

# Chironomidae larvae associated with *Eichhornia azurea* leaf detritus: decomposition community structure and colonization dynamics

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**Abstract** Chironomidae stand out among aquatic insects associated with organic matter decomposition due to their abundance, cosmopolitan distribution, the varied forms in which they use detritus, as well as the feeding plasticity of their larvae. The objective of this study was to investigate the structure and composition of the Chironomidae community (Diptera) in the decomposition of *Eichhornia azurea* leaves in a marginal lake. The working hypothesis is that the taxonomic and functional density and richness of Chironomidae increase over time during the degradation of *E. azurea* leaves. Decomposition was analyzed in leaves kept in 2-mm mesh litter bags and collected at set successive sampling intervals. Significant differences were found in Chironomidae density and composition in the time scale. The density of individuals increased significantly during the experiment, in contrast to the taxonomic and functional richness. Subfamily Chironominae was the most representative in terms of density and taxonomic richness. The densities of taxa *Labrundinia* sp., *Tanytarsus* sp., *Dicrotendipes* sp., *Endotribelos* sp. *Chironomus* sp. and *Ablabesmyia* sp. were mainly responsible for intragroup similarity in the groups formed at each sampling time. In contrast, the taxonomic composition varied throughout the experiment with characteristic ecologic succession and dynamic stabilization of the colonizing community towards the end of the experiment. In conclusion, the Chironomidae community structure presented an increase in larva density during the experimental period associated with changes in taxon composition; however, the total taxonomic richness variation was low and functional richness did not vary.

**Keywords** Macroinvertebrates · Aquatic insects · Macrophytes · Ecologic succession · Lentic ecosystem

## Introduction

Decomposition is a key process in the metabolism of aquatic ecosystems (Gimenes et al. 2010) and is often the focus of various ecological studies (Graça and Canhoto 2006). When considering that plants serve as the base for aquatic food webs, the degradation of plant material is ideal for analyses of aquatic biodiversity. Aquatic plants have a high growth potential and contribute to the production of allochthonous material, in addition to serving as an important source of organic matter in the detritus food chain. The production of detritus is more intense in tropical lentic ecosystems, which are characterized by high temperatures and high availability of nutrients (Bianchini 2007). A large amount of detritus is consumed by larvae of the family Chironomidae

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(Henriques-Oliveira et al. 2003; Silveira et al. 2013; Saito and Fonseca-Gessner 2014), which consists mostly of omnivorous species (Berg 1995; Galizzi et al. 2012).

Chironomidae larvae can be divided into six functional trophic groups based on their feeding habits: gathering collectors, filtering collectors, scrapers, shredders and predators. However, most Chironomids are not restricted to a single feeding habit, and taxa of the same genus may vary in feeding “preferences” according to resource availability, nutritional value, size and type (Berg 1995). Shredders are suggested to consume conditioned plant organic matter, which is organic matter colonized and degraded by microorganisms during decomposition (Graça et al. 2001). However, relationships between invertebrates and plant detritus are considered complex due to the physical and chemical alterations that occur during the decomposition of organic matter (Gonçalves et al. 2004).

The mechanisms to colonize detritus are determined by the compositions of microorganisms and other fauna. Microorganisms colonize decomposing organic matter and increase in biomass through cell division. In contrast, the biomass of macroinvertebrates associated with plant detritus increases mainly through immigration of individuals to the new substrate for colonization (Hieber and Gessner 2002). The colonization of decomposing plant matter by macroinvertebrates is related to their feeding habits, which may include the ingestion of detritus or predation on smaller detritivorous invertebrates (Lancaster and Downes 2013).

The relationship between decomposing macrophytes and associated organisms requires further investigation to improve the understanding of the ecological processes that drive the metabolism of aquatic ecosystems, such as nutrient cycling, intra- and interspecific interactions, organic matter degradation, food chain, etc. Therefore, this study examined changes in the structure and composition of the Chironomid community in decomposing *E. azurea* leaf detritus and its role in the degradation of organic material.

The objective of this study was to examine changes in the structure and composition of the Chironomidae community in decomposing *E. azurea* leaf detritus and its role in the decomposition of organic matter. Exponential increases in density and taxonomic and functional richness during the decomposition process and a tendency towards stabilization at the end of the experiment are expected. As to taxonomic richness, the number of Chironomidae genera is presumed to increase significantly, mostly in the beginning of the decomposition process, when *E. azurea* leaves make up a “new substrate” available for colonization.

## Materials and methods

### Study area

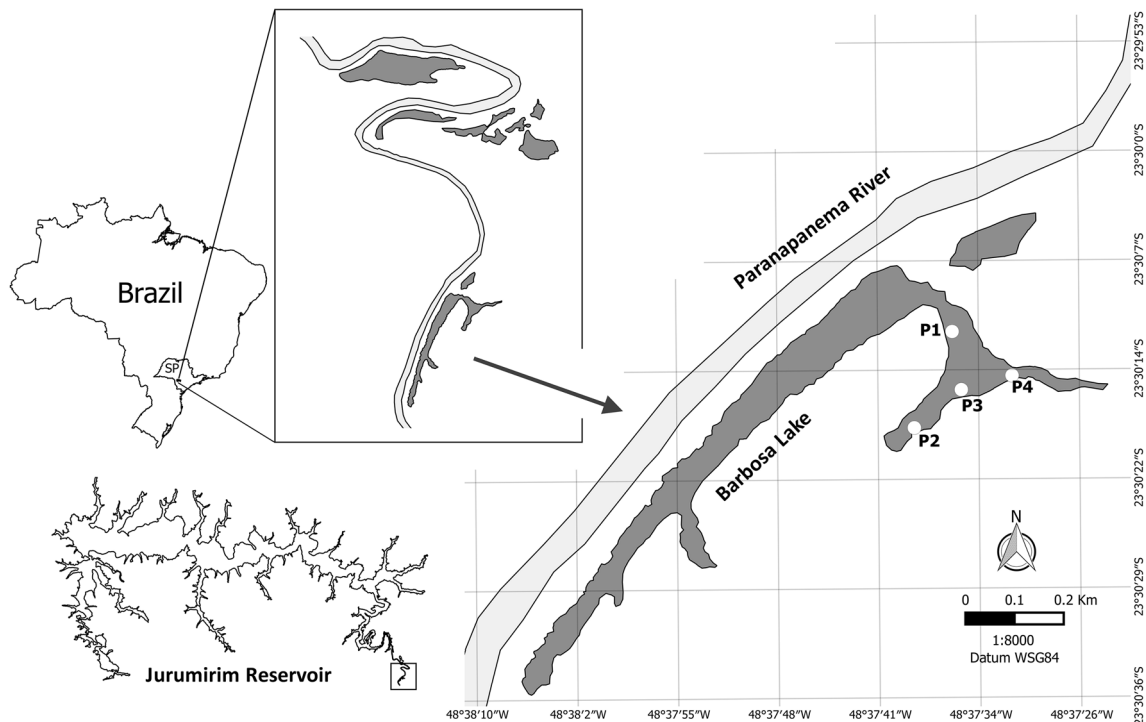
This study was conducted on a marginal lake at the mouth of the Paranapanema River into Jurumirim Reservoir (Fig. 1) in the municipality of Angatuba, state of São Paulo, Brazil. This region is characterized by a high diversity of aquatic ecosystems, consisting of marginal lakes with distinct connections to the river. The hydrologic connectivity, as well as the river bed outflow and lateral flooding, is controlled by the Jurumirim Reservoir located downstream (Henry 2003, 2005).

### Experimental design and sampling interval

The *E. azurea* leaf decomposition experiment was performed between April and July 2013, which corresponds to the end of the rainy season and beginning of the dry season, respectively. Litter bags of 2-mm mesh and measuring 20 × 25 cm were used to hold 20.0 g of *E. azurea* leaves. The leaves were previously dried at room temperature for 3 weeks before being incubated at 30 cm under the water surface. The litter bags were tied to floaters located at four sites, where seven litter bags were placed at each site on Barbosa Lake (Fig. 1). Four litter bags, one from each sampling site, were collected at days 1, 3, 7, 14, 35, 56 and 70, totaling 28 litter bags in whole study.

The litter bags were stored in plastic bags upon sampling and kept in thermo boxes with ice until analyses in the laboratory. For analysis, the leaf detritus was carefully washed with running water over a stack of sieves organized by decreasing mesh size (0.25, 0.125, 0.105 and 0.053 mm) for retention of the associated invertebrate fauna. The material collected from each sieve was stored in a plastic jar with a 70% alcohol solution.





**Fig. 1** Study area: Barbossa Lake, marginal to and at the mouth zone of the Paranapanema River into Jurumirim Reservoir (São Paulo, Brazil)

The invertebrates were sorted under a stereoscopic microscope and identified through specialized dichotomous key (Trivinho-Strixino 2011).

After the invertebrates were collected, three sets of five 1.5-cm diameter disks were taken from five *E. azurea* leaves from each litter bag, labeled and stored frozen at  $-20\text{ }^{\circ}\text{C}$ . They were used for determination of dry mass, organic matter, microbial and fungal biomass. Ash-free dry mass (AFDM) and organic matter content were determined, using a muffle furnace at  $550\text{ }^{\circ}\text{C}$  for 4 h (Taylor and Chauvet 2014; Martins et al. 2017). Carbon content, were calculated based on the rate of 47% of the organic matter (Wetzel 1975). Total microbial biomass, in  $\text{gAFDM}^{-1}$ , was estimated from the ATP content found in detritus (in nmoles), determined by enzymatic activity bioluminescence, following Abelho (2005). Fungal biomass, in  $\mu\text{g gAFDM}^{-1}$ , was determined by ergosterol content following Gessner (2005).

#### Abiotic and biotic variables

Water variables were determined on the water surface within macrophyte stands at each of the four sampling sites. Dissolved oxygen was determined using Winkler's method. Water pH and electrical conductivity (corrected to  $25\text{ }^{\circ}\text{C}$ ) were measured using laboratory bench meters. Suspended solids were determined by gravimetry, water temperature with mercury thermometer, water transparency with a Secchi disk, and photosynthetic pigments were extracted in acetone (90%) for 12 h and the concentration determined with a spectrophotometer. Suspended solids were determined according to Teixeira and Kutner (1962) and all the others according to Golterman et al. (1978). Daily precipitation data during the study period (from April 26 to July 05, 2013) were obtained from the pluviometric station at Departamento de Água and Energia elétrica in the Municipality of Angatuba.

The functional trophic group of each Chironomid genus was determined following Coffman and Ferrington (1996), Henriques-Oliveira et al. (2003) and Galizzi et al. (2012). The functional trophic groups were defined following methods described in Gonçalves et al. (2003), Janke and Trivinho-Strixino (2007), Zilli et al. (2008), Silva et al. (2008), Ligeiro et al. (2010), Silva et al. (2010), and Silva et al. (2011).

## Analysis of the decomposition process

The decomposition coefficient ( $k$ ) was determined by fitting the percent mass loss to the exponential model (Olson 1963).

The variation of the ATP content was estimated using a first-order mathematical model that considered two processes simultaneously, microorganism growth and ATP concentration decrease (Levenspiel 1974). Fitting was performed by non-linear regressions using the Levenberg–Marquardt iterative algorithm (Press et al. 2007).

$$\text{ATP}_t = \text{ATP}_{\max} \times \mu \times \left( \frac{e^{-\mu t}}{k - \mu} + \frac{e^{-kt}}{\mu - k} \right),$$

where  $\text{ATP}$  = ATP concentration,  $\mu$  = coefficient of increase in ATP concentration ( $\text{day}^{-1}$ ),  $k$  = coefficient of decrease in ATP concentration ( $\text{day}^{-1}$ ),  $t$  = time (day).

The variation of the concentration of ergosterol was evaluated using the exponential growth model (Eq. 1). The duplication time ( $T_d$ ) was estimated with Eq. (2). Fitting was performed with non-linear regressions using the iterative Levenberg–Marquardt algorithm (Press et al. 2007).

$$N_t = N_0 \times e^{\mu \times t}, \quad (1)$$

where  $N_t$  = value of the biotic variable in time;  $N_0$  = initial value of the biotic variable;  $\mu$  = growth coefficient ( $\text{day}^{-1}$ );  $t$  = time (day).

$$t_d = \frac{\ln 2}{\mu}, \quad (2)$$

where  $t_d$  = duplication time in days,  $\ln 2$  = Neper logarithm of 2,  $\mu$  = growth coefficient of the biotic variable.

## Quantitative analysis of invertebrates

Density ( $\text{ind.}100 \text{ g DM}^{-1}$ ) was calculated from the total abundance of Chironomidae in the remaining ash-free dry mass of *E. azurea* leaf detritus from each of the seven sampling periods. The mean daily colonization rate ( $x$ ) of macrophyte detritus by Chironomidae, expressed in terms of abundance (daily variation rate of individual abundance  $\text{day}^{-1}$ ) and richness (daily variation rate of taxon richness  $\text{day}^{-1}$ ), in the successive sampling intervals was estimated by Chironomidae abundance and richness over time using  $x_A = (A_2 - A_1)/(t_2 - t_1)$  ( $A$  = abundance and  $t$  = time) and  $x_R = (R_2 - R_1)/(t_2 - t_1)$  ( $R$  = richness and  $t$  = time).

## Statistical analysis

Statistically significant differences ( $p < 0.05$ ) in variables between sampling days were examined by variance analysis using Sigma Plot 11 software. Multiple data comparisons were carried out through Tukey test. “One-way” ANOVA was used when the data were normally distributed and the Kruskal–Wallis test when normality was not observed.

Chironomidae associated with *E. azurea* leaf detritus and their respective biotic were related to Barbosa Lake environmental variables, by means of simple correlation matrix/Spearman correlation coefficient, using Statistica 7 (Statsoft 2009) software. Chironomidae density values recorded at each sampling time were used. The similarity in Chironomidae density and composition (presence or absence) between leaf detritus samples on successive sampling days was tested by Non-Metric Multidimensional Scaling analysis (NMDS) using the Bray–Curtis dissimilarity coefficient. The main taxa responsible for groupings shaped by NMDS were identified by SIMPER analysis and the differences in Chironomidae density and composition by ANOSIM analysis. All analyses were carried out with Primer v6 (Clarke and Gorley 2006) software using square root-transformed data (Clarke and Warwick 2001).



Statistical tests were carried out using  $\log(x + 1)$  transformed data, except pH values and NMDS, SIMPER, and ANOSIM analyses.

## Results

### Abiotic variables

All values of the abiotic variables are showed in Table 1. The highest water temperature was recorded in the beginning of the experiment, which then decreased until day 56 and showed increase on day 70. The mean dissolved oxygen concentration varied little between successive sampling days, while the percent saturation showed a higher degree of variation. Higher pH, suspended solids and total nitrogen values were observed on day 56. Conductivity increased after day 7 and peaked on day 35. The lowest water transparency value was recorded during the period with the greatest depth. The total phosphorus concentration in the water column was the highest on day 70.

### Biotic variables

Values of the biotic variables are showed in Table 2. Higher values of total pigments were observed at the end of the experiment (days 35 to 70), with a peak on day 56 ( $222.6 \mu\text{g L}^{-1}$ ). The remaining *E. azurea* leaf biomass showed a loss of 1.81% after the first seven days. The decomposition rates at the subsequent sampling periods were low as well, demonstrating a small loss of mass during the entire experiment. The percent mass loss was the highest at day 35 (4.4% of the initial value), followed by mass increases at days 56 and 70. The ash content of the remaining dry biomass was the highest at day 35 (4.8%) and decreased thereafter until the end of the experiment. In contrast, the carbon content was the lowest on day 35 (44.9%) and then increased until the end of the experiment. The nitrogen and phosphorus concentrations of the remaining dry biomass showed little variation and both concentrations were low at the end of the experiment. Ergosterol was detected

**Table 1** Variation of mean values and standard deviations ( $N = 4$ ) of Barbosa Lake environmental variables between April and July 2013

Variables/days	Initial	1st	3rd	7th	14th	35th	56th	70th
Water temperature (°C)	28 ± 0	26 ± 1	26 ± 1	26 ± 1	21 ± 1	19 ± 0	19 ± 0	21 ± 1
Dissolved oxygen concentration (mg L <sup>-1</sup> )	7 ± 2	8 ± 2	8 ± 1	10 ± 2	9 ± 3	8 ± 2	7 ± 2	7 ± 1
Oxygen saturation (%)	101 ± 22	110 ± 29	110 ± 20	124 ± 20	105 ± 38	96 ± 23	78 ± 23	82 ± 8
Water pH	6 ± 0	6 ± 0	6 ± 0	6 ± 0	6 ± 0	7 ± 0	8 ± 1	6 ± 0
Organic suspended matter (mg L <sup>-1</sup> )	5 ± 2	10 ± 5	13 ± 7	11 ± 4	12 ± 7	25 ± 13	45 ± 32	20 ± 22
Inorganic suspended matter (mg L <sup>-1</sup> )	3 ± 1	4 ± 2	3 ± 1	3 ± 2	4 ± 2	3 ± 2	7 ± 6	12 ± 8
Water electrical conductivity (μS cm <sup>-1</sup> )	33 ± 1	33 ± 1	33 ± 1	32 ± 2	36 ± 1	38 ± 4	35 ± 1	34 ± 2
Water transparency (m)	1.1 ± 0	1.5 ± 0	1.5 ± 0	1.4 ± 0	1.2 ± 0	1.6 ± 0	1.5 ± 0	0.7 ± 0
Water depth (m)	1.8 ± 0	1.8 ± 0	1.8 ± 0	1.8 ± 0	1.7 ± 0	1.6 ± 0	1.8 ± 0	2.3 ± 1
Total nitrogen concentration (μg L <sup>-1</sup> )	490 ± 141	507 ± 160	458 ± 27	487 ± 36	592 ± 110	792 ± 78	975 ± 364	752 ± 297
Total phosphorus concentration (μg L <sup>-1</sup> )	22 ± 3	37 ± 16	25 ± 9	34 ± 15	26 ± 7	46 ± 23	46 ± 46	57 ± 24



**Table 2** Variation in means and standard deviation ( $N = 4$ ) values of total pigments and the variables determined from the remaining biomass of *E. azurea* leaves during decomposition on Barbosa Lake between April and July 2013

Variables/days	1st	3rd	7th	14th	35th	56th	70th
Total pigments ( $\mu\text{g L}^{-1}$ )	58.1 $\pm$ $\pm$ 47.9	60.6 $\pm$ 39.6	68.8 $\pm$ 33.6	43.5 $\pm$ 22.6	192.3 $\pm$ 111.5	222.6 $\pm$ 190.7	102.3 $\pm$ 124.2
Remaining biomass (%)	98.5 $\pm$ 0.2	98.3 $\pm$ 0.1	98.2 $\pm$ 0.2	97.1 $\pm$ 1.1	95.6 $\pm$ 0.6	97.7 $\pm$ 0.5	98.1 $\pm$ 0.6
Ash content (%)	2.0 $\pm$ 0.1	2.2 $\pm$ 0.1	2.3 $\pm$ 0.2	3.4 $\pm$ 1.0	4.8 $\pm$ 0.6	2.9 $\pm$ 0.5	2.5 $\pm$ 0.6
Carbon content (%)	46.3 $\pm$ 0.1	46.2 $\pm$ 0.1	46.1 $\pm$ 0.1	45.6 $\pm$ 0.5	44.9 $\pm$ 0.3	45.9 $\pm$ 0.2	46.1 $\pm$ 0.3
Nitrogen content ( $\text{mg g}^{-1}$ )	0.5 $\pm$ 0.0	0.7 $\pm$ 0.2	1.0 $\pm$ 0.6	1.1 $\pm$ 0.7	1.0 $\pm$ 0.8	0.7 $\pm$ 0.1	0.8 $\pm$ 0.2
Phosphorus content ( $\text{mg g}^{-1}$ )	0.2 $\pm$ 0.1	0.1 $\pm$ 0.0	0.1 $\pm$ 0.0	0.2 $\pm$ 0.0	0.1 $\pm$ 0.1	0.1 $\pm$ 0.0	0.1 $\pm$ 0.0
Ergosterol biomass ( $\mu\text{g g}^{-1}$ AFDM)	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	19.7 $\pm$ 23.8	25.9 $\pm$ 10.1	58.8 $\pm$ 19.4
ATP biomass (nmoles $\text{g}^{-1}$ AFDM)	145.5 $\pm$ 105.7	45.3 $\pm$ 25.3	62.2 $\pm$ 35.2	39.1 $\pm$ 7.0	34.9 $\pm$ 8.9	25.8 $\pm$ 14.7	27.6 $\pm$ 9.4



on day 35 and its concentration gradually increased thereafter. In contrast, the microbial community biomass was high on day 1 and decreased until day 7, and showed little variation until day 70.

The remaining decay rate of *E. crassipes* was extremely low, while the half-life was very high (Table 3). Excluding data on days 56 and 70, it was obtained  $k = 0.00148 \text{ day}^{-1}$ ,  $r^2 = 0.52$  and  $t_{1/2} = 468$  days.

The density of Chironomidae increased over time from  $72 \pm 69 \text{ ind.}100 \text{ g DM}^{-1}$  at days 1 to  $3,049 \pm 915 \text{ ind.}100 \text{ g DM}^{-1}$  at day 70. The subfamily Chironominae showed the highest density and taxonomic richness (Fig. 2a, b). The mean rate of colonization by the Chironomids (richness; taxa  $\text{day}^{-1}$ ) was highest at day 1, but remained low for the rest of the experiment (Fig. 2c). The mean taxonomic richness increased over time, with the highest richness observed on day 70 (Fig. 2d). Three peaks were observed at days 1, 7 and 70 for the abundance of invertebrate fauna ( $\text{ind day}^{-1}$ ), with  $11 \text{ ind day}^{-1}$ ,  $8 \text{ ind day}^{-1}$  and  $9 \text{ ind day}^{-1}$ , respectively (Fig. 2e).

Analyses of abundance over time showed that *Endotribelos* sp. (Chironominae subfamily) was the dominant genus at most of the sampling periods, with the greatest relative abundance shown at day 70 (38.5%). *Corynoneura* sp. (Orthoclaadiinae subfamily) and *Larsia* sp. (Tanypodinae subfamily) showed the lowest relative abundance (Fig. 3).

The subfamily Chironominae had the greatest number of taxa, which showed a peak in richness on day 56 (Table 4). The richness of the functional trophic groups showed no variation over time, but six functional categories were observed throughout the entire experimental period with the exception of *Stenochironomus* sp. (subgenus *Petalopholius*), which was observed from day 35 onwards. This particular genus is a miner of submersed aquatic macrophyte leaves (Trivinho-Strixino 2011).

The functional taxonomic richness of Chironomidae showed no variation throughout the experimental period. On the other hand, variation was shown for the relative abundance of trophic groups (Fig. 4). Only *Polypedilum* sp., the most representative taxon at the beginning of the experiment, was classified in the three functional groups of collectors, shredders and scrapers. As shown in Table 4, *Ablabesmyia* sp. was a collector only in its first larval instars. Nevertheless, developmental stages were not considered for the richness of the functional trophic groups. Therefore, *Ablabesmyia* sp. was included in the collector and predator functional groups, together with *Parachironomus* sp., and its relative abundance did not vary significantly from days 3 to 70. On the first day of colonization, no larvae were observed from either *Ablabesmyia* sp. or *Parachironomus* sp. From day 7, the collectors and shredders were the most representative groups at all sampling periods (Fig. 4). *Endotribelos* sp. and *Chironomus* sp. composed a large fraction of the two groups, especially towards the end of the experiment (Fig. 3).

Statistically significant differences were shown for most environmental variables over time, with the exception of the dissolved oxygen (Kruskal–Wallis:  $H = 7.795$ ;  $p = 0.351$ ), oxygen saturation (Kruskal–Wallis:  $H = 10.358$ ;  $p = 0.169$ ) suspended inorganic matter (Kruskal–Wallis:  $H = 9.091$ ;  $p = 0.246$ ) and phosphorus (ANOVA:  $F = 1.406$ ;  $p = 0.249$ ). For the ecological attributes of the invertebrate community and variables determined for the *E. azurea* leaf detritus, only the total nitrogen in detritus showed no significant changes over time (Kruskal–Wallis:  $H = 10.974$ ;  $p = 0.089$ ).

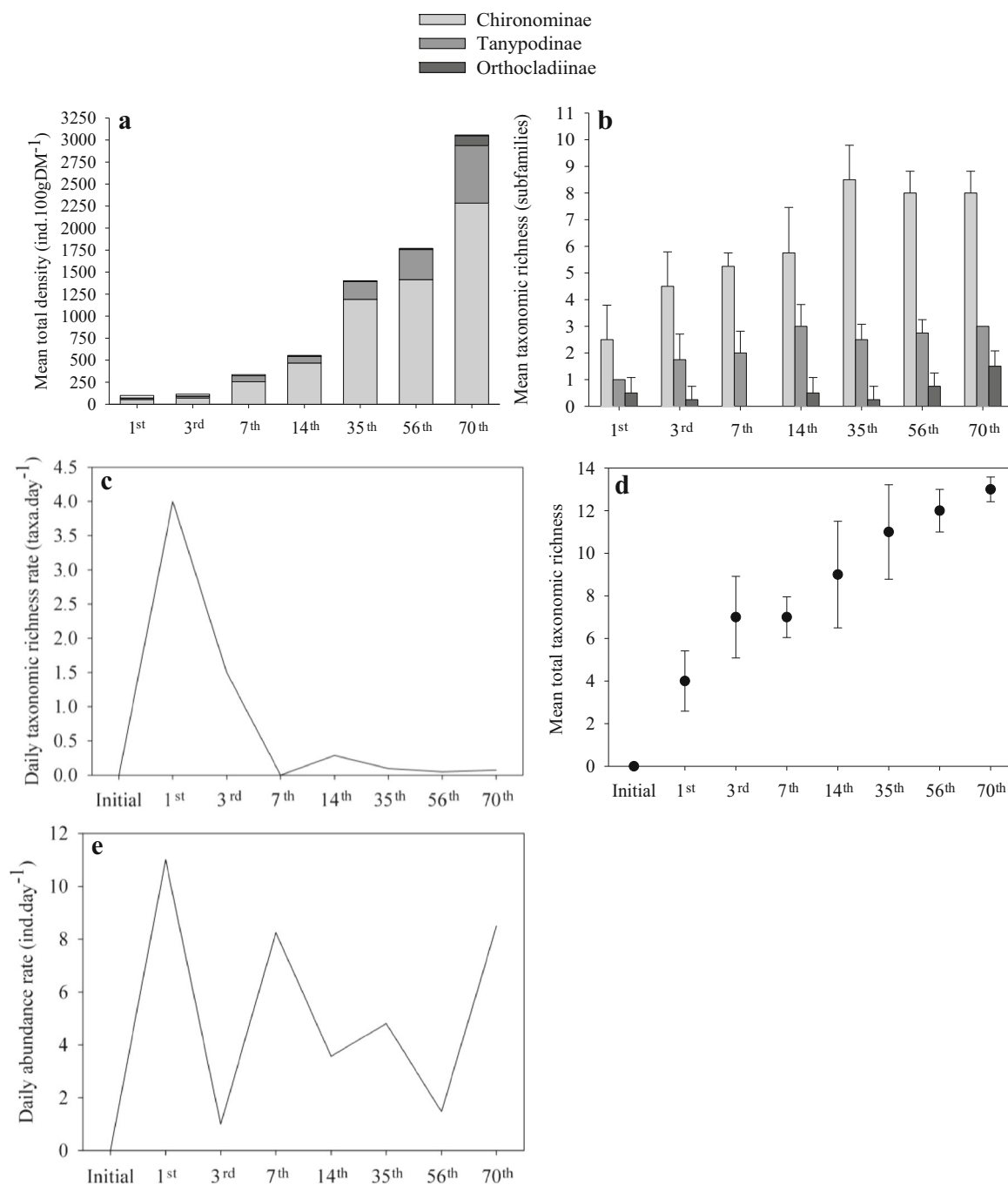
The density (ANOVA:  $F = 41.159$ ,  $p = <0.001$ ) and richness (ANOVA:  $F = 14.540$ ,  $p = <0.001$ ) of the Chironomid subfamilies associated with *E. azurea* leaf detritus were statistically different between sampling periods (Table 5).

NMDS and ANOSIM analyses revealed significant differences in the density (Fig. 5a) (ANOSIM:  $p = 0.001$ ;  $R$  global = 0.6) and taxon composition (Fig. 5b) (ANOSIM:  $p = 0.001$ ;  $R$  global = 0.5) of

**Table 3** Values of decay rate ( $k$ ), growth ( $\mu$ ) and coefficient of determination ( $r^2$ ) recorded for half-life ( $t_{1/2}$ ) and duplication ( $t_d$ ) times of the models used in the analysis of the decomposition process (1), of the ATP content (2), the ergosterol concentration (3) in the remaining biomass of the *E. azurea* leaves at successive sampling times on Barbosa Lake from April to July 2013

Models	$K$	$\mu$	$R^2$	$T_{1/2}$	$T_d$
(1) Remaining leaf biomass	$0.00051 \text{ day}^{-1}$	–	0.92	1.359 days	–
(2) Microorganism biomass (ATP)	$0.01808 \text{ day}^{-1}$	$0.61029 \text{ day}^{-1}$	0.86	7 days	3 days
(3) Fungal biomass (ergosterol)	–	$0.0261 \text{ day}^{-1}$	0.84	–	26 days



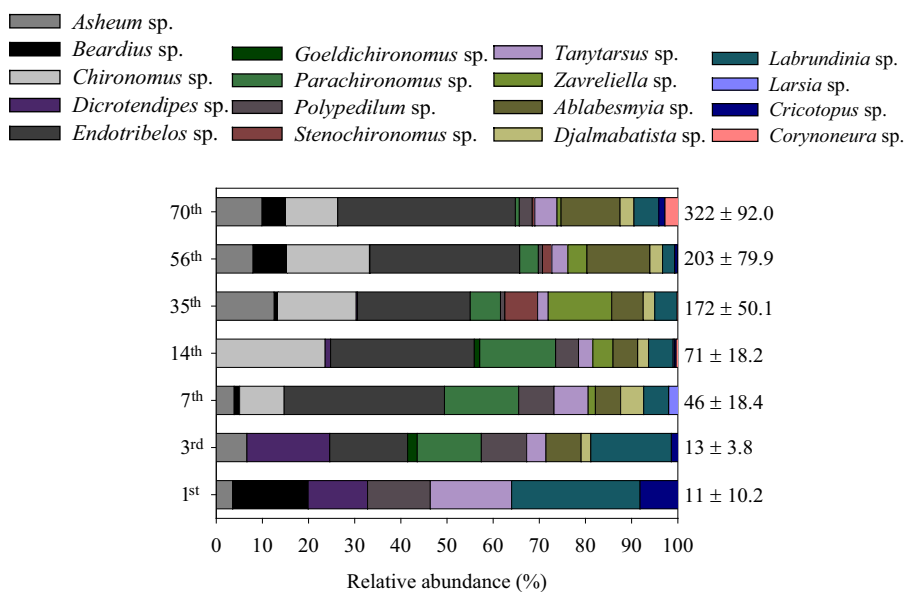


**Fig. 2** Variation in mean values ( $N = 4$ ) of total density (ind.100 g DM<sup>-1</sup>) of Chironomidae (a) subfamilies, taxonomic richness per Chironomidae subfamily (b), daily variation rate of taxon colonization (richness) (taxa day<sup>-1</sup>) (c), total taxonomic richness (d) and daily mean variation of the number of colonizing individuals (abundance) of Chironomidae fauna (ind day<sup>-1</sup>) (e) associated with leaf detritus of *E. azurea* on Barbosa Lake in successive sampling times between April and July 2013

Chironomidae sampled at the seven periods, which suggests a change in the Chironomid community structure and composition over time during the experimental period. However, from day 35 on, the sample data were similar, indicating that the community was stable (Fig. 5a, b).

In the beginning of the experiment, *Labrundinia* sp. (SIMPER: 46.8%), *Tanytarsus* sp. (SIMPER: 21.3%) and *Dicrotendipes* sp. (SIMPER: 19.1%) were the main taxa responsible for the similarity within the groups at each sampling period. From day 7 on, *Endotribelos* sp. (27.7%) contributed the most to the NMDS result. At



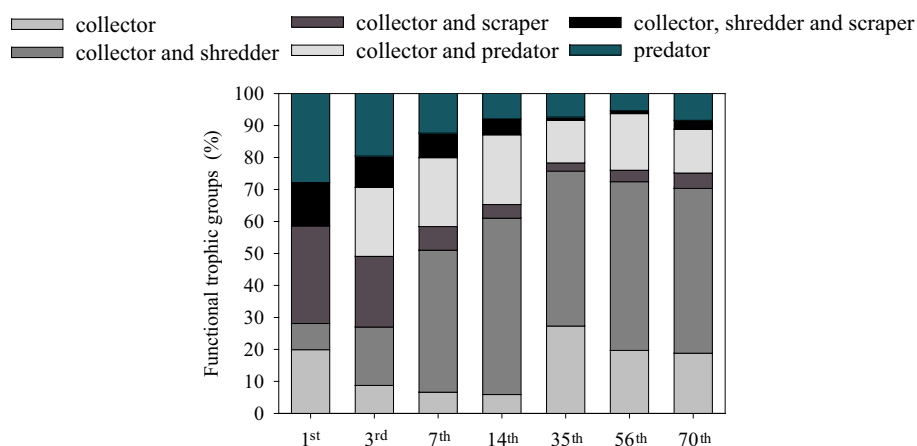


**Fig. 3** Variation of mean values ( $N = 4$ ) of relative abundance (%), total abundance (right column) and standard deviations ( $\pm$ ) of Chironomidae genera associated with leaf detritus of *E. azurea* on Barbosa Lake in successive sampling times between April and July 2013

**Table 4** Taxon occurrence, functional trophic groups, subfamily richness (Chironominae, Tanypodinae and Orthoclaadiinae) and total richness of the Chironomidae community associated with *E. azurea* leaf detritus on Barbosa Lake in successive sampling times between April and July 2013

Taxa	Functional trophic groups	Sampling day						
		1st	3rd	7th	14th	35th	56th	70th
<b>Chironominae</b>								
<i>Asheum</i> sp.	GC	*	*	*		*	*	*
<i>Beardius</i> sp.	GC	*		*		*	*	*
<i>Chironomus</i> sp.	GC; FC—few spp.; HS (miner)			*	*	*	*	*
<i>Dicrotendipes</i> sp.	GC; FC; S?	*	*		*	*	*	
<i>Endotribelos</i> sp.	GC; HS—facultative		*	*	*	*	*	*
<i>Goeldichironomus</i> sp.	GC		*		*			
<i>Parachironomus</i> sp.	P (engulfer); GC; PA		*	*	*	*	*	*
<i>Polypedilum</i> sp.	HS (miner); GC; FC?; P (engulfer)	*	*	*	*	*	*	*
<i>Stenochironomus</i> sp.	GC; HS (miner); FX					*	*	*
<i>Tanytarsus</i> sp.	GC; FC; S—few spp.	*	*	*	*	*	*	*
<i>Zavreliella</i> sp.	GC			*	*	*	*	*
Subfamily richness		5	7	8	8	10	10	9
<b>Tanypodinae</b>								
<i>Ablabesmyia</i> sp.	P (engulfer/piercer); GC—1st instars		*	*	*	*	*	*
<i>Djalmbatista</i> sp.	P (engulfer)		*	*	*	*	*	*
<i>Labrundinia</i> sp.	P (engulfer/piercer)	*	*	*	*	*	*	*
<i>Larsia</i> sp.	P (engulfer)			*	*			
Subfamily richness		1	3	4	4	3	3	3
<b>Orthoclaadiinae</b>								
<i>Cricotopus</i> sp.	HS (miner/shredder); GC	*	*		*		*	*
<i>Corynoneura</i> sp.	GC				*	*	*	*
Subfamily richness		1	1	0	2	1	2	2
Total richness		7	11	12	14	14	15	14

Chironomidae functional groups, GC gathering collector; FC filtering collector; HS herbivorous shredder; XS xylophage shredder; P predator; PA parasite; S scraper

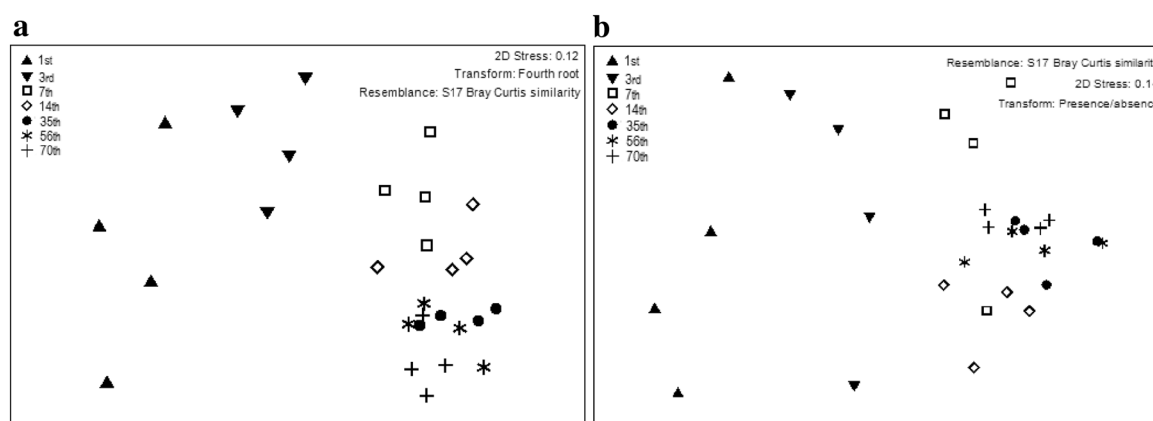


**Fig. 4** Variation of mean values ( $N = 4$ ) of relative abundance (%) of functional trophic groups of the Chironomidae community associated with *E. azurea* leaf detritus on Barbosa Lake at successive sampling times between April and July 2013

**Table 5**  $p$  values obtained in statistical analyses (ANOVA “one way”/Kruskal–Wallis) and differences indicated by Tukey test for Chironomidae community density and richness and the respective subfamily densities (ind.100 g DM<sup>-1</sup>) associated with leaf detritus of *E. azurea* on Barbosa Lake at successive sampling times between April and July 2013

Variables analyzed	$p$	Tukey test
Total Density (ind.100 g DM <sup>-1</sup> )	<b>&lt; 0.001</b>	(70 <sup>th</sup> ≠ 1st, 3rd, 7th, 14th); (56th ≠ 1st, 3rd, 7th, 14th); (35th ≠ 1st, 3rd, 7th); (14th ≠ 1st, 3rd, 70th); (7th ≠ 1st, 3rd, 35th, 70th)
Total Taxonomic Richness	<b>&lt; 0.001</b>	(70th ≠ 1st, 3rd, 7th); (56th ≠ 1st, 3rd); (35th ≠ 1st, 3rd); (14th ≠ 1st); (7th ≠ 1st, 70th)
Chironominae	<b>&lt; 0.001</b>	(70th ≠ 1st, 3rd, 7th, 14th); (56th ≠ 1st, 3rd, 7th); (35th ≠ 1st, 3rd, 7th); (14th ≠ 1st, 3rd, 70th); (7th ≠ 1st, 3rd, 35th, 56th, 70th)
Tanytopodinae	<b>&lt; 0.001</b>	(70th ≠ 1st, 3rd, 7th, 14th); (56th ≠ 1st, 3rd, 7th, 14th); (35th ≠ 1st, 3rd); (14th ≠ 1st, 56th, 70th)
Orthocladiinae	<b>0.001</b>	(70th ≠ 1st, 3rd, 7th, 14th, 35th)

Significant differences ( $p < 0.05$ ) in bold



**Fig. 5** Non-metric multidimensional scaling analysis (NMDS) of taxon density (a) and composition (presence or absence) (b) of the Chironomidae community associated with *E. azurea* leaf detritus on Barbosa Lake at successive sampling times between April and July 2013

days 35, 56 and 70, *Chironomus* sp., *Ablabesmyia* sp. and *Endotribelos* sp. contributed the most to the NMDS result. The ergosterol concentration and remaining detrital biomass of *E. azurea* had the greatest significant correlations with the various invertebrate taxa (Table 6).

## Discussion

The procedures adopted in this experiment sought to reproduce the decomposition of aquatic macrophytes in natural conditions as close as possible; so leaves were dried naturally at room temperature before incubation on Barbosa Lake. However, the methodological procedures used may have interfered with the dynamics of decomposition of *E. azurea*, as it was slower than in other studies (Cunha-Santino et al. 2010; Martins et al. 2011; Bianchini et al. 2014). Since aquatic plants generally begin to decompose at the senescence stage, part of the labile compounds may have been lost even before incubation in water (Pagioro and Thomaz 2006). Additionally, factors like decreasing water temperature through the experiment, occasional inhibition of microorganism growth by leachate, predominance of an oligotrophic environment and low abrasion due to the environment lentic regime may have contributed to a low decomposition rate of *E. azurea* (Battle and Mihuc 2000; Grattan and Suberkropp 2001; Sangiorgio et al. 2004; Carvalho et al. 2005; Sangiorgio et al. 2008; Song

**Table 6** Density of Chironomidae taxa associated with *E. azurea* leaf detritus on Barbosa Lake with significant Spearman correlations ( $p \leq 0.05$ ) with abiotic and biotic variables in successive sampling times between April and July 2013

Taxa	Variables									
	ERG	ATP	BIO	WT	TN	pH	K	DP	%A	%CA
Total density	+ 0.804	- 0.450	- 0.896	- 0.762	+ 0.707	+ 0.499	+ 0.490	- 0.446	+ 0.485	- 0.433
Total Richness	+ 0.780	- 0.432	- 0.728	- 0.714	+ 0.595	+ 0.448	+ 0.533		+ 0.507	- 0.481
Chironominae										
<i>Asheum</i> sp.	+ 0.813	- 0.454	- 0.727	- 0.596	+ 0.462			- 0.465		
<i>Beardius</i> sp.	+ 0.719		- 0.588	- 0.412	+ 0.447	+ 0.423		- 0.473		
<i>Chironomus</i> sp.	+ 0.679		- 0.838	- 0.782	+ 0.756	+ 0.637	+ 0.552	- 0.493	+ 0.492	- 0.458
<i>Dicrotendipes</i> sp.			+ 0.392			- 0.444				
<i>Endotribelos</i> sp.	+ 0.814	- 0.497	- 0.921	- 0.764	+ 0.701	+ 0.486	+ 0.494	- 0.494	+ 0.497	- 0.444
<i>Goeldichironomus</i> sp.			+ 0.374							
<i>Parachironomus</i> sp.				- 0.615	+ 0.504	+ 0.568	+ 0.403		+ 0.719	- 0.715
<i>Polypedilum</i> sp.	+ 0.380									
<i>Stenochironomus</i> sp.	+ 0.555		- 0.522	- 0.722	+ 0.554	+ 0.587	+ 0.585			
<i>Tanytarsus</i> sp.	+ 0.782	- 0.491	- 0.739	- 0.574	+ 0.567					
<i>Zavreliella</i> sp.	+ 0.397		- 0.594	- 0.776	+ 0.750	+ 0.736	+ 0.642		+ 0.547	- 0.545
Tanypodinae										
<i>Ablabesmyia</i> sp.	+ 0.832	- 0.548	- 0.863	- 0.724	+ 0.659	+ 0.514	+ 0.422	- 0.495	+ 0.404	
<i>Djalmabatista</i> sp.	+ 0.766		- 0.688	- 0.530	+ 0.471	+ 0.384	+ 0.497	- 0.530		
<i>Labrundinia</i> sp.	+ 0.562		- 0.507	- 0.421						
<i>Larsia</i> sp.										
Orthoclaadiinae										
<i>Cricotopus</i> sp.	+ 0.386									
<i>Corynoneura</i> sp.	+ 0.616		- 0.553							

ERG ergosterol, ATP microorganism biomass, BIO detritus biomass, WT water temperature, SOM suspended organic matter, TN total nitrogen, T transparency, DN detritus nitrogen, DP detritus phosphorus, % A ash percentage in detritus, %CA carbon percentage in detritus, - negative, + positive

-/+ signals = negative and positive correlations, and the R values



et al. 2013). However, colonization of the remaining biomass by Chironomidae increased with a significant increase in the total density over time as decomposition progressed.

The feeding behavior of Chironomid larvae is also influenced by local environmental characteristics, changes in substrate, and input of allochthonous organic matter (Silva et al. 2008). Size and stage of development may also determine variations in larval feeding habits (Berg 1995). For example, Shimabukuro and Henry (in press) described the diet of *Chironomus sancticarloi* larvae as a high ingestion of coarse particulate organic matter and algae in later development stages. The consumption of coarse particulate organic matter was also reported for *Chironomus paragigas*, even in young individuals, due to their relatively large size in all stages of development (Shimabukuro and Henry in press).

The functional richness of the Chironomid community in this study showed no variation throughout the experiment, as five of the trophic groups were observed at all sampling periods (Table 2). In contrast, prior research suggested that the functional complexity of Chironomid feeding habits increases during the decomposition of macrophytes (Gonçalves et al. 2003; Silva et al. 2010). Collectors were the most representative functional group in this study. However, the same Chironomidae taxon has more than one feeding habit, such as *Polypedilum* sp. (Table 2), which can be a collector, a shredder or a predator, making classification under a single and specific functional trophic group difficult. Therefore, care must be taken with generalizations of feeding habits of closely related taxa as this approach may result in misrepresentations of the Chironomid trophic ecology (Berg 1995).

Most Chironomids are omnivorous (Berg 1995; Galizzi et al. 2012). Analysis of the Chironomid trophic structure with stable isotopes showed a broad variety of feeding behaviors between taxa, suggesting that Chironomids do not belong to specific groups in the aquatic trophic web (Henriques-Oliveira et al. 2003; Reuss et al. 2013; Silveira et al. 2013; Saito and Fonseca-Gessner 2014). Reuss et al. (2013) also found that the stomach contents of Tanypodinae (e.g., *Djalmabatista* sp., *Labrundinia* sp. and *Larsia* sp.) contained detritus, macroalgae and invertebrates, despite being commonly classified as predators. This shows that the feeding habits of Chironomidae are still relatively unknown and that further investigation of their larval feeding behavior is necessary to understand their complex trophic ecology. In an analysis of the digestive tube of Chironomidae, Shimabukuro and Henry (in press) identified algae (Diatomacea, *Closterium* sp., *Peridinium* sp., Zygnemaphyceae and *Spirogyra* sp.), animal origin resources (Rotifera, Ostracoda, Protozoa, Cladocera and animal fragments), and fine and coarse particulate organic matter. The Chironomidae studied in Shimabukuro and Henry (in press) were sampled in two lentic environments of the same location as the present study.

The collectors and shredders were the most abundant functional groups, comprised of *Chironomus* sp., *Endotribelos* sp., *Stenochironomus* sp. and *Cricotopus* sp. The genus *Endotribelos* sp. had the greatest density from day 7 to the end of the experiment. According to Coffman and Ferrington (1996), this genus is classified as both a collector and a facultative herbivorous shredder. The capacity of Chironomids to adapt their feeding strategy to their habitat (Reuss et al. 2014) affirms that *Endotribelos* sp. individuals observed in the present study may have fed on both fine and coarse particulate organic matter from *E. azurea* leaf fragmentation detritus. Galizzi and Marchese (2007) reported that *Endotribelos* sp. are also shredders and accelerate the decomposition process, as they are observed in high abundances forming miners in detritus leaf mesophyll. Herbivory in aquatic macroinvertebrates and its effects on the macrophyte biomass are well documented (Lodge 1991; Nachtrieb et al. 2011). The biomass of fungus associated with *E. azurea* leaf detritus had the greatest number of positive correlations with Chironomidae genera in this study, which affirms that the degradation of plant organic matter leads to a reduction of the polyphenol content and the simultaneous colonization by bacteria and fungi, which in turn improves the palatability and nutritional value of detritus (Newman 1991; Stripari and Henry 2002).

The presence of all functional Chironomid groups at all decomposition stages may be related to a generalist strategy to obtain food, since most taxa in this group are omnivorous (Berg 1995; Galizzi et al. 2012) and consume a large amount of detritus (Henriques-Oliveira et al. 2003; Silveira et al. 2013; Saito and Fonseca-Gessner 2014). In macrophyte decomposition experiments, detritus is noted as the most abundant food resource, which accounts for the high density of Chironomids observed in decomposition studies.

The taxonomic richness of Chironomidae observed during the experimental period increased over time with the exception of day 70. Richness was greatest on day 14, which was twofold of that observed on day 1. Richness showed no variation at the other sampling times, except on day 56. Taxon composition differed



significantly over time, with smaller variations towards the end of the experiment, suggesting that the number of individuals reached equilibrium to keep the community stable in terms of number of taxa throughout most of the experiment, despite the variation in the taxonomic composition.

## Conclusion

The decomposition of *E. azurea* leaves was slow when compared to previous research. For the colonization of the remaining plant biomass, however, the total density of Chironomids increased significantly as decomposition progressed with time, and no tendency towards stability at the final sampling periods was observed; so one of our working hypotheses was partially confirmed. The taxonomic and functional richness of Chironomidae followed a distinct pattern, but taxon composition varied during the experiment in a characteristic ecological succession process, with a tendency towards stability at the final sampling periods (days 35, 56 and 70), confirming another initial working hypothesis just for taxonomic richness, since the richness of the functional trophic groups showed no variation over time. On the other hand, variation was shown for the relative abundance of trophic groups, where from day 7 on, the collectors and shredders were the most representative groups. The varied forms of use of detritus by Chironomidae (e.g. as a food resource or as a feeding site), as well as their feeding plasticity, may have contributed to the present results.

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