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PRIMARY RESEARCH PAPER

What is more important for invertebrate colonization in a stream with low-quality litter inputs: exposure time or leaf species?

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Abstract The objective of this study was to evaluate the influences of detritus from the leaves of different species, and of exposure time on invertebrate colonization of leaves in a shaded Cerrado stream. We hypothesized that the exposure time is the main factor that influences the colonization of leaves by invertebrates. We used leaves of five tree species native to the Brazilian Cerrado: *Protium heptaphyllum* and *Protium brasiliense* (Burseraceae), *Ocotea* sp. (Lauraceae), *Myrcia guyanensis* (Myrtaceae), and *Miconia chartacea* (Melastomataceae), which are characterized by their toughness and low-nutritional quality. Litter bags, each containing leaves from one species, were placed in a headwater stream and removed after 7, 15, 30, 60, 90, and 120 days. The dominant taxon was Chironomidae, which comprised ca. 52% of all organisms and ca. 20% of the total biomass. The taxonomic richness of colonizing organisms did not vary among the leaf species. However, the density and biomass of the associated organisms varied differently among the kinds of detritus during the course of the incubation. The collector-gatherers and shredders reached higher densities in the detritus that decomposed more rapidly (*Ocotea* sp. and *M. guyanensis*), principally in the more advanced stages of colonization. The collector-filterers reached higher densities in the detritus that decomposed more slowly (*P. heptaphyllum*, *P. brasiliense*, and *M. chartacea*), principally in the initial stages of incubation. A cluster analysis divided the detritus samples of different leaf species according to the exposure time (initial phase: up to 7 days; intermediate phase: 7–30 days; advanced phase: 30–120 days), suggesting some succession in invertebrate colonization, with differences in taxon composition (indicator taxa analysis). These results suggest that regardless of the leaf-detritus species, exposure time was the main factor that influenced the colonization process of aquatic invertebrates.

Keywords Brazilian Savanna (Cerrado) · Functional feeding groups · Invertebrate assemblages · Leaf patches · Tropical streams

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Introduction

In headwater streams where the streambed is shaded by the riparian vegetation, the autochthonous primary productivity is reduced (Vannote et al., 1980). In these environments, leaves from the riparian vegetation are an important energy source for aquatic organisms (Cummins et al., 1989; Wallace et al., 1997; Bastian et al., 2008). In many tropical regions, where leaf abscission is not seasonal, riparian vegetation provides abundant and diverse leaf litter throughout the year (Dobson et al., 2002; Gonçalves et al., 2006a; Chara et al., 2007).

The capacity for leaf retention depends on the hydraulic and geomorphological characteristics of a stream and, to a lesser extent, on intrinsic characteristics of the leaves, such as size, texture, and shape (Canhoto & Graça, 1998). The patchy retention of litter on the streambed causes high-spatial heterogeneity in organic-matter accumulation (Prochazka et al., 1991; Gjerlov & Richardson, 2004). Aquatic invertebrates quickly respond to aggregations of feeding resources, turning leaf detritus patches into "hotspots" of abundance of organisms (Kobayashi & Kagaya, 2004, 2005).

Some types of detritus types are more attractive to invertebrates than others, as a function of their chemical composition, physical structure, and levels of degradation and microbial conditioning. Since the characteristics of detritus vary with the time of exposure in the water, the attractiveness of detritus can also change with time (Abelho, 2001; Graça et al., 2001). Several studies in temperate regions have demonstrated the importance of invertebrates, especially shredders, in the decomposition of leaf detritus (Webster & Benfield, 1986; Graça, 2001; Haapala et al., 2001). However, in tropical regions, the role of invertebrates in this process is still not completely understood (Dobson et al., 2002; Ribas et al., 2006; Wantzen & Wagner, 2006). Despite the intense invertebrate colonization described in many leaf decomposition studies, typical shredders are not abundant in many tropical streams (e.g., Mathuriau & Chauvet, 2002; Callisto et al., 2004; Gonçalves et al., 2006b, c; Moretti et al., 2007a; but see Cheshire et al., 2005). According to Irons et al. (1994), higher temperatures in tropical streams may enhance the activity of microorganisms, making them the main decomposers in these environments.

The intrinsic traits of each type of detritus determine its use by aquatic invertebrates and, consequently, the way that these detritus types are colonized by invertebrates over time (Gonçalves et al., 2004). Leaf detritus with low palatability is usually poor in nutrients, tough, and slow to decompose. However, it constitutes a resource that is more temporally stable than that formed by more palatable detritus, which is soft and decomposes rapidly. In other words, good-quality resources are normally ephemeral and thus not always available for consumers (Dudgeon & Wu, 1999; Haapala et al., 2001).

As a response to intense herbivory and hydric stresses, the majority of the tree species native to the Brazilian Cerrado (savanna) have tough leaves, which are poor in nutrients and contain large amounts of secondary compounds, such as tannins and polyphenols (Nolen & Pearson, 1993; Oliveira & Marquis, 2002; Wantzen & Wagner, 2006). Consequently, most of these species have leaves that decompose very slowly after entering streams, and therefore accumulate on the streambed (Gonçalves et al., 2007).

In an effort to understand better the patterns that control leaf decomposition in tropical streams, including colonization by aquatic invertebrates, we compared the relative importance of leaf species and exposure time in a Cerrado stream, using five native tree species (*Protium heptaphyllum* March., *Protium brasiliense* Engl., *Ocotea* sp. Aubl., *Myrcia guyanensis* Aubl., and *Miconia chartacea* Triana). Data on breakdown rates and chemistry of these leaves are already available (Moretti et al., 2007b). We hypothesized that in an environment where leaf detritus has low-nutritional quality, the exposure time is the main factor that influences the colonization of leaves by invertebrates.

Methods

Study area

The study was carried out in a third-order reach (sensu Strahler, 1963) of Garcia stream (20°21′S, 43°41′W), 1,300 m asl; Doce River basin, Serra do Ouro Branco, in southeastern Brazil. The site is located in the Cerrado biome, one of the 25 "biodiversity hotspots" in the world (Myers et al.,

2000). In the reach studied, the riparian vegetation was a well-developed forest with a canopy totally covering the streambed. Yearly air temperatures vary between 13 and 22°C (annual mean 17°C), and the mean annual precipitation is 1,200 mm.

Leaves

Leaves from five native tree species that are common in the riparian vegetation of Brazilian Cerrado headwater streams were used: *Protium heptaphyllum*, *Protium brasiliense* (Burseraceae), *Ocotea* sp. (Lauraceae), *Myrcia guyanensis* (Myrtaceae), and *Miconia chartacea* (Melastomataceae). These species differ in their decomposition rates in the stream; *Ocotea* sp. decomposes fastest ($k = 0.0088$/day), and *P. brasiliense* and *P. heptaphyllum* slowest ($k = 0.0042$/day and 0.0040/day, respectively). *M. guyanensis* and *M. chartacea* have intermediate decomposition rates ($k = 0.0053$/day and 0.0051/day, respectively). They are poor in nutrients (nitrogen concentrations between 0.88 and 1.11% g^{-1} dry mass; phosphorus concentrations between 0.023 and 0.030% g^{-1} dry mass), tough (toughness between 481.66 and 869.90 g), and contain large amounts of secondary compounds (concentrations of polyphenols between 6.31 and 8.48% g^{-1} dry mass). More information about the physical and chemical characteristics of these leaf species can be found in Table 2 from Moretti et al. (2007b).

Leaves were collected using plastic nets (1 m^2, 10-mm mesh size) fixed at a height of 1.5 m in the riparian zone. Leaves deposited in the nets were taken to the laboratory, dried at room temperature, sorted by species, and stored until needed (approximately 6 months).

Experimental procedures

Leaves were placed in single-species litter bags of 10 × 15 cm (10-mm mesh size) and incubated in Garcia stream between April and August 2004. In total, 120 litter bags (24 samples of each species) were fixed in place with the help of iron bars and rocks, and incubated under similar conditions of turbulence and water flow (glides), mean water velocity of 1.85 ± 0.51 m/s. We placed 1 ± 0.005 g of leaves in each litter bag.

Four litter bags of each species were collected after 7, 15, 30, 60, 90, and 120 days and transported to the laboratory inside a cool, insulated box. The leaf material was washed over 120 µm sieves, dried at 60°C for 72 h, and weighed to determine leaf dry mass (leaf DM).

The invertebrates retained on the sieves were preserved in 70% ethanol, sorted, and identified to family level using a stereomicroscope (32×) and taxonomic keys (Pérez, 1988; Merritt & Cummins, 1996; Fernández & Domínguez, 2001; Costa et al., 2006). After identification, the organisms were dried (60°C, 72 h) and weighed (0.1 mg precision balance) to estimate the total invertebrate biomass of each sample. Chironomid larvae were weighed separately, in order to evaluate the importance of this group in relation to the total biomass. Invertebrates were assigned to the following functional feeding groups: gathering-collectors, filtering-collectors, predators, scrapers, and shredders (Table 1). For taxa that are reported to belong to more than one functional group, the specimens were evenly divided among each possible trophic category. Chironomid larvae were not assigned to any functional feeding group because they have multiple, and poorly known, feeding habits

Table 1 Classification of invertebrate taxa in functional feeding groups (FFG) according to Brazilian or Neotropical references (Fernández & Domínguez, 2001; Cummins et al., 2005; Costa et al., 2006; Wantzen & Wagner, 2006)

FFG	Taxa
Gathering-collectors	Baetidae, Leptohyphidae, Leptophlebiidae, Elmidae, Hydroptilidae, Leptoceridae, Oligochaeta
Filtering-collectors	Hydropsychidae, Simuliidae
Predators	Coenagrionidae, Calopterygidae, Perlidae, Hydropsychidae, Hydrobiosidae, Leptoceridae, Empididae, Ceratopogonidae, Hydracarina, Hirudinea
Shredders	Gripopterygidae, Odontoceridae, Leptoceridae
Scrapers	Baetidae, Leptophlebiidae, Elmidae, Hydroptilidae, Glossosomatidae

(Stout & Taft, 1985; Oertli, 1993; Callisto et al., 2007). In any event, we must be cautious when allocating tropical macroinvertebrates to feeding categories, because of the uncertainty about their trophic ecology (Camacho et al., 2009).

Data analysis

We used the rarefaction methodology to calculate expected taxon richness values at standardized sample sizes $E(Sn)$, because the total number of invertebrates ranged widely across all samples (from 16 to 302 individuals). The effects of leaf species and exposure time (factors) on taxon richness, total biomass (mg organisms/g leaf DM), total density, and densities of each functional feeding group (no. individuals/g leaf DM) were tested with factorial two-way ANOVA (log-transformed data). Tukey's HSD test was used for post-hoc comparisons (Zar, 1999).

The similarities among samples of different leaf species and exposure times were examined with a Cluster analysis using Bray–Curtis distance (log-transformed data) and the mean distance between groups (UPGMA) as the amalgamation method.

An indicator taxa analysis (Dufrêne & Legendre, 1997) was used to determine which taxa were characteristic of groups of samples. This method combines information on species abundance and relative frequency in a particular group. Then, the analysis assigns to each taxon, indication values (IV) that range between 0 and 100, according to its abundance and relative frequency in each previously defined group (in our case, the incubation times). These values are tested statistically using a Monte Carlo technique. If significant differences are found for the IV of the same taxon in different groups ($P < 0.05$), this taxon can be considered as an indicator for one or more groups.

All statistical analyses were performed using Statistica 6.0 (Statsoft Inc., 2002), Primer 6 Beta (Primer-E Ltd, 2004), and PC-Ord 3.11 (MjM Software, 1997).

Results

We identified 10,367 organisms classified into 21 families. The most abundant taxa were Chironomidae (Diptera, 52% of all organisms collected), followed by Leptohyphidae (Ephemeroptera, 13%), Oligochaeta (Annelida, 9%), Simuliidae (Diptera, 6%), Hydropsychidae (Trichoptera, 5%), and Gripopterygidae (Plecoptera, 4%). These six taxa represented approximately 90% of the invertebrates associated with the leaves.

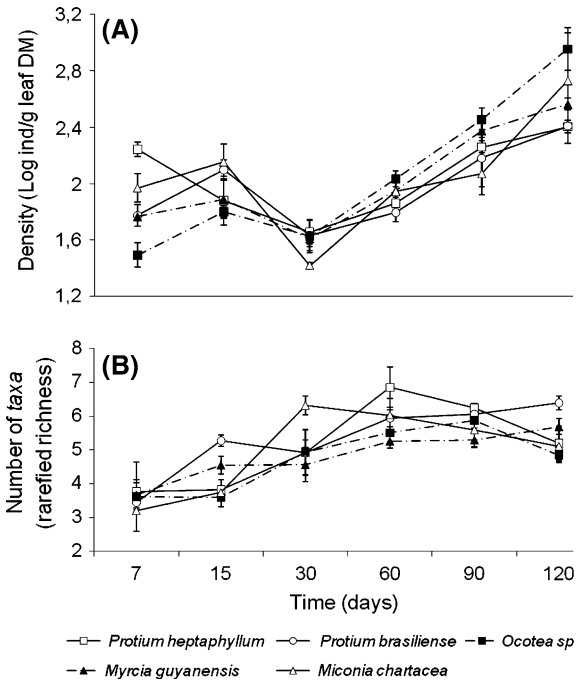

Fig. 1 Total density (mean ± SE) (**A**) and taxon richness (mean ± SE) (**B**) of invertebrate communities associated with leaf detritus in Garcia stream

Invertebrate total density reached 87 ± 13 individuals/g leaf DM (mean ± SE) during the first week of incubation, decreased to the lowest level on the 30th day (42 ± 4 individuals/g leaf DM), and then increased continuously until the end of the experiment, reaching 708 ± 265 individuals/g leaf DM after 120 days (Fig. 1A). The variation of the total density of invertebrates among the leaf species depended on the incubation period (leaf species × time: $F_{(20, 89)} = 2.82$, $P < 0.001$). *P. heptaphyllum* harbored the highest density during the first week, and *Ocotea* sp. had the lowest. Beginning with day 60 of incubation until the end of the experiment, *Ocotea* sp. harbored higher densities than *P. brasiliense* and *P. heptaphyllum*.

Taxa richness per litter-bag sample increased from 3.5 ± 0.2 taxa on day 7, to 5.9 ± 0.2 on day 60, and then remained stable until day 120 (Fig. 1B). Taxa richness only differed significantly among exposure

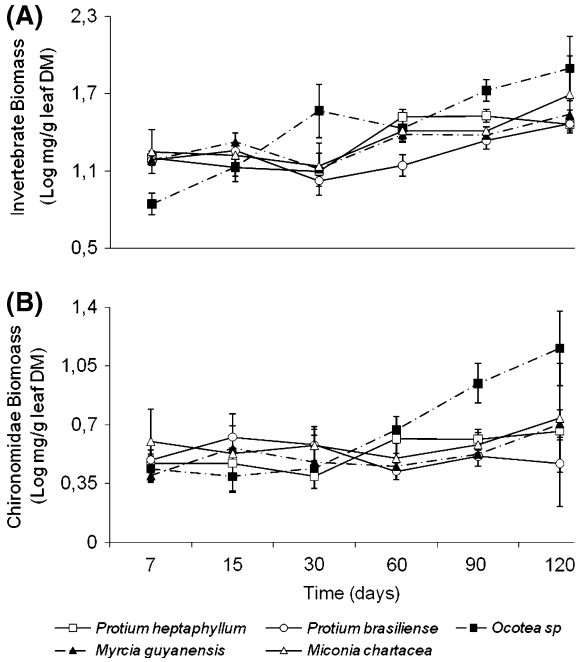

Fig. 2 Total invertebrate biomass (mean ± SE) (**A**) and chironomid biomass (mean ± SE) (**B**) associated with leaf detritus in Garcia stream

times (leaf species: $F_{(4,\ 89)} = 1.89$, $P = 0.12$; time: $F_{(5,\ 89)} = 26.57$, $P < 0.001$; leaf species × time: $F_{(20,\ 89)} = 1.48$, $P = 0.11$).

The mean invertebrate biomass of all leaves was 14.3 ± 1.2 mg/g leaf DM during the first week, which increased after the 30th day of incubation, and reached 61.9 ± 21.5 mg/g leaf DM after 120 days (Fig. 2A). The variation of the biomass of associated invertebrates among the leaf species depended on the incubation time (leaf species × time: $F_{(20,\ 79)} = 2.05$, $P = 0.01$). On the seventh day of incubation, the biomass of associated invertebrates was lower on *Ocotea* sp. than on the other leaf species. At 15 days of incubation, all the leaf species harbored similar levels of biomass. From day 30 on, *Ocotea* sp. showed biomass levels higher than the others during almost the entire remaining period of the experiment.

Chironomid biomass did not differ among leaf species ($F_{(4,\ 79)} = 2.06$, $P = 0.09$). The mean initial levels were 3.1 ± 0.3 mg/g leaf DM during the first week, and reached 8.8 ± 2.7 mg/g leaf DM at the end of the experiment (Fig. 2B). In this group, differences in biomass among exposure times were significant ($F_{(5,\ 79)} = 4.28$, $P < 0.001$). The interaction effect between leaf species and exposure time on chironomid biomass was not significant ($F_{(20,\ 79)} = 1.34$, $P = 0.18$). The percentage of Chironomidae in the total invertebrate biomass ranged from 2 to 94 across all collected samples, with a mean of 20%.

Gathering-collectors were the most abundant functional feeding group (50% of the total number of organisms), followed by filtering-collectors (18%) and predators (17%). Shredders constituted 9%, while scrapers represented 5% of the total number of organisms collected. The differences in the densities of the functional trophic groups among the leaf species depended on the incubation time (Table 2). After 15 days of incubation, the filtering-collectors were the most abundant trophic group on the detritus of *P. heptaphyllum*, *P. brasiliense*, and *M. chartacea*

Table 2 Densities (mean ± SE) of functional feeding groups (FFG) associated with leaf detritus species in Garcia stream, and two-way ANOVA results

FFG	Density (ind/g leaf DM)					*F*/*P* values		
	Mg	Oc	Mc	Pb	Ph	Leaf species	Time	Leaf species × time
Gathering-collectors	58.6 ± 13.6	93.8 ± 40.5	39.4 ± 17.4	37.0 ± 8.8	17.8 ± 3.9	10.978**	86.889**	1.816*
Filtering-collectors	2.9 ± 1.5	2.4 ± 1.6	24.7 ± 7.8	5.1 ± 2.0	16.8 ± 4.6	16.84**	15.393**	2.756**
Predators	10.4 ± 2.6	12.6 ± 3.8	21.8 ± 11.2	10.7 ± 2.1	16.9 ± 2.4	4.92*	28.58**	1.861*
Shredders	8.6 ± 2.0	15.1 ± 4.8	12.5 ± 8.5	6.0 ± 1.1	3.7 ± 0.9	5.44**	35.889**	2.146*
Scrapers	3.8 ± 1.1	5.8 ± 1.9	2.6 ± 0.6	5.0 ± 1.2	2.7 ± 0.7	1.101	20.552**	1.889*

Mg, *Myrcia guyanensis*; Oc, *Ocotea* sp.; Mc, *Miconia chartacea*; Pb, *Protium brasiliense*; Ph, *Protium heptaphyllum*

Degrees of freedom: leaf species = 4, time = 5, leaf species × time = 20

* $P < 0.05$, ** $P < 0.001$

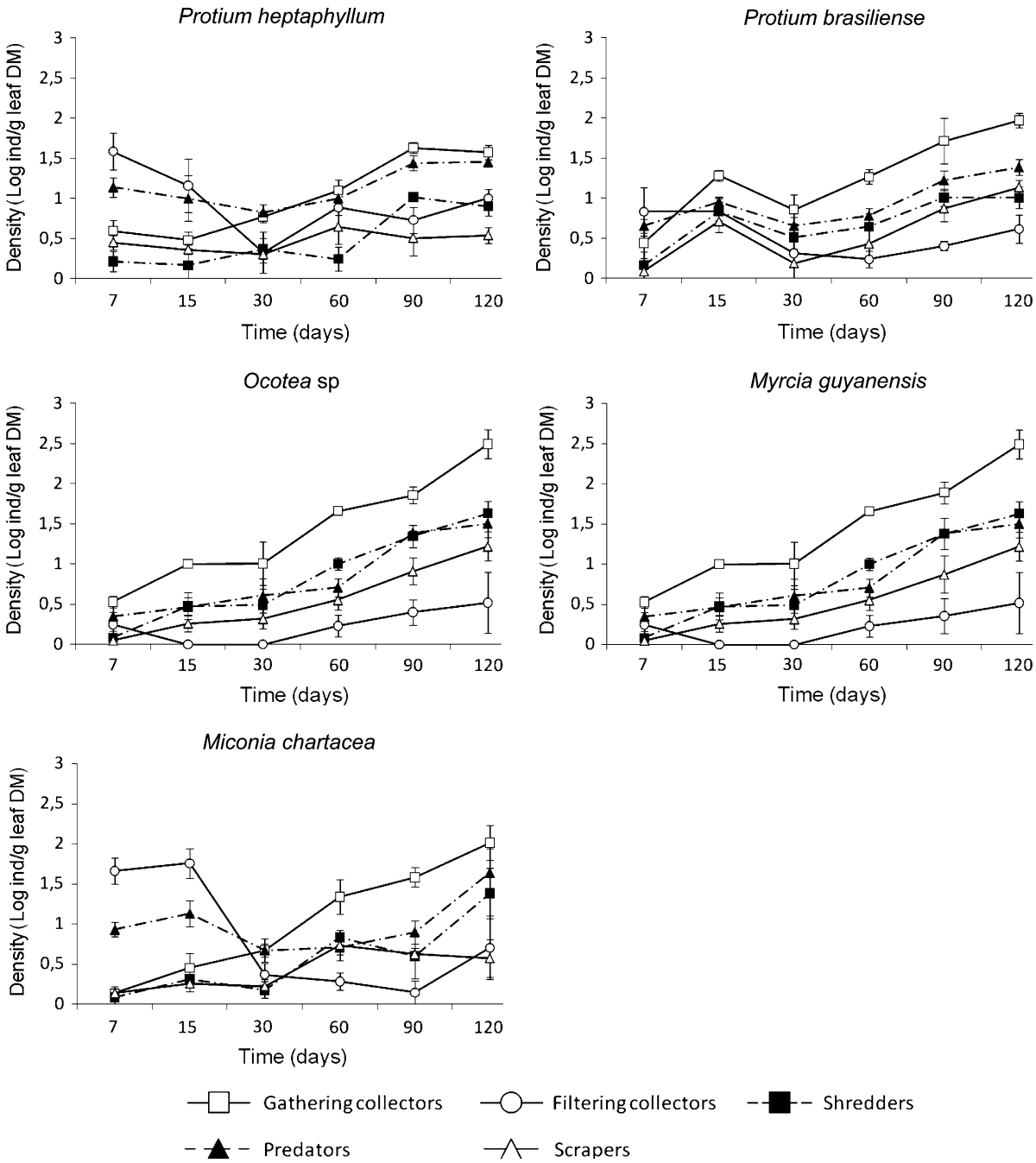

Fig. 3 Densities (mean ± SE) of functional feeding groups (FFG) associated with leaf detritus species in Garcia stream

(Fig. 3). On *Ocotea* sp. and *M. guyanensis*, the gathering-collectors were the most abundant trophic group throughout the entire experiment. On the other leaf species, the gathering-collectors were the most abundant trophic group after the 60th day of incubation. In *P. heptaphyllum*, *P. brasiliense*, and *M. chartacea* no great variations were observed in the densities of predators and scrapers between the initial and final incubation periods. In *Ocotea* sp. and *M. guyanensis*, the densities of predators and scrapers increased continuously during the entire experiment. In all the leaf species, the shredders were more

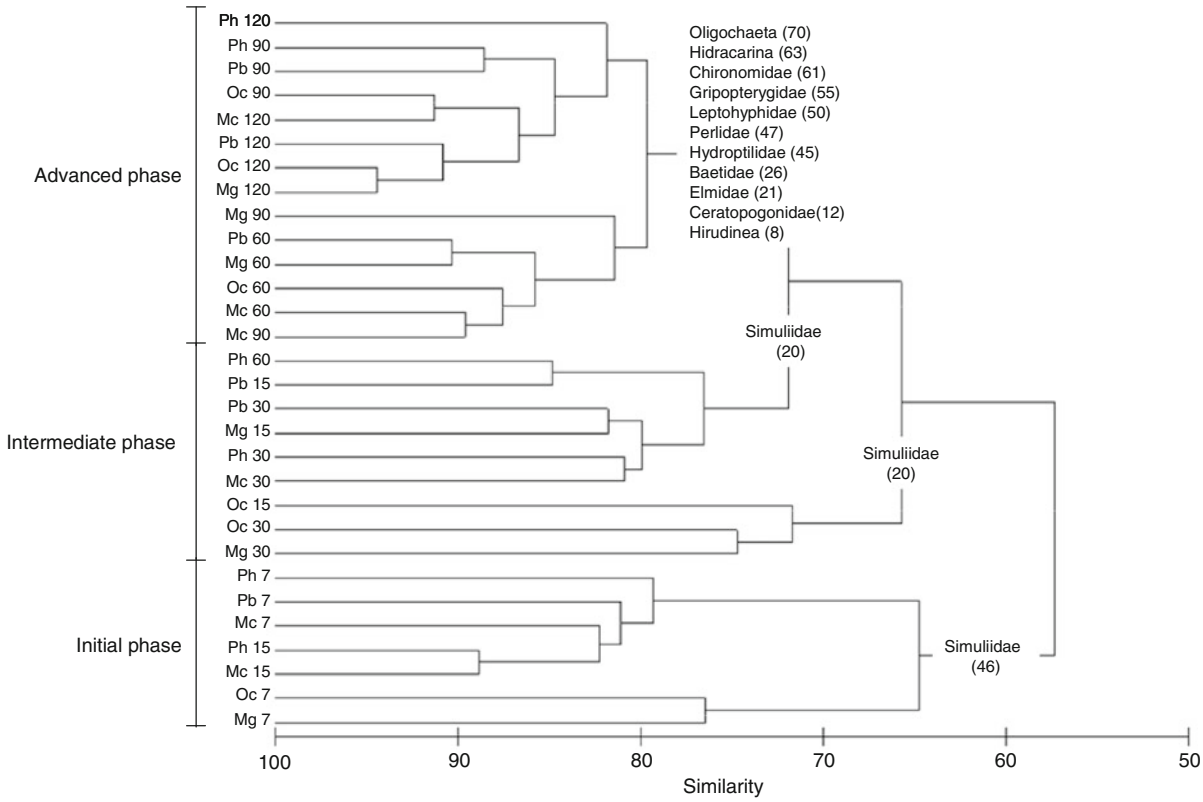

Fig. 4 Cluster analysis dendrogram generated for the invertebrate communities associated with leaf detritus in Garcia stream. Each treatment is indicated with the leaf species (Ph *Protium heptaphyllum*, Pb *Protium brasiliense*, Oc *Ocotea* sp., Mg *Myrcia guyanensis*, and Mc *Miconia chartacea*), followed by exposure time. The indicator taxa are listed for each group, with their respective indication values (IV) in parentheses

abundant after the longer incubation periods (90 and 120 days). Leaves from *Ocotea* sp. and *M. guyanensis* showed the highest densities of shredders.

The cluster analysis evidenced a minimum similarity of 57% among all samples. Invertebrate assemblages showed different structures according to exposure time. The clusters separated the initial (7 days), intermediate (15 and 30 days), and advanced (60, 90, and 120 days) colonization phases (Fig. 4). The formation of these clusters was not influenced by leaf species, because all five species were found mixed in each cluster.

The indicator taxa analysis showed that only Simuliidae was an indicator of the initial (IV = 46%) and intermediate (IV = 20%) phases of the colonization process (Fig. 4). Oligochaeta (IV = 70%), Hydracarina (63%), Chironomidae (61%), Gripopterygidae (55%), Leptohyphidae (50%), Perlidae (47%), Hydroptilidae (45%), Baetidae (26%), Elmidae (21%), Ceratopogonidae (12%), and Hirudinea (8%) were indicators of the advanced phase.

Discussion

The accumulation of leaves in streambeds provides shelter and protection to invertebrates, as well as being a food resource for some of them (Oberndorfer et al., 1984; Lancaster & Hildrew, 1993; Dudgeon & Wu, 1999). Accordingly, the distribution of leaf detritus along the streambed directly influences the distribution of invertebrate populations, turning these leaf patches into "islands" with high richness and densities of aquatic organisms (Wallace et al., 1997; Kobayashi & Kagaya, 2005). The availability of leaf detritus can also be influenced by the presence of invertebrates (Graça, 2001; Haapala et al., 2001). These, by shredding, scraping, and mining leaves,

accelerate the loss of leaf mass (Webster & Benfield, 1986; Cheshire et al., 2005). Consequently, there is a relationship among leaf-detritus species, breakdown rates, and the associated invertebrate assemblages in aquatic environments.

Several studies assessing invertebrate colonization in leaf detritus have observed a relatively constant increase in taxon richness and density from the beginning to the end of the experiment (Anderson & Sedell, 1979; Dudgeon, 1982; Webster & Benfield, 1986; Bunn, 1988; Benstead, 1996). In the present study, these variables showed similar patterns, although the taxon richness increased only until the 60th day, and total density values decreased on the 30th day of incubation. However, the values of both variables were high compared to those found in other studies in tropical regions (see Gonçalves et al., 2006b; Chara et al., 2007; Moretti et al., 2007a).

Taxon richness did not vary among the different leaf species, although the leaves differ in physical (toughness) and chemical (polyphenols) traits and in decomposition rates (Moretti et al., 2007b). On the other hand, total invertebrate biomass and density varied among leaf species in different ways during the incubation times. *Ocotea* sp. (which was reported to decompose fastest of the five) was the leaf species that supported the smallest density and biomass of invertebrates in the first week of incubation. However, after the 60th day the detritus of this species showed higher levels than the detritus of *P. brasiliense* and *P. heptaphyllum*, which were reported to decompose slowly. More rapidly decomposing detritus may have provided food resources of better quality (e.g., presence of biofilm, fungal colonization, adhered fine particles; see Gonçalves et al., 2006b, 2007) for shredders, gathering-collectors, and scrapers, resulting in higher invertebrate density and biomass during the more advanced decomposition stages.

Studies assessing the colonization of leaf detritus have found higher abundances of invertebrates during intermediate incubation stages, and lower taxon richness and density in advanced stages (Gessner & Dobson, 1993; Tanaka et al., 2006), following the general patterns of degradative ecological succession (sensu Begon et al., 2006). However, in the present study, invertebrate richness, biomass, density, and number of indicator taxa were higher during the last incubation time. This may be related to the slow decomposition rates of the five leaf species, which after 120 days of incubation still had substantial biomass remaining (a mean of 50%, see Moretti et al., 2007b). Thus, our results suggest that at the end of the experiment, the detritus was still in an intermediate stage of decomposition, when a larger amount of resources is still available to the associated invertebrates and degradative ecological succession reaches its most advanced and complex stage (Cummins et al., 1989; Begon et al., 2006).

The observed dominance of Chironomidae on all leaf species agrees with other reports by Dudgeon & Wu (1999), Haapala et al. (2001), Mathuriau & Chauvet (2002), Sylvestre & Bailey (2005), and Gonçalves et al. (2006b). The lower proportion of chironomids in the invertebrate biomass (20% of the total biomass) reflects the small sizes of the larvae. However, chironomids are important for the maintenance of nutrient cycling and trophic webs in aquatic ecosystems (Armitage et al., 1994). The role of these larvae in the decomposition process has been studied by many researchers (Oertli, 1993; Grubbs et al., 1995; Gonçalves et al., 2000; Callisto et al., 2007), and some of them have suggested that chironomid larvae can, in some situations, feed on the detritus by scraping and mining the leaf surface (Rosemond et al., 1998). Given their abundance and feeding habits, chironomids have the potential to be important in litter decomposition.

We observed that the five leaf species studied supported different densities of functional feeding groups, and that these differences changed during the course of the incubation. Higher densities of gathering-collectors and shredders were found in the faster-decomposing leaves (*Ocotea* sp. and *M. guyanensis*). Shredders were almost exclusively represented by larvae of Gripopterygidae. Leaves with higher decomposition rates are usually more palatable to shredders (Graça, 2001; Graça et al., 2001), which in turn increase the availability of fine particulate organic matter (FPOM), the main food resource for gathering-collectors (Hoffmann, 2005). The proportion of shredders found in our samples was low, as reported in other studies in tropical streams (e.g., Pringle & Ramírez, 1998; Dudgeon & Wu, 1999; Dobson et al., 2002; Gonçalves et al., 2006b, c; Wantzen & Wagner, 2006; Gonçalves et al., 2007). The proportion of shredders probably would be even lower if chironomids were included in this analysis.

Higher densities of filtering-collectors (mainly represented by simuliid larvae) were observed during the initial times of incubation, principally in leaves that decompose slowly (*P. heptaphyllum*, *P. brasiliense*, and *M. chartacea*), which are probably less palatable and more temporally stable. This trophic group had lower densities in more rapidly decomposing leaves. In this context, our results suggest that the filtering-collectors were using the leaf detritus only as a substrate, as suggested by Dudgeon & Wu (1999).

In all the leaf species, the density of predators was high during almost all the incubation periods, suggesting that prey items were continuously available in the detritus. The density of scrapers was low in all the samples; this may be related to shading by the riparian vegetation over the streambed, which reduces sunlight incidence and limits periphyton productivity (see Gjerlov & Richardson, 2004; Dudgeon & Wu, 1999).

Cheshire et al. (2005) and Tomanova et al. (2006), who allocated invertebrates to feeding groups according to their gut contents and mouthparts, found little specialization among tropical invertebrates, even at the genus level. In this study, because we analyzed functional feeding groups at the family level, even less-specialized behaviors might be expected. Therefore, some caution is needed in comparing these data with other studies.

The three phases of invertebrate colonization found in the cluster analysis fit with the temporal patterns of the invertebrate densities. The indicator taxa analysis revealed that the first two phases (up to 30 days of incubation) were dominated by Simuliidae. In these phases, the more slowly decomposing detritus (*P. heptaphyllum*, *P. brasiliense*, and *M. chartacea*), because it supported higher densities of simuliid larvae, also showed higher total densities. The decrease in density observed on the 30th day of incubation may represent a period when the dominant taxa were being replaced. As indicated by the various indicator taxa, the last phase was characterized by a more heterogeneous use of the leaf detritus, which allowed the colonization and coexistence of a larger number of invertebrates with different feeding habits and resource requirements. In this phase, the more rapidly decomposing detritus (*Ocotea* sp. and *M. guyanensis*), which is probably more palatable and offers more food resources, showed the highest densities.

From the cluster analysis it appeared that the exposure time was more important than leaf species in determining the taxon composition of associated invertebrate communities, corroborating our initial hypothesis. In spite of this, a small gradient can be observed among the leaf species with respect to the time of arrival of each of the stages. We noted that the detritus that decomposed more slowly took longer to reach the intermediate and advanced stages of colonization. The samples at 15 days of incubation of the detritus of *P. heptaphyllum* and *M. chartacea* were more similar to the samples at 7 days. After 60 days of incubation, the detritus of *P. heptaphyllum* was still in the intermediate stage, whereas the others were in the advanced stage. This reinforces the idea that the detritus that decomposes more slowly constitutes a temporally more stable habitat for the invertebrates. The high degree of similarity among the communities associated with the different detritus types might be related to the homogenous quality of the leaf species studied. We probably would have found different results if more attractive and rapidly decomposing leaves had been included. However, this type of leaf is rarely found in the riparian zones of the Cerrado biome, where the majority of native trees have leaves with homogeneous traits and low palatability to invertebrates. Accordingly, our results and interpretations were generated in a natural environment that provides resources with low quality and high-temporal stability to the invertebrates.

Conclusions

We observed that the species of leaf had an indirect effect on the process of colonization of the leaf detritus. The total biomass and density of the associated invertebrates and the densities of the functional trophic groups varied differently among the types of detritus during the different incubation periods, as was indicated by the significant values for interaction. At the beginning of the experiment, the slower-decomposing leaves, which are temporally more stable, were more intensely colonized than the rapidly decomposing leaves, indicating that these leaves were being used primarily as habitat (mainly by larvae of Simuliidae). In the more advanced decomposition periods, the more rapidly decomposing detritus was colonized more intensely, showing higher levels of biomass, total

density, and density of trophic groups, especially shredders. This, together with the results of the analysis of indicator taxa, may indicate that the importance of the detritus as a trophic resource for the invertebrates may have increased as the incubation progressed.

Despite this, our results demonstrated that, for the determination of the structure and composition of the invertebrate assemblages, exposure time is more important than leaf species in streams that contain patches of detritus of low-nutritional quality and high-temporal stability, such as Brazilian Cerrado streams.

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