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### Invertebrate colonisation during leaf processing of native, exotic and artificial detritus in a tropical stream

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**Abstract.** The relationship between leaf breakdown and colonisation by invertebrates in tropical aquatic ecosystems is poorly understood, especially in regard to the added problem of the potential effects of exotic species. To assess the colonisation by invertebrates during leaf breakdown in a third-order headwater stream in south-eastern Brazil, we conducted an experiment using the native species *Miconia chartacea*, the exotic species *Eucalyptus grandis* and artificial leaves. We hypothesised that the quality of the detritus and the leaf shape influence invertebrate colonisation because of the quality of the food and refuge offered by leaf detritus. Invertebrate density and richness were higher on leaves of *E. grandis* than on those of *M. chartacea*. Taxon richness did not differ among *M. chartacea* and the two sizes of artificial leaves offered, probably as a function of the chemical composition of *E. grandis*. Total invertebrate density was significantly higher in the organic detritus, suggesting that detritus provides food for the organisms. Our results indicate that the colonisation of invertebrates had no difficulty in colonising *E. grandis*, although it is an exotic species. In addition, the shredder activity did not influence leaf breakdown. These results may indicate that the invertebrates in this stream tend to behave as generalist feeders.

Additional keywords: artificial detritus, breakdown, Cerrado, chemical composition, Eucalyptus, exotic species.

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#### Introduction

In water, leaves break down as a consequence of the actions of decomposers (bacteria and fungi), invertebrates and abiotic processes (e.g. leaching and physical fragmentation) (Gessner *et al.* 1999). The incorporation of leaf litter in secondary production produces abundant fine particles of organic matter, which are used as food by collectors and filterers (Romito *et al.* 2010). However, the role of invertebrates in leaf breakdown in tropical regions is still unclear and requires further investigation (Boyero *et al.* 2012). Similarly, the reasons for the low abundance and proportion of shredders found during the colonisation processes remain unclear (Mathuriau and Chauvet 2002; Moulton *et al.* 2010).

Colonisation of detritus by invertebrates in lotic systems is influenced by factors such as conditioning of leaves by the microbial community (Gessner *et al.* 1999), chemical composition (Moretti *et al.* 2007) and the use of detritus as a substrate and habitat (Godoy and Coutinho 2002). Together, these factors influence the community structure and the relative abundance of the organisms and their trophic interactions (competition and predation) (Warfe and Barmuta 2004). Some studies have shown that invertebrate colonisation can be influenced by the degradative ecological succession in the breakdown of the decomposing detritus (Gonçalves *et al.* 2004; Ligeiro *et al.* 2010). Others have demonstrated an influence of altitude on the distribution of these organisms, principally the presence of shredders (Chara *et al.* 2007; Camacho *et al.* 2009). In the present study we sought to fill a gap in knowledge regarding invertebrate colonisation of detritus in tropical streams.

Freshwater ecosystems are undergoing many anthropogenic impacts, such as deforestation of native riparian vegetation, invasions by exotic plant species and the spread of monoculture crops (Vörösmarty *et al.* 2010). These changes affect the ecological processes in aquatic systems, especially invertebrate– detritus relationships (Gessner and Chauvet 2002; Graça *et al.* 2002). Problems involved in the consumption of leaves of *Eucalyptus* spp. by aquatic insects likely result from physical impediments (e.g. toughness) and the leaves' chemical composition (e.g. low nitrogen concentration, high tannin content), which may lead to low decomposition rates (Davies and Boulton 2009). Gonçalves and Canhoto (2009) suggested another effect: a delay in the colonisation of leaves by insects. Few studies have so far evaluated the ecological effects of *Eucalyptus* plantations on Brazilian freshwater ecosystems.

Here, we report the results of an experiment comparing breakdown of leaves from a common native plant species of the Cerrado biome in Brazil with those from an exotic eucalypt species, placed in a third-order tropical stream. The experiment was designed to examine the possible ecological implications of landscape changes involving exotic plant species for leaf detritus colonisation by invertebrates. In addition to breakdown rates, we evaluated invertebrate colonisation on different types of organic (exotic and native) and artificial substrates, testing the effects of the shape and quality of leaf detritus on invertebrate colonisation. This experiment tested the hypothesis: if aquatic invertebrates use detritus as a refuge and food source, then colonisation of detritus from the native species Miconia chartacea will be more rapid than colonisation of detritus from the exotic species Eucalyptus grandis. We expected that the density and richness of invertebrates would be higher on the detritus from the native than from the exotic species and higher on the natural leaves than on the artificial ones, because the real native leaves offer the best refuge, space (habitat), calories and nutrients for invertebrate colonisation. Our aims were to: (1) assess the effect of the form of leaf detritus (potential for refuge by invertebrates) by comparing colonisation on the larger leaves of M. chartacea with that on the smaller leaves of E. grandis; (2) differentiate the effect of size from that of the nutritional quality of detritus (i.e. artificial v. natural leaves) because the synthetic leaves offered only refuge (habitat); and (3) test the food resource (quality) by comparing decay rates of leaves of a common native species (M. chartacea, Melastomataceae) with leaves of an exotic species (E. grandis) during the process of invertebrate colonisation.

#### Materials and methods

#### Study area

The Cerrado biome of Brazil is composed of plant physiognomies ranging from tropical savanna at lower altitudes (below 1000 m above sea level) to rupestrian fields above 1000 m and riparian forest in the wetter valleys along riverbanks. The number of endemic plant species is high. The predominant soil type is deep and infertile latosols. The climate is a high-altitude tropical one with wet summers and dry winters. The mean annual rainfall is >1500 mm.

The study area was in the Serra do Cipó National Park (33 800 ha) in the southern portion of the Espinhaço mountain range, which divides two important Brazilian watersheds: the São Francisco and Doce rivers. The site is  $\sim$  1400 m above sea level, with vegetation typical of rupestrian fields, except near the streams where it is gallery forest. The landscape is dissected by many streams flowing from the mountains. The upper reaches of these streams are vegetated by shrubs and are exposed to constant insolation. Conversely, many of the lower reaches are shaded completely, or nearly so, by riparian forest.

The experiment was conducted in a third-order stretch of Indaiá stream (19°16′S–43°31′W) at 1450 m above sea level. This stretch is 3 m wide and the mean current velocity during the study period was ~0.27 m s<sup>-1</sup>. The water was well oxygenated (>6.65 mg L<sup>-1</sup>) and acidic (pH 5.3), with a mean temperature of 18°C, low electrical conductivity (9  $\mu$ S cm<sup>-1</sup>) and low nutrient concentrations (total P = 27.95  $\mu$ g L<sup>-1</sup> and total N = 203.6  $\mu$ g L<sup>-1</sup>) (Callisto *et al.* 2004). The riparian forest along the banks in this stretch is narrow (<7 m wide) and surrounded by rupestrian fields dotted with small shrubs (Gonçalves *et al.* 2006).

#### Field sampling

Senescent leaves of Miconia chartacea (Mc) (Melastomataceae) and Eucalyptus grandis (Eg) (Myrtaceae) were used as detritus in the experiment. M. chartacea is the most abundant species in the local riparian vegetation. Because Indaiá stream receives no eucalyptus leaves, E. grandis leaves were collected from a reforested area  $\sim$ 7 km from the stream. Artificial leaves simulating the two species were prepared from brown synthetic nylon cloth, to evaluate the influence of size and shape on invertebrate colonisation. We used detritus of the two plant species collected locally as a model to prepare the two sizes of artificial leaves: artificial – *Miconia*: AM;  $18 \pm 4.44$  cm long (all values are means and standard deviations) and  $7 \pm 1.38$  cm wide and artificial – *Eucalyptus*: AE;  $13 \pm 1.69$  cm long and  $2 \pm 0.75$  cm wide. The artificial leaves for each species were placed in a separate bag, which was shaken to mix the leaves and then they were removed for weighing and used in the litter bags, avoiding individual selection.

The approximate weights of leaves used were: *E. grandis*  $9.5 \pm 0.1$  g, *M. chartacea*  $4.5 \pm 0.1$  g and artificial leaves  $10.0 \pm 0.1$  g dry weight (DW). The leaves were placed in individual litter bags ( $30 \times 30$  cm with 6 mm mesh). The decomposition experiments ran from April through to July 2001. Each litter bag was placed in sequences of the same leaf species, with replicates spaced 30 cm apart and  $\sim 0.3$  m deep, using stones to fix the bag on the stream bed (the total stream area used was  $\sim 15$  m<sup>2</sup>). Three replicates were collected from the stream on each date, after 2, 20, 30, 60 and 90 days and the litter bags were transported in ice chests to the laboratory.

#### Laboratory processing

After the samples were retrieved from the stream, they were washed with tap water in a 120 µm mesh sieve. The leaves were oven-dried at 60°C for 72 h (to constant weight) and then weighed. Decomposition rates were estimated using the non-linear exponential negative model  $W_t = W_0 \cdot e^{-kt}$  ( $W_t$  = remaining weight;  $W_0$  = initial weight; -k = decay rate; t = time). The invertebrates retained on the sieve were preserved in 10% formalin for later identification and counting. The invertebrates were classified in five feeding categories (Pérez 1988; Merritt and Cummin 1996; Fernández and Domíngues 2001; Cummin *et al.* 2005; Costa *et al.* 2006): gathering-collectors (G-C), filtering-collectors (F-C), shredders (Sh), scrapers (Sc) and predators (P).

On each sampling date, dry leaves were ground to a fine powder for subsequent chemical analysis. The lignin content was measured according to Van Soest (1963), the nitrogen content by the Kjeldahl method (Malavolta and Netto 1989), the phosphorus content according to Malavolta and Netto (1989) and Miyazawa *et al.* (1992) and the carbohydrate content according to Deriaz (1961) and Conn and Stumpf (1975).

#### Data analyses

To evaluate the differences in mass loss, we used the generalised linear model (GLM), analysed by using the quasi-binomial distribution (link = logit, test = Chi-square). The data for mass (response variable) were analysed in terms of sampling periods (time), type of detritus (E. grandis and M. chartacea leaves) and the interaction between these two factors. To evaluate the influence of the sampling periods (time), type of detritus (E. grandis, M. chartacea leaves, artificial - Eucalyptus and artificial - Miconia) and the interaction between these two factors on the richness and diversity of aquatic invertebrates, four GLMs were constructed. The two models for richness were analysed using the Poisson distribution (link = log, test = Chisquare), correcting the cases of under- or overdispersion. The other two models for density were analysed using the Gaussian distribution (link  $= \log$ , test = F), also noting if there was underor overdispersion. The densities of each functional trophic group was analysed using separate GLMs (one for each trophic group: gathering-collectors, filtering-collectors, scrapers, shredders and predators), where the quasi-binomial data distribution was used (link = logit, test = Chi-square), with sampling periods (time), type of detritus (E. grandis, M. chartacea leaves, artificial - Eucalyptus and artificial - Miconia) and the interaction between these two factors as the explanatory variables. To compare the different concentrations of nutrients between E. grandis and M. chartacea, four models were constructed (one for each nutrient type) and the ANOVAs of these GLMs were conducted using the Gaussian distribution (F-test).

To analyse the overall effects of the plant detritus (*E. grandis*, *M. chartacea* leaves, artificial – *Eucalyptus* and artificial – *Miconia*), sampling periods (time) and interaction between the two factors on the functional trophic groups of the invertebrate J. F. Gonçalves Jr. et al.

community, we used a MANOVA/Pillai Trace test. The MANOVA can be used in cases where multiple dependent variables that remain interdependent are analysed (Scheiner 2001). To detect specific differences among the types of detritus (*E. grandis, M. chartacea* leaves, artificial – *Eucalyptus* and artificial – *Miconia*) over time and the interaction among the factors in all the tests (GLMs and MANOVAs), pair-contrast analyses were done (using P = 0.05). For the MANOVA, a sequential *post hoc* Bonferroni correction was used for multiple comparison/adjustment (Rice 1989). All analyses were carried out in the R-Program (R Development Core Team 2008).

An indicator species analysis was performed to determine which taxa of invertebrates were most important to the invertebrate community structure over time, during the process of colonisation of the natural and artificial detritus. This method combines the abundance and frequency of each group during the study and the fidelity of occurrence of a taxon in a particular group to yield indicator values (IV) for each species in each group (Dufrêne and Legendre 1997). These are tested for statistical significance using a Monte Carlo technique with 1000 permutations. Groups are commonly defined by categorical environmental variables, levels of disturbance, experimental treatments, presence/absence of a target species, or habitat types.

#### Results

#### Leaf breakdown and detritus chemical composition

We found differences between the decay rates of the two leaf species in the interaction between time and type of detritus and when only time was assessed (Fig. 1; Table 1). However, we observed no difference when only detritus was considered. The *E. grandis* leaves lost 44% of their mass by day 90 ( $k = 0.005 \text{ day}^{-1}$ ), when the *M. chartacea* leaves had lost 36% ( $k = 0.003 \text{ day}^{-1}$ ).

*E. grandis* and *M. chartacea* contained similar amounts of nitrogen and total carbohydrates (Table 2). However,



Fig. 1. Percentage of leaf weight remaining (mean and s.e.) of *Miconia chartacea* and *Eucalyptus grandis* leaves during breakdown in Indaiá stream, Serra do Cipó National Park.

phosphorus and lignin contents were significantly higher in *M. chartacea* than in *E. grandis*.

#### Invertebrate communities

Chironomidae (Diptera) and Leptophlebiidae (Ephemeroptera) were the predominant insect groups on the leaves. Oligochaeta, Cladocera, Leptoceridae (Trichoptera) and Elmidae (Coleoptera) also showed high densities (Tables 3, 4). The analysis of indicator species during invertebrate colonisation selected Chironomidae (IV 61.2%, P = 0.002), Oligochaeta (IV 57.5%, P = 0.006), Leptoceridae (IV 45.8%, P = 0.002), Cladocera (IV 40.1%, P = 0.042) and Leptophlebiidae (IV 37.7%, P = 0.048) as important taxa in the community on the *E. grandis* substrate. No indicator species were found on the other substrates.

Invertebrate colonisation of the four types of detritus showed significantly similar patterns, with high densities midway during the decomposition period; maximum values occurred on day 30. The highest density was observed on *E. grandis*, whereas the densities on *M. chartacea*, artificial – *Eucalyptus* and artificial – *Miconia* were similar to each other (Fig. 2; Table 5). The taxonomic richness of invertebrates was not significantly different among the types of detritus, or in the interaction between time and type of detritus. However, taxonomic richness was least at 90 days and highest at 30 days (Fig. 2; Table 5).

#### Functional feeding groups

The invertebrate community structure, in terms of the functional trophic groups, differed significantly among the types of detritus, sampling period (time) and the interaction of these two factors (Table 6). Analysis of the detritus revealed that only artificial – *Eucalyptus* and artificial – *Miconia* showed no

Table 1. Values of significance (P) of the generalised linear model (GLM) test, degrees of freedom (d.f.) and residual (residual d.f.) and values of deviance (Chi-square test,  $\chi^2$ ), in the analysis of the percentage mass loss in terms of time, detritus and the interaction between two factors (detritus × time)

	d.f.	d.f. residual	Deviance $(\chi^2)$	P-value
		29	9.74	
Detritus	1	29	9.74	0.879
Time	1	27	1.79	< 0.001
Detritus × time	1	26	1.48	0.018

## Table 2. Nitrogen, phosphorus, lignin and carbohydrate contents (%) of senescent leaves (at time zero) of *Eucalyptus grandis* and *Miconia* chartacea

F-value and P-value are results of ANOVA/generalised linear model (GLM)

	Eucalyptus grandis		Miconia c	hartacea	F-value	P-value
	Mean	s.d.	Mean	s.d.		
Nitrogen	0.934	0.053	0.974	0.033	2.05	0.190
Phosphorus	0.031	0.004	0.036	0.002	6.44	0.034
Lignin	29.040	1.635	37.740	7.256	6.84	0.030
Carbohydrates	12.538	1.368	15.158	3.687	2.22	0.174

significant difference in their invertebrate communities (FFG). With respect to the time of sampling, 2 v. 20, 2 v. 90 and 20 v. 90 days did not differ significantly (Table 6). The abundance of filtering-collectors was significantly different (Table 7) among the detritus types, with the highest values observed on *M. chartacea* (Fig. 3*a*). The highest values were observed after 20 days and the remaining sampling times were similar to each other (Fig. 3*b*). Abundances of gathering-collectors also differed (Table 7), peaking on *E. grandis* (Fig. 3*c*). This functional trophic group showed the lowest densities after 2, 20 and 90 days and the highest at 30 days, followed by 60 days (Fig. 3*d*).

Predators varied in abundance (Table 7) and were most numerous on *M. chartacea* (Fig. 3*e*). Predators reached their highest abundance after 20 days (Fig. 3*f*). Scrapers also differed in abundance (Table 7), with the lowest levels observed on the natural detritus (*E. grandis* and *M. chartacea*) and the highest on the artificial detritus (artificial – *Miconia* and artificial – *Eucalyptus*) (Fig. 3*g*). The lowest abundances were observed after 20 and 30 days (Fig. 3*h*). The abundance of shredders was significantly different (Table 7) between the detritus types, although no difference was observed between *E. grandis* and *M. chartacea*. Artificial – *Eucalyptus* and artificial – *Miconia* showed the highest values (Fig. 3*i*). The sampling times were significantly different and the lowest abundance was observed after 90 days (Fig. 3*j*).

#### Discussion

## Relationship between leaf breakdown and chemical composition

The decay rates of *E. grandis* and *M. chartacea*, based on work by Graça *et al.* (2002), were intermediate. Comparable studies of *Eucalyptus* spp. and native riparian species in Portugal (Canhoto and Graça 1996) and Australia (Yeates and Barmuta 1999) showed that decay rates of *Eucalyptus* detritus were lower, except when native species have higher lignin contents, in concordance with our data. The quality of detritus, as evaluated by its chemical composition, is important for the breakdown rate. Some molecules can facilitate the decomposition of detritus (e.g. nitrogen and phosphorus), whereas others can hinder it (e.g. lignin and phenol) (Chergui and Pattee 1991; Golladay and Sinsabaugh 1991).

Our data indicated that lignin and phosphorus contents affected the breakdown of *E. grandis* and *M. chartacea* whereas nitrogen and carbohydrate contents had no effect. Phosphorus is a limiting and labile compound, which is lost in the initial periods of decomposition; this may explain the more rapid loss of *M. chartacea* in the first 7 days of the study. The lignin content was the most important factor causing a difference between the leaf breakdown rates of the two species. According to Ostrofsky (1997) and Gonçalves *et al.* (2004), refractory compounds such as lignin and cellulose retard decomposition whereas others, such as phosphorus, may facilitate this process. Differences in chemical characteristics may also influence invertebrate colonisation on each detritus type, as reported by Dudgeon and Wu (1999) and discussed below.

#### Invertebrate colonisation: time and source

Maximum densities and diversities were found after a month, corroborating the observations by Gessner and Dobson (1993)

## Table 3. Means (and s.e.) of densities of invertebrates colonising (ind. g<sup>-1</sup>) artificial – *Eucalyptus* (AE) and artificial – *Miconia* (AM) leaves during breakdown

Functional feeding groups (FFG): P, predators; Ga-Co, gathering-collectors; Fil-Co, filtering-collectors; Shr, shredders; Scr, scrapers

Taxa	FFG		Artif	ficial – Eucal	vptus			Artif	icial – Mico	nia	
		2 days	20 days	30 days	60 days	90 days	2 days	20 days	30 days	60 days	90 days
Annelida											
Oligochaeta Arthropoda Arachnida	Ga-Co	$4\pm3$	$145\pm13$	$191\pm14$	$0\pm 0$	$0\pm 0$	$25\pm5$	$243\pm18$	$302\pm13$	$399\pm24$	$0\pm 0$
Hydracarina Branchiopoda	Р	$4\pm3$	$0\pm 0$	$45\pm 6$	$0\pm 0$	$0\pm 0$	$25\pm5$	$51\pm9$	$77\pm7$	$10\pm 4$	$0\pm 0$
Cladocera	Fil-Co/P	$19\pm4$	$167 \pm 11$	$399 \pm 16$	$4\pm 2$	$0\pm 0$	$126\pm12$	$1303\pm41$	$957\pm22$	$527\pm21$	$0\pm 0$
Copepoda Insecta	Fil-Co/P	$4\pm3$	$7\pm 2$	$7\pm3$	$0\pm 0$	$0\pm 0$	$0\pm 0$	$453\pm26$	$9\pm4$	$265\pm17$	$0\pm 0$
Coleoptera	C C /C /C1	11 1 4	11 1 4	170   0	50 L 7	4 + 2	10 1 6	17   4	70 + 11	0   0	0   0
Elmidae	Ga-Co/Scr/Shr	$11 \pm 4$	$11 \pm 4$	$1/0 \pm 8$	$52 \pm 7$	$4\pm 2$	$18 \pm 6$	$1/\pm 4$	$79 \pm 11$	$0\pm 0$	$0\pm 0$
Scirtidae	Ga-Co/Scr/Shr	$4 \pm 3$	$0\pm 0$	$0\pm 0$	$0 \pm 0$	$0\pm 0$	$0\pm 0$	$0\pm 0$	$0\pm 0$	$0\pm 0$	$0\pm 0$
Stanbalinidae	Ga-Co/P	$0\pm 0$	$0\pm 0$	$3\pm 2$	$14 \pm 3$	$0\pm 0$	$0\pm 0$	$0\pm 0$	$20 \pm 6$	$0\pm 0$	$0\pm 0$
Staphylinidae	Ga-Co/P/Snr	$4\pm 3$	$0\pm 0$	$0\pm 0$	$0\pm 0$	$0\pm 0$	$0\pm 0$				
Diptera	Ga-Co	$0\pm 0$	$0\pm 0$	$3\pm 2$	$0\pm 0$	$0\pm 0$	$0\pm 0$	$35\pm8$	$0\pm 0$	$0\pm 0$	$0\pm 0$
Chirominidae	-	$85\pm9$	$217\pm16$	$1624\pm45$	$128\pm9$	$33\pm5$	$243\pm11$	$658\pm24$	$471\pm13$	$723\pm29$	$154 \pm 4$
Simuliidae Ephemeroptera	Fil-Co	$4\pm3$	$0\pm 0$	$35\pm8$	$0\pm 0$	$0\pm 0$	$0\pm 0$				
Leptophlebiidae	Ga-Co/Scr	$58\pm8$	$46 \pm 4$	$120 \pm 9$	$209\pm7$	$4\pm3$	$197 \pm 14$	$101 \pm 5$	$166 \pm 12$	$348 \pm 13$	$43\pm5$
Baetidae Trichoptera	Ga-Co/Scr	$4\pm3$	$19\pm 4$	$31\pm 5$	$31\pm7$	$0\pm 0$	$0\pm 0$	$0\pm 0$	$39\pm8$	$0\pm 0$	$0\pm 0$
Philopotamidae	Fil-Co	$0\pm 0$	$0\pm 0$	$10\pm4$	$0\pm 0$	$0\pm 0$	$0\pm 0$	$0\pm 0$	$79 \pm 11$	$98 \pm 10$	$0\pm 0$
Leptoceridae	Ga-Co/P/Shr	$18 \pm 4$	$50 \pm 4$	$90 \pm 10$	$137 \pm 9$	$16 \pm 3$	$71 \pm 11$	$96 \pm 7$	49 + 7	0 + 0	23 + 4
Polvcentropodidae	Fil-Co/P	$0\pm 0$	$0\pm 0$	$0\pm 0$	$0\pm 0$	$0\pm 0$	$0\pm 0$	$0\pm 0$	$0\pm 0$	$9\pm4$	$0\pm 0$
Hemiptera	Р	$0\pm 0$	$4\pm3$	$24 \pm 5$	$31\pm5$	$0\pm 0$	$18 \pm 6$	$9\pm4$	$34\pm8$	$0\pm 0$	$12 \pm 4$
Odonata	Р	$0\pm 0$	$4\pm 2$	$7\pm 2$	$0\pm 0$	$0\pm 0$	$18 \pm 6$	$9\pm4$	$9\pm4$	$0\pm 0$	$10\pm4$
Plecoptera											
Perlidae Lepidoptera	Р	$0\pm 0$	$4\pm 2$	$0\pm 0$	$0\pm 0$	$0\pm 0$	$0\pm 0$	$0\pm 0$	$0\pm 0$	$0\pm 0$	$0\pm 0$
Pyralidae	Fil-Co/Scr	$0\pm 0$	$0\pm 0$	$0\pm 0$	$0\pm 0$	$0\pm 0$	$0\pm 0$	$0\pm 0$	$9\pm4$	$0\pm 0$	$0\pm 0$
Hydra Mollusca	Р	$0\pm 0$	$81\pm10$	$24\pm 6$	$0\pm 0$	$0\pm 0$	$0\pm 0$	$17\pm 5$	$92\pm10$	$0\pm 0$	$0\pm 0$
Gastropoda	Scr	0 + 0	0 + 0	3 + 2	0 + 0	0 + 0	0 + 0	0 + 0	9 + 4	0 + 0	0 + 0
Rotifera	P	$0 \pm 0$ 0 + 0	$0 \pm 0$ 0 + 0	$0 \pm 2$ 0 + 0	$0 \pm 0$ 0 + 0	$0 \pm 0$ 0 + 0	$0 \pm 0$ 0 + 0	111 + 11	0 + 0	$9 \pm 3$ 9 + 4	$0 \pm 0$
Mean $\pm$ s.e.	-	$5\pm 0$ $7\pm 3$	$25\pm5$	$92 \pm 10$	$20\pm 3$	$2\pm 1$	$26\pm5$	$102 \pm 11$	$79\pm7$	$80 \pm 9$	$8\pm 2$

and Dudgeon and Wu (1999). This seems to be a general tendency, which might be explained by the relationship between invertebrate colonisation and detritus conditioning by the microbial community. This is illustrated by the analysis of indicator species, richness and functional feeding groups, which showed shifts of taxa occurred mainly after 30 days of incubation. Moreover, the total invertebrate density was higher in the organic detritus, suggesting that it is important as a source of food, probably by supporting a larger microbial community (Casey and Kendall 1996; Stockley *et al.* 1998; Dudgeon and Wu 1999).

Moreover, as shown by Gonçalves *et al.* (2004) and Ligeiro *et al.* (2010), the degradative ecological succession process occurs during a sequence of changes in colonisation by organisms, which modifies the properties of the surface and improves the habitat for subsequent colonists. The sampling time is

important because the passage of time allows other changes to occur in the detritus. During the initial and final stages of decomposition, we found similar community structures. This could occur because a well structured community does not form during the first days of decomposition, when the greatest lixiviation and release of inhibitory (anti-herbivore) compounds occurs and there is little time for large numbers of invertebrates to arrive in the detritus. Conversely, during the intermediate decomposition period, a large amount of leaf mass still exists and a considerable exposure time allows colonisation by a wide diversity of organisms, resulting in a well structured community. During the final decomposition period, the invertebrate community returns to its original simplicity when habitat quantity and quality decline because the small amount of detrital mass remaining contains a larger proportion of refractory compounds. We note that these stages do not last for the same

## Table 4. Means (and s.e.) of densities of invertebrates colonising (ind. g<sup>-1</sup>) Eucalyptus grandis (Eg) and Miconia chartacea (Mc) leaves during breakdown

Functional feeding groups (FFG): P, predators; Ga-Co, gathering-collectors; Fil-Co, filtering-collectors; Shr, shredders; Scr, scrapers

Taxa	FFG	Eucalyptus grandis					Miconia chartacea				
		2 days	20 days	30 days	60 days	90 days	2 days	20 days	30 days	60 days	90 days
Annelida											
Oligochaeta Arthropoda	Ga-Co	8±3	$69\pm10$	$3990\pm59$	$1494\pm36$	$44\pm7$	$3\pm 2$	$17\pm5$	$204\pm12$	$10\pm4$	$0\pm 0$
Arachnida											
Hydracarina Branchiopoda	Р	$4\pm3$	$17\pm5$	$67\pm8$	$42\pm 6$	$6\pm3$	$0\pm 0$	$28\pm5$	$55\pm4$	$10\pm3$	$0\pm 0$
Cladocera	Fil-Co/P	$442\pm12$	$245\pm16$	$1126\pm29$	$1354\pm26$	$25\pm5$	$0\pm 0$	$76\pm8$	$145\pm11$	$24\pm5$	$0\pm 0$
Copepoda Insecta	Fil-Co/P	$4\pm3$	$17\pm4$	$362\pm17$	$247\pm18$	$49\pm9$	$14\pm4$	$28\pm7$	$103\pm12$	$10\pm4$	$0\pm 0$
Coleoptera											
Elmidae	Ga-Co/Scr/Shr	$12\pm3$	$17\pm4$	$101\pm10$	$73\pm 6$	$0\pm 0$	$0\pm 0$	$10\pm3$	$7\pm 2$	$24\pm5$	$3\pm 2$
Hydrophilidae	Ga-Co/P	$0\pm 0$	$0\pm 0$	$4\pm3$	$15\pm5$	$6\pm3$	$3\pm 2$	$0\pm 0$	$0\pm 0$	$0\pm 0$	$0\pm 0$
Psephenidae	Scr	$0\pm 0$	$0\pm 0$	$4\pm3$	$0\pm 0$	$6\pm3$	$0\pm 0$	$0\pm 0$	$0\pm 0$	$8\pm4$	$0\pm 0$
Gyrinidae	Р	$0\pm 0$	$0\pm 0$	$0\pm 0$	$5\pm3$	$0\pm 0$	$0\pm 0$	$0\pm 0$	$0\pm 0$	$0\pm 0$	$0\pm 0$
Collembola Diptera	Ga-Co	$0\pm 0$	$31\pm7$	$0\pm 0$	$5\pm3$	$0\pm 0$	$3\pm 2$	$0\pm 0$	$3\pm 2$	$0\pm 0$	$0\pm 0$
Chaoboridae	р	4 + 3	0 + 0	0 + 0	0 + 0	0 + 0	0 + 0	0 + 0	0 + 0	0 + 0	0 + 0
Chironomidae	_	$156 \pm 5$	$687 \pm 31$	$5628 \pm 22$	$1736 \pm 25$	$971 \pm 24$	$83 \pm 7$	$69 \pm 9$	$196 \pm 11$	$140 \pm 8$	$7 \pm 3$
Simuliidae	Fil-Co	4+3	$0 \pm 0$	0 + 0	$0 \pm 0$	0+0	$0 \pm 0$	0 + 0	$0 \pm 0$	0 + 0	0 + 0
Ceratopogonidae	P	$0 \pm 0$	$0 \pm 0$ 0 + 0	$3 \pm 2$	$0 \pm 0$ 0 + 0	$0 \pm 0$ 0 + 0					
Ephemeroptera	1	010	010	0 1 0	010	010	0 - 0	0 ± 0	5 ± 2	010	0 ± 0
Leptophlebiidae	GA-Co/Scr	$178\pm10$	$101\pm12$	$402\pm 6$	$557\pm16$	$27\pm 6$	$101\pm9$	$23\pm 4$	$116\pm7$	$108\pm 6$	$0\pm 0$
Baetidae	GA-Co/Scr	$39\pm3$	$0\pm 0$	$50\pm7$	$0\pm 0$	$0\pm 0$	$0\pm 0$	$0\pm 0$	$12\pm4$	$0\pm 0$	$8\pm4$
Leptohyphidae Trichoptera	Ga-Co	$0\pm 0$	$0\pm 0$	$18\pm 6$	$0\pm 0$	$0\pm 0$	$0\pm 0$	$0\pm 0$	$0\pm 0$	$0\pm 0$	$0\pm 0$
Philopotamidae	Fil-Co	$0\pm 0$	$0\pm 0$	$45\pm7$	$51\pm9$	$0\pm 0$	$0\pm 0$	$0\pm 0$	$14 \pm 4$	$0\pm 0$	$0\pm 0$
Leptoceridae	Ga-Co/P/Shr	$43\pm5$	$82\pm10$	$164 \pm 5$	$339\pm10$	$107 \pm 5$	$17 \pm 3$	$35\pm3$	$14\pm5$	$99 \pm 8$	$48\pm 6$
Helicopsychidae	Scr	$0\pm 0$	$0\pm 0$	$18\pm 6$	$0\pm 0$	$0\pm 0$	$0\pm 0$	$0\pm 0$	$0\pm 0$	$0\pm 0$	$0\pm 0$
Hemiptera	Р	$12 \pm 3$	$0\pm 0$	$0\pm 0$	$58\pm8$	$0\pm 0$	$0\pm 0$	$3\pm 2$	$0\pm 0$	$4\pm3$	$0\pm 0$
Odonata Placentera	Р	$0\pm 0$	$9\pm4$	$4\pm3$	$10\pm3$	$0\pm 0$	$0\pm 0$	$0\pm 0$	$10\pm0$	$3\pm 2$	$0\pm 0$
Parlidae	D	$0 \pm 0$	$0 \pm 0$	0 + 0	0 + 0	$0 \pm 0$	$0 \pm 0$	$0 \pm 0$	$0 \pm 0$	$3 \pm 2$	$0 \pm 0$
Lepidoptera	1	0 ± 0	$0 \pm 0$	$0 \pm 0$	0 ± 0	$0 \pm 0$	0 ± 0	$0 \pm 0$	$0 \pm 0$	$J \perp Z$	0 ± 0
Pyralidae	Fil-CO/Scr	$0\pm 0$	$3\pm 2$	$0\pm 0$	$0\pm 0$						
Megaloptera	D	0   0	0   0	0   0	0   0	0   0		2   2	0   0	0   0	
Corydalidae Hydrozoa	К	$0\pm 0$	$3\pm 2$	$0\pm 0$	$0\pm 0$	$0\pm 0$					
Hydra	Р	$0\pm 0$	$4\pm3$	$636\pm24$	$208\pm13$	$0\pm 0$	$0\pm 0$	$14\pm4$	$135\pm10$	$38\pm 6$	$0\pm 0$
Rotifera	Р	$0\pm 0$	$0\pm 0$	$84\pm11$	$5\pm3$	$0\pm 0$	$0\pm 0$	$0\pm 0$	$10\pm4$	$0\pm 0$	$0\pm 0$
Mean $\pm$ s.e.		$30\pm3$	$44\pm8$	$423\pm14$	$207\pm11$	$41\pm 5$	$8\pm 2$	$10\pm3$	$34\pm 5$	$16\pm3$	$2\pm 1$

amount of time in each type of detritus because this depends on the intrinsic decay rate.

#### Invertebrate colonisation: size and shape of the detritus

We also assessed whether the size and shape of the detritus could influence the number and diversity of invertebrates, expecting that larger detritus would be more densely colonised (Corkum 1992). In our study, artificial synthetic leaves of different sizes (large and small) were incubated, mimicking the natural variability. When synthetic leaves were used, there was no variation in the chemical composition, so we expected that only physical effects would influence invertebrate colonisation. Our results showed no significant differences in the invertebrate structure during the colonisation process of artificial – *Miconia* and artificial – *Eucalyptus* leaves, suggesting that differences in size and shape did not affect the colonisation process.

If the leaf shape was not important, then the chemical composition of leaves during the incubation period might be a good alternative explanation for the effects on invertebrate colonisation on detritus. We found that *E. grandis* leaves supported the highest invertebrate densities, indicating that detritus with lower levels of refractory compounds would support larger numbers of organisms, in concordance with the observations by Dudgeon and Wu (1999), even though



**Fig. 2.** Mean and s.e. of (*a*) density of invertebrates, (*b*) density over time, (*c*) taxonomic richness of detritus and (*d*) taxonomic richness over time of associated invertebrates during colonisation in Indaiá stream, Serra do Cipó National Park. Different letters over the bars indicate a statistically significant difference (contrast analysis; P < 0.05), where A represents the highest value, followed by B and C. Eg, *Eucalyptus grandis*; Mc, *Miconia chartacea*; EA, artificial – *Eucalyptus*; MA, artificial – *Miconia*.

Table 5. Values of significance (P) of the generalised linear model (GLM) test, degrees of freedom (d.f.) and residual (residual d.f.), F-test and values of the deviance (Chi-square test,  $\chi^2$ ), in the analysis of density and richness of aquatic invertebrates in terms of time, detritus and the interaction between two factors (detritus × time)

	d.f. d.f. residual		Test		
			F	Р	
Density of invertebrates					
Null		59			
Detritus	3	56	16.12	< 0.001	
Time	4	52	12.36	< 0.001	
Detritus  imes time	12	40	5.27	< 0.001	
			Deviance $(\chi^2)$		
Richness of invertebrate	S				
Null		59	124.63		
Detritus	3	56	117.47	0.097	
Time	4	52	62.61	< 0.001	
Detritus  imes time	12	40	50.69	0.573	

# Table 6. Values of MANOVA/Pillai Trace test, F, Effect d.f., Error d.f., significance and for the contrast analysis showing the overall effects, of detritus, time and interaction between the factors, including five response variables of the functional trophic groups (FFG) of the invertebrate community (gathering-collectors, filtering-collectors, scrapers, predators and shredders)

Eg, Eucalyptus grandis; Mc, Miconia chartacea; EA, artificial - Eucalyptus; MA, artificial - Miconia, d.f., degrees of freedom

	Pillai Trace	F	Effect d.f.	Error d.f.	Р
MANOVA of FFG					
Intercept	0.257	20.791	5	36	P < 0.001
Detritus	0.263	4.139	15	100	P < 0.001
Time	0.271	2.906	20	120	P < 0.001
Detritus × time	0.086	1.984	60	172	P < 0.001
Contrast analysis					
$Eg \times EA$	0.396	4.728	5	36	0.002
$Eg \times MA$	0.429	5.417	5	36	0.001
$Eg \times Mc$	0.399	4.779	5	36	0.002
$EA \times MA$	0.049	0.371	5	36	0.865
$EA \times Mc$	0.461	6.148	5	36	0.000
$MA \times Mc$	0.451	5.907	5	36	0.000
2 days $\times$ 20 days	0.153	1.298	5	36	0.287
2 days $\times$ 30 days	0.330	3.553	5	36	0.010
2 days $\times$ 60 days	0.271	2.670	5	36	0.037
2 days $\times$ 90 days	0.125	1.024	5	36	0.418
20 days $\times$ 30 days	0.358	4.008	5	36	0.005
20 days $\times$ 60 days	0.404	4.888	5	36	0.002
20 days $\times$ 90 days	0.106	0.853	5	36	0.522
$30 \text{ days} \times 60 \text{ days}$	0.285	2.872	5	36	0.028
30 days $\times$ 90 days	0.420	5.219	5	36	0.001
60 days $\times$ 90 days	0.449	5.859	5	36	0.000

Table 7. Values of significance (P) of the generalised linear model (GLM) test, degrees of freedom (d.f.) and residual (residual d.f.) and values of the deviance (Chi-square test,  $\chi^2$ ), in the analysis of filtering-collectors, gathering-collectors, predators, scrapers and shredders, in terms of time, detritus and the interaction between two factors (detritus × time)

	d.f.	d.f. residual	Deviance $(\chi^2)$	Р
Filtering-collectors				
Null		59	51.23	
Detritus	3	56	30.42	< 0.001
Time	4	52	25.32	< 0.001
Detritus × time	12	40	8.23	< 0.001
Gathering-collectors				
Null		59	98.89	
Detritus	3	56	55.98	< 0.001
Time	4	52	37.09	< 0.001
Detritus × time	12	40	17.39	< 0.001
Predators				
Null		59	31.65	
Detritus	3	56	22.84	< 0.001
Time	4	52	17.49	< 0.001
Detritus × time	12	40	10.11	0.004
Scrapers				
Null		59	49.52	
Detritus	3	56	39.12	< 0.001
Time	4	52	21.58	< 0.001
Detritus × time	12	40	16.57	0.045
Shredders				
Null		59	21.81	
Detritus	3	56	15.21	< 0.001
Time	4	52	10.32	< 0.001
Detritus  imes time	12	40	4.43	< 0.001

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**Fig. 3.** Functional feeding groups of invertebrates ( $\log_{10}$  of percentage) in detritus (a, c, e, g) and over time (b, d, f, h) during colonisation in Indaiá stream, Serra do Cipó National Park. Different letters over the bars indicate a statistically significant difference (contrast analysis; P < 0.05), where A represents the highest value, followed by B and C. Eg, *Eucalyptus grandis*; Mc, *Miconia chartacea*; EA, artificial – *Eucalyptus*; MA, artificial – *Miconia*; P, predators; Ga-Co, gathering-collectors; Fil-Co, filtering-collectors; Shr, shredders; Scr, scrapers.



Fig. 3. (Continued)

*E. grandis* is an exotic species. The likely reason is that invertebrates may colonise detritus at different rates because of chemical differences among leaves (Gessner and Dobson 1993). In contrast, Godoy and Coutinho (2002) pointed out that the chemical composition of leaves is presumably not the key factor affecting changes in invertebrate colonisation on different types of detritus. In our opinion, this question needs to be studied further, using other plant species, mainly tropical species that are rich in different compounds (Dudgeon and Wu 1999; Moretti *et al.* 2007; Downes *et al.* 2011).

#### Functional feeding groups

The activity of shredders profoundly affects leaf decay rates (Bastian et al. 2007). However, shredders are reportedly not abundant in tropical regions (Mathuriau and Chauvet 2002; Cheshire et al. 2005; Boyero et al. 2012), suggesting that they have little influence on the leaf breakdown process. In our study, shredders were rare (<10%) and occurred in similar numbers on natural and artificial detritus, suggesting that these organisms use detritus not only as food but also as a refuge (protected in the spaces between leaves) to avoid predators. In tropical systems, scrapers can act indirectly as shredders when they scrape the periphyton on substrate surfaces (Wantzen and Wagner 2006). However, in our study, scrapers reached a higher density on the artificial detritus. Shredders and scrapers were abundant principally in the final periods of decomposition, as a result of the increased palatability of the detritus because of the nutritional value added from microbial and periphyton colonisation (Gessner et al. 1999; Gonçalves et al. 2006; Yule et al. 2009). These facts concord with the observations by Downes et al. (2011) and Dudgeon and Wu (1999) in tropical streams, that most species are not specialised for living in leaves, because of the diversity of resources and the low quality of detritus. Our data also indicated that shredders and scrapers are more abundant in artificial leaves, reflecting their generalist behaviour.

Gathering-collectors and filtering-collectors use fine organic particles as a resource (Cummin *et al.* 2005; Ligeiro *et al.* 2010). Therefore, with the transformation of natural substrates into increasingly smaller particles by decomposition and the consequent production of fine particles (FPOM) (Gessner *et al.* 1999), we observed that this group was more abundant on the natural substrates (Gonçalves *et al.* 2004), mainly after 20 or 30 days of incubation (with 80–75% of mass remaining). This higher abundance of organisms may attract predators, explaining the greater abundance of the latter on the natural substrate (Ligeiro *et al.* 2010).

#### Conclusion

In summary, our hypothesis was not confirmed because invertebrates did not heavily colonise the natural leaves and invertebrate colonisation differed between the leaves of native and exotic species. Also, the shape of the leaves did not affect colonisation by invertebrates. However, the chemical composition of the detritus could have affected the aquatic invertebrates. This indicates that the chemical composition of the species in riparian zones may be of fundamental importance for the aquatic biota. Our study, together with others conducted in the Cerrado, suggests that one hypothesis to be tested in future studies is that the lack of shredders may be related to the effect of the natural selection exercised by the chemical composition of the plant species that inhabit riparian zones in the Cerrado.

The negative consequences of using exotic species for reforestation and charcoal production are well known (Graça *et al.* 2002; Bañuelos *et al.* 2004). However, our data do not indicate any negative influence of *E. grandis* leaves on invertebrate colonisation of decomposing leaves in Indaiá stream. The results obtained in this study should be considered in the evaluation of reforestation programs and carbon sequestration through silviculture using exotic species. The findings reported here contribute to the knowledge of invertebrates, chemical composition and leaf shape in high-altitude tropical headwaters of streams in the Brazilian Cerrado biome, which is among the most threatened hotspots of tropical biodiversity. Moreover, we must improve our knowledge of tropical functional feeding groups, in view of the many inconsistent results regarding the true role of invertebrates in decomposition.

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