ELSEVIER

Eucalyptus leaves are preferred to cerrado native species but do not constitute a better food resource to stream shredders

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A B S T R A C T

We investigated food preferences, growth and survival of the caddisfly shredder *Phylloicus angustior* while exposed to leaves of *Eucalyptus camaldulensis* and three native tree species (*Myrcia guianensis*, *Miconia chartacea*, and *Protium brasiliense*) of the Brazilian Cerrado. Because of the low quality of native leaves, we hypothesized that *E. camaldulensis* would be preferred and would promote higher growth and survival of shredders than Cerrado species. Except for *P. brasiliense*, all leaves were consumed in the food preference experiment and *E. camaldulensis* was preferred to native species. Shredder preferences were similar in an *in situ* experiment, and the consumption rates did not differ between the laboratory and field conditions. In the monodietary experiment, shredder daily growth rates were positive (4.76–6.83%) and did not differ among leaves. Survival of larvae that fed on *E. camaldulensis* and *M. chartacea* was significantly higher than those that fed on *M. guianensis* and *P. brasiliense*. Our results showed that *E. camaldulensis* can be an attractive food resource for *P. angustior* in Cerrado streams. However, the lack of differences in growth do not fully support the proposed hypothesis and suggests that *E. camaldulensis* does not constitute a better food resource than native leaves of worse quality.

1. Introduction

Allochthonous inputs of leaf litter are an important energy source for aquatic communities living in shaded headwater streams (Webster and Benfield, 1986; Abelho, 2001). After entering streams, leaves are retained on the streambed where they are used as food and habitat resources by different detritivores (Mathuriau et al., 2008). Previous studies concerning the feeding ecology of invertebrate shredders revealed that they prefer to feed on leaves that promote higher growth and survival (Balibrea et al., 2017; Canhoto and Graça, 1995), rejecting leaves that are tough and poor in nutrients and that contain high amounts of secondary compounds (Li and Dudgeon, 2008; Rincón and Martínez, 2006). It is also known that invertebrate shredders prefer conditioned leaves, i.e., leaves colonized by aquatic microorganisms, over poor conditioned or unconditioned leaf material (Foucreau et al., 2013). The composition of tree species in riparian vegetation can also influence the behavior and distribution of shredders because both are directly related to the quality and availability of leaves on the streambed (Marcarelli et al., 2011). Bastian et al. (2007), who manipulated the diversity of shredders and leaf litter in a detritus food web in Australia, suggested that lowered leaf diversity promotes competitive interactions among shredders.

Riparian zones are highly susceptible to invasion by exotic species since streams work as dispersal corridors (Naiman et al., 2005). On the other hand, many of the species used in commercial forestry around the world are exotic, and these plantations are frequently close to or replace riparian vegetation (Hood and Naiman, 2000). Most of the studies that assess the effects of exotic leaves on shredder performance were developed in environments in which these leaves have relatively poor quality, such as the Iberian Peninsula and other temperate regions in Europe and North America. These studies reported low leaf consumption, growth and survival of shredders when feeding on exotic species (Alonso et al., 2010; Canhoto and Graça, 1995; Reinhart and VandeVoort, 2006). However, in some streams of Australia and New Zealand, exotic species in riparian zones produce leaf litter of high quality, which is processed more rapidly than that of native species by

microbial and invertebrate decomposers (Greenwood et al., 2004). In the tropics, it is expected that the effects of exotic leaves on stream processes vary across different biomes and geographic regions because streams are naturally surrounded by a high diversity of plant species (Tonin et al., 2017) that present a wide range of leaf characteristics (Hättenschwiler et al., 2011). In a meta-analysis study, Ferreira et al. (2016) suggested that *Eucalyptus* plantations may have stronger negative effects on leaf decomposition rates in streams naturally receiving high-quality litter inputs and where detritivores abundance is high.

In Brazil, *Eucalyptus* trees were first introduced in 1868 (Miritz et al., 2008). Currently, *Eucalyptus* plantations occupy an area of 6 million hectares and are one of the greatest threats to the Brazilian Cerrado, a savanna-like ecosystem that is considered to be a biodiversity hotspot in South America (Myers et al., 2000). Many areas with native vegetation, including riparian zones, are being deforested and replaced with *Eucalyptus* monocultures (Maquere et al., 2008) to provide wood for a variety of purposes (e.g., charcoal, paper industry, furniture). Compared with other tropical biomes, in the Cerrado, leaves of tree species are considered to be low quality and present higher concentrations of secondary and structural compounds (Moretti et al., 2007a, 2007b).

To evaluate the effects of exotic *Eucalyptus* leaves on the performance of shredders found in Brazilian Cerrado streams, we investigated the food preferences, growth, and survival of larvae of *Phylloicus angustior* (Ulmer, 1905) that were exposed to the leaves of *Eucalyptus camaldulensis* Dehn. and that of three native tree species (*Myrcia guianensis* Aubl., *Miconia chartacea* Triana, and *Protium brasiliense* Engl.). Because of the low quality of native leaves, we hypothesized that *Eucalyptus* leaves would be preferred and would promote higher growth and survival of shredders than do Cerrado native species. Laboratory trials were used to evaluate food preferences (multiple-choice experiments), growth and survival (monodietary experiments) of *P. angustior*. Food preferences and consumption rates of *P. angustior* were also determined in an *in situ* experiment to validate the results from the laboratory trials, i.e. to evaluate if they are similar to those observed in nature. Additionally, leaf palatability may change in field conditions because leaves are continually exposed to water flow and microbial colonization during the experiment.

2. Materials and methods

2.1. Shredders

The caddisfly genus *Phylloicus* (Trichoptera, Calamoceratidae) used in our experiments is one of the few invertebrate taxa considered to be a shredder in Cerrado streams. Individuals of this genus can be found throughout the Americas (Prather, 2003) and have been used in laboratory experiments that evaluate the behavior of tropical shredders (see Becker et al., 2009; Graça et al., 2001; Moretti et al., 2009; Rezende et al., 2015; Rincón and Martínez, 2006). In Brazil, *P. angustior* was recorded in the South, Southeast and Central-West regions (Paprocki and França, 2014). A total of 384 larvae of this species were collected by hand on several occasions between August and December 2006 in Taboões (20° 03′ 38″ S - 44° 03′ 03″ W). This spring is located within the Serra do Rola Moça State Park, Minas Gerais State, southeastern Brazil. Taboões spring is surrounded by a native forest (ca. 92 hectares) with diverse woody riparian vegetation (ca. 90 tree species) that is mainly composed of Cerrado plant species (e.g., *Aspidosperma subincanum* Mart., *Casearia sylvestris* Sw., *Ocotea corymbose* (Meisn.) Mez). Some tree species, such as *Inga marginata* Willd. and *Tabebuia serratifolia* (Vahl) G. Nichols., characteristic of the transition zone between Cerrado and Atlantic Forest are also present (Meyer et al., 2004). Fallen leaves form patches along the spring margins year-round, and this substrate supports a large population of *P. angustior* (ca. 110 ind.m^2). Spring waters were well oxygenated (7.2 mg.L^{-1}), alkaline (pH 7.9) with low conductivity (13.0 μS cm^{-1}) and nutrient

concentrations (Total N: 35.0 μg.L^{-1}; Total P: 3.0 μg.L^{-1}). Values of water temperature ranged from 20.2 to 21.3 °C. More information of Taboões spring can be found in Moretti et al. (2009).

After collection, the larvae were placed in an isothermic box with spring water and were brought to the laboratory, where they starved for two days in an aquarium (80 cm long, 20 cm wide, 40 cm high) filled with spring water and had a bottom layer of fine gravel (which had been sterilized previously by incinerating for 4 h at 500 °C) to not constrain larvae movement. The aquarium was aerated continuously and maintained at 21 °C under a 12:12 light-dark photoperiod.

2.2. Leaves

We used senescent leaf material in all experiments. Leaves of *M. guianensis*, *M. chartacea*, and *P. brasiliense* were chosen because they are abundant in the riparian zones of Cerrado streams in Minas Gerais (Gonçalves et al., 2006). These are low quality leaves that are used for case-building by larvae of *Phylloicus* (Moretti et al., 2009). All the leaves were collected at the same time from the litter traps (1 m^2, 10 mm mesh size, approximately 1.5 m height) fixed in the riparian zone of Taboões (native species) and in a monoculture of *E. camaldulensis* located nearby. Leaves were air-dried and stored at room temperature until needed. Before use in the experiments, the leaves were conditioned by incubating in fine-mesh bags (10 × 15 cm; 0.5 mm mesh size) for two weeks in the spring. The initial chemical composition of the four species was determined from leaves randomly selected from different litter bags. The total nitrogen content of the leaves was determined using the Kjeldahl method, and the total phosphorus was measured by the ascorbic-acid method (Flindt and Lillebø, 2005). Nitrogen to phosphorus (N:P) ratios were calculated from the dry mass by dividing the nitrogen fraction (%N) by the phosphorus fraction (%P). Tannins were determined as tannic-acid equivalents by a radial-diffusion assay (Graça and Bärlocher, 2005), and the approximate lignin and cellulose contents were determined gravimetrically according to Gessner (2005). All analyses were performed with 4 replicates.

2.3. Food preference experiments

We assessed the food preference of the larvae of *P. angustior* using the multiple-choice approach described in Graça et al. (2005) under laboratory and field conditions. In the laboratory, the feeding arenas consisted of plastic cups (12 cm diameter, 9 cm high) that contained sterilized fine gravel and 400 ml filtered spring water (Whatman Glass Microfiber filters, Grade 934-AH). All cups were maintained under the same temperature and the photoperiod conditions described above, and were aerated through pipette tips connected to an aquarium pump. In Taboões, the feeding arenas consisted of PVC pipes (5 cm diameter, 20 cm long) closed with a fine mesh (0.5 mm mesh size) on both sides. The pipes were tied randomly, at a distance of 20 cm from each other, to five nylon ropes (1.5 m long) that were fixed parallel to the spring bottom with iron bars, under similar conditions of depth and flow.

Larvae of *P. angustior* of similar size (2nd–3rd instars) were visually selected from the pool of organisms and were placed individually in each arena. Food was offered in the form of leaf discs (1.4 cm diameter). Paired discs were cut from symmetrical areas of leaves, in relation to the main vein, with a cork borer. For each arena (replicate), we cut one pair of each of the four leaf species. One disc of each pair was used as the control, and the other was offered to the shredder. The control discs were placed inside small 0.5 mm mesh bags marked with colored pins (one color for each leaf species). These small mesh bags were suspended from the rim of the cups or were tied close to the inner surface of the pipe so that the discs were fully submerged but inaccessible to the larvae. The leaf discs offered to the larvae were also marked with colored pins. The number of replicates (feeding arenas) was 80 in both the laboratory and field trials.

The larvae were allowed to feed until one of the leaf discs was

reduced to about two-thirds of its initial size, which was achieved within 1–4 days, in both the laboratory and field conditions. The leaf material remaining after the feeding period (control and exposed discs) was dried at 60 °C for 72 h and weighed to the nearest 0.01 mg. The larvae were also dried and weighed. The individual consumption of each leaf species was expressed in terms of the mg of the leaf dry mass ingested (the difference between the weight of the control and the exposed discs) per individual biomass (mg) over the feeding period (days).

2.4. Monodietary experiment

To assess the food value of each leaf species, we determined, in the laboratory, the growth and survival of the larvae fed exclusively on *E. camaldulensis*, *M. guianensis*, *M. chartacea*, or *P. brasiliense*. The larvae selected for these experiments had an initial interocular distance between 0.54 mm and 1.11 mm. The initial dry mass of each larva was estimated by relating the interocular distance (mm) to the animal dry mass (mg). The established relationship for this population of *P. angustior*, after Becker et al. (2009), was:

$$\ln DM = 2.50 + 3.84 (\ln ID) \ r^2 = 0.71, n = 54$$

where ID = interocular distance and DM = animal dry mass. The interocular distance was measured as the minimum distance between the eyes, parallel to the head width, with a Zeiss dissecting microscope fitted with an ocular micrometer ($50 \times$ magnification).

After acclimatization, the larvae were individually allocated into the aerated feeding arenas as described above. Each arena contained 5 discs (1.4 cm diameter) from one of the four leaf species (treatments). Food, gravel, and filtered spring water were replaced every week, and the arenas were maintained under the same temperature and photoperiod conditions as above. The monodietary trials were to be maintained until pupal development was first observed or until other factors, such as high mortality, made termination necessary. The final dry mass of each larva was measured directly. Because of the limited number of organisms collected per sampling day, we used a randomized block design, and the trials were run in 3 blocks across 3 months (one block per month). The same number of replicates of each food treatment was assigned to each block (20, 18 and 18 replicates per treatment in blocks 1, 2 and 3, respectively), and a total of 56 replicates per treatment was used.

The larval daily growth rates (DGR) and specific growth rates (SDGR) were obtained according to Feio and Graça (2000):

$$DGR = (DM_f - DM_i) / t$$

$$SDGR = (DGR / DM_i) \times 100$$

where DM_i is the initial dry mass, DM_f is the final dry mass, and t is the feeding period (days). The feeding arenas were checked every day, and the survival (% of larvae alive on each day) was calculated for each treatment.

2.5. Statistical analysis

The differences in the leaf chemical properties were tested using one-way ANOVA and Tukey's HSD test after an arcsine square-root transformation. In the food preference experiments, the first procedure consisted of analyzing the data to determine whether the larvae had consumed a significant amount of each leaf species. For this, we used paired *t*-tests to compare the mean weights of the exposed leaf discs and the corresponding control discs. If no differences were found, then the larvae had not significantly consumed that leaf species and it was not used in further analysis. Consumption rates were evaluated by permutation tests (Graça et al., 2005). Permutation tests were used because the consumer choice is not independent in multiple-choice experiments. These tests are more flexible than standard tests and do not require a normal distribution of data and errors. For each possible pair of leaf species, we calculated the differences between the original consumption values. These differences were shuffled and were randomly assigned among the pairs. For each pair of leaf species, the average of shuffled differences was compared with the average of original differences 10,000 times. The *P*-value was determined by dividing the number of times that the average of shuffled differences was larger than the average of the original differences by the number of permutations used. *P*-values were adjusted by False Discovery Rate (FDR), a method of conceptualizing the rate of type I errors in null hypothesis testing when conducting multiple comparisons. By convention, $P < 0.05$ would lead to the rejection of H_0, which assumes that there is no significant difference in the consumption of the two leaf species that constitute the pair. We used *t*-tests (for independent samples) to determine if there were significant differences in the larvae consumption rates of each leaf species under laboratory and field conditions.

In the monodietary experiment, the effect of leaf species on larval growth was analyzed by Generalized Linear Mixed Models (GLMM). The food treatment was treated as fixed factor and blocks as random factor. Only larvae surviving until the end of the experiment were included in the analyses. The log-rank test was used to compare survivorship of larvae in the four food treatments (Hutchings et al., 1991). The normality and homogeneity of variances of all data were tested, and the ANOVA and GLMM models were validated by the analysis of the residuals. The statistical analyses were performed using R (R Development Core Team, 2017) and the packages 'coin' and 'rcompanion' (permutation test), 'lme4', and 'survival'.

3. Results

3.1. Leaf characteristics

The leaf litters of *E. camaldulensis*, *M. guianensis*, *M. chartacea*, and *P. brasiliense* differed in their initial chemical composition (Table 1). The nitrogen and phosphorus contents varied among the leaf species. *E. camaldulensis* had two-fold the nutrient content of *P. brasiliense*, which is the native species with the highest nitrogen and phosphorus contents. The N:P ratio for *M. chartacea* was the highest (83:1) and differed from those for *M. guianensis* (37:1), *P. brasiliense* (26:1), and *E. camaldulensis* (22:1). *P. brasiliense* had the lowest amount of tannins (2.4%), while the

Table 1
Leaf chemistry values for *Eucalyptus camaldulensis*, *Myrcia guianensis*, *Miconia chartacea*, and *Protium brasiliense* (mean $\pm$ SE; n = 4) and ANOVA F values.

Leaf chemistry	E. camaldulensis	M. guianensis	M. chartacea	P. brasiliense	F
Nitrogen (%)	1.65 ± 0.03[a]	0.66 ± 0.02[b]	0.59 ± 0.01[c]	0.74 ± 0.01[d]	656.4*
Phosphorus (%)	0.076 ± 0.002[a]	0.018 ± 0.001[b]	0.007 ± 0.001[c]	0.029 ± 0.001[d]	678.0*
Nitrogen:Phosphorus	21.87 ± 0.14[a]	37.13 ± 0.30[a]	82.89 ± 2.96[b]	25.98 ± 0.25[a]	24.8*
Tannins (%)	8.16 ± 1.06[a]	8.11 ± 0.39[a]	6.00 ± 0.52[a]	2.44 ± 0.28[b]	25.2*
Lignin (%)	12.87 ± 0.74[a]	30.68 ± 1.07[b]	36.23 ± 0.20[c]	28.85 ± 1.07[b]	148.4*
Cellulose (%)	15.93 ± 0.59[a]	23.07 ± 1.16[b]	23.69 ± 0.49[b]	26.93 ± 0.97[b]	31.8*

*$P < 0.001$. Values sharing superscript letters are not significantly different ($P > 0.05$).
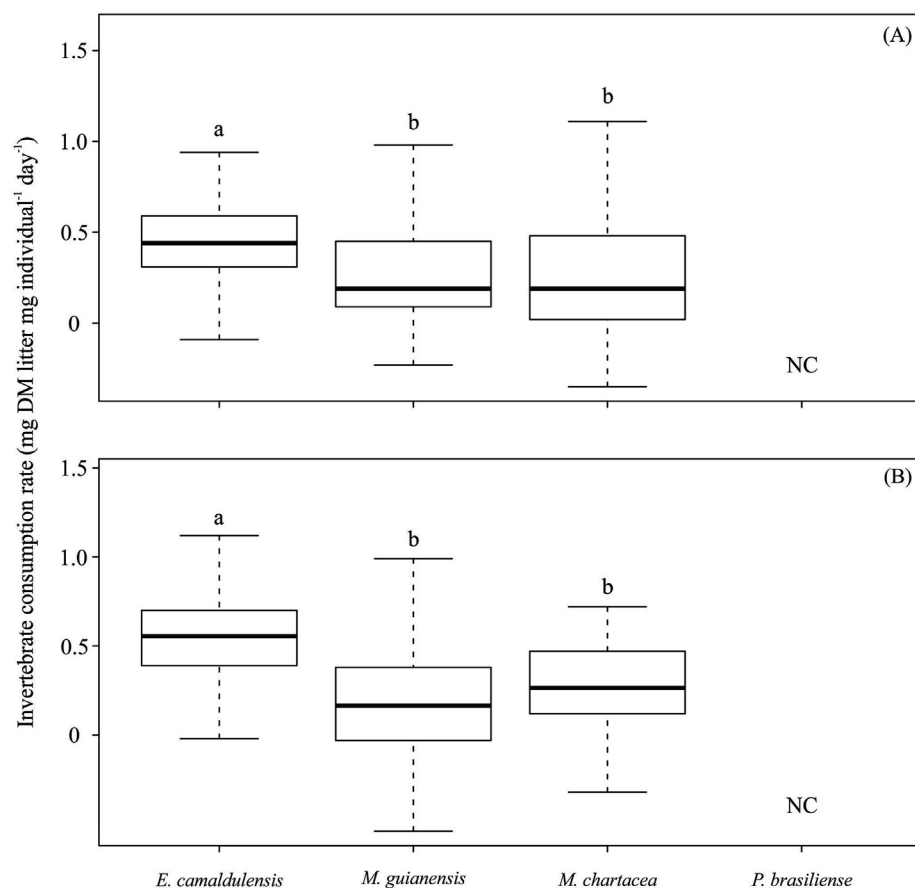
Fig. 1. Food preference of larvae of *Phylloicus angustior* exposed to *Eucalyptus camaldulensis*, *Myrcia guianensis*, *Miconia chartacea*, and *Protium brasiliense* in multiple-choice feeding experiments conducted in the laboratory (A) and in the field (B). NC = no consumption. Boxplot legend: Median (midline), 25th and 75th percentiles (box), maximum and minimum values (whiskers). Values sharing superscript letters are not significantly different ($P > 0.05$).

other three species contained similar amounts (6–8%). *M. chartacea* had the highest amount of lignin (36%). The highest cellulose contents were found in *P. brasiliense*, *M. chartacea*, and *M. guianensis* (26-23%). The lowest amounts of lignin and cellulose were found in *E. camaldulensis* (12 and 15%, respectively; Table 1).

3.2. Food preference experiments

In the food preference experiments, the mortality rates of *P. angustior* were low (approximately 1% in both experiments: laboratory and field), and none of the larvae used the leaf discs for case-building. This could be noticed because larvae cut the leaf discs differently when they are feeding (rough cuts) and building their cases (smooth cuts). The larvae consumed a significant amount of all the leaf species, with the exception of *P. brasiliense* (paired *t*-test, $P > 0.05$), under both laboratory and field conditions. The discs of *E. camaldulensis* were consumed more than those of *M. chartacea* and *M. guianensis* in both experiments (Fig. 1A and B; Table 2). The consumption rates observed under laboratory and field conditions did not differ in any leaf species

Table 2
Analysis of leaf consumption data in the food preference experiments. Differences between the averages of consumption of each possible pair of leaf species and the *P* values of permutation tests. *Protium brasiliense* was not consumed in both laboratory and field trials.

	Difference		*P*	
	Laboratory	Field	Laboratory	Field
E. camaldulensis – M. guianensis	+0.163	+0.346	0.001	< 0.001
E. camaldulensis – M. chartacea	+0.140	+0.256	0.017	< 0.001
M. guianensis – M. chartacea	−0.023	−0.090	0.709	0.081

Table 3
Consumption rates (mg mg^{-1} day^{-1}) of *Eucalyptus camaldulensis*, *Myrcia guianensis*, and *Miconia chartacea* (mean ± SE) in the food preference experiments and the *t*-tests results. *Protium brasiliense* was not consumed (NC) in both laboratory and field trials.

	Consumption				
	Laboratory	Field	*t*	df	*P*
E. camaldulensis	0.456 ± 0.031	0.537 ± 0.034	−1.77	151	0.080
M. guianensis	0.292 ± 0.038	0.191 ± 0.038	1.90	152	0.059
M. chartacea	0.316 ± 0.049	0.281 ± 0.035	0.57	137	0.572
P. brasiliense	NC	NC			

(Table 3).

3.3. Monodietary experiment

The monodietary experiment ended after 21 days, when the larval mortality under the *P. brasiliense* food treatment became excessive (68%). Only a few larvae (approximately 5%) in all food treatments used the leaf discs for case-building and none of the larvae pupate. The larvae of *P. angustior* grew positively in the four food treatments, with the daily growth rates ranging from 0.08 to 0.14 mg day^{-1} and the specific daily growth rates ranging from 4.76 to 6.83% (Fig. 2). However, none of these growth rates differed significantly among the food treatments (Table 4). At the end of 21 days, 55% of the 224 larvae that started the experiment had died. The survival of larvae fed on *E. camaldulensis* and *M. chartacea* was significantly higher than those fed on *M. guianensis* and *P. brasiliense* (logrank statistic > −2.88, $P < 0.05$; Fig. 3). No significant differences were found in larval survival within these two groups (logrank statistic < 1.05, $P > 0.05$).
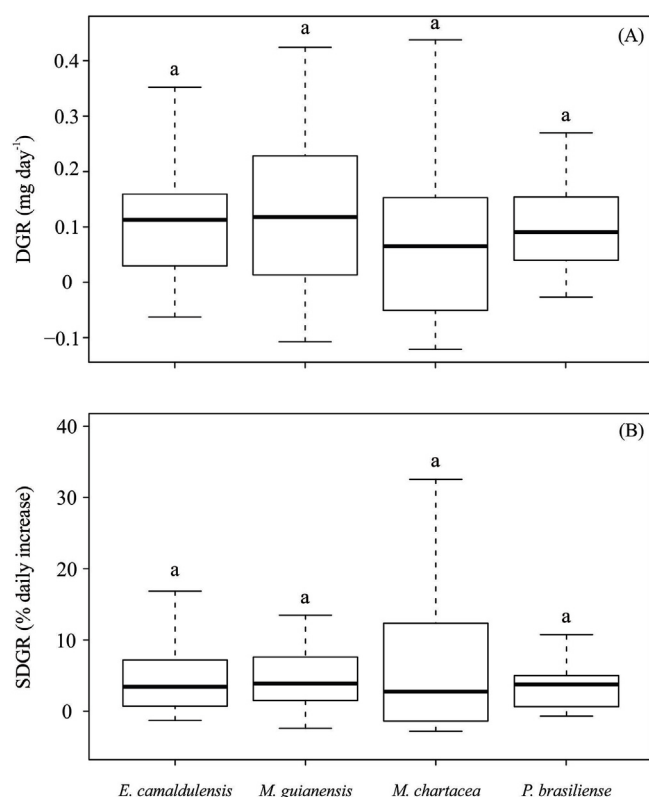
Fig. 2. Daily growth rates (DGR, A) and specific growth rates (SDGR, B) of larvae of *Phylloicus angustior* fed on *Eucalyptus camaldulensis*, *Myrcia guianensis*, *Miconia chartacea* or *Protium brasiliense* for 21 days in the monodietary experiment. Boxplot legend: Median (midline), 25th and 75th percentiles (box), maximum and minimum values (whiskers). Values sharing superscript letters are not significantly different ($P > 0.05$).

Table 4
Variation in the daily growth rates (DGR) and specific growth rates (SDGR) of larvae of *Phylloicus angustior* in monodietary experiments depending on leaf species (fixed factor) and block of replicates (random factor) tested by Generalized Linear Mixed Models (GLMM).

	Factor	SS	MS	*F*	df	*P*
DGR	Leaf species	0.017	0.009	0.717	2	0.532
	Block	0.650	0.325	27.230	2	0.003
	Error	0.992	0.013		77	
SDGR	Leaf species	43.197	21.599	0.272	2	0.772
	Block	1190.552	595.276	7.607	2	0.036
	Error	7452.353	96.784		77	

4. Discussion

The leaves of *E. camaldulensis* had the highest nutrient content and the lowest amounts of lignin and cellulose among the four leaf species. These leaf characteristics were probably responsible for the attractiveness of this exotic species to the larvae of *P. angustior*. As expected, the discs of *E. camaldulensis* were preferred over those of *M. chartacea* and *M. guianensis*, which are the native leaves that were consumed in the food preference experiments under laboratory and field conditions. These results suggest that other chemical compounds present in the leaves of *E. camaldulensis*, such as essential oils, did not diminish nutrient effects on shredder preferences. The essential oils of *Eucalyptus* leaves are known to decrease leaf palatability and may detain leaf consumption, mainly when shredders are not able to avoid the oil glands (Canhoto and Graça, 1995). In addition, the consumption rates of *E. camaldulensis* that were observed here contrast with those from

other studies that also evaluated the food preferences of shredders in the presence of *Eucalyptus* leaves (see Canhoto and Graça, 1995; Correa-Araneda et al., 2015; Yeates and Barmuta, 1999) and found lower consumption of these leaves. Beyond these studies have used different eucalypt species, which may differ in their intrinsic characteristics (e.g., cuticular thickness, phenol content, and the components and quantities of essential oils), the conditioning status of the leaves offered to shredders (see Bastian et al., 2007) and the low quality of native leaves used might have contributed to the high consumption rates of *E. camaldulensis* that was observed in the present study.

The lack of consumption of *P. brasiliense* in the presence of other species with lower nutrient content and higher tannin concentrations suggests that leaves of this species may contain other defensive compounds that limit microbial conditioning and make it difficult for shredders to consume. This species and other neotropical species of the family Burseraceae have leaves with epicuticular wax and many oil ducts (Watson and Dallwitz, 1992) that may act as a barrier to microbial colonization and shredder feeding. Rüdiger et al. (2007) demonstrated that some of these leaf oils have antimicrobial properties. The slow decomposition rate of *Protium* leaves observed by Moretti et al. (2007a) in Cerrado streams ($k = -0.0020$ d^{-1}) and the low survivorship of the larvae of *P. angustior* feeding on this species in our monodietary experiment (32% after 21 days) also support this hypothesis.

Several studies have reported the effects of leaf chemistry and toughness on the feeding of shredders (see Ardón et al., 2009; Balibrea et al., 2017; Graça et al., 2001). Rincón and Martínez (2006) observed that the larvae of *Phylloicus* sp. from Venezuela preferred to feed on leaves with a high nutrient content and low lignin and polyphenol concentrations, while Kiffer et al. (2018) observed that the larvae of *Triplectides gracilis* (Burmeister, 1839) preferred leaves with a low N content and intermediate values of toughness, even those that resulted in high mortality rates. In Hong Kong, Li and Dudgeon (2008) found that leaf toughness was the primary determinant of feeding and fitness of *Anisocentropus maculatus* Ulmer, 1926. In the present study, the food preference results of *P. angustior* could not be totally explained by the initial chemistry values of litter. This may be a consequence of the high lignin contents and the low nutrient quality of the native species, which had N:P ratios that were among the highest reported for leaf litter (see Correa-Araneda et al., 2017; Frost et al., 2002). These characteristics prevented us from evaluating food preferences using a broad ranking of leaf toughness and nutritional quality. On the other hand, the majority of Cerrado leaves have similar characteristics, and shredders are naturally exposed to this type of leaf litter in streams (Oliveira and Marquis, 2002).

The larvae of *P. angustior* showed similar food preferences under laboratory and field conditions. Because of the constant water flow, leaf microbial colonization and water physical abrasion, we expected an increase in the palatability of native leaves in relation to *E. camaldulensis* in the field setting, thus enhancing the consumption of the native leaves (Northington and Webster, 2017). However, our results suggested that field conditions did not provide an increase on litter quality during the experiment and the intrinsic characteristics of the leaves were the most important determinant to shredder food preferences. Because no differences were found between the consumption rates observed under laboratory and field conditions for each leaf species, our study supports the applicability of the laboratory approach to evaluate shredder behavior and consumption.

The stoichiometric theory implies that food quality depends on the nutritional requirements of individual consumers (Cross et al., 2003; Frost et al., 2002). Although leaves of *E. camaldulensis* have a higher nutrient content than native leaves, the growth experiments revealed that this leaf species was not a better-quality food resource for *P. angustior*. The growth rates were highly variable, but no differences were found among the food treatments. Similar patterns were observed by Rincón and Martínez (2006) in assessing the growth of *Phylloicus* sp. when exposed to leaves of the tropical *Ficus* sp. L. and *Tabebuia rosea*
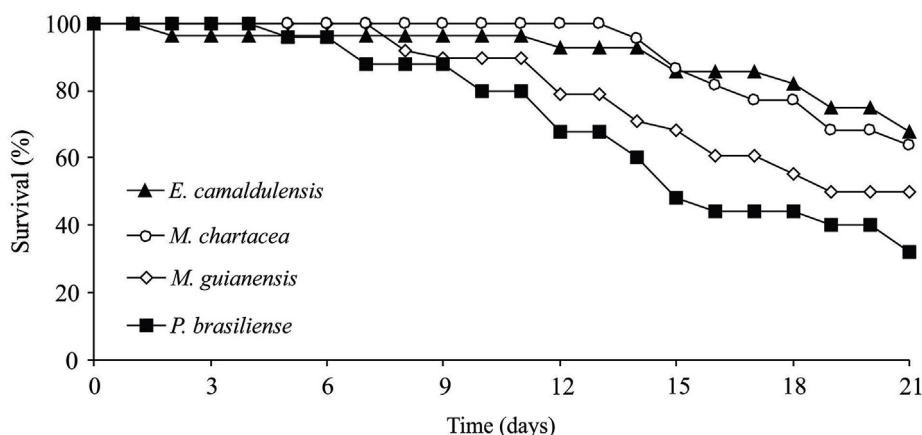
Fig. 3. Survival (%) of larvae of *Phylloicus angustior* fed on *Eucalyptus camaldulensis*, *Myrcia guianensis*, *Miconia chartacea* or *Protium brasiliense* for 21 days in the monodietary experiment.

(Bertol.) DC. Compared to the present study, these authors also found higher specific daily growth rates than those reported here, which corroborated the low food value of the leaf species that were used in our experiments. In addition, the daily growth rates that were measured in our study were almost 3 times lower than that measured in a similar experiment, when the larvae of *P. angustior* from the same population were fed on leaves of *Alnus glutinosa* (L.) Gaertn., a fast-decomposing and nitrogen-rich leaf species from temperate latitudes (M.S. Moretti, *unpublished data*). Therefore, we believe that larval growth in this study was probably limited by nutrients and the presence of secondary compounds.

The survival rates of *P. angustior* were low compared to shredders from temperate streams (see Canhoto and Graça, 1995; Going and Dudley, 2008). Furthermore, the survival of larvae fed on *E. camaldulensis* and *M. chartacea* was higher than that of larvae fed on *M. guianensis* and *P. brasiliense*, which suggested that among the three consumed leaf species in the food preference experiments, *M. guianensis* was the worst food resource in terms of quality. The same leaves used in this study were also used to assess the *Phylloicus* case-building behavior (Moretti et al., 2009). Surprisingly, the species that were more used to building cases (*E. camaldulensis* and *M. guianensis*) were also consumed by the larvae. Taken together, the results of these two studies confirmed the low attractiveness of *P. brasiliense* leaves in multiple-choice trials, which were not consumed and were less used for case-building.

5. Conclusion

In summary, our results showed that the leaves of *E. camaldulensis* can be an attractive food resource for *P. angustior* in Cerrado streams, thus promoting higher consumption rates than native leaves of worse quality. However, the lack of differences observed in the growth rates does not fully support the proposed hypothesis and suggests that exotic *Eucalyptus* leaves did not constitute a better food resource to shredders in our experiments. The low quality of food resources naturally available in Cerrado streams might impose a constraint to shredder consumption and survival, which probably reflects their lower abundance and the slow decomposition rates of native species in these ecosystems. The assimilation efficiency and survival of *P. angustior* feeding on the leaves of *Eucalyptus* during longer periods should also be evaluated to completely understand the effects of these exotic leaves on shredders performance and, consequently, on detritus-based food webs.

CRediT authorship contribution statement

Marcelo S. Moretti: Formal analysis, Writing - original draft. **Bárbara Becker:** Formal analysis, Writing - original draft. **Walace P.**

Kiffer: Formal analysis, Writing - original draft. **Lyandra O. da Penha:** Formal analysis, Writing - original draft. **Marcos Callisto:** Writing - original draft.

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.

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