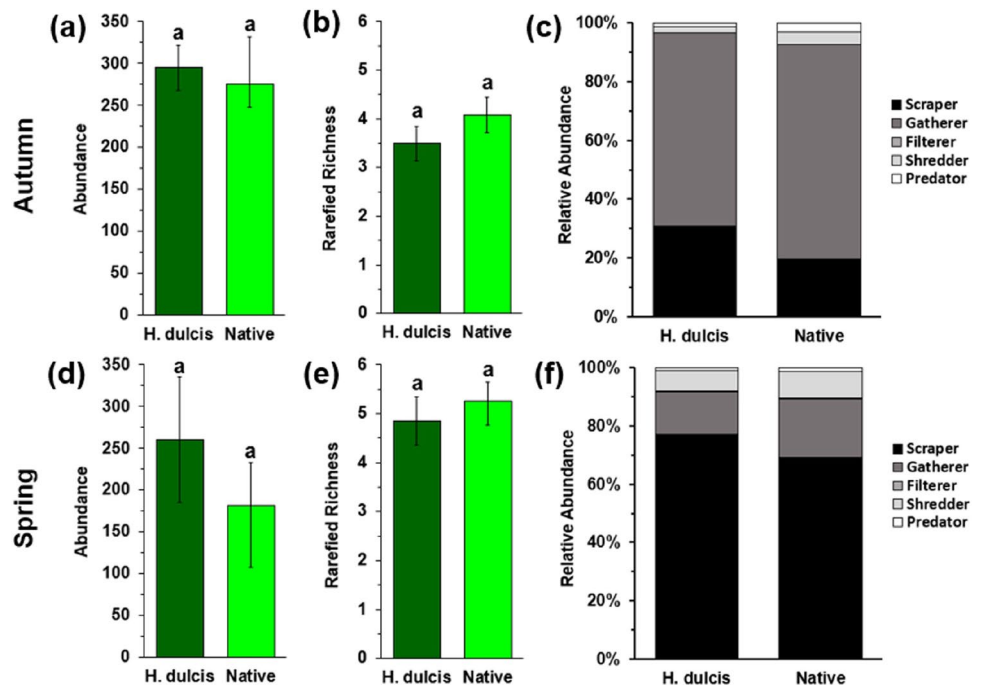
Chironomidae among collectors, whereas Calamoceratidae (genus *Phylloicus* sp.) and Leptoceridae (*Nectopsyche* sp. and *Triplectides* sp.) were the most abundant shredders. However, the relative abundance of FFG did not vary between leaf litter types (Fig. 4c, f). The invertebrate taxonomic composition was similar between the native and non-native leaf litter ($F_{(1;\ 32)} = 0.02$; $p = 0.80$), but differed between Spring and Autumn ($F_{(1;\ 32)} = 5.9$; $p = 0.001$).

Discussion

In this study, we evaluated the effects of the invasion of the non-native species *Hovenia dulcis* on the functioning of small streams in the Brazilian Atlantic Forest biome. We observed that the stream allochthonous input of organic matter to streams was significantly altered with the presence of *H. dulcis* in the riparian zone and that decomposition of the *H. dulcis* leaf litter was higher than that of native litter. However, we found no clear evidence of differences in the structure and composition of the aquatic invertebrate community associated with native and non-native leaf litter.

During the study period, the native organic matter input was twofold higher than *H. dulcis* input. However, in Autumn, with the highest *H. dulcis* input, the leaf litter input in streams was higher. The high levels of native organic matter in the Winter were due to leaf renewal, where plant species eliminated old leaves to grow new ones (Turchetto and Fortes 2014). We also observed that native organic matter input was related to rainfall, in accordance with other studies (Dick et al. 2015; Tonin et al. 2017). The average rainfall during the study period was slightly lower than the average for last 10 years. Thus, we can expect that this rainfall-organic matter relationship is common throughout the year in the region under study.

Hovenia dulcis leaf fall is dependent on lower temperatures (Schumacher et al. 2008), occurring from beginning of Autumn until mid-Winter. Other non-natives' (e.g., *Eucalyptus*) peak of organic matter input occurs normally in Summer months (Abelho and Graça 1996; Pozo et al. 1997), demonstrating that species identity is important in determining organic matter dynamics. In this study, this was clear when we observed that the input of native organic matter was higher than that of *H. dulcis*, again indicating the importance of identity for litter dynamics (Capellesso et al. 2016; Rezende et al. 2017).

The Atlantic Forest is characterized by the presence of tree species with specific phenological characteristics and different litterfall periods (Ruschel et al. 2005) leading to a consistency of energy and material input (Lisboa et al. 2015). In riparian vegetation in which *H. dulcis* predominates, vegetal allochthonous resources are limited due to restricted leaf fall patterns that occur at specific periods throughout the year (i.e., Autumn).

The leaf decomposition rates of the *H. dulcis* leaf litter were higher than those of native leaf litter, possibly because of its low toughness. Studies indicate that shredders abundance accelerates leaf decomposition (Tonin et al. 2014b; Tonello et al. 2016). However, in the present study, the accelerated decomposition of *H. dulcis* was not a direct effect of shredders that presented similar abundances between both leaf litters.

Leaf litter decomposition rates are determined by its structural and chemical characteristics and not by its origin (Zhang et al. 2019). Thus, we have shown that decomposition is faster in non-native than in native species, as seen in other studies (König et al. 2014; Medina-Villar et al. 2015). In some cases, the structure of the aquatic invertebrate community that colonizes the non-native litter may alter the aquatic invertebrate community (see Castro-Díez and Alonso 2017), possibly due to reduce nutritional quality, but we found no difference in the community between the native and non-native litter (König et al. 2014). This result was contrary to our expectations, since it is apparent that greater plant diversity typically sustains a greater diversity of consumers (Abelho 2009). It is possible that the lower toughness of the non-native species countered any litter diversity effect. We observed that litter-dwelling invertebrate communities varied between seasons. Similarly, invertebrate assemblages have been shown to be structured by season rather than the type of litter available (Larrañaga et al. 2014).

Conclusion

Our main conclusion was that the establishment of *H. dulcis* in riparian vegetation altered the organic matter dynamics and litter decomposition in the streams. While native organic matter input was relatively constant throughout the year, varying with rainfall intensity, the input of *H. dulcis* was seasonal. Although we found no differences in invertebrate communities between litter types, the changes in organic matter dynamics may affect ecosystem functioning, although we have no evidence of this. The *H. dulcis* input in a single period of year and its rapid decomposition can alter the availability of allochthonous resources, affecting the use of this resource by stream organisms. In addition, when *H. dulcis* is dominant in riparian zones, it can potentially decrease the diversity of allochthonous plant resource in streams.

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