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RESEARCH ARTICLE

Intra-annual colonization of Chironomidae on leaf litter in a Brazilian Cerrado stream

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ABSTRACT. In low-order streams, the processing of allochthonous leaf litter is essential in the carbon/energy flow dynamics. Benthic macroinvertebrates, such as chironomids, play critical roles in the breakdown of allochthonous materials, because their larvae take part in intricate trophic networks and have varied trophic ecologies. We evaluated the effects of intra-annual variability on the input of allochthonous leaf litter, and the interactions of leaf-detritus on the succession of Chironomidae assemblages in the dry, rainy, and transition seasons (rainy-dry and dry-rainy). The study took place in a stream in the Brazilian Cerrado. Leaves were incubated in the stream to ascertain the colonization process by Chironomidae and the loss of leaf litter mass after 90 days. Functional feeding groups (FFG) were less rich and less abundant in the dry and dry-rainy seasons, than in the other seasons. The FFG composition of Chironomidae demonstrated that temporal variation between seasons was affected by the exposure time of the leaf-detritus in the stream, and there was more segregation during the dry and rainy seasons. In conclusion, the colonization of leaf-detritus by Chironomidae larvae depended on how long allochthonous plant material remained in the stream, and the variability of the organic matter dynamics input into the stream.

KEY WORDS. Allochthonous materials, benthic macroinvertebrates, functional feeding group, leaf-detritus, richness, temporal variation.

INTRODUCTION

The process of organic matter decomposition is fundamental for the functioning of streams (Graça et al. 2015) and deserves special attention in ecological studies. In conserved riparian vegetation, allochthonous organic matter is one of the primary sources of energy for ecological processes (Warren et al. 2017). Allochthonous organic matter is processed inside the stream, and provide food for benthic macroinvertebrates, and shelter against the flow of water and predators (Moretti et al. 2007, Alonso et al. 2010).

In tropical ecosystems, leaves fall continuously throughout the year, with peaks associated with the rainy season, when more organic matter is available (Tonin et al. 2017). In the dry season, litterfall is often associated with water stress (Gonçalves-Jr and Callisto 2013, Gonçalves-Jr et al. 2014, Sales et al. 2015). In the Brazilian Cerrado (also known as Brazilian savanna), the greatest litterfall occurs in the transition from the dry to the rainy season (dry-rainy transition season). The fallen debris supply plant biomass to the streams (Bambi et al. 2017). The accumulation of detritus during the dry seasons and its subsequent incorporation into the aquatic ecosystem when water flow is resumed may also increase food sources for aquatic organisms (Acuña et al. 2007).

When allochthonous organic matter is input into the aquatic ecosystem, it undergoes modifications in a continuous process that includes leaching (loss of the soluble compounds; Silva et al. 2018), microbial conditioning (degradation of structural compounds, especially by fungi; Graça and Cressa 2010, Ligeiro et al. 2010), and fragmentation (reduction of coarse particles into fine particles by shredders; Graça et al. 2015).

On a small scale, these processes are influenced by the characteristics of plant species in the riparian zone (Alonso et al. 2021), which favor the action of microorganisms and shredders (Biasi et al. 2017). On a larger scale, the geology and climate also influence the decomposition of litter in streams (Graça et al. 2015). In addition, the small-scale effects influence the larger-scale changes, in a complex hierarchical system (Peters et al. 2007). Hard leaves, which are poor in nutrients and contain many secondary compounds (this is the case of most of the native tree species of the Brazilian Cerrado), are initially colonized by microorganisms and are less palatable to invertebrates (Graça and Cressa 2010, Ligeiro et al. 2010). Microorganisms play a fundamental role in the transformation of detritus into food. Therefore, the chemical composition of leaf-detritus subsequently becomes more homogeneous due to the loss of soluble compounds (Kominoski and Pringle 2009). Consequently, it is necessary to consider smaller scale (intra-annual variations) temporal changes in the composition and decomposition of leaf-detritus, to determine the nature of trophic processes in streams (Wootton et al. 2019).

Chironomidae larvae stand out during the decomposition process, as they are generally the most abundant taxon of benthic macroinvertebrates in tropical streams (>70% species; Gonçalves-Jr et al. 2006, Pio et al. 2018). However, the ecological importance of Chironomidae may have been neglected in decomposition studies, because the family is very diverse and the taxonomic identification of species is difficult (Gonçalves et al. 2007, Trivinho-Strixino 2011). More importantly, Chironomidae larvae play an essential role in nutrient cycling in the freshwater environment (König et al. 2014, Pereira et al. 2017, Rezende et al. 2016). Species of different genera of Chironomidae can modify some properties of the habitat for subsequent colonizers. This is because the various species of chironomids have differing feeding habits, such as shredders, collectors, predators, and miners of leaves, fruits, and wood (Trivinho-Strixino 2011, Biasi et al. 2013).

The intrinsic characteristics of plant species and length of environmental exposure of the leaf-detritus determine the succession of species in a Chironomidae assembly in freshwater ecosystems (Hepp et al. 2008, Biasi et al. 2013, Leite-Rossi et al. 2016). Despite the relative importance of Chironomidae in the dynamics of tropical streams, their role in the decomposition process of leaf-detritus is still not well-known in these environments, since only a few genera are classified as shredders (Hepp et al. 2008). Therefore, the importance of the leaf litter for these organisms means that the seasonal composition of plant species and the residence time of leaf-detritus in streams in the Brazilian Cerrado can be guiding factors for the richness and abundance of the Chironomidae assembly.

In this study, we tested the influence of intra-annual patterns on the allochthonous leaf litter and interactions among Chironomidae assemblages in a stream of the Brazilian Cerrado. Our hypotheses were: (i) the input of leaves in streams in the Brazilian Cerrado is higher in the dry season and when there is high rainfall (Bambi et al. 2017, Tonin et al. 2017); thus, the highest abundance and richness of Chironomidae in detritus will be in transition seasons; (ii) the loss of secondary compounds and microbial conditioning occur over time (Biasi et al. 2013); therefore, we expect a higher abundance of Chironomidae shredders in the later periods of decomposition; and (iii) throughout the year, the input of leaves into the stream varies according to plant species phenology (Bambi et al. 2017); thus, the composition of Chironomidae assemblages will vary according to the seasons of the year.

MATERIAL AND METHODS

Study area

The study was carried out in the Córrego Boiadeiro located in Parque Nacional da Chapada Diamantina (NE Brazil, 12°59′43.8″ S, 41°19′35.6″ W, 900 m a.s.l.). The stream is second-order, 20 cm deep and 0.3 m s^{-1} flux. The vegetation is predominantly Cerrado and some areas of Caatinga and seasonal rainforest (Juncá et al. 2005). The climate is Subtropical highland climate (Cwb) type, according to the Köppen classification, with an average annual air temperature of ~18°C and 700 mm of precipitation (Alvares et al. 2013). This region has two well-defined climatic seasons: a dry season (May to July) and a rainy season (November to January). There are also two transition seasons: a rainy-dry season (February to April) and a dry-rainy season (August to October) (Sales et al. 2015, Rezende et al. 2017). This study used information on temperature and monthly rainfall obtained from the database Hidroweb (2021).

Field experiment

Collection of Chironomidae associated with leaf litter was conducted between February 2015 and January 2016. Leaves were collected every three months (corresponding to the leaves falling in the last 30 ± 2 days in buckets) between January and October 2015. Leaves were collected at three sampling points spaced 40 m apart. Leaves were stored in buckets (25 cm in diameter, n = 6 per row) fixed at 1 m above the stream and collected after 30 days (see Calderón del Cid et al. 2019).

After a collection period of 30 days, only the two buckets with the highest weight in each row (corresponding to 6 buckets per point) were selected to remove the leaves. The leaves of each selected bucket were then placed in a decomposition bag (30 × 30 cm, 10 mm diameter mesh) and incubated in the stream for 90 days (see Supplementary Material, Fig. S1). After 30, 60, and 90 days of incubation, six litter bags were removed to wash litter for the collection of associated organisms. This procedure was repeated four times, in February, May, August, and November 2015 (rainy-dry, dry, dry-rainy, and rainy seasons, respectively). Precipitation fluctuations did not affect the organic matter entering the system or the litterfall triggers, and the physicochemical properties of the leaves did not vary between seasons (according to data previously published by Calderón del Cid et al. 2019).

Chironomidae larvae identification

After removing the litter bags, leaves were washed in a 250 mm sieve. A stereomicroscope was used to examine associated Chironomidae. After segregation, specimens were preserved in 70% ethanol for later identification. Leaves were inspected to verify the presence of Chironomidae. The larvae were then mounted on semi-permanent slides using Hoyer's medium and were determined to genus using taxonomic keys by Trivinho-Strixino (2011) and Silva et al. (2018). Functional feeding groups (FFG) were categorized according to Cummins et al. (2005), Trivinho-Strixino (2011), Saito and Fonseca-Gessner (2014), and Cuda et al. (2019). The FFG was based on the dominant resource present in the diet description of larvae.

The specimens were deposited at the Museu de História Natural da Bahia (MHNBA), Instituto de Biologia, Universidade Federal da Bahia with the following deposit numbers: *Chironomus* sp.: MHNBA Diptera 1921; *Endotribelos* sp.: MHNBA Diptera 1922; *Oukuriella* sp.: MHNBA Diptera 1923; *Polypedilum* sp.: MHNBA Diptera 1924; *Rheotanytarsus* sp.: MHNBA Diptera 1925; *Stempellinella* sp.: MHNBA Diptera 1926; *Stenochironomus* sp.: MHNBA Diptera 1927; *Tanytarsus* sp.: MHNBA Diptera 1928; *Coryneura* sp.: MHNBA Diptera 1929; *Cricotopus* sp.: MHNBA Diptera 1930; *Onconeura* sp.: MHNBA Diptera 1931; *Ablabesmyia* sp.: MHNBA Diptera 1932; *Pentaneura* sp.: MHNBA Diptera 1933.

Data analysis

We used a Shapiro-Wilk test to assess the normality of the data, and a Levene test was used to assess the homoscedasticity of the variances. We log-transformed (x+1) datasets that did not meet the assumptions of normality and homoscedasticity. We evaluated the abundance and richness of FFG identified in the Chironomidae assemblage using a two-way analysis of variance (two-way ANOVA). In this analysis, we individually assessed the categorical factors of the season (four levels; rainy-dry, dry, dry-rainy, and rainy) and time (three levels; 30, 60, and 90 days) and the interaction between them. We repeated this same analysis approach for the abundances of each FFG (collector-gatherer, collector-filter, shredder, scraper, and predator). We considered 95% as the level of significance ($p < 0.05$). We used a non-metric multidimensional scaling (NMDS) ordination based on Bray-Curtis dissimilarity (abundance log-transformed) to evaluate the composition of Chironomidae assemblage FFG associated in leaf litter. We used a permutational multivariate analysis of variance (PERMANOVA; 999 repetitions) to verify the existence of differences between the studied seasons. The analyses were performed using the R software (R Core Team 2019).

RESULTS

The temperature ranged from 21 to 24 °C between February and June 2015 (rainy-dry and beginning of the dry season). It ranged from 12 to 15 °C in August 2015 and between October 2015 and January 2016 (dry-rainy and rainy seasons). Precipitation in the rainy-dry, dry, dry-rainy, and rainy seasons were 136.0 (± 5.3), 49.3 (± 22.4), 41.3 (± 20.8), and 210.7 (± 191.4) mm, respectively. January 2016 was the month with the highest rainfall (593 mm), and September and December 2015 were the months with the lowest rainfall (4 mm) (Fig. 1).

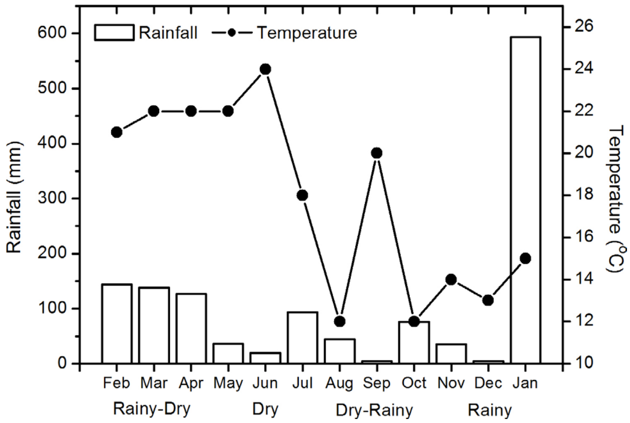


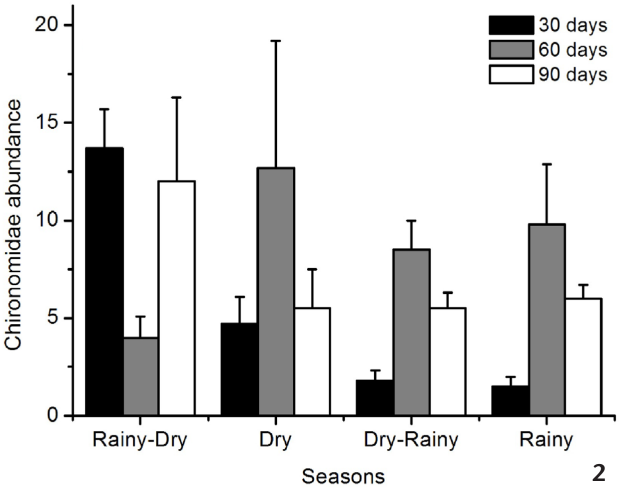
Figure 1. Air temperature and rainfall during the study between February 2015 and January 2016 in the Boiadeiro stream, Mucugê, BA, Brazilian Cerrado. Data: http://www.snirh.gov.br/hidroweb/serieshistoricas (Hidroweb 2020).

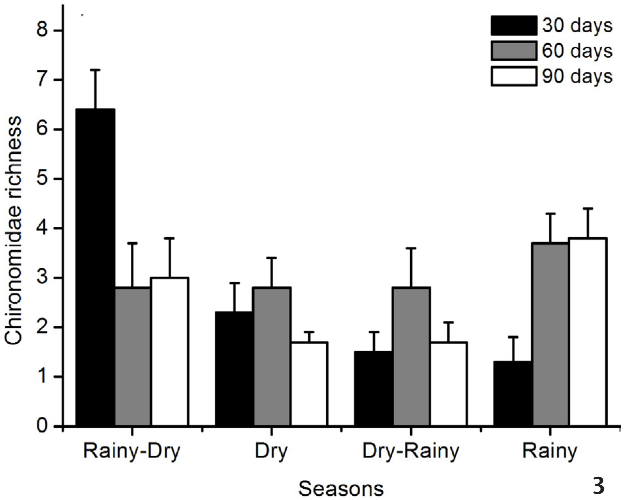
We identified 500 Chironomidae larvae associated with leaf litter during the experiment, distributed into three subfamilies (Chinonominae, Orthocladiinae, and Tanypodinae) and 13 genera (Table 1). Chironominae showed the highest total richness and abundance (8 genera and 224 individuals, 45% of

Table 1. Chironomidae larvae associated with decomposing leaf-detritus in the Boiadeiro stream, Mucugê, BA, Brazilian Cerrado. FTG = Functional trophic group. (C-G) Collector-gatherer, (C-F) Collector-filter, (Shr) Shredder, (Scr) Scraper, (Pre) Predator.

Taxa	Rainy-dry	Dry	Dry-rainy	Rainy	FFG	Total
Chironominae						
Chironomus	1	0	0	0	C-G	1
Endotribelos	7	0	0	10	Shr	17
Oukuriella	11	0	1	5	C-F	17
Polypedilum	31	3	10	17	Shr	61
Rheotanytarsus	6	59	0	3	C-F	68
Stempellinella	0	0	0	3	C-G	3
Stenochironomus	1	0	2	1	Shr	4
Tanytarsus	13	8	11	21	C-F	53
Orthocladiinae						
Corynoneura	78	42	44	13	C-G	177
Cricotopus	1	0	0	0	Scr	1
Onconeura	3	23	0	1	Scr	27
Tanypodinae						
Ablabesmyia	18	0	6	17	Pre	41
Pentaneura	8	2	7	13	Pre	30
Total	178	137	81	104		500

the total), followed by Orthocladiinae (3 genera and 205 individuals, 41%) and Tanypodinae (2 genera and 71 individuals, 14%). *Corynoneura*, *Rheotanytarsus*, *Polypedilum,* and *Tanytarsus*, were the most abundant genera (359 individuals, 71.8% of the total). *Chironomus* and *Cricotopus* were exclusive to the rainy-dry season, and *Stempellinella* was exclusive to the rainy season (Table 1). The highest abundance of individuals (178 and 137 individuals, respectively) was found in the rainy-dry and dry seasons, whereas the highest total richness (12 and 11 genera, respectively) (Table 2) was found in the rainy-dry and rainy seasons. The variation in abundance and richness of Chironomidae was mediated by the amount of time the detritus remained in the stream (Table 2). We did not observe a pattern of abundance and richness over time (Figs 2, 3).





Figures 2–3. Abundance (2) and richness (3) (mean ± SEM) of Chironomidae assemblages associated at leaf litter on 30, 60, and 90 days during inter-annual seasons in Boiadeiro stream, Mucugê, BA, Brazilian Cerrado.

Table 2. Results of the two-way ANOVA of abundance and richness of Chironomidae assemblages associated at leaf litter during inter-annual seasons in Boiadeiro stream, Mucugê, BA, Brazilian Cerrado.

	df	SS	MS	F	p-value
Abundance					
Season	3	4.63	1.54	3.15	0.031
Time	2	2.33	1.16	2.39	0.100
Season:Time	6	13.41	2.23	4.57	<0.001
Residuals	60	29.33	0.48		
Richness					
Season	3	28.72	9.57	5.06	0.003
Time	2	3.03	1.51	0.80	0.453
Season:Time	6	14.19	12.36	6.54	<0.001
Residuals	60	113.33	1.88		

We classified the chironomid genera into five FFG: shredders, collector-gatherers, collector-filterers, scrapers, and predators. Collector-gatherer (36.2% of the total) and collector-filterers (27.6% of the total) were the most abundant FFG (Table 1). Shredders, predators, and scrapers presented 16.4%, 12.2%, and 5.6%, respectively.

The FFG varied between seasons, except collector-filter (Fig. 4, Table 3). In general, collector-gatherers were more abundant in the rainy-dry, dry, and dry-rainy seasons, while shredders were more abundant in the rainy season (Fig. 4). However, we did not observe a clear pattern in FFG abundance during the experiment period. Shredders were more abundant in the rainy-dry season, especially during the initial period of colonization (30 days); however, in the dry-rainy and rainy seasons, the abundance was more significant in the final periods of colonization (60 and 90 days). Predators were more abundant in 60 days in rainy-dry and rainy seasons (Fig. 4).

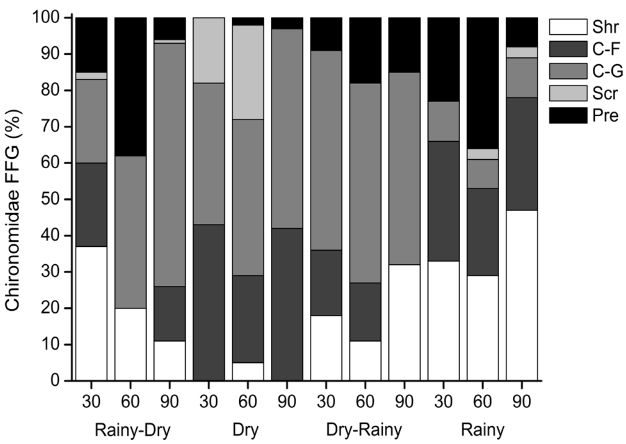


Figure 4. Functional feeding group (FFG) proportion of Chironomidae assemblages associated at leaf litter during inter-annual seasons in Boiadeiro stream, Mucugê, BA, Brazilian Cerrado. (Shr) Shredder, (C-F) Collector-filter, (C-G) Collector-Gatherer, (Scr) Scraper, (Pre) Predator.

Chironomidae FFG composition varied between seasons, especially between rainy, dry, and dry-rainy (PERMANOVA, $F_{3,20} = 4.9$, p = 0.001). We observed segregation between rainy and dry-rainy and rainy and dry seasons (Fig. 5). We observed greater dispersion in the FFG composition in the dry season (Fig. 5). On the other hand, the FFG composition showed less variability in the rainy and dry-rainy seasons.

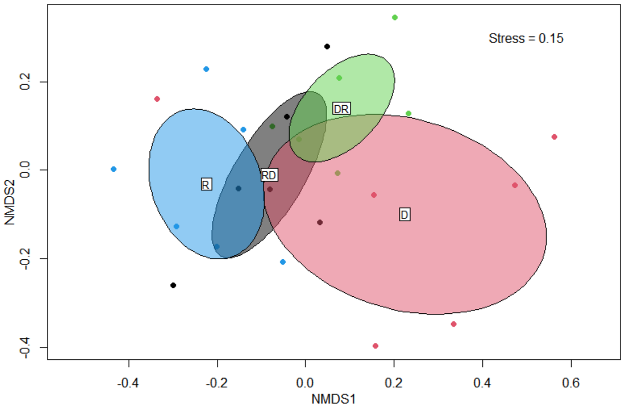


Figure 5. Non-metric multidimensional scaling (NMDS) of Chironomidae assemblages functional feeding group at leaf litter during inter-annual seasons in Boiadeiro stream, Mucugê, BA, Brazilian Cerrado. RD-Rainy-dry (brown). (D) Dry (red), (DR) Dry-rainy (green), (R) Rainy (blue).

Table 3. The two-way ANOVA of functional feeding groups of Chironomidae assemblages associated with leaf litter during inter-annual seasons in Boiadeiro stream, Mucugê, BA, Brazilian Cerrado.

	df	SS	MS	F	p-value
Shredder					
Season	3	3.09	10.30	9.37	<0.001
Time	2	0.01	0.01	0.08	0.922
Season:Time	6	2.46	0.41	3.73	0.003
Residuals	60	6.59	0.11		
Collector-filter					
Season	3	2.23	0.74	1.51	0.218
Time	2	0.09	0.04	0.10	0.903
Season:Time	6	7.89	1.31	2.68	0.022
Residuals	60	29.38	0.48		
Collector-gatherer					
Season	3	7.34	2.44	3.80	0.014
Time	2	1.67	0.83	1.30	0.279
Season:Time	6	3.84	0.64	0.99	0.435
Residuals	60	38.53	0.64		
Scraper					
Season	3	1.75	0.58	3.18	0.030
Time	2	0.35	0.17	0.96	0.387
Season:Time	6	1.49	0.24	1.36	0.245
Residuals	60	11.00	0.18		
Predator					
Season	3	4.28	1.42	5.93	0.001
Time	2	2.28	1.14	4.74	0.012
Season:Time	6	3.19	0.53	2.20	0.054
Residuals	60	14.45	0.24		

DISCUSSION

In this study, we observed an intra-annual variation in Chironomidae assemblages associated with allochthonous plant litter in a Brazilian Cerrado stream, especially during the transition seasons (i.e., rainy-dry and dry-rainy). In addition, the structure and composition of the Chironomidae assemblage varied between seasons, which was directly reflected on the FFG composition. Thus, our study demonstrates an essential interaction between the organic matter dynamics in tropical streams with the stream Chironomidae fauna.

Colonization by benthic macroinvertebrates can be influenced by ecological or stochastic factors (Ge et al. 2021). In general, seasonal variations of precipitation and temperature can affect the diversity of these organisms, especially chironomids (Pereira et al. 2017, Pio et al. 2018, 2020). We found that the richness and abundance of organisms and FFG were higher in the rainy-dry season, especially within 30 (richness and abundance) and 90 (abundance) days of incubation time. Rainfall is an essential predictor of invertebrate community structure, especially in extreme seasons (i.e., rainy and dry) (Nava et al. 2015). In this way, in the rainy-dry season there is less disturbance in the streams, which keeps the local communities more stable. In the present study, we observed changes in the rainfall pattern (mean of 49.33 and 210.67 mm, respectively) in the dry and rainy seasons, compared with the historical average rainfall (30.8 and 159.7 mm, respectively) (Calderón del Cid et al. 2019). The highest rainfall recorded for the last month of the dry season (93.4 mm in July 2015) may have provided an unstable environment, which prompted a lower total richness and abundance of Chironomidae for the dry-rainy season.

The trophic web of small streams depends on the input of allochthonous matter as a source of energy (Irons et al. 1994). However, the exposure time of leaf-detritus is an essential factor in determining the characteristics of the Chironomidae assemblage in a stream (Biasi et al. 2013). In addition, when the chemical composition of the leaves is similar across the seasons, the amount of organic material reaching the stream is essential to the structure of associated detritus communities. We found that the abundance of Chironomidae associated with detritus was low compared to other streams in the Brazilian Cerrado (Ligeiro et al. 2010, Rezende et al. 2016). Considering that decomposing leaf-detritus is initially colonized by the microbial community (Shearer 1992), we believe that the lower abundance of Chironomidae in the current study must be associated with the characteristics of the leaf litter and the reduced activity of decomposing microorganisms in the study stream.

The tropical streams of the Brazilian Cerrado have a high diversity of leaf-detritus that is rich in chemical defense against herbivory (Sales et al. 2015). In the riparian areas of the Brazilian Cerrado, most native trees have leaves with homogeneous characteristics and low palatability for invertebrates (Ligeiro et al. 2010). Chironomidae larvae commonly appear later, when their colonization has already been facilitated by microbial conditioning (Shearer 1992) and by the physical fragmentation of leaf-detritus (Calderón del Cid et al. 2019). Fungi and their interactions with the amount of organic matter and the duration of the plant material in streams positively affect the richness and abundance of Chironomidae in tropical streams (Biasi et al. 2013, Leite-Rossi et al. 2016, Rezende et al. 2019).

The effectiveness of Chironomidae shredders as co-participants in the decomposition process in tropical streams is widely known, given the emphasis that FFG receives in studies of leaf decomposition (Leite-Rossi et al. 2019). Despite this, the activity of fungi seems to be more important than the activity of shredder organisms for the decomposition of detritus (Boyero et al. 2012) at the beginning of the decomposition process. The attractiveness of leaf-detritus to the shredder depends on their colonization by microorganisms, their degradation stages, and the residence time of allochthonous material in the stream (Ligeiro et al. 2010, Leite-Rossi and Trivinho-Strixino 2012). According to Ligeiro et al. (2010), regardless of the plant species that originated the leaf-detritus, exposure time is the main factor affecting the colonization process of aquatic invertebrates. Microbial conditioning can reduce leaf hardness, stimulating colonization by shredder macroinvertebrates and improving the decomposition process (Biasi et al. 2016). This reinforces the importance of the residence time of the detritus in the stream (30, 60, and 90 days), verified in our findings for the structure of the Chironomidae assemblages and their FFG. In addition, we suggest that future studies are based on a two-year sampling, to ascertain the role of inter-annual variations.

The trophic structure in a stream in south-eastern Brazil (subtropical climate) was strongly correlated with the organic matter available as a food resource in the diet of Chironomids (Silva et al. 2009). Chironomidae larvae can consume a variety of food items (Leite-Rossi and Trivinho-Strixino 2012), and adjust their foraging strategies to consume all available resources. In the present study, the composition of the FFG of Chironomidae showed a slight overlap during the transition seasons. On the other hand, there was more segregation during the dry and rainy seasons, indicating niche specialization. According to Rezende et al. (2019), an increase in the input of leaf litter in the stream decreases the biomass of microorganisms. Still, it may increase the use of leaf-detritus by different FFG of benthic macroinvertebrates during the transition seasons.

The Chironomidae assemblages were represented mainly by *Corynoneura* (collector-gatherers), *Tanytarsus*, and *Rheotanytarsus* (both collector-filters). Generally, collector invertebrates are more abundant in environments with greater stability and a higher concentration of particles (Cheshire et al. 2005). According to Henriques-Oliveira et al. (2003), leaf-detritus can represent more than 90% of the food items found in the gut contents of *Corynoneura*, *Tanytarsus*, and *Rheotanytarsus* larvae, even though they are not typical shredders, which suggests the possible contribution of these Chironomidae larvae to the leaf decomposition process. So, we highlight that colonization of leaf-detritus by Chironomidae larvae shows an intra-annual pattern that can be regulated by the amount of time the allochthonous plant material remains in the stream but is mainly due to the organic matter dynamics input into the stream.

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Author Contributions

JFGP: identification of Chironomidae larvae, statistical analysis, and paper writing. LUH: statistical analysis, interpretation of results, and participated in the article's report. AOM: conception and design, carried out the collection, financial support, and participated in the paper report. FLS: provided support for identifying Chironomidae larvae, revised the English language, and participated in writing of the paper. CEC: statistical analysis, supervised the findings, writing of the paper and final text. All the authors have read and approved the manuscript.

Competing Interests

The authors have declared that no competing interests exist.

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Supplementary material 1

Figure S1. Sampling design of the leaf debris collection system (A) and the choice of buckets with the highest weight for the preparation of decomposition bags (B) (adapted from Bambi et al. 2017).

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