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Chemical change of leaves during breakdown affects associated invertebrates in a subtropical stream

Mudanças químicas dos detritos foliares durante a decomposição afetam os invertebrados associados em um riacho subtropical

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Abstract: Aims: Our objective was assess the effects of leaf chemical change during breakdown on the associated invertebrates. **Methods:** We evaluate the chemical composition of leaves (of two tree species; *Sebastiania brasiliensis* and *Campomanesia xanthocarpa*) and the density of invertebrates during leaf breakdown (on four incubation times; 3, 7, 14 and 22 days) in a subtropical stream. Linear multiple regression analysis were performed to evaluate the relationship between invertebrate density and changes in leaf chemical during breakdown. **Results:** Density of invertebrates was related to the chemical composition of leaves. There was a positive correlation of K ($\beta = 3.48$) and a negative of C:N ($\beta = -0.34$), polyphenols ($\beta = -0.16$), Ca ($\beta = -2.98$) and Mg ($\beta = -2.58$) with the total density of invertebrates. Density of invertebrates on leaves reached 38 ± 9 and 192 ± 31 individuals g^{-1} leaf DM during the first 3 and 7 days of incubation, had decreased by the 14th day (117 ± 18) and then increased after 22 days (270 ± 41). **Conclusions:** We conclude that changes in the chemistry of decomposing leaves affect invertebrate colonization process. This conclusion reinforce the importance of understand the dynamic of energy and nutrients and its association with the biological communities of tropical riparian ecosystems.

Keywords: leaf chemistry, chemical composition, litter decomposition, tropical stream, functional feeding group.

Resumo: Objetivos: Nosso objetivo foi avaliar o efeito de mudanças na composição química dos detritos foliares durante a decomposição sobre os invertebrados associados. **Métodos:** Avaliamos a composição química dos detritos foliares (de duas espécies arbóreas, *Sebastiania brasiliensis* e *Campomanesia xanthocarpa*) e a densidade de invertebrados durante a decomposição (em quatro tempos de incubação; 3, 7, 14 e 22 dias) em um riacho subtropical. Realizamos análises de regressão linear múltipla para avaliar a relação entre a densidade de invertebrados e as mudanças na composição química dos detritos foliares durante a decomposição. **Resultados:** A densidade de invertebrados foi relacionada com a composição química dos detritos foliares. Houve uma correlação positiva de K ($\beta = 3.48$) e uma negativa de C:N ($\beta = -0.34$), polifenóis ($\beta = -0.16$), Ca ($\beta = -2.98$) e Mg ($\beta = -2.58$) com a densidade total de invertebrados. A densidade de invertebrados nos detritos foliares alcançou 38 ± 9 e 192 ± 31 indivíduos por grama de massa seca durante os primeiros três e sete dias de incubação, diminuindo no 14° (117 ± 18) e então aumentando no 22° dia (270 ± 41). **Conclusões:** Concluímos que as mudanças na química dos detritos foliares em decomposição afetam o processo de colonização por invertebrados. Essa conclusão reforça a importância do entendimento da dinâmica de energia e de nutrientes e sua associação com as comunidades biológicas em ecossistemas ripários tropicais.

Palavras-chave: química foliar, composição química, decomposição de detritos, riacho tropical, grupo trófico funcional.

1. Introduction

Leaf litter from riparian trees is fundamental for the functioning of forested headwater streams because it provides the main source of carbon and nutrients for the ecosystem (Wallace, 1997). After reaching a stream, these leaves suffer various physical and chemical processes including an initial rapid leaching phase when water-soluble compounds are lost, bacterial and fungal colonisation, and mechanical breakdown of leaf structure due to water flow and shredder invertebrates (Graça, 2001). The single-effect or interaction of these processes is responsible to chemical change of leaf litter over breakdown that affect invertebrate and microbial communities (Ardón and Pringle, 2008).

The leaching of soluble compounds may account for considerable loss of leaf initial mass and can be responsible for greater reduction of secondary compounds concentration (Gonçalves et al., 2012). Microbial colonization (especially fungi) enhance leaf breakdown by macerating and metabolizing the leaf tissue and indirectly increases the concentration of leaf nutrients (e.g. N and P), increasing the palatability of leaves to invertebrates (Hieber and Gessner, 2002). The fragmentation of leaves occurs due to fungal and invertebrate activity that produce fine and dissolved particles, and physical abrasion caused by current and transported sediment (Ferreira et al., 2006). The effect of these fragmentation types is responsible for leaf tissue breakdown that result in changes of leaf chemical composition and faster decomposition (Ferreira et al., 2006; Santos Fonseca et al., 2013).

Leaf chemical characteristics known to increase breakdown rates and nutritional quality of leaves for invertebrates in streams included high N and P (Ardón et al., 2009), low C:N ratio (Enríquez et al., 1993), secondary compounds (Hepp et al., 2009) and lignin content (Ardón et al., 2009). In contrast to the existing information from temperate streams, high diversity of tree species in the tropical riparian vegetation has prompted suggestions that leaf quality plays a more important role on decomposition than in temperate streams (Wantzen et al., 2008). Thus, assesses of the subsequent changes in leaf litter chemistry during breakdown is ecologically essential to understand the dynamics of energy and nutrients in the ecosystem.

We examined chemical changes and invertebrate colonization of leaves from tree species with contrasting chemistry during breakdown in a subtropical stream. Our hypothesis was that changes in the chemistry of leaves during breakdown affects leaf associated invertebrates. We expect that chemical changes of leaf litter (e.g. nutrients, tannins and metals) during breakdown would be related to invertebrates.

2. Material and Methods

2.1. Study area

The study was conducted in a second-order stream of the Suzana River basin, Southern Brazil (27°36'45.4"S, 52°13'48.9"W; 701 m a.s.l.). The area has a subtropical regional climate, a mean annual temperature of 17.6°C, a mean annual precipitation of 1,912 mm and no dry season. The vegetation is characterized by a mix of Araucaria Forest and Subtropical Atlantic Forest (Oliveira-Filho et al., 2013). The riparian trees bordering the stream included *Araucaria angustifolia* (Bertol.) Kuntze, *Ocotea puberula* (Rich.) Nees, *Cabraela canjerana* (Vell.) Mart., *Nectandra megapotamica* (Spreng) Mez., *Sebastiania brasiliensis* Spreng. and *Campomanesia xanthocarpa* O. Berg.

The study stream was nearly 2 m wide and 0.3 m deep. During the experimental period, the mean water temperature (±SD) was 20 (± 1°C). The water had low conductivity (62 ± 1 µS cm^{-1}) and was circumneutral (pH 7.6 ± 0.5) and well oxygenated (9 ± 1 mg O_2 L^{-1}, n = 4). The stream has a turbidity of 7 ± 0.5 NTU and alkalinity of 18 ± 2 mg $CaCO_3$ L^{-1}. Moreover, the stream water has 13 ± 0 µg NH_4 L^{-1} and 0.08 ± 0.01 mg PO_4 L^{-1} (n = 2). The average current velocity across sampling dates was 0.7 ± 0.1 m s^{-1} (n = 4).

2.2. Experimental design and leaf litter decomposition

We used leaves of two native tree of Brazilian Atlantic Forest: *Sebastiania brasiliensis* Spreng. (Euphorbiaceae) and *Campomanesia xanthocarpa* O.Berg (Myrtaceae), because these leaves offer contrasting characteristics (for chemical details, Biasi et al., 2013). The leaves of *S. brasiliensis* are thin and soft, with a low C:N ratio (< 17), whereas those of *C. xanthocarpa* are thick and tough, with a high C:N ratio (> 20). Freshly fallen leaves were collected from the ground under a group of trees near the experimental site in spring 2009 and air-dried.

The leaves were placed in single-species litter bags of 15 × 20 cm (10 mm mesh size) and incubated in the stream between November and December 2009. We prepared 32 litter bags (16 litter bags of each species), each containing 2.5 ± 0.1 g of air-dried leaves. The bags were fixed in place with the help of iron bars and incubated under similar conditions of turbulence and water flow.

Four replicate samples of each leaf species were randomly withdrawn after 3, 7, 14 and 22 days. The retrieved litter bags were enclosed in individual plastic bags and taken to the laboratory. The leaf material was washed over 250 µm sieves, then dried in an oven (60°C/72h) and weighed to determine leaf dry mass (leaf DM) and for subsequent chemical analysis. In addition, four replicate samples per species were prepared on day 0 for assessment of mass loss in preparation, handling and transport. Moreover, those replicates were used for determination of initial chemical composition. The invertebrates retained on the sieves were preserved in 70% ethanol and sorted. They were identified to family level with a stereomicroscope and taxonomic keys (Fernández and Domínguez, 2001; Mugnai et al., 2010; Pes et al., 2005).

2.3. Leaf chemistry

We determined the chemical composition of decomposing leaves analysing the content of nitrogen, phosphorus, C:N, polyphenols, tannins, calcium, potassium, and magnesium over the experimental period. All determinations were done on four replicate samples.

The dry leaves were ground in knife mills of 1 mm mesh for chemical analyses. Samples of powdered dry leaves were used to determine total nitrogen concentration by the Kjeldahl method (Flindt and Lillebø, 2005), total phosphorus after acid digestion (HCl) followed by reaction with ascorbic acid (Flindt and Lillebø, 2005) and tannins with the Folin-Ciocalteu method (Bärlocher and Graça, 2005). Samples of dry powder were used to obtain ash-free dry mass (AFDM) by gravimetry after incineration at 550°C for 4 hours. Part of the inorganic material resulting from incineration was diluted with HNO_3 (1 mol L^{-1}) and the resulting solution was analysed with atomic absorption spectrophotometry to quantify the calcium, potassium and magnesium concentrations. Leaf carbon was estimated as 0.47 × AFDM (Westlake, 1963).

2.4. Data analysis

We estimated litter breakdown rates (k day^{-1}) of the tree species by linear regressions of percentage mass (ln transformed) over time to facilitate comparison of decomposition process of leaves between studies done in different locations and with different species of leaves. The initial chemistry of leaves was compared using Student's *t*-tests. The relationship between density of invertebrates (log x+1-transformed data) and chemical compounds of leaves was examined by multiple linear regression analysis (stepwise method, excluding non-significant variables at P > 0.05; Logan, 2010a). We assessed the chemical changes of leaves and the variability of density of each functional feeding group during breakdown by two-way analysis of variance. We used the incubation time as a proxy for temporal changes of leaves and the interaction of time and leaves as different temporal dynamic between two tree species of leaves (Logan, 2010b). The response variables were log (x+1)-transformed prior analysis of variance to normalised the data and reduced the difference in the variance. All analyses were run using the R software (R Core Team, 2013).

3. Results

The density of invertebrates was related to the chemical composition of leaves ($F_{5,26}$ = 42.85; $P < 0.001$). The multiple regression model revealed a positive correlation of K and a negative correlation of the C:N ratio, total polyphenols, Ca and Mg with the invertebrate density (Table 1). Leaf chemistry varied widely over the experimental period (Figure 1, Table 2). N on leaves increased over time, while P decreases until 14^{th} day increasing after this. Tannins, polyphenols and the metals K and Mg followed similar dynamics with fast leaching of leaves. The C:N ratio followed the opposed N patterns, while Ca concentration fluctuated during incubation time.

After 22 days of incubation, the leaves of *S. brasiliensis* lost an average of 77% ± 6 SD of their initial AFDM, while *C. xanthocarpa* lost an average of 41% ± 8. The leaf breakdown were relatively high for both species (k = -0.0640 day^{-1} and k = -0.0219 day^{-1}, respectively).

Table 1. Summary of final multiple regression model to test for correlation (β) between concentrations of chemical compounds of leaves and density of associated invertebrates during leaf breakdown.

Chemical compounds	*β*	*P*-value
Nitrogen	–0.93	0.719
Phosphorus	1.78	0.397
C:N	–0.34	**0.048**
Polyphenols	–0.16	**< 0.001**
Tannins	–0.11	0.340
Magnesium	–2.58	**< 0.001**
Potassium	3.48	**< 0.001**
Calcium	–2.98	**0.001**

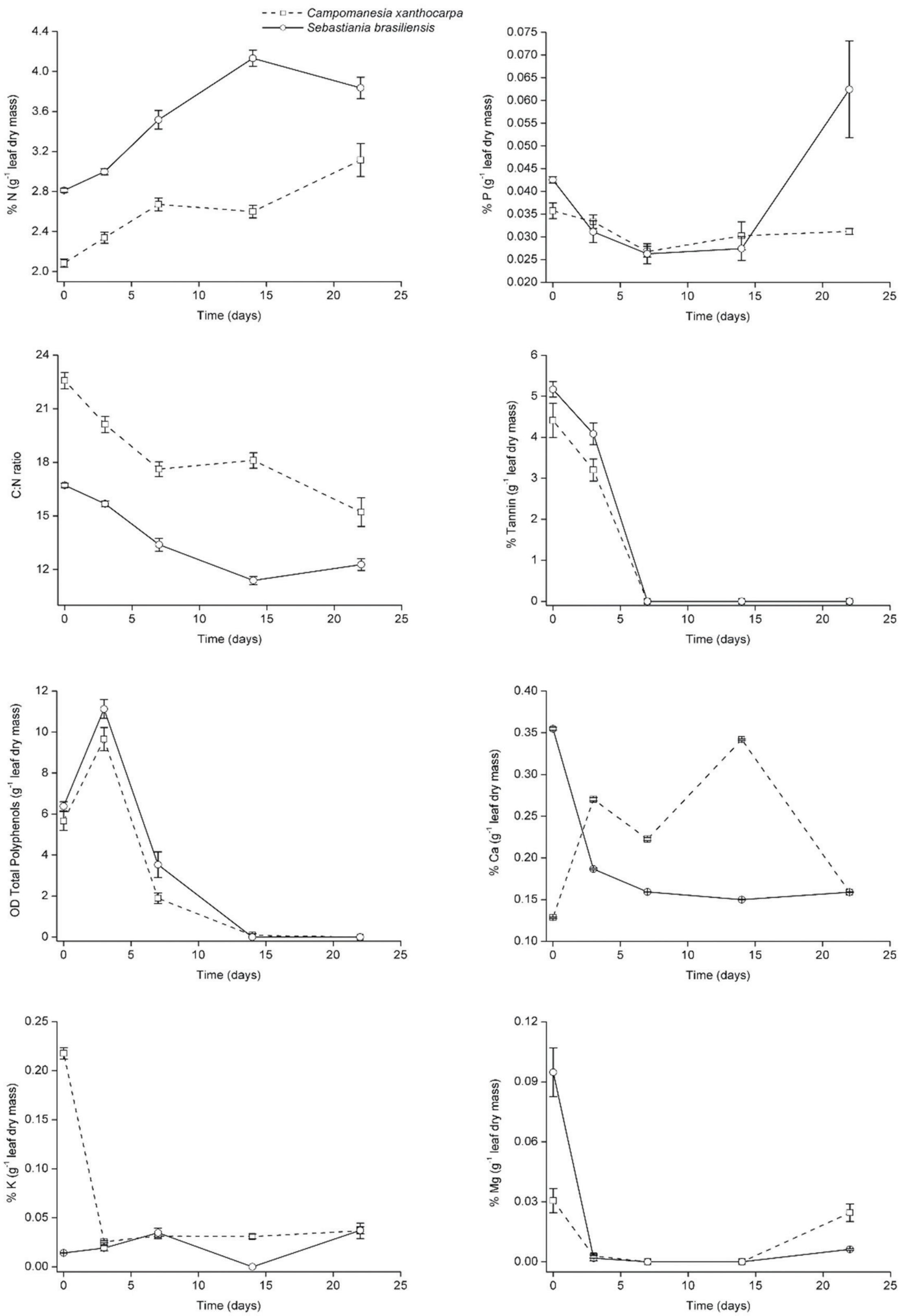

Figure 1. Temporal variations of chemical compounds of leaves of tree species in a subtropical stream. OD = optical density.

We collected 7245 organisms, classified into 17 families. The Chironomidae (Diptera) was the most abundant family, with 71.91% of all organisms collected. The family Simuliidae (Diptera) was the second most abundant, with 20.11% of the total organisms. These two taxa represented approximately 92% of the invertebrates associated with the leaf litter (Table 3). Density of invertebrates

Table 2. Summary for two-way ANOVAs results to test for changes in concentration of leaf chemical compounds and the density of each functional feeding group during breakdown.

	Incubation time		Leaves × incubation time	
	F-value	*P*-value	*F*-value	*P*-value
Chemical compounds	$F_{3,24}$		$F_{3,24}$	
Nitrogen	32.5	**< 0.001**	8.3	**< 0.001**
Phosphorus	9.3	**< 0.001**	7.6	**0.001**
C:N	32.7	**< 0.001**	7.7	**< 0.001**
Tannins	1324.4	**< 0.001**	5.3	**0.006**
Polyphenols	561.0	**< 0.001**	5.1	**0.007**
Magnesium	40.1	**< 0.001**	14.7	**< 0.001**
Potassium	13.7	**< 0.001**	8.6	**< 0.001**
Calcium	2504.0	**< 0.001**	2616.2	**< 0.001**
Functional feeding groups	$F_{3,24}$		$F_{3,24}$	
Gathering-collectors	4.6	**0.011**	0.3	0.83
Filtering-collectors	8.8	**< 0.001**	0.9	0.44
Predators	13.1	**< 0.001**	1.2	0.34
Shredders	1.8	0.17	0.2	0.87
Scrapers	2.4	**0.093**	0.6	0.64
Chironomids	71.1	**< 0.001**	0.5	0.69

Table 3. Means ± SE combined over time of densities (individuals g^{-1} leaf dry mass), relative abundance (%) and corresponding Feeding Functional Group (FFG) of total invertebrates associated on leaves of tree species in a subtropical stream ."-" = FFG not assigned, GC = gathering-collectors, FC = filtering-collectors, P = predators, Sc = scrapers, Sh = shredders.

Taxa	*C. xanthocarpa*		*S. brasiliensis*		FFG
	Density	Abundance	Density	Abundance	
COLEOPTERA					
Elmidae	0.1 ± 0.0	0.03	1 ± 0.4	0.09	GC/Sc
Gyrinidae	0	0	0.3 ± 0.1	0.02	P
DIPTERA					
Chironomidae	303 ± 60.8	71.91	638 ± 120.9	75.05	-
Ceratopogonidae	0	0	0.2 ± 0.0	0.02	P
Empididae	0	0	0.6 ± 0.3	0.05	P
Simuliidae	75 ± 17.6	20.11	120 ± 12.9	17.05	FC
Psychodidae	0	0	0.2 ± 0.0	0.02	GC
EPHEMEROPTERA					
Baetidae	21 ± 1.8	5.21	36 ± 4.1	4.72	GC/Sc
Caenidae	6 ± 1.7	0.49	8 ± 1.6	0.83	GC
Leptophlebiidae	1 ± 0.4	0.26	2 ± 0.1	0.21	GC/Sc
ODONATA					
Coenagrionidae	0.1 ± 0.0	0.03	0	0	P
Calopterygidae	0.1 ± 0.0	0.03	0.1 ± 0.0	0.02	P
PLECOPTERA					
Grypopterigidae	0.2 ± 0.1	0.07	1 ± 0.2	0.14	Sh
TRICHOPTERA					
Calamoceratidae	1 ± 0.2	0.16	0	0	Sh
Hydropsychidae	7 ± 1.7	1.65	18 ± 5.9	1.61	FC/P
Leptoceridae	0	0	0.4 ± 0.2	0.05	GC/Sh/P
Odontoceridae	0.1 ± 0.0	0.03	0.3 ± 0.1	0.05	Sh
Unknown	0	0	0.2 ± 0.1	0.05	-
Total Density	414.5 ± 64		825.2 ± 134		

on leaves reached 38 ± 9 and 192 ± 31 individuals g^{-1} leaf DM (mean of density in both leaf species ± SE) during the first 3 and 7 days of incubation, had decreased by the 14th day (117 ± 18 individuals g^{-1} leaf DM) and then increased, reaching 270 ± 41 individuals g^{-1} leaf DM after 22 days (Figure 2). In terms of trophic groups, scrapers and gathering-collectors densities increased over time, reaching highest values on 14-22 days. Densities of filtering-collectors were higher in intermediate incubation times (7-14 days), while predators and chironomids reach highest densities in final period of incubation (22 day; Figure 3).

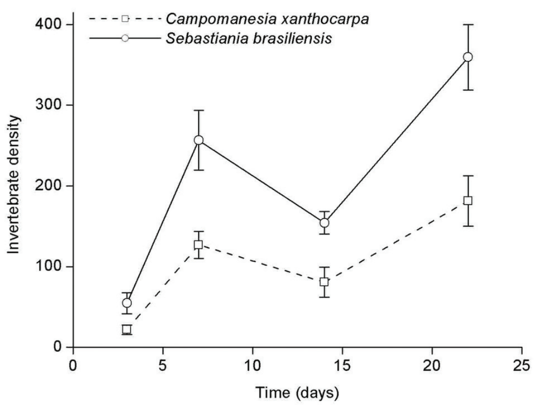

Figure 3. Percentage of functional feeding groups (excluding chironomids for functional feeding classification) of invertebrate community on leaves of tree species during breakdown of *C. xanthocarpa* a) and *S. brasiliensis* b) leaves in a subtropical stream.

4. Discussion

The invertebrate density was correlated with the chemistry of leaves during breakdown. The negative correlation of polyphenols and invertebrate densities may be due to progress of breakdown that leached this compound and elevated the nutritional quality of leaves to invertebrates. Furthermore, we suggest that the ions (K, Mg and Ca) were only correlated with the density of invertebrates due to its rapid leached (K and Mg) or oscillation (Ca) from leaves. Leaves of *S. brasiliensis* exhibited the fastest breakdown, lower C:N ratio and consequently the greatest density of invertebrates over time. Mathuriau and Chauvet (2002) found a similar pattern in a tropical stream where softer texture and lower C:N leaves breakdown more rapidly and supported higher densities of invertebrates.

The leaching of soluble compounds was responsible for the initial mass loss of leaves (Gonçalves et al., 2006; Hepp et al., 2008). The relatively high water temperatures and water flow in the stream can potentially accelerate the decomposition through physical or biological effects on the leaf litter (Ferreira et al., 2006; Irons III et al., 1994). The difference in breakdown rates between tree species were partly explained by the high N and P contents in *S. brasiliensis* leaves (Richardson et al., 2004; Shieh et al., 2008). The N content in *S. brasiliensis* leaves is among the highest found in 53 temperate tree species by Flindt and Lillebø (2005) and in 8 tropical tree species analysed by Ardón et al. (2009). Leaves of *C. xanthocarpa*

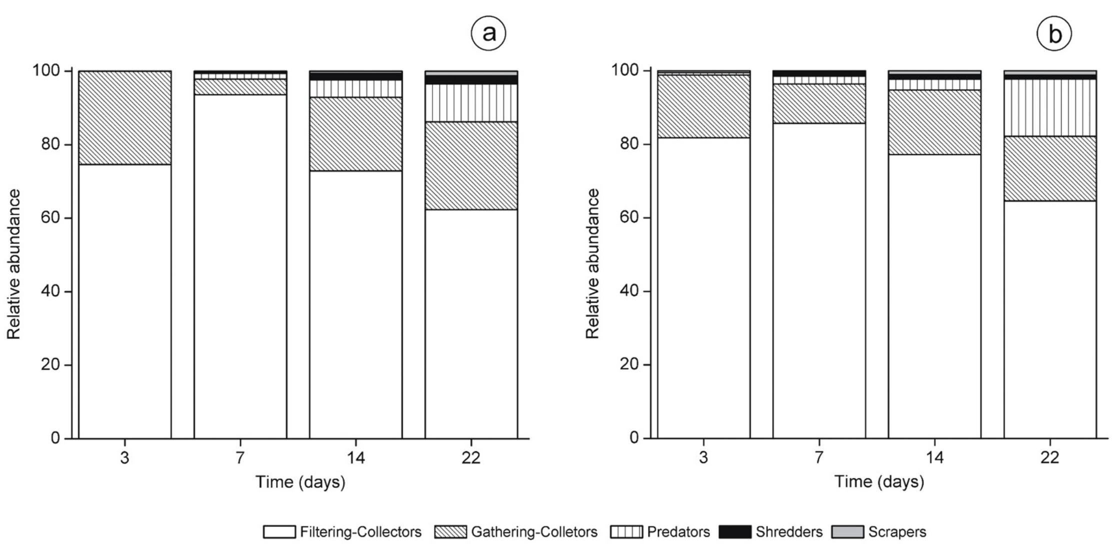

Figure 2. Temporal variations in invertebrate density individuals per gram of ash free dry mass [AFDM]; mean ± SE) on leaves of tree species in a subtropical stream.

had an intermediate concentration of this nutrient. We hypothesised that the increase in leaf N concentration is due to microbial conditioning of leaves through time (Graça et al., 2001). This increase leads to an increment in nutritional quality and the attractiveness of the detritus for invertebrates (Mathuriau and Chauvet, 2002).

Secondary compounds (i.e., total polyphenols and tannins) were rapidly leached at rates four times greater than the rates reported for temperate leaves by Bärlocher et al. (1995) and for tropical leaves by Ardón and Pringle (2008). Both species lost more than 50% of their secondary compounds during the first week of incubation in the stream. Previous studies have suggested that high concentrations of these compounds inhibit colonisation by invertebrates, slowing leaf breakdown (Hepp et al., 2009; Stout, 1989; Wantzen et al., 2002). However, the rapid leaching of these leaf compounds may have reduced the inhibitory effect on invertebrates. Our results are in accordance with Ardón and Pringle (2008) and Ardón et al. (2009) who conclude that secondary compounds are rapidly leached, and thus does not play a direct role in leaf breakdown.

The general decrease in the concentrations of metals (Ca, Mg and K) in the detritus, especially during the initial period of the incubation, can be related to the breakdown of leaf tissue and the associated loss of soluble compounds. Shieh et al. (2008) observed high release rates of K, Mg and Ca from leaf litter in a subtropical stream and hypothesised that the dissolution of these compounds accelerated leaf degradation.

The decay rates for *C. xanthocarpa* and *S. brasiliensis* can be considered rapid according to Gonçalves et al. (2013). The decomposition rates obtained are among the highest observed for tropical streams (see Gimenes et al., 2010). The rapid breakdown may be due to intrinsic characteristics of the leaves (e.g., chemical composition and texture), and/or the hydrological and chemical features of the stream (high water flow and nutrients such as P and N in water).

Higher densities of filtering and gathering-collectors in intermediate times of incubation (7 and 14 days) may be explained by the availability of fine particulate organic matter (FPOM) as a food resource, mainly in leaves that decompose rapidly (*S. brasiliensis*). The two rainfall events over the experimental period increased the water flow and may have intensified the release of FPOM to the water column. Furthermore, collectors may be using leaf detritus as substrate to cling to (Dudgeon and Wu, 1999), certainly in the early stages of the experiment when FPOM is most likely from an outside source. Wantzen et al. (2006) expected a reduction in leaf-feeding specialist and an increase in organisms with generalized and opportunistic feeding strategies where frequent spates interfere with biological degradation (e.g., some tropical streams). This increase is evident for collectors, particularly for chironomids, that dominate the food webs of small tropical streams (Rueda-Delgado et al., 2006). Despite chironomids dominance, their role on leaf breakdown is uncertainly, especially considering the low density of shredder or miner chironomids in the community (Biasi et al., 2013; Landeiro et al., 2008).

We observed a low density of invertebrate shredders in relation to other functional groups. This trophic group have a key factor in low-order stream ecosystems because they feed organic detritus and shred into small particles, providing other forms of C for stream food webs (Graça, 2001; Wallace et al., 1982). The low percentage of shredder invertebrates were observed in some tropical streams (Gonçalves et al., 2007; Moretti et al., 2007; Moulton et al., 2010), suggesting that their occurrence were more variability in these systems (but see Cheshire et al., 2005; Tonin et al., 2014). Furthermore, the density of shredders tended to increase over time as the leaf litter started to breakdown. This tendency may be due to increased nutritional quality of leaf detritus over time (N and P content, and C:N ratio).

We conclude that changes in the chemistry of decomposing leaves affect invertebrate colonization process. We also conclude that leaves become more attractive as a food source to invertebrates through time. These conclusions reinforce the importance in follow leaf litter chemistry over time, especially in tropical streams where the dynamic of organic matter breakdown is poorly studied.

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