Leaf breakdown in an Atlantic Rain Forest stream

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Abstract The hypothesis of this study was that colonizers in decaying leaf litter prefer native species (Erythrina verna) to exotic ones (Eucalyptus camaldulensis and Protium heptaphyllum). Therefore, native species are expected to show higher breakdown rates, increased biomass, richness and density of invertebrate species, and increased biomass of decomposer fungi. Breakdown of leaf litter from these three species was assessed in an Atlantic Rain Forest stream. Four samples were collected during a period of 90 days and washed on a sieve to separate the invertebrates. Then, a series of leaf disks were cut to determine ash-free dry mass and fungal biomass, and the remaining material was oven-dried to determine the dry weight. Eucalyptus camaldulensis and E. verna showed higher breakdown rates than P. heptaphyllum, due to differences in leaf physical and chemical characteristics. The harder detritus (P. heptaphyllum) broke down more slowly than detritus with high concentrations of labile compounds (E. camaldulensis). The density of the invertebrates associated with detritus increased with time. There were no differences in density, taxonomic richness or biomass of invertebrates among the leaf types, which indicated that the invertebrates did not distinguish between exotic and native detritus. Fungal colonization varied among samples; E. camaldulensis showed the lowest ergosterol concentrations, mainly due to a high concentration of total phenolics. The detritus with the highest hardness value was colonized most slowly by fungi. These results showed that leaf breakdown in Atlantic Rain Forest streams could be affected either by changes in riparian vegetation, or by becoming more savanna-like process due to climate change.

Key words: exotic species, fungi, invertebrate, litter decomposition, Neotropical stream.

INTRODUCTION

In headwater-stream ecosystems, the growth of photosynthetic organisms is limited by shading from riparian vegetation, which makes these systems dependent on allochthonous organic detritus for energy (Minshall 1967; Benfield 1997). Most of the nutrients available in these environments derive from terrestrial ecosystems (Webster & Benfield 1986). Therefore, processing allochthonous organic matter is essential to preserve the biodiversity of lotic ecosystems (Wantzen & Junk 2000). Studying the breakdown of allochthonous plant litter is especially important in order to understand energy flows and the maintenance of stream metabolism (Benfield 1997; Wallace et al. 1997; Gessner et al. 1999).

Leaf litter breakdown in lotic ecosystems can be divided into three stages: leaching of soluble compounds, microbial conditioning, and fragmentation by invertebrates and physical abrasion. During these stages, detritus is simultaneously reduced, transformed and incorporated into the food web (Gessner et al. 1999). This process is affected primarily by the chemical composition of detritus, and may be influenced by water temperature, pH, nutrient concentrations and stream discharge (Petersen et al. 1989; Suberkropp & Chauvet 1995; Lecerf et al. 2005). The most important decomposers of leaves are microorganisms (Rincón & Santellocchio 2009). Aquatic invertebrates can also influence leaf decomposition directly (especially by shedding) or indirectly (e.g. excretion on leaves), facilitating microbial colonization (Graça 2001).

Microbial communities, especially fungi, accelerate litter processing by decomposing the structural components of plants (e.g. cellulose and lignin) (Gaudes et al. 2009). Fungi also improve the nutritional quality of leaf detritus and its palatability to aquatic invertebrates (Suberkropp 1998; Baschien et al. 2009). Nevertheless, few studies on litter processing have been carried out in tropical ecosystems in comparison with temperate regions (Li et al. 2009), even in countries with large areas covered by forests and rivers, such as Brazil.

Among the priority conservation areas in Brazil is the Atlantic Rain Forest biome, which is currently...
threated by severe environmental degradation. This biome is reduced to less than 8% of its original extent and has become excessively fragmented (Mittermier et al. 2004), with the occupation and expansion of urban areas, farming and ranching, and the development of large-scale silviculture of exotic trees such as Australian Eucalyptus spp. (Petrucio & Barbosa 2004). It is important to assess the effects of these tree plantations on ecological processes in riparian zones. Additionally, many locations in the Atlantic Rain Forest region experience an increase of locally exotic Cerrado plant species after an area is abandoned (Majer & Recher 1999). At present, there exists no functional assessment of the consequences of an increase in abundance of typical Cerrado (Brazilian savanna) species, for energy flow and nutrient cycling in waterbodies in areas of the Atlantic Rain Forest undergoing this process.

The hypothesis tested in this study was that colonizers in decomposing leaf detritus prefer native species (Erythrina verna) over exotic ones (Eucalyptus camaldulensis, a species now widely planted in Brazil, and Protium heptaphyllum, a native tree of the Cerrado). Higher breakdown rates, biomass values, density and richness of invertebrates, and higher biomass of decomposer fungi would be expected in native species. The aims of this study were to: (i) determine the breakdown rates of E. verna, E. camaldulensis and P. heptaphyllum, examining the chemical composition of their leaves, in an Atlantic Rain Forest stream; (ii) assess the composition and structure of the invertebrate community associated with decomposing leaves of these three species; and (iii) assess the effect of fungal biomass on the processing of these three types of leaf detritus.

MATERIALS AND METHODS

Study site

The study was carried out in a second-order Zé Adão stream (19°34′23.1″S, 42°37′55.17″W), located in an Atlantic Rain Forest remnant (923 ha) in the state of Minas Gerais, Brazil. The area is near the Doce River State Park, the largest continuous area of Atlantic Rain Forest in the state (35 974 ha), and is currently in the process of ecological regeneration.

The study site is part of the Doce River watershed, an 83 400-km² drainage basin in eastern Brazil. The regional climate is humid and megathermal tropical, with a well-defined rainy period from October to March, and a dry period from April to September. According to the Brazilian Meteorological Institute (INMET), mean monthly precipitation reaches 235 mm in December, and decreases to 9 mm in August. Based on records over the past 20 years, the mean annual precipitation, relative humidity and temperature are around 1300 mm, 79% and 23°C, respectively.

The canopy of the riparian zone of Zé Adão stream was composed of secondary Atlantic Rain Forest (semi-evergreen) characterized by trees such as Guarea guidonea (318 individuals per hectare), Cupania oblongifolia (91), Trichilia pallida (52), Piptadenia gonoacantha (26), Sparattosperma leucanthum (22), Dalbergia nigra (21), Luehea glandiflora (19), Platycyamus regnellii (18) and Anadenanthera peregrina (13).

Procedures

We used approximately 3 ± 0.01-g dry weight of leaf detritus for the exotic plant species (E. camaldulensis and P. heptaphyllum), and 2 ± 0.01 g of a native species (E. verna). The leaves were enclosed in separate litter bags (15 × 20 cm, 10-mm mesh). Six groups of four bags of each leaf type were fixed to the stream bed. The litter bags were spaced 20 cm apart at a depth of 15 cm and tied with a rope. Four bags of each leaf type were retrieved from the stream after 3, 7, 15, 30, 60 and 90 days, placed in individual plastic bags, and taken to the laboratory in a cooler for processing.

On each sampling day, we measured the temperature, pH, electrical conductivity and dissolved oxygen in situ (around 5 m upstream from the experimental site) using a digital multi-analyzer (YSI-85) and specific sensors (Tecnal, Tecn-3MP). We collected 1 L of water to determine the nitrogen and total phosphorus concentrations (American Public Health Association 1992). The contents of the bags were washed over a 120-μm sieve, and the invertebrates retained were stored in 70% ethanol for later identification (Roldan 1992) under a magnifying glass (30x). The organisms collected were assigned to functional feeding groups proposed by Merritt and Cummins (1996) and Cummins et al. (2005): gathering collectors, filtering collectors, shredders, scrapers and predators.

Five leaves of each sample were collected randomly to extract two disks (1.2-cm diameter), forming two five-disk sets. One set was used to determine the ash-free dry mass remaining (AFDM; calculated after incineration in a muffle furnace at 550°C for 4 h), and another set to assess the ergosterol concentration. The remaining material was oven-dried at 60°C for 72 h.

The ergosterol content (used to indicate fungal biomass) was estimated according to Gessner (2005). The disks were preserved in methanol, and lipid extraction and saponification were carried out in boiling KOH-methanol. The extract was purified in a cartridge Solid Phase Extraction manifold equipped with a vacuum port. Ergosterol was then eluted with isopropanol and analysed for isocratic operation by high-performance liquid chromatography (UV detector set to 282 nm).

After each sample was ground, the polyphenol concentrations in leaf tissues of the three species were assessed by the Folin-Denis method according to Bärlocher and Graça (2005), nitrogen according to the method proposed by Kjeldahl (Sarruge & Haag 1974; Malavolta & Netto 1989) and phosphorus according to Malavolta and Netto (1989). A device that measures leaf resistance to rupture (Graça & Zimmer 2005) was used to assess the hardness of intact leaves. Five leaves of each species at time ‘0’ were moistened and five disks were removed, always avoiding the central rib.

The strength necessary to break each disc was read, and the mean strength of the five disks from each leaf was used to estimate the initial average hardness of the species (expressed in grams).

Data analysis

Breakdown rates (k) were calculated according to the negative exponential model, using the percentage data for mass loss and time (Wt = W0e^-kt). Differences among mass loss (ln-transformed; dependent variable) by sampling times (continuous variable) were compared by covariance analyses (ANCOVA, R-program; R Development Core Team 2008). Differences among nutrient concentrations (nitrogen and phosphorus), total phenolics, initial hardness of detritus and functional feeding groups of invertebrates (dependent variable) among the plant species (categorical variable) were tested by analysis of variance (ANOVA). The colonization of invertebrates (density, richness and biomass) and ergosterol content (dependent variable) among the plant species (categorical variable) were tested by analysis of variance (one-way ANOVA). The colonization of invertebrates (density, richness and biomass) and ergosterol content (dependent variable) among the plant species, sampling times and its interaction (categorical variable) were tested by analysis of variance (factorial two-way ANOVA). Data normality was tested according to Kolmogorov–Smirnov, and the data were transformed whenever necessary with the neperian logarithm (ln). The Tukey test (Zar 1996) was used to discriminate among the categorical variables.

RESULTS

Stream characteristics

The water parameters in this stream were: mean temperature 20.2°C ± 1.1, water depth 0.3 m ± 0.15, dissolved oxygen content 8.0 mg L^-1 ± 0.04, pH 7 ± 0.2, electrical conductivity 77.8 μS cm^-1 ± 7.7, total nitrogen 0.07 mg L^-1 and total phosphorus 0.0176 mg L^-1.

Breakdown rate

The breakdown rates for *Eucalyptus camaldulensis* (k = 0.0445; R^2 = 0.976) and *E. verna* (k = 0.0202; R^2 = 0.956) were the most rapid, requiring 60 and 90 days, respectively, for total decay. The breakdown rate of *P. heptaphyllum* leaves was slower than the others, with 49% AFDM remaining (k = 0.0085; R^2 = 0.927) 90 days after the experiment began (Fig. 1). The differences among these rates were statistically significant (ANCOVA, F_{2,85} = 36.0; P < 0.001).

Chemical composition

The three species differed in initial hardness (Table 1). *Erythrina verna* (60.3 ± 6.7 g) showed the lowest values for initial hardness, followed by *E. camaldulensis* (154.2 ± 36.1 g) and *P. heptaphyllum* (249.8 ± 51.1 g) (Tukey test, P < 0.001). Both nitrogen and phosphorus contents were significantly different among the species (Table 1). *Protium heptaphyllum* showed the lowest values for nitrogen (Tukey test, P = 0.012 and P = 0.028 for *E. camaldulensis* and *E. verna*, respectively) and phosphorus (Tukey test, P = 0.006 and P = 0.006 for *E. camaldulensis* and *E. verna*, respectively).

We found a significant decrease in total phenolics concentration during the study period, and differences in the concentrations among leaves (Table 1). The lowest concentration was observed in *E. verna*, and the highest in *E. camaldulensis* and *P. heptaphyllum* after incubation (Tukey test, P < 0.001; Table 2).

Biological colonization

There was a significant interaction of leaves × time in the analysis of the ergosterol concentrations (Table 2). *Eucalyptus camaldulensis* had the lowest ergosterol content (Tukey test, P = 0.001), and in this species the maximum was observed on day 30 of incubation (150 μg g^-1). In *P. heptaphyllum*, the peak concentration of 274 μg g^-1 occurred on day 15. After the beginning of breakdown, *E. verna* showed its highest ergosterol content on day 30 (243 μg g^-1) (Fig. 2).

There was also a significant leaves × time interaction for the density of invertebrates colonizing the leaves (Table 2). Although the density of invertebrates increased over time for all leaf species, *E. camaldulensis* showed the highest density after 60 days of incubation (574.8 ind g^-1), whereas *P. heptaphyllum* and *E. verna* had the highest density after 90 days (45.7 ind g^-1 and 1161.5 ind g^-1, respectively; Fig. 3A).

*Eucalyptus camaldulensis* showed the highest taxonomic richness after 7 days of incubation, *P. hep-
E. verna reached its highest value only at an advanced stage of breakdown (after 90 days of incubation; Table 2). However, we did not found difference in the taxonomic richness of invertebrates over time, and among leaves (Table 2; Fig. 3B).

Invertebrate biomass was not significantly influenced by either leaf species or sampling time (Table 2; Fig. 3C). Among the groups of invertebrates, Chironomidae (Diptera) was the most abundant in all leaves and periods (Appendix S1), amounting to 78% of the total of invertebrates collected, followed by Elmidae (Coleoptera, 7%), Hydropsychidae (Trichoptera, 3%) and Leptophyphidae (Ephemeroptera, 2%).

The most frequent functional feeding groups in E. camaldulensis were filtering collectors (28%), gathering collectors (24%) and predators (23%); in P. heptaphyllum, gathering collectors (27%), filtering collectors (25%) and scrapers (23%); and in E. verna, gathering collectors (30%), scrapers (24%) and filtering collectors (23%). With respect to functional feeding groups, shredder densities did not vary among the leaves (Table 2). Densities of predators, filtering collectors, gathering collectors and scrapers were all the lowest in E. verna (Table 2; Fig. 4).

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**Table 1.** Nitrogen, phosphorus, lignin and carbohydrate content (% g⁻¹ dry mass) of the leaf litter of *Eucalyptus camaldulensis*, *Protium heptaphyllum* and *Erythrina verna* in the Zé Adão stream over time

<table>
<thead>
<tr>
<th>Detritus</th>
<th>Nutrient</th>
<th>3 days</th>
<th>7 days</th>
<th>15 days</th>
<th>30 days</th>
<th>60 days</th>
<th>90 days</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>E. verna</em></td>
<td>Nitrogen</td>
<td>2.017</td>
<td>1.87</td>
<td>2.365</td>
<td>1.978</td>
<td>2.04</td>
<td>†</td>
</tr>
<tr>
<td></td>
<td>Phosphorus</td>
<td>0.068</td>
<td>0.073</td>
<td>0.128</td>
<td>0.128</td>
<td>0.092</td>
<td>†</td>
</tr>
<tr>
<td></td>
<td>Phenols</td>
<td>14.05</td>
<td>17.35</td>
<td>15.56</td>
<td>7.33</td>
<td>3.43</td>
<td></td>
</tr>
<tr>
<td><em>E. camaldulensis</em></td>
<td>Nitrogen</td>
<td>1.963</td>
<td>2.117</td>
<td>2.89</td>
<td>†</td>
<td>†</td>
<td>†</td>
</tr>
<tr>
<td></td>
<td>Phosphorus</td>
<td>0.065</td>
<td>0.073</td>
<td>0.099</td>
<td>†</td>
<td>†</td>
<td>†</td>
</tr>
<tr>
<td></td>
<td>Phenols</td>
<td>89.48</td>
<td>80.63</td>
<td>37.21</td>
<td>39.19</td>
<td>33.46</td>
<td>†</td>
</tr>
<tr>
<td><em>P. heptaphyllum</em></td>
<td>Nitrogen</td>
<td>0.958</td>
<td>1.036</td>
<td>1.221</td>
<td>1.499</td>
<td>1.082</td>
<td>1.654</td>
</tr>
<tr>
<td></td>
<td>Phosphorus</td>
<td>0.028</td>
<td>0.029</td>
<td>0.046</td>
<td>0.062</td>
<td>0.036</td>
<td>0.083</td>
</tr>
<tr>
<td></td>
<td>Phenols</td>
<td>87.66</td>
<td>74.12</td>
<td>28.75</td>
<td>31.66</td>
<td>20.74</td>
<td>13.23</td>
</tr>
</tbody>
</table>

†Insufficient sample for analysis.

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**Table 2.** The results of statistical analyses (ANOVA¹ and factorial ANOVA²) among *Eucalyptus camaldulensis*, *Protium heptaphyllum* and *Erythrina verna* during time in the Zé Adão stream

<table>
<thead>
<tr>
<th>Dependent variable</th>
<th>Categorical predictors</th>
<th>d.f.</th>
<th>d.f. residual</th>
<th>Value of <em>F</em></th>
<th><em>P</em></th>
</tr>
</thead>
<tbody>
<tr>
<td>Initial hardness</td>
<td>Leaves †</td>
<td>2</td>
<td>25</td>
<td>55.234</td>
<td>0.0010***</td>
</tr>
<tr>
<td>Nitrogen</td>
<td>Leaves †</td>
<td>2</td>
<td>13</td>
<td>7.1127</td>
<td>0.0086**</td>
</tr>
<tr>
<td>Phosphorus</td>
<td>Leaves †</td>
<td>2</td>
<td>13</td>
<td>7.5714</td>
<td>0.0063**</td>
</tr>
<tr>
<td>Phenols</td>
<td>Leaves †</td>
<td>2</td>
<td>53</td>
<td>51.434</td>
<td>0.0010***</td>
</tr>
<tr>
<td>Phenols</td>
<td>Time †</td>
<td>2</td>
<td>53</td>
<td>23.967</td>
<td>0.0010***</td>
</tr>
<tr>
<td>Ergosterol</td>
<td>Leaves †</td>
<td>2</td>
<td>4</td>
<td>8.9558</td>
<td>0.0010***</td>
</tr>
<tr>
<td></td>
<td>Time †</td>
<td>2</td>
<td>38</td>
<td>3.7574</td>
<td>0.0034**</td>
</tr>
<tr>
<td>Density of invertebrates</td>
<td>Leaves †</td>
<td>2</td>
<td>5</td>
<td>0.0387</td>
<td>0.8448</td>
</tr>
<tr>
<td></td>
<td>Time †</td>
<td>2</td>
<td>5</td>
<td>2.4451</td>
<td>0.0484*</td>
</tr>
<tr>
<td></td>
<td>Leaves × time †</td>
<td>9</td>
<td>50</td>
<td>2.2538</td>
<td>0.0333*</td>
</tr>
<tr>
<td>Richness of invertebrates</td>
<td>Leaves †</td>
<td>2</td>
<td>5</td>
<td>0.0172</td>
<td>0.8960</td>
</tr>
<tr>
<td></td>
<td>Time †</td>
<td>2</td>
<td>5</td>
<td>1.5375</td>
<td>0.2056</td>
</tr>
<tr>
<td></td>
<td>Leaves × time †</td>
<td>9</td>
<td>50</td>
<td>3.4832</td>
<td>0.0020**</td>
</tr>
<tr>
<td>Biomass of invertebrates</td>
<td>Leaves †</td>
<td>2</td>
<td>5</td>
<td>3.9377</td>
<td>0.0527</td>
</tr>
<tr>
<td></td>
<td>Time †</td>
<td>2</td>
<td>5</td>
<td>0.5393</td>
<td>0.7074</td>
</tr>
<tr>
<td></td>
<td>Leaves × time †</td>
<td>9</td>
<td>50</td>
<td>1.3824</td>
<td>0.2213</td>
</tr>
<tr>
<td>Shredder</td>
<td>Leaves †</td>
<td>2</td>
<td>64</td>
<td>1.7041</td>
<td>0.1977</td>
</tr>
<tr>
<td>Predators</td>
<td>Leaves †</td>
<td>2</td>
<td>64</td>
<td>14.779</td>
<td>0.0005*</td>
</tr>
<tr>
<td>Filtering collectors</td>
<td>Leaves †</td>
<td>2</td>
<td>64</td>
<td>12.044</td>
<td>0.0010***</td>
</tr>
<tr>
<td>Gathering collectors</td>
<td>Leaves †</td>
<td>2</td>
<td>64</td>
<td>10.976</td>
<td>0.0017**</td>
</tr>
<tr>
<td>Scrapers</td>
<td>Leaves †</td>
<td>2</td>
<td>64</td>
<td>11.711</td>
<td>0.0012**</td>
</tr>
</tbody>
</table>

*P < 0.05, **P < 0.01 and ***P < 0.001. d.f., degrees of freedom.
DISCUSSION

Breakdown rates and chemical properties of leaf detritus

According to the categories developed by Petersen and Cummins (1974), the observed breakdown rates of *E. camaldulensis* and *E. verna* detritus can be classified as rapid ($k > 0.010$), whereas the breakdown rates of *P. heptaphyllum* are intermediate ($0.010 > k > 0.005$). Nevertheless, the rate found for *P. heptaphyllum* was higher than rates reported by Moretti *et al.* (2007) in the Cerrado biome, where this species is native ($k = 0.0019$ per day and 0.0040 per day; Indaiá and Garcia streams, respectively). The difference between the breakdown rates of *P. heptaphyllum* in the two studies may be due to abiotic features of the streams. Higher temperatures and pH values were observed in the experimental stream (Atlantic Rain Forest), and both factors are known to accelerate the decomposition process as well as the colonization and activity of microorganism communities in leaf detritus (Petersen & Cummins 1974; Swan & Palmer 2004).

Decreases in phenolic total concentration, especially in the initial period of the experiment, are due to the hydrophilic property of phenol, which leaches rapidly from detritus (Webster & Benfield 1986). According to Canhoto and Graça (1996), it is necessary to totally or partially remove the cuticle to allow the polyphenol to dissolve. Thus, hard leaves such as those of *P. heptaphyllum* leach slowly because the cuticle is difficult to remove (Oliveira *et al.* 2003; Moretti *et al.* 2007). This may explain their slow breakdown rates.

The highest breakdown rate was observed in *E. camaldulensis*, which showed intermediate hardness and high concentrations of phenol, nitrogen and phosphorus (Suberkropp & Klug 1976). This finding corroborates those of Swan and Palmer (2004) and Ardón and Pringle (2008), who observed high concentrations of these compounds, suggesting that their solubility accelerated litter degradation. Leaves of *E. camaldulensis* contain hydrophilic compounds, which may accelerate leaching. The rapid breakdown of *E. verna* may be explained by its low hardness and high concentrations of nitrogen and phosphorus. This would increase its attractiveness and facilitate detritus
metabolization by the microbial community, thus increasing its palatability to aquatic invertebrates (Mathuriau & Chauvet 2002). In contrast, the leaves of *P. heptaphyllum*, a common Cerrado species, have a thick cuticle to better withstand water stress (Waldhoff et al. 2002), high concentrations of structural compounds (Oliveira et al. 2003), low nutrient contents (nitrogen and phosphorus) and high values of hardness (Moretti et al. 2007). The synergistic effects of these attributes lead to the lowest breakdown rates observed (Suberkropp 1998; Ardón et al. 2006). Moreover, according to Ribeiro et al. (1999), inhibitory chemical compounds (e.g. phenolics and tannin), used for defence against herbivores, that are present in Cerrado plant species (such as *P. heptaphyllum*) lead to very slow leaching due to the thick cuticle of their leaves, which may decrease breakdown rates compared to leaves with lower hardness and a thinner cuticle. This also explains the acceleration in breakdown after 60 days of incubation, owing to cuticle degradation (Delgado et al. 2006).

These results reinforce the importance of the chemical composition of leaves for the dynamics of the breakdown process (Webster & Benfield 1986). We propose the following hypothesis: considering that in many tropical ecosystems the plants contain more secondary substances, the inhibitory effects of polyphenols are surmounted by the rapid degradation of less-hard leaves due to the strong attraction of tissue-forming molecules to water, and by the adaptation of the local aquatic invertebrates and microorganisms to tolerate the presence of these compounds, to explain the smaller effects of *Eucalyptus* spp. in the same tropical streams.

**Fungi effects**

Studies have shown the effects of leaf quality on microbial activity and biomass (mainly fungi), leading to differences in breakdown rates (Mathuriau & Chauvet 2002; Gonçalves et al. 2007; Lecerf et al. 2005). The highest biomass was found in *P. heptaphyllum* and the lowest in *E. camaldulensis*, whereas the breakdown rates were the reverse of this pattern. Gonçalves et al. (2007), studying a species of the same genus in the Cerrado, suggested that in the stream with lower nutrient contents in the water, the fungal community had difficulty in colonizing leaves of *Protium braziliense*, probably due to the difficulty in extracting nutrients from the leaves themselves. However, the present study found favourable conditions of nutrients, temperature and pH, which favoured fungal colonization. In addition to the better conditions, we believe that substrate stability favoured the development of this community in *P. heptaphyllum*.

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Fig. 4. Percentage of predators (A), gathering collectors (B), filtering collectors (C) and scrapers (D) functional feeding groups significantly different, during leaf breakdown of *Eucalyptus camaldulensis* (diamond), *Protium heptaphyllum* (square) and *Erythrina verna* (triangle) in the Zé Adão stream over time.
Gessner et al. (1999) showed that by the seventh day, 20% of the mass of the detritus is already lost; also, possible competition with bacteria for substrate and low fungal colonization rates could explain the low values of fungal biomass found in E. camaldulensis. This could also be related to the presence of labile substances such as polyphenol, as explained above (Jugnia et al. 2000). Our data showed an increase of fungi and decrease of phenolic compounds between 7 and 15 days of immersion, in agreement with the delay fungi and decrease of phenolic compounds between 7 days, 20% of the mass of the detritus is already lost; and Canhoto and Graça (1996).

Although P. heptaphyllum and E. verna showed similar amounts of total fungal biomass after 15 days of incubation, at the beginning of the experiment the highest values were observed in E. verna. This may be due to the low concentration of polyphenolic compounds, allelopathic substances, hardness, and high concentrations of nitrogen and phosphorus, favouring rapid colonization and degradation of detritus (Canhoto & Graça 1996; Rosemond et al. 2002), in addition to the low variation in fungal biomass during the entire breakdown process (Mathuriau & Chauvet 2002; Oliveira et al. 2003).

Invertebrate community

The Chironomidae was the most abundant group of invertebrates during the entire breakdown process in all three leaf species, in agreement with studies in other tropical streams (Mathuriau & Chauvet 2002; Wantzen & Wagner 2006; Moretti et al. 2007; Landeiro et al. 2008). According to Gonçalves et al. (2006a) and Callisto et al. (2007), chironomids may be responsible for structuring the entire community of invertebrates, because they are disturbance-tolerant and able to colonize detritus regardless of its quality and/or breakdown time. In this study, these invertebrates were able to colonize all types of detritus, illustrating their importance for aquatic systems in the Atlantic Rain Forest, and their plasticity in selecting different kinds of detritus regardless of origin (exotic or natural).

Although P. heptaphyllum, E. verna and E. camaldulensis showed different physical and chemical characteristics, no effect was observed on the density, richness and biomass of aquatic invertebrates, and only one difference was found among sampling times. Rezende et al. (2010) obtained similar results when studying the breakdown of Eucalyptus grandis (exotic species) and Hirtella glandulosa (native species) in the same watershed. These reports suggest that the community of invertebrates is structured only by the process of ecological succession that litter undergoes over time (Gonçalves et al. 2004; Ligeiro et al. 2010). This indicates that the initial nutritional quality of leaves does not play a central role in the process of colonization by invertebrates, contradicting the results found by Davies and Boulton (2009) and O’Connor et al. (2000) who observed a negative effect of exotic detritus on invertebrates, especially shredders. This was probably because of the scarcity (>10%) of shredders in tropical streams (Wantzen & Wagner 2006; Gonçalves et al. 2007).

In advanced stages of breakdown, colonization by invertebrates may be correlated with leaf conditioning by the microbial community (Gessner & Dobson 1993). Our findings showed that the peaks of density and richness of invertebrates coincided with the peaks of ergosterol concentration. Working in the Amazon basin, Henderson and Walker (1986) suggested that variations in the microbial community are important to structure the community of invertebrates associated with the leaf breakdown process. These data reinforce the idea that detritus becomes more attractive and palatable to invertebrates after microbial colonization (Suberkropp 1998; Gessner et al. 1999), even in tropical systems with low densities of shredders.

We observed a low density of shredders, which are important for transforming detritus into fine particulate organic matter. This finding corroborates other studies carried out in many regions of Brazil (Gonçalves et al. 2006b, 2007; Moretti et al. 2007; Hepp et al. 2009; Moulton et al. 2010), suggesting that aquatic invertebrates make only a small contribution to the breakdown process in these environments. The highest densities of aquatic invertebrates in E. camaldulensis and E. verna occurred after 60 and 90 days of incubation, respectively, when the leaves were in an advanced stage of breakdown, thus releasing large amounts of coarse organic matter. This may explain the high density of collectors using this material as a food resource (Dobson et al. 2002). The density of scrapers increased in the initial stages of leaf breakdown of E. camaldulensis, P. heptaphyllum and E. verna, probably due to the continual amassing of biofilm on the detritus surface (Moretti et al. 2007). This is related to the establishment and activities of microorganism communities, which shows their importance for the food web of streams and nutrient cycling, linking detritus and the invertebrate communities (Graça 2001).

Our hypothesis that organisms colonizing decomposing leaf detritus prefer native species (E. verna) rather than exotic ones (E. camaldulensis and P. heptaphyllum) was only partly confirmed. These results are important because they enlarge the data set and inform discussions in tropical regions, where it has been shown that leaf breakdown in Atlantic Rain Forest streams could be affected either by changes in riparian vegetation or by becoming more savanna-like due to climate change. However, more specific investigations in different tropical systems are necessary in order to determine general patterns for these processes.

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Additional Supporting Information may be found in the online version of this article:

Appendix S1. Data from samples of aquatic invertebrates.