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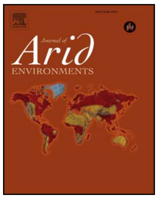

Aquatic invertebrates increase litter breakdown in Neotropical shallow semi-arid lakes

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ABSTRACT

The feeding behavior of shredders and scrapers (invertebrates) is important for litter processing in aquatic ecosystems. We assessed the importance of invertebrate activity for organic matter breakdown in shallow lakes (macrophyte covered or macrophyte free), testing whether the abundance of scrapers was greater than that of shredders, and if macrophytes increased scraper density and consequently, the rate of leaf litter breakdown. We used litter bags with senescent leaves to assess the density, richness and biomass of invertebrates and assessed the mass loss of litter after oven drying. The mean decomposition coefficient (k = -0.0037day^{-1}) was lower than reported rates for other semi-arid lakes. We observed greater leaf breakdown in litter bags with coarse mesh, indicating the importance of scrapers, but potentially also microbes. However, leaf-associated invertebrates (averaged across both types of lakes) had low densities (4.7 ind.g^{-1}), biomass (8.3 mg g^{-1}) and richness (12 *taxa*), which may explain similar breakdown rates between lakes. Semi-aquatic Coleoptera and Mollusca were the most diverse *taxa* because they are capable of tolerating high hydrological stress associated with shallow lakes in semiarid areas. Planorbidae, which are intermediate hosts for the human parasitic trematode *Schistosomamansoni*, were almost absent in the macrophytic lake, suggesting that macrophytes may reduce the Planorbidae density and play an important role in human health.

1. Introduction

Shallow lakes are small water bodies, with dominance particularly in semi-arid regions as the Australian "Mallee" and "Mulga", the Chilean and Argentinean "Chacos" and the Brazilian "Caatinga", that often provide water and habitat for biota (Barbosa et al., 2012; Casco et al., 2016; Neiff et al., 2006). For example, shallow artificial lakes (called "açudes") and small dams provide most of the water storage within Brazilian semi-arid regions. Apart from water storage, shallow lakes also provide water recharge, water purification and recreational fisheries to their adjacent communities (Sayer et al., 2016). Although most studies published worldwide have highlighted the importance of deep lakes, shallow lakes cover a larger area of Earth's surface and often have greater biological activity per unit area than deep lakes (Downing et al., 2006). Despite the clear importance of these small lakes, ecological aspects such as nutrient cycling and energy flow through leaf litter breakdown are still poorly understood.

The diversity of aquatic communities may be influenced by environmental factors such as rainfall and water pollutants (Mooney et al., 2009), biological interactions (e.g. predation and competition; Padial et al., 2014; Ziegler et al., 2015) and ecological processes (e.g. input and decomposition of organic matter; Carvalho et al., 2015; Song et al., 2013). The effects of these factors (environmental, interactions process conditions) may be evaluated through the analysis of leaf litter breakdown (Graça et al., 2015; Rezende et al., 2014). Although many studies have examined the processes of autochthonous litter and/or dead macrophytes breakdown (Carvalho et al., 2015; Li et al., 2013; Song et al., 2013; Ziegler et al., 2015), we still have a poor understanding of breakdown dynamics (mainly allochthonous leaf litter; Rezende et al., 2010) in shallow lakes (Ilmavirta, 1980; Telöken et al., 2011).

Dead macrophytes (a type of autochthonous litter), provide food and refuge to fish and invertebrates, contribute to habitat heterogeneity, and increase habitat productivity and biodiversity (Thomaz and Cunha, 2010). The contribution of allochthonous litter may be more important in shallow than deep lakes because of their greater

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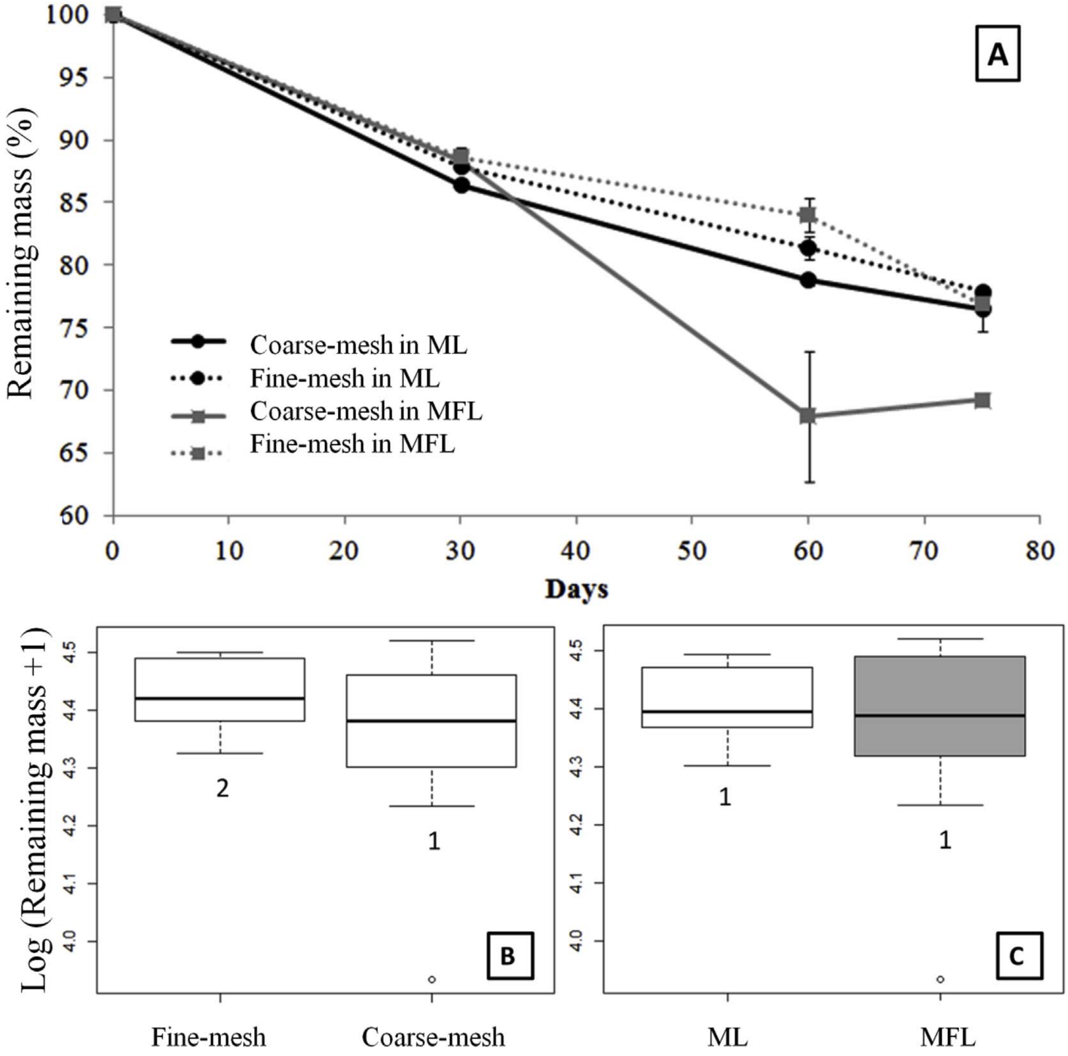

Fig. 1. Mean values and standard errors for the remaining mass in the ML (black line) and MFL (grey line) from fine mesh (dotted line) and coarse mesh (continuous line) litter bags (A). For B (remaining mass between litter bags mesh sizes) and C (remaining mass between lake types), the upper and lower lines of the boxes represent the quartiles, the bold line represents the median, the dashed lines represent the upper and lower limits, and the circles represent outliers. Different numbers (1 and 2) indicate significant differences.

surface-area (Ilmavirta, 1980). Also, allochthonous litter influences the production of methane, which is an important greenhouse gas, in the sediments of shallow lakes (Furlanetto et al., 2012). Therefore, allochthonous input (i.e., driven by rain and wind) and subsequent decomposition processes should be better studied to understand the ecology of semi-arid shallow lake sand interactions within the associated decomposer communities (Telöken et al., 2011). Leaf litter breakdown can also be influenced by many factors, such as physical and chemical variables of water and detritus and decomposers such as micro-organisms and aquatic invertebrates (Carvalho et al., 2015; Li et al., 2013; Quintão et al., 2013; Rezende et al., 2010; Song et al., 2013).

Aquatic fungi (hyphomycetes), mineralize leaf litter through enzymatic action, and drive the breakdown of structural and recalcitrant compounds such as lignin and cellulose (Graça et al., 2015; Quintão et al., 2013). Bacteria then decompose labile molecules as secondary metabolites (Graça et al., 2015; Quintão et al., 2013). Microbial communities are also responsible for the nutritional enrichment of leaf litter, increasing their palatability and enabling the colonization and consumption of leaves by invertebrates (Graça et al., 2015; Quintão et al., 2013; Rezende et al., 2010). The density and richness of shredders are low, and often absent, in semi-arid Brazilian lakes (Barbosa et al., 2012), but the relative abundance of scrapers is high (Barbosa et al., 2012; Rodríguez-Lozano et al., 2015, 2016).The high abundance of scrapers is important for leaf breakdown, once leaves are fragmented when the consumption of periphyton in litter tissues (Rezende et al., 2010). The role of aquatic organisms in breaking down allochthonous litter in tropical shallow lakes is not well studied (Barbosa et al., 2012; Carvalho et al., 2015) and there are no published studies of these dynamics in Brazilian semi-arid regions.

Our objective was to assess the importance of the invertebrate community in leaf breakdown of *Inga laurina*in two Brazilian semi-arid shallow lakes (covered by macrophytes or macrophyte-free), specifically testing two working hypotheses: (1) scrapers will be relatively more abundant than shredders (which are generally absent in lentic systems; Rezende et al., 2010), resulting in a high importance of scrapers in leaf breakdown; and (2) increase in the density of macrophytes in shallow lakes will lead to a high density of invertebrates (mostly scrapers) indirectly increasing leaf breakdown rates. We tested these hypotheses by comparing the invertebrate colonization and the rate of leaf breakdown in litter bags with different mesh sizes, allowing us to remove the effects of invertebrates on decomposition using a fine mesh size.

2. Materials and methods

2.1. Study area

In this study, two eutrophic, shallow, semi-arid lakes (maximum depth of 1.5 m) were investigated. The first (0.011 km^2; 5°12′27.9″S, 37°19′11.8″W), hereafter "ML" (macrophyticlake), presents a limnetic region covered by macrophytes (70–80%). The second (0.016 km^2; 5°12′35.6″S, 37°19′00.3″W), hereafter "MFL" is macrophyte-free lake. Both lakes are located in a semi-arid region (Fig. MS1) in the permanent protection area of the Federal Rural University of the Semi-arid Region (Mossoró, Brazil). The two shallow lakes have high mean water temperature (29 °C), neutral pH (pH ∼6.8), high electrical conductivity ($\sim 0.201^{e+10} pSm^{-1}$) and low dissolved oxygen content ($\sim 5.41\ mgL^{-1}$; Electronic Appendix Table 2). However, ML presented higher temperature, conductivity and TDS than MFL. Dissolved oxygen and turbidity were greater in MFL (Table MS2). Semi-arid regions represent transition zones between arid and sub-humid regions where precipitation is lower than evaporation (Barbosa et al., 2012). The Brazilian semi-arid regions are delimited by i) average annual precipitation lower than 800 mm; ii) aridity index (hydric balance between precipitation and evapotranspiration) below 0.5; and iii) chance of drought higher than 60% (Barbosa et al., 2012).The most abundant macrophyte species present in the studied shallow lakes was *Lemna minor* (Electronic Appendix Fig. 1). However, the low leaf size of these macrophytes preclude their use in breakdown experiments. In the present study, we used senescent leaves of *Inga laurina* (tree), which has broad demographic distribution in South America riparian zones. *Inga laurina* has also been used repeatedly in tropical aquatic studies in Brazil, making it a standard litter type for studies of leaf breakdown in this region (Gomes et al., 2016; Navarro et al., 2013; Rezende et al., 2014, 2015).

2.2. Procedures

Leaves of *Inga laurina* were dried, weighed and pulverized prior to incubation for analysis of the total polyphenol and tannic acid concentration (Bärlocher and Graça, 2005), lignin and cellulose content (Gessner, 2005) and the resistance of leaves to rupture by toughness of intact leaves using a penetrometer (Graça et al., 2005). The total nitrogen content was determined using a CHN basic analyzer (Carlo Erba 1500 for WI; Thermo Electron Corp. Milan, Italy), and the total phosphorus content was determined using the ascorbic acid method after acid digestion. The leaves of *I. laurina* were thus chemically characterized as follows (mean values): total polyphenols (18.29 ± 1.8 mgg^{-1}), total tannic acids (0.002 ± 0.0004 mgg^{-1}), lignin (45.94 ± 0.5%), cellulose (37.39 ± 1.2%), toughness (0.6 ± 0.3 kPa), nitrogen (16.41 ± 1.0 gkg^{-1}) and phosphorus (0.53 ± 0.07 gkg^{-1}).

A second set of *I. lurina* leaves was dried at room temperature until a constant weight was achieved. Then, 32 litter bags (10 × 20 cm) of two mesh sizes (10 mm for coarse and 0.5 mm for fine) were prepared. Each litter bag contained 2 g (± 0.1) of dry leaves. Three litter bags (subreplicates) were incubated in each lake during April 2017 for 30, 60and 75 days (ending in June 2017). The samples were then removed and placed individually into insulated plastic bags and transported in thermal containers to the laboratory, where they were transferred to a refrigerator (4 °C) until processing. Temperature, electrical conductivity, pH, dissolved oxygen, total dissolved solids, water turbidity and reduction potential of water oxidation were determined *in situ* with a multi-analyzer at the time of litter bag recovery.

In the laboratory, leaves from the litter bags were washed with tap water in a 120-μm mesh sieve. The invertebrates retained on the sieve were preserved in 70% alcohol for later identification and enumeration (Hamada et al., 2014; Merritt and Cummins, 1996). The numbers of *taxa* and individuals were calculated for the aquatic invertebrate community, and the biomass was obtained by desiccation at 60 °C for 72 h. The invertebrates were classified into five feeding categories (Cummins et al., 2005; Hamada et al., 2014; Merritt and Cummins, 1996): gathering-collectors, filtering-collectors, shredders, scrapers, and predators. Among these categories, only the frequencies of shredders and scrapers were used to determine the direct effects on leaf litter.

Leaves from each litter bag were randomly collected, and one disk (1.2 cm diameter) was cut from each leaf and used to determine the ash-free dry mass (AFDM; calculated after incineration in a muffle furnace at 550 °C for 4 h). The material was oven-dried at 60 °C for 72 h to determine the dry weight (Graça et al., 2005) and use in leaf breakdown rates determination. A literature search was carried out including personal literature databases and journal indices (Web of Science n = 4, and Scopus n = 3), of material published after 1980. The search terms used in online databases were "leaf breakdown", "litter", "decomposition" and "semi-arid". Studies were included if they satisfied the following criteria: (i) they contained data for leaf breakdown rates; (ii) they were performed in natural aquatic systems; (iii) they contained data for leaf species and/or litter bag size.

2.3. Statistical analysis

Leaf litter breakdown rates (k) were calculated using a negative exponential model of the percent of mass lost over time ($W_t = W_0\ e^{-kt}$; W_t = remaining weight; W_0 = initial weight; $-k$ = decay rate; t = time). We tested the remaining mass (dependent variable) through a factorial two-way repeated measures ANOVA (RM-ANOVA) and the density of invertebrates, invertebrate richness, density of scrapers, and biomass of scrapers (dependent variable) by one-way RM-ANOVA.

To run the RM-ANOVA, we used the time in days (30, 60 and 75 days) as repeated measurements (Crawley, 2007). The RM-ANOVA is typical for experiments with different error variances and pseudoreplication corrections (see Crawley, 2007 for further details). Differences among the categorical variables were assessed through orthogonal contrast analysis (Crawley, 2007). In this analysis, the dependent variables for the different shallow lakes (ML and MFL) and mesh sizes (coarse and fine) were ordered (increasingly) and tested pairwise (with the closest values) and sequentially by adding to the model values with no differences and testing with the next model in a stepwise model simplification process (Crawley, 2007). The specific contribution of invertebrates to leaf litter breakdown was estimated by the difference between the AFDM remaining in total (coarse-mesh) and microbial (fine-mesh) leaf breakdown in each sampling time for each sampling time and then calculating a new k value according to Tonin et al. (2017).

Indicator Species Analysis (*sensu* Dufrêne and Legendre, 1997), was used to determine which organisms were characteristic of the shallow lakes. This analysis uses the frequency and density of organisms in the previously defined groups and produces an indicator value ranging from 0 (non-indicator) to 100 (perfect indicator). Significance was tested using Monte Carlo tests with 1000 permutations and set to $P < 0.05$. Only significant results are reported.

3. Results

3.1. Leaf litter breakdown rates

After 75 days, the average remaining litter mass was 75 (± 3%) (Table 1; Fig. 1), with lower values on the coarse mesh of the MFL (69%) and higher values in fine mesh of ML (77%; Fig. 1). The mean decomposition coefficient ("k") was $-0.0039 day^{-1}$and ranged from −0.0031 (fine-mesh in both lakes) to −0.0055 (coarse-mesh in MFL). Conversely, the k values specific for invertebrates was −0.5425 $day^{-1}$to ML and −0.09011 $day^{-1}$to MFL, whit the higher breakdown rates of −0.9323 $day^{-1}$to ML (60 days) and −0.4165 $day^{-1}$to MFL (30 days). The higher values of remaining mass were found in the fine-mesh compared to the coarse-mesh (Table 1; Fig. 1). However, there were no

Table 1
Degrees of freedom (DF), residuals, sums of squares (%), F-tests and contrast analyses for comparisons among remaining mass (A), density of invertebrates (B), invertebrate richness (C - number of taxa) and biomass (D), density of scrapers (E) and biomass of scrapers (F) among two different types of shallow lakes (with macrophytes or without) and mesh sizes, and the interactions by RM-ANOVA.

RM-ANOVA	DF	Sum Sq %	F value	Pr > F	Contrast Analysis
A. Remaining mass					
Lake	1	1.34	0.537	0.469	
Mesh size	1	16.34	6.535	0.016	Coarse mesh < Fine mesh
Lake: Mesh size	1	7.28	2.912	0.098	
Residuals	30	75.03			
B. Density of invertebrates					
Lake	1	7.66	1.246	0.282	
Residuals	15	92.34			
C. Number of taxa					
Lake	1	0.03	0.005	0.947	
Residuals	15	99.97			
D. Biomass of invertebrates					
Lake	1	15.26	5.945	0.021	MFL < ML
Residuals	15	84.73			
E. Density of scrapers					
Lake	1	21.40	8.991	0.005	MFL < ML
Residuals	15	78.59			
F. Biomass of scrapers					
Lake	1	54.47	19.461	< 0.001	MFL < ML
Residuals	15	43.52			

differences in the remaining mass between lakes and the interaction factor with mesh size was non-significant (Table 1; Fig. 1). The fine mesh in both lakes showed higher and similar values of remaining mass (Fig. 1).

3.2. *Invertebrate community*

The mean density of leaf-associated invertebrates found in this study ranged from 4.7 to 8.3 individuals g^{-1} for both lakes and among the three experimental periods. The most abundant *taxa* were the class Ostracoda (51%) and the family Lymnaeidae (32%). The mean species richness was 5 *taxa* (range from 7 at 60 days to 3 at 75 days). However, density and species richness (number of *taxa*) in the invertebrate community did not vary significantly between shallow lakes or sampling times, and the interactions between these factors were non-significant (Table 1; Fig. 2 and MS3). The most important trophic group (shedders, that break down matter) was not found in our study (Table 2). However, the biomass and density of scrapers (important in tropical aquatic systems) were higher in ML (24.42 individuals g^{-1}, 0.39 g individual^{-1}g^{-1}, respectively) than in MFL (11.50 individuals g^{-1}, 0.14 g individual^{-1} g^{-1}, respectively; Table 1; Fig. 2, MS3 and MS4). The scraper trophic functional group was represented by the Planorbidae (Gastropoda), Lymnaeidae (Gastropoda) and Scirtidae (Coleoptera; Table 2). The analysis of the indicator species showed that the families Lymnaeidae (Indicator Value = 0.71; p = 0.031) and Planorbidae (Indicator Value = 0.58; p = 0.034) were indicator species for ML and MFL, respectively.

4. Discussion

4.1. *Leaf litter breakdown rates*

The leaf litter decomposition rates in our study ($k \approx -0.0039$; range -0.0031 to -0.0055 day^{-1}) were relatively low compared to other semi-arid lake systems worldwide (range -0.001 to -0.022 day^{-1}; Casco et al., 2016; Neiff and Casco, 2001; Neiff et al., 2006; Zozaya and Neiff, 1991). The breakdown of *Inga laurina* is classified as intermediate to slow in tropical systems (according to Gonçalves et al., 2014) because the high quantity of refractory compounds (e.g. lignin and hemicelluloses) inhibits weight loss (Carvalho et al., 2015; Li et al., 2013; Neiff et al., 2006). The greater weight loss observed after 30 days of incubation compared to other sampling days may be attributed to the higher metabolism of labile molecules or leaching (Rezende et al., 2010), except forfine mesh in MFL. Given that the macrophyte *Eichhornia crassipes* decomposes quickly ($k = -0.022$day^{-1}; Neiff et al., 2006 Table 3), removing it from the global decomposition estimates results in a k-range from -0.001 to -0.006day^{-1}. Under these new data, our estimates indicate a decomposition rate that is average compared to other studies worldwide. Studies conducted in tropical streams (e.g. Rezende et al., 2014) and in the laboratory (e.g. Gomes et al., 2016; Navarro et al., 2013) have shown that intermediate temperature variation (from 20 to 32 °C) does not influence litter breakdown for low-quality leaves (as *I. laurina*). Two inferences may arise from these results: (1) litter type influences leaf breakdown rates (see also Carvalho et al., 2015; Li et al., 2013; Neiff et al., 2006); and (2) leaf breakdown is slow in semi-arid tropical lakes (Monroy et al., 2016;

Table 2
Invertebrate density (individuals.g^{-1}) in the sampling sites (ML and MFL) and among sampling periods (30, 60 and 75 days) presented as means ± standard error.

Taxon	FFG	Macrophyte lake			Macrophyte-free lake		
		30	60	75	30	60	75
Annelida							
Oligocheta	Gathering-collectors	5.46 ± 1.04	3.14 ± 0.54	0.85 ± 0.49	0.21 ± 0.12	0.83 ± 0.27	1.26 ± 0.38
Hirudinae	Predators	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.35 ± 0.12	0.79 ± 0.27
Arthropoda							
Insecta							
Coleoptera							
Hydrophilidae	Gathering-collectors	0.39 ± 0.23	2.38 ± 0.50	4.55 ± 0.92	4.98 ± 0.45	3.19 ± 0.27	1.50 ± 0.49
Staphylinidae	Predators	0.00 ± 0.17	0.57 ± 0.33	1.12 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
Dytiscidae	Predators	0.00 ± 0.00	0.57 ± 0.18	1.15 ± 0.36	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
Scirtidae	Scrapers	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.30 ± 0.09	0.51 ± 0.15
Diptera							
Chironomidae	Gathering-collectors	3.26 ± 0.71	1.81 ± 0.39	0.00 ± 0.00	2.31 ± 0.82	1.97 ± 0.84	0.00 ± 0.00
Mollusca							
Gastropoda							
Planorbidae	Scrapers	0.39 ± 0.23	0.22 ± 0.13	0.00 ± 0.00	2.58 ± 0.41	1.90 ± 0.43	0.00 ± 0.00
Lymnaeidae	Scrapers	20.93 ± 8.80	20.88 ± 2.08	30.85 ± 4.96	6.19 ± 0.81	9.68 ± 2.06	13.35 ± 3.55
Crustacea							
Ostracoda	Filtering-collectors	3.78 ± 1.13	6.10 ± 1.03	10.38 ± 2.31	1.14 ± 0.66	47.66 ± 8.25	94.01 ± 21.38
Entognatha							
Collembola	Gathering-collectors	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.21 ± 0.12	0.12 ± 0.07	0.00 ± 0.00

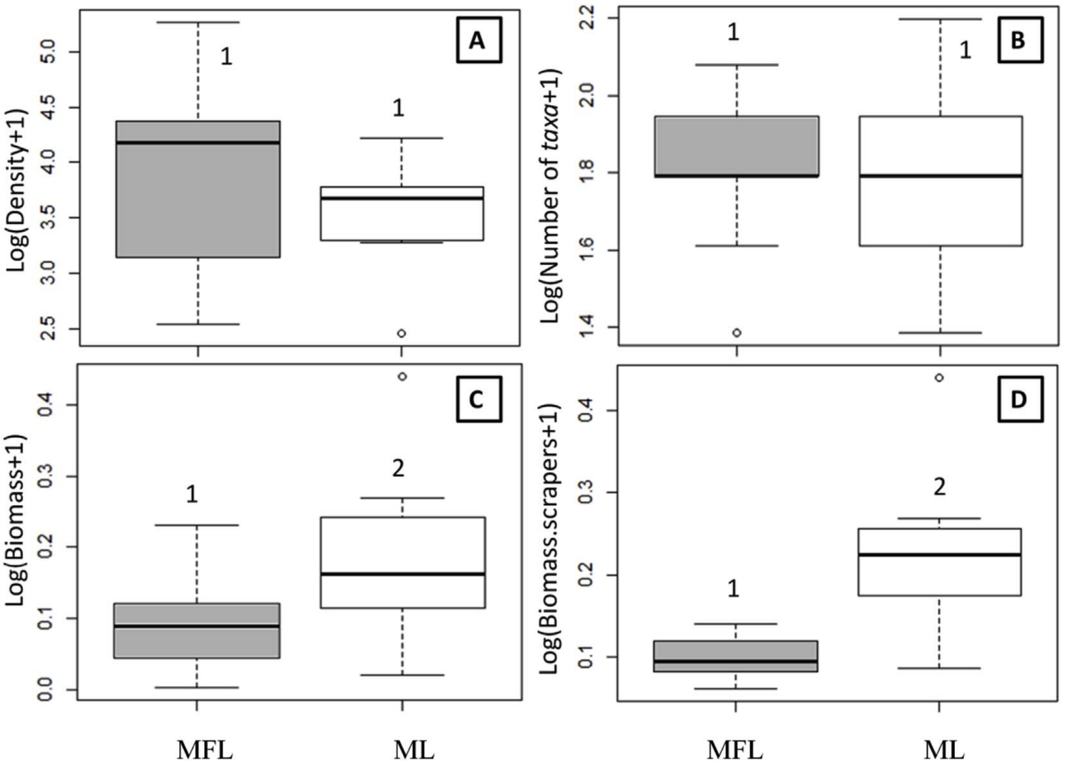

Fig. 2. The effects of density (A), number of taxa (richness; B), biomass of invertebrates (C) and biomass of scrapers (D) in ML (white) MFL (grey) on *I. laurina* leaf litter breakdown colonization over 75 days. The lower and higher lines of the boxes represent the quartiles, the bold line represents the median, the dashed lines represent the upper and lower limits, and the circles represent outliers. Different numbers (1 and 2) indicate significant differences.

Moody and Sabo, 2013; Neiff et al., 2006). Therefore, despite the high biological activity per unit area in shallow semi-arid lakes (Downing et al., 2006), the low litter breakdown rates indicate that these habitats accumulate organic matter and nutrients by delaying biomass cycling.

Despite the small difference in k values among treatments, our results may indicate that the invertebrate community influences litter breakdown in semi-arid shallow lakes (mainly in ML), consistent with our first hypothesis. This is corroborated by the remaining litter mass in fine mesh bags exceeded the coarse mesh ones. As expected in this hypothesis, no shredder invertebrates were found in our study. Shredders are the most important functional group among the invertebrates influencing the leaf litter breakdown process (Graça et al., 2015). Their ecological niche was consequently occupied by Gastropoda scrapers, which scrap the leaf surfaces with their radulae and increase litter breakdown rates (Casas and Gessner, 1999; Rezende et al., 2010), supporting our first hypothesis. However, similarities in invertebrate community (density and richness) and remaining litter in both lakes (ML and MFL) support the general understanding that macrophytes do not influence litter breakdown in semi-arid shallow lakes. In fact, macrophytes are known to influence the diversity and distribution of invertebrates in aquatic systems (Damanik-Ambarita et al., 2016; Mykra et al., 2008) by increasing substrate and food (Thomaz and Cunha, 2010); but this was not observed in our experiment for all community. The absence of macrophytic influence on litter breakdown in our study may be due to (1) similarity in the decomposer community by the close geographical proximity between the lakes, which facilitates migration (Durães et al., 2016; Padial et al., 2014) and (2) the low environmental (physical and chemical water characteristics) difference between lakes by high homogeneity of lentic systems (Rezende et al., 2010). Also, the distance from high-diversity systems (e.g. lotic systems) hinders migration and isolates populations that contribute to the regional invertebrate diversity (Durães et al., 2016; Padial et al., 2014).

4.2. *Invertebrate community*

Although the biomass of invertebrates and scrapers and the density of scrapers in ML significantly surpassed that of MFL (see Table 1), the invertebrate biomass did not influence litter breakdown because the remaining litter percentage in the ML was roughly equal to that of the MFL, refuting our second hypothesis. The low contribution of invertebrate decomposers to litter breakdown is due higher toughness of *I. laurina* compared to other specie leaves, like aquatic macrophytes (when present), which may be preferred (Carvalho et al., 2015; Li et al., 2013; Rezende et al., 2010). These results challenge the current understanding that invertebrate biomass is a dominant environmental factor influencing litter breakdown in tropical ecosystems (Tonin et al., 2014). The composition of invertebrate communities appears to be particularly important for litter breakdown given that invertebrate scrapers such as gastropods, planorbids and lymnaeids are relatively larger (body size) than other invertebrate groups (by higher density of scrapers), therefore decreasing the effect of total invertebrate biomass on litter breakdown (Rezende et al., 2015). Planorbidae was more abundant on MFL than on ML, while Lymaneide showed an opposite pattern. However, once the biomass of Lymnaeide individuals exceeded that of Planorbidae (by a factor of 2 or 3), we observed a greater biomass of scrapers in ML compared to MFL. The low invertebrate biomass importance to leaf breakdown maybe explained due to high temperature in study systems that may increase the biological metabolism and activity of decomposers (Graça et al., 2015; Rezende et al., 2010). Thus, the average temperature observed in our experiment was 30 °C; thus the increased activity of decomposers may have also reduced the biomass effect on litter breakdown (for more, see Rezende et al., 2014). Therefore, we hypothesize that litter breakdown in semi-arid shallow lakes is driven mostly by the composition of invertebrate community (i.e., through low natural biodiversity).

Although the diversity of benthic invertebrates in Brazilian semi-arid systems is higher than that of other warm-dry systems (Barbosa

Table 3
Comparison of leaf breakdown rates (k d^{-1}) and litter bag sizes (L.B. size) in different types of litter in l aquatic system lentic (A) and lotic (B) zones in various semi-arid regions of the world.

References	Country	L.B. Size	Leaf Litter Type	k d^{-1}	Observations
A. Aquatic lentic systems					
Current study	Brazil	Coarse	*Inga laurina*	−0.004 to −0.005	ML and MFL
Current study	Brazil	Fine	*Inga laurina*	−0.003	ML and MFL
Zozaya and Neiff (1991)	Argentina	Coarse	*Typha latifolia*	−0.001 to −0.004	Floating island (above, under and air)
Neiff and Casco (2001)	Argentina	Coarse	*Copernicia alba*	−0.006 to −0.007	Chaco - Palm Swamp Forest
Neiff et al. (2006)	Argentina	Coarse	Mixed leaves	−0.006 to −0.007	Oxbow Lake
Neiff et al. (2006)	Argentina	Coarse	*Eichhornia crassipes*	−0.022	Oxbow Lake
Neiff et al. (2006)	Argentina	Coarse	*Typha latifolia*	−0.004	Palm Swamp Forest
Neiff et al. (2006)	Argentina	Coarse	*Paspalum repens*	−0.008	Palm Swamp Forest
Neiff et al. (2006)	Argentina	Coarse	*Eichhornia crassipes*	−0.021	Palm Swamp Forest
Neiff et al. (2006)	Argentina	Coarse	*Copernicia alba*	−0.003	Palm Swamp Forest
Casco et al. (2016)	Argentina	Coarse	Mixed leaves	−0.004 to −0.008	Oxbow lake
Total range/mean				**−0.001 to -0.022**	
Total mean				**−0.007**	
B. Aquatic lotic systems					
Schade and Fisher (1997)	USA	Coarse	*Populus fremontii*	−0.017	Sonoran desert stream
Pomeroy et al. (2000)	USA	Coarse	*Populus fremontii*	−0.006	Glen Canyon Dam
Andersen and Nelson (2006)	USA	Coarse	*Populus deltoides*	−0.001 to −0.016	Desert river floodplains
Neiff et al. (2006)	Argentina	Coarse	*Tessaria integrifolia*	−0.072	Riverine Forest
Neiff et al. (2006)	Argentina	Coarse	*Salix humboldtiana*	−0.019	Riverine Forest
Neiff et al. (2006)	Argentina	Coarse	*Polygonum acuminatum*	−0.022	Riverine Forest
Neiff et al. (2006)	Argentina	Coarse	*Panicum elephantipes*	−0.011	Riverine Forest
Neiff et al. (2006)	Argentina	Coarse	*Eichhornia crassipes*	−0.067	Riverine Forest
Nelson and Andersen (2007)	USA	Coarse	*Populus* sp.	−0.006 to −0.029	–
Nelson and Andersen (2007)	USA	Fine	*Populus* sp.	−0.006 to −0.016	–
Casas et al. (2011)	Spain	Coarse	*Alnus glutinosa*	−0.016 to −0.094	Sub-humid forests
Moody and Sabo (2013)	USA	Coarse	*Tamarix* sp.	−0.041 to −0.081	In Crayfish and no Crayfish area
Moody and Sabo (2013)	USA	Coarse	*Baccharis* sp.	−0.111 to −0.141	In Crayfish and no Crayfish area
Moody and Sabo (2013)	USA	Coarse	*Populus* sp.	−0.055 to −0.061	In Crayfish and no Crayfish area
Moody and Sabo (2013)	USA	Coarse	*Salix* sp.	−0.045 to −0.046	In Crayfish and no Crayfish area
Arroita et al. (2013)	Spain	Coarse	*Alnus glutinosa*	−0.005 to −0.011	In canal, cropland and gully area
Arroita et al. (2013)	Spain	Fine	*Alnus glutinosa*	−0.006 to −0.010	In canal, cropland and gully area
Martinez et al. (2015)	Spain	Fine	*Alnus glutinosa*	−0.039 to −0.058	–
Martinez et al. (2015)	Spain	Coarse	*Alnus glutinosa*	−0.052 to −0.164	–
Monroy et al. (2016)	Spain	Fine	*Alnus glutinosa*	−0.0006 to −0.001	Ebro basin in a regional gradient of aridity
Monroy et al. (2016)	Spain	Coarse	*Alnus glutinosa*	−0.001 to −0.005	Ebro basin in a regional gradient of aridity
Monroy et al. (2016)	Spain	Fine	*Quercus robur*	−0.0002 to −0.0007	Ebro basin in a regional gradient of aridity
Monroy et al. (2016)	Spain	Coarse	*Quercus robur*	−0.0001 to −0.0008	Ebro basin in a regional gradient of aridity
Overall range/mean				**−0.0001 to -0.164**	
Overall mean				**−0.034**	

et al., 2012), we found low species density and richness compared with other semi-arid lakes (Neiff and Casco, 2001; Neiff et al., 2006) and tropical lakes worldwide (Carvalho et al., 2015; Rezende et al., 2010; Telöken et al., 2011). In semi-arid regions, evaporation exceeds precipitation (Barbosa et al., 2012) and this phenomenon causes seasonal drying of small water bodies, particularly during prolonged droughts (Barbosa et al., 2012). Because of the small size and depth of our experimental lakes, the recent drought that occurred during the last El Niño event (2015–2016) dried the lakes and consequently reduced the invertebrate density and diversity. Species dominance in our study also differed from other breakdown studies in tropical systems. For example, Chironomidae and Oligochaeta occurred at low densities in the current study, but usually dominate the invertebrate community in tropical lakes and reservoirs (Carvalho et al., 2015; Quintão et al., 2013; Rezende et al., 2010; Telöken et al., 2011) and semi-arid lakes (Barbosa et al., 2012). The most dense and diverse invertebrate groups found here were the Coleoptera (represented by the families Hydrophilidae, Staphylinidae, Dytiscidae and Scirtidae) and Mollusca (families Gastropoda, Planorbidae and Lymnaeidae), and the Lymnaeidae and Planorbidae had the highest indicator values in the ML and MFL lakes, respectively. This result indicates that Lymnaeidae species may outcompete the Planorbidae (both families are composed by scraper species), thereby restricting the latter to the less-productive MFL habitat.

5. Conclusion

The decomposition of *I. laurina* litter was classified as intermediate to slow due to the presence of highly refractory compounds such as lignin and hemicellulose, highlighting the importance of litter quality for breakdown rates. Thus, semi-arid lakes may function as sinks for organic matter and nutrients. The lower remaining biomass in coarse mesh bags indicates the importance of invertebrate scrapers for litter breakdown in macrophytic lakes, corroborating our first hypothesis. However, despite the importance of scrapers importance to leaf breakdown, the microbial contribution cannot be excluded, mainly by low difference between fine and coarse-mesh. However, these results also indicated a lack of macrophyte influence on litter breakdown rates, providing no support for our second hypothesis. The presence of macrophytes positively influenced the biomass of invertebrates, likely through increased food availability, and the biomass of scrappers, which may be due to the increased presence of biofilm.

We observed low species richness and density that were possibly induced by the hydric stress typical of semi-arid regions. The high diversity of coleopterans and molluscs in both lakes corroborates the hydric stress explanation, as they are semi-aquatic invertebrates that can survive drought events. Molluscs from Lymnaeidae and Planorbidae were indicator species for ML and MFL, respectively, and we highlight the occurrence of the planorbid *Biomphalaria straminea*, which represents a potential public health problem in the study area through its role as a host of the human parasitic trematode *Schistosomamansoni*.

Given that lymnaeids (with no medical importance) out competed planorbids in the presence of macrophytes, these aquatic plants may provide an important ecosystem service to public health. Finally, ecological processes such as leaf litter breakdown are important environmental indicators and can be managed in the semi-arid ecosystem. Therefore, continued evaluation of this ecological process may aid the development of future public policies for semi-arid water conservation and public health services.

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Appendix A. Supplementary data

Supplementary data related to this article can be found at http://dx.doi.org/10.1016/j.jaridenv.2018.03.002.

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