



LEAF LITTER WITH CONTRASTING CHEMICAL TRAITS AND DECOMPOSITION PROMOTE SIMILAR BENTHIC MACROINVERTEBRATES COMMUNITIES

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Abstract: In aquatic ecosystems, allochthonous inputs of leaf litter are common substrates for the invertebrates communities. The quality and physical structure of these substrates are expected to strongly determine benthic invertebrates structure and functioning. Therefore, we carried out an experiment to evaluate the association between these organisms and the chemical traits of leaf litter from 16 *restinga* plant species in Jurubatiba lagoon, a coastal aquatic ecosystem at Restinga de Jurubatiba National Park. After 123 days, litter mass loss varied from 14 - 30%, indicating that decomposition was in the initial stage for most species. Litter converged to have a similar nutritional quality after this time submerged. Initial K concentration positively affected, whereas initial lignin and C concentration negatively affected species richness and diversity. It indicates that nutrients attract whereas structural compounds limit benthic species colonization. Chemical compounds such as C, nutrients (N, P, K and Na), lignin and cellulose tended to be positively associated with the dominant taxa (*Chironominae* n.i. and *Heleobia australis*) and functional feeding groups (scrapers and collector-gatherers). However, no significant associations were detected by the redundancy analyses. We may conclude that litter quality affect benthic structure, but

not community composition nor FFG distribution at Jurubatiba lagoon. The benthic composition and FFG may be randomly distributed among litter substrates or may be better explained by some other litter aspect(s) different from those considered in this study. Future studies may also consider the temporal dynamic of litter colonization to better elucidate the relationship between litter traits and invertebrate community.

Keywords: litterbags, invertebrates, colonization, coastal lagoon, restinga.

INTRODUCTION

Aquatic ecosystems play an important role in the processing of energy and matter on natural landscapes and are responsible for the dynamics (production, consumption, transport, decomposition, immobilization, *etc.*) of a considerable amount of organic matter (OM) through their drainage systems (Molnar *et al.* 2002). Riparian vegetation contributes to a large portion of OM inputs to aquatic ecosystems, mainly via leaf litter (Wetzel 2001). Leaf litter is a common substrate for invertebrates' colonization, shaping their community structure and metabolic dynamics (Cummins 1974).

Benthic macroinvertebrates are particularly important on OM dynamics on aquatic ecosystems (Abelho 2009). They live associated with the substrates deposited on the bottom of these ecosystems, and contribute substantially to the burial, consumption, and processing of OM and for its mobilization from this compartment to the water column (Hutchinson 1993). The benthic community composition is mostly constituted of insect larvae and nymphs, crustaceans, annelids, mollusks, nematodes, among others (Cummins 1974). They occupy a wide range of substrates, from mineral (clay, silt, sand, gravel, and stones) to organic ones (logs, aquatic plants, litter, *etc.*), to which they associate for food, shelter or refuge (Van Looy *et al.* 2019).

Substrate quality is a fundamental aspect for the occurrence, distribution, and composition of benthic macroinvertebrates assemblages (Janke & Trivinho-Strixino 2007). Leaf litter, for example, has a wide range of variation in its chemical and structural quality, aspects that constitute an important environmental filter for colonization by macroinvertebrates (Gonçalves Jr. *et al.* 2004, Martínez *et al.* 2016, Rezende *et al.* 2019). Initial litter quality represents the enormous variation

in the chemical and morphological composition of litter species and is a good predictor of litter decomposition (Cornwell *et al.* 2006). It mediates litter decomposition process through the regulation of microbial decomposers, which tend to prefer litter resources that are richer in nutrients and labile compounds (Gessner *et al.* 2007). High availability of nutrients such as nitrogen and phosphorous facilitates microbial and periphytic colonization, improving litter quality and its importance as a food source for invertebrates (Brum & Esteves 2001a, b, Gonçalves Jr. *et al.* 2004).

By their turn, benthic macroinvertebrates have great phylogenetic diversity and their communities are formed by highly diverse organisms that differently exploit the resources and perform a wide range of functions in these ecosystems. This can be evidenced by the great variety of functional feeding groups found in these communities, with ability to scrape, fragment, collect, resuspend and ingest litter (Cummins 1974). On leaf litter, a considerable attraction of detritivorous invertebrates is expected, mainly comprising shredders and scrapers (Martínez *et al.* 2016). These groups are closely linked to litter, using it as a refuge and as a grazing source, because they are primary consumers that feed on periphyton that colonizes litter (Jacobsen *et al.* 2008). As a result, they are commonly associated with allochthonous production, and can dominate the communities in ecosystems where litter is the primary source of energy, such as in low-order streams (Neres-Lima *et al.* 2017). The action of shredders increases litter surface area, stimulating colonization by microorganisms. The presence and activity of these organisms promote intense bioturbation, resuspension, and, consequently, improve the availability of organic matter and nutrients to the sediment surface and to the water column (Caliman *et al.* 2012),

increasing substrate availability for collectors and filter-feeding macroinvertebrates. Predators are also associated with litter, seeking for refuge or preys (Ono 2018).

Because macroinvertebrates have relatively quick responses to changes in environmental conditions, they are commonly associated to substrate quality (Hutchinson 1993, König *et al.* 2014, Martínez *et al.* 2016, Rezende *et al.* 2019). However, most of these studies evaluating the relationship between aquatic macroinvertebrates community structure and function, and litter characteristics were carried out in temperate and tropical lotic ecosystems neglecting their importance on tropical lentic ones (but see Gonçalves Jr. *et al.* 2004). Also, not a single study to date reported the association between invertebrates and terrestrial litter quality on tropical lentic coastal ecosystems, to our knowledge. So, the great diversity and importance of invertebrates and terrestrial litter in the trophic structure of aquatic ecosystems contrasts with the scarcity of data in the literature on the structure and feeding habits of the first with the quality of the second in tropical lentic ecosystems.

Therefore, this research aimed at evaluating how benthic macroinvertebrates structure and function are associated with riparian leaf litter quality on a tropical lentic ecosystem. To achieve this, we experimentally evaluated how the benthic community composition, abundance, diversity, evenness and functional feeding groups are associated with litter quality, considering a litter quality gradient composed of 16 chemically distinct leaf litter species from restinga ecosystem, decomposing at Jurubatiba lagoon. Based on previous essays considering litter from aquatic macrophytes decomposing at Jurubatiba lagoon, Gonçalves Jr. *et al.* (2008) found that scrapers tended to prefer harsh substrates, with a higher proportion of lignin and cell wall fractions, what is associated to the stability provided by the low rates of substrate degradation; collector–filterer abundances were influenced by concentrations of nitrogen and phosphorus, and collector–gatherers and shredders were mainly influenced by coarse organic matter availability. Therefore, we can also expect benthic invertebrate dynamics to be highly responsive to variations in terrestrial litter quality in Jurubatiba lagoon. So, we hypothesized

that litter species chemical composition affect the structure and function of invertebrates, such that litter with higher amounts of organic matter and nutrients will present a higher diversity of taxa, and a greater amount of collector–filterer and collector–gatherers, whereas litter with higher amounts of lignin and cellulose will present a greater amount of scrapers and shredders.

MATERIAL AND METHODS

Study area

To evaluate how benthic macroinvertebrates are associated with *restinga* leaf litter species, an experiment was carried out at Jurubatiba Lagoon, situated in the Restinga de Jurubatiba National Park, in Macaé - RJ (22° 22' 30" S e 41° 15' 45" W; Figure 1). This is a shallow and oligotrophic ecosystem, where salinity varies from freshwater to brackish (Marinho *et al.* 2010, Gripp *et al.* 2018; Figure 1).

The mean annual rainfall in the area varies between 1,100 to 1,250 mm (Alvares *et al.* 2013), and is concentrated between November and January, whereas precipitation minima are registered from June to August. The mean annual temperature varies between 21.3 to 22.4 °C, with small oscillations throughout the year. Climate is characterized as Tropical with dry winters according to Köppen classification (Alvares *et al.* 2013).

Experimental design

The experiment was carried out considering leaf litter from 16 *restinga* plant species, commonly found around Jurubatiba lagoon: *Amaioua pilosa* (K. Schum.) (AP), *Byrsonima sericea* (DC) (BS), *Clusia hilariana* (Schltdl.) (CH), *Cupania emarginata* (Cambess) (CE), *Erythroxylum ovalifolium* (Peyr) (EO), *Eugenia nitida* (Benth) (EN), *Eugenia umbelliflora* (Berg) (EU), *Gomidesia martiana* (Berg) (GM), *Heisteria perianthomega* ((Vell.) Sleumer) (HP), *Inga maritima* (Benth.) (IN), *Manilkara subsericea* ((Mart.) Dubard) (MS), *Maytenus obtusifolia* (Mart.) (MA), *Ocotea notata* ((Nees) Mez) (ON), *Ouratea cuspidata* ((St.-Hil.) Engl.) (OC), *Protium icicariba* ((DC.) Marchand) (PI), and *Senna australis* (Vell) (SA). Leaf litter (hereafter, litter) consisted of senescent leaves, with less than 50% of green-chlorophyll surface,

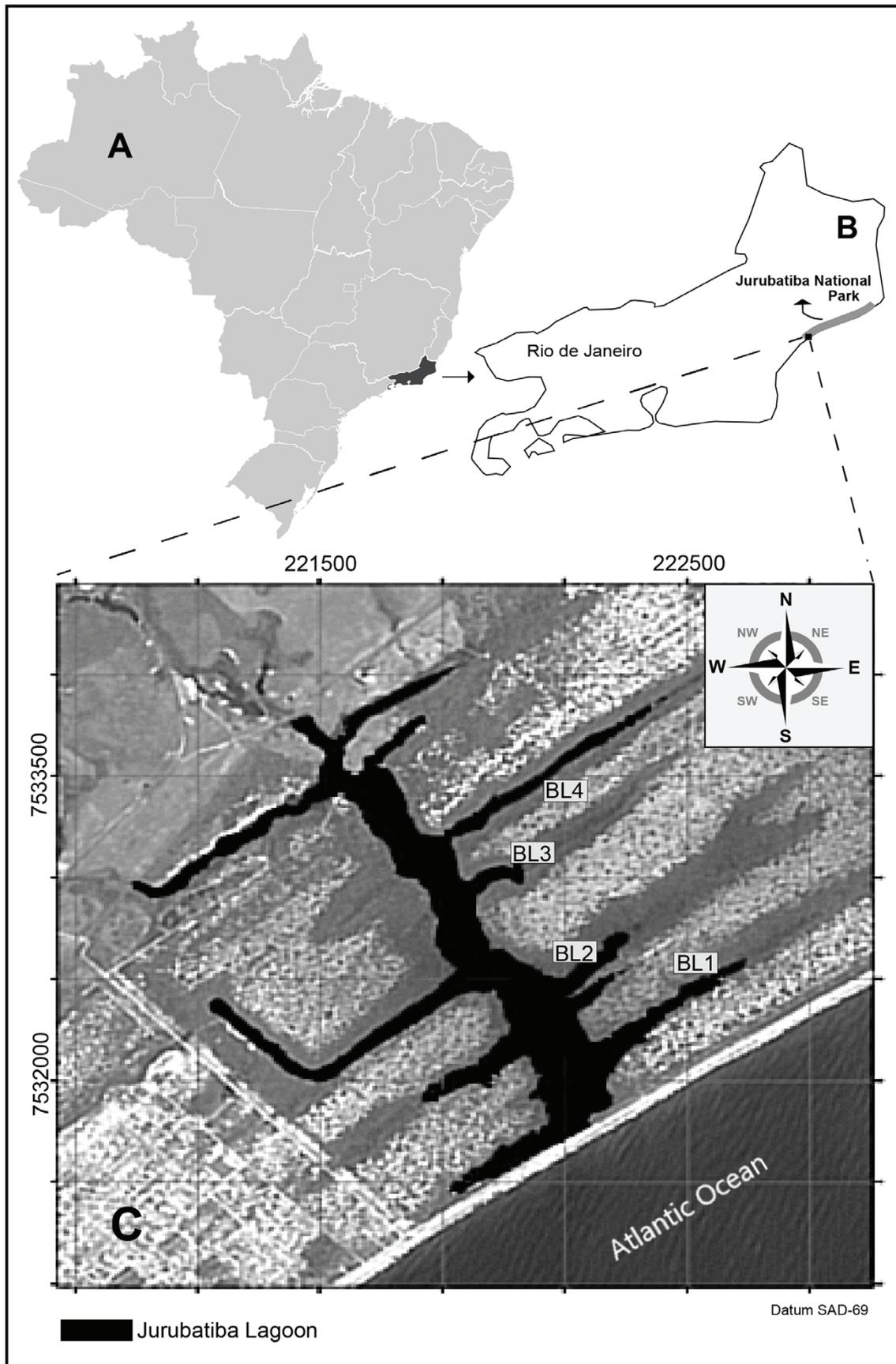


Figure 1. Location of Jurubatiba Lagoon in Rio de Janeiro state, indicating the experimental blocks (BL1 – BL4) where this study was carried out.

collected from the trees just before they were shed as litterfall, and oven-dried at 40 ± 5 °C until they reach a constant weight (Gripp 2018).

About five grams of litter dry weight from each of these species were incubated in 5-mm mesh *litterbags* in Jurubatiba lagoon from May 21 to September 22, 2014. This design was replicated four times, and each replicate was arranged in one of our four experimental blocks, totaling 64 samples. Each block was situated on the lateral projections, along the longitudinal gradient of the lagoon (Figure 1). After 123 days, the period in which the less recalcitrant litter species showed ca. 30% mass loss, the litterbags were collected and taken to the laboratory. There, the remaining litter was washed under running water in 0.25 mm mesh sieves, and oven-dried at 40 ± 5 °C for 48 hours, and then weighed.

Small litter fragments as well as the macroinvertebrates retained in the sieves were later transferred to transilluminated trays and immediately sorted. Subsequently, macroinvertebrates were preserved at 80% alcohol to posterior identification to the lowest taxonomic level possible and functional feeding groups (FFG) classification, according to Mugnai *et al.* (2010) and Hamada *et al.* (2014). Small litter fragments retained in the sieves accounted for less than 2% of the final dry weight.

Chemical analyzes were carried out for the initial and the final (after 123 days) litter content. Carbon (C) were quantified on Shimadzu TOC-5000 (Wieder *et al.* 2009). Nitrogen (N) and phosphorus (P) were determined according to Graça *et al.* (2005). Calcium (Ca), Sodium (Na), Potassium (K), and Magnesium (Mg) were determined employing ion chromatography methods. Secondary and structural compounds, such as polyphenols, lignin, and cellulose were determined according to Bärlocher & Graça (2005) and Gessner *et al.* (2005). Decomposition was estimated as the percentage of litter mass loss (%ML), according to Graça *et al.* (2005).

Data analysis

To describe and characterize the benthic macroinvertebrates community, their abundance, richness, diversity (Simpson's index) and evenness were estimated in each sample. To evaluate possible differences in these metrics

among litter species, a Kruskal-Wallis test was performed. Significant differences among litter species concerning decomposition (mass loss rates) were tested by one-way ANOVA, and Tukey post-hoc tests were performed in order to identify specific differences. Litter mass loss data were transformed and checked for normality with the Kolmogorov–Smirnov test (Crawley 2007).

To evaluate the relationship between the benthic macroinvertebrates community composition and functional groups and litter quality, at initial and final conditions, Redundancy Analyses (RDA) were performed. The biotic data were previously transformed by the Hellinger function. Finally, an analysis of variance (ANOVA) was performed to evaluate the significance of the association between biotic and abiotic matrix from RDA data sets. Before the experiment, cellulose and Mg were strongly correlated with Lignin ($r_{\text{Pearson}} = -0.88$) and Ca ($r_{\text{Pearson}} = 0.90$), respectively (Table S.3), and were removed from the RDA analyses. Mg was also strongly correlated with Ca ($r_{\text{Pearson}} = 0.92$) and K ($r_{\text{Pearson}} = 0.82$) after the experiment (Table S.4), and was removed from the referred data set considered on RDA analyses too.

To evaluate how litter quality affects invertebrate community structure, we used multiple linear regressions. They were carried out to investigate the relationship between litter chemical trait values, at initial and final conditions, on invertebrate richness, abundance, diversity and evenness. Multiple regressions were calculated considering the “lm” function and the selected models were chosen using the “stepAIC” function, that performs backward model selection, from the package ‘MASS’, available in R. For each selected model, the variance inflation factor (VIF), estimated using the “vif” function from the package ‘car’, was used to investigate collinearity between explanatory predictors. All models' predictors presented VIF values < 2 , indicating that factors are not correlated and that models are valid. For all data set, outliers were identified using R's “mahalanobis” function and excluded from the models.

To characterize how litter quality was affected along decomposition process, we used chemical litter traits to evaluate how functional richness (FRic) changed before and

after the experiment. FRic indicates how much of the functional niche space is fulfilled by the species in a community, and is represented by a value of a convex hull volume (Villéger *et al.* 2008). Convex hull volume quantifies the smallest envelope enclosing the points in an n -dimensional space, being n the number of traits evaluated. In our case, FRic represents the volume of the functional space ‘occupied’ by litter species chemical traits, in the beginning and at the end of the experiment. FRic was estimated based on mean chemical trait values weighted by litter mass present at initial and final experimental conditions, considering the function “*dbFD*” from package *FD* in R v. 4.1.0 (R Core Team 2021).

RESULTS

Litter species selected for the experiment have a wide range of C and nutrients concentrations: C (49.9 – 60.5% dry mass), N (0.34 – 1.15%), P (0.023 – 0.076%), Ca (<0.001 - 0.339%), K (0.066 – 0.417%), Mg (0.006 – 0.372%), and Na (0.072 – 0.665%; Table S.1). They also present a considerable variability and contain large amounts of structural and secondary compounds, such as cellulose (19.7 – 35.8%), lignin (38.9 – 52.0%) and polyphenols (4.8 – 12.3%; Table S.1).

Litter mass loss varied between 14% and 30% after four months decomposing at Jurubatiba lagoon (Figure 2a). We found three significantly different groups concerning litter mass loss ($F_{1,15} = 5.687$, $p < 0.001$). The first group was composed by *A. pilosa*, *E. umbelliflora*, *I. maritima*, and *G. martiana*, which were the most refractory species, with a mass loss varying between 14% and 18% (Figure 2a). The second group was composed by *C. emarginata*, *C. hilariana*, *E. ovalifolium*, *H. perianthomega*, and *S. australis*, the most labile litter species, with mass loss above 28% (Figure 2a). Finally, there was a transition group between refractory and labile species, composed of the other litter species in the experiment, not significantly distinct from the others (Figure 2a).

Altogether, 1,353 macroinvertebrate individuals were collected, comprising 24 taxa. Tanypodinae n.i., Chironominae n.i. (both Diptera - Chironomidae) and *Heleobia australis* (Gastropoda - Hydrobiidae) were found associated

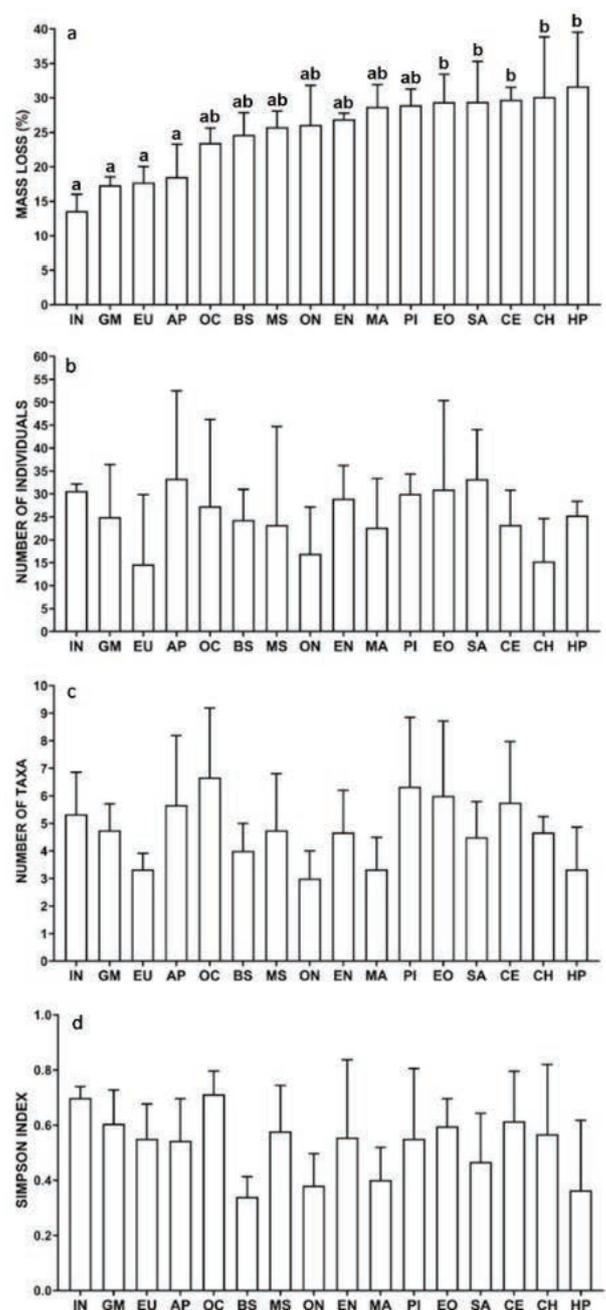


Figure 2. Litter mass loss (%) of *restinga* plant species after four months in Jurubatiba lagoon (a), and benthic macroinvertebrates’ (b) abundance, (c) richness, (d) diversity, and (e) evenness associated with litter species. Litter species are indicated by acronyms: *Amaioua pilosa* (AP), *Byrsonima sericea* (BS), *Clusia hilariana* (CH), *Cupania emarginata* (CE), *Erythroxylum ovalifolium* (EO), *Eugenia nitida* (EN), *Eugenia umbelliflora* (EU), *Gomidesia martiana* (GM), *Heisteria perianthomega* (HP), *Inga maritima* (IN), *Manilkara subsericea* (MS), *Maytenus obtusifolia* (MA), *Ocotea notata* (ON), *Ouratea cuspidata* (OC), *Protium icicariba* (PI), e *Senna australis* (SA). Error bars indicates standard deviations.

Table 1. Benthic macroinvertebrates associated with resting litter species at Jurubatiba lagoon, in September, 2014. Litter species acronyms are as described on methods and Figure 2 legend. Benthic functional feeding groups classified as: P – Predators; GC – Gathering collectors; FC – Filter collector; SH – Shredders; SC – Scrapers.

Taxa	Functional Group	AP	BS	CE	CH	EM	EO	EU	GM	HP	IN	MA	MS	OC	ON	PI	SA
Classe Insecta																	
Diptera																	
Chaoboridae	P																
Ceratopogoninae	P																
Chironominae n.i.	GC																
Tanypodinae n.i.	P																
Orthoclaadiinae n.i.	GC																
Ephemeroptera																	
<i>Caenis</i> sp.	GC																
<i>Brasilocaenis</i> sp.	GC																
<i>Campsurus</i> sp.	FC																
Trichoptera																	
<i>Nectopsyche</i> sp.	SH																
<i>Cynellus</i> sp.	FC																
<i>Oecetis</i> sp.	SH																
Odonata																	
<i>Acanthagrion</i> sp.	P																
Libellulidae n.i.	P																
Coleoptera n.i.	GC																
Classe Arachnida																	
Acari n.i.	P																
Annelida																	
Classe Clitellata																	
Hirudinea n.i.	P																
<i>Pristina</i> sp.	GC																
Oligochaeta n.i.	GC																
<i>Branchiura sowerbyi</i>	GC																

Table 1. Continues on next page...

Table 1. ...continued

Taxa	Functional Group	AP	BS	CE	CH	EM	EO	EU	GM	HP	IN	MA	MS	OC	ON	PI	SA
<i>Haemonais</i> sp.	GC																
<i>Nais variabilis</i>	GC																
Subphylum Crustacea																	
Ostracoda n.i.	FC																
<i>Macrobriachium</i> sp.	P																
Kalliapseudidae n.i.	GC																
Filo Mollusca																	
<i>Heleobia australis</i>	SC																
Bivalvia n.i.	FC																
<i>Eupera</i> sp.	FC																
Ancilidae n.i.	SC																
<i>Antillorbis</i> sp.	SC																
Filo Nemertea																	
Nemertea n.i.	P																

with all litter species (Table 1), and these last two taxa were the dominant in the experiment, corresponding to 1,046 individuals recorded. Nemertea n.i. (ribbon worms), Tanypodinae n.i., Ostracoda n.i. (Crustacea) and *Cyrnellus* sp. (Trichoptera - Insecta) summed 220 individuals. Other groups were less abundant, accounting for less than 10 individuals each, and were considered rare taxa. Gathering-collectors and predators were the most abundant functional feeding groups (11 and 9 taxa each, which accounted to 30% and 36% of the total number of organisms, respectively), followed by filtering-collectors (5 taxa - 17%), scrapers (3 taxa - 10%), and shredders (2 taxa - 7%).

The abundance of benthic invertebrates ranged from 14 ± 11 to 38 ± 9 individuals on litter species (Figure 2b), while the invertebrates richness ranged from 2.9 ± 0.5 to 7.4 ± 0.3 taxa (Figure 2c). The diversity, estimated by Simpson's index, ranged from 0.33 ± 0.05 to 0.70 ± 0.05 (Figure 2d), and Simpson's evenness ranged from 0.63 ± 0.68 to 0.69 ± 0.23 (Figure 2e). The Kruskal-Wallis test for each of these metrics showed that there is no significant difference on macroinvertebrates' richness, abundance, diversity and evenness among litter species ($H_{(15)} = 16.77$, $p = 0.299$; $H_{(15)} = 10.97$, $p = 0.753$; $H_{(15)} = 19.4$, $p = 0.196$; and $H_{(15)} = 12.84$, $p = 0.615$, respectively).

The selected model explaining invertebrate richness indicated it is negatively associated to initial lignin, C and Na concentrations, and positively to initial and final K concentration (Table 2). But the contribution of initial litter traits was much larger than that of final conditions, accounting for about 25.3% and 1.9% of richness variability, respectively (Table 2 and 3, respectively). These same effects of initial lignin, C and K concentrations on richness were registered for invertebrates diversity, with an adjusted R² value equal to 0.21 (Table 2). Initial lignin concentrations were the single best predictor of invertebrate richness and diversity, accounting for more than 50% of the variance explained by the selected models (Table 2). Final K and N concentrations were also positively related to invertebrates abundance, but explained only 11.2% of its variability (Table 3). No initial or final chemical traits predicted invertebrates evenness (Table 2 and 3).

The relationship between litter quality and

Table 2. Results of multiple regression analysis for predicting initial litter quality effects on invertebrate structure (richness, abundance, diversity and evenness). Only selected variables are depicted in the table. R^2 (%) indicates the contribution (and percent contribution) of each selected variable to model R^2 . AIC indicates the Akaike's Information Criterion value for the selected model, while Δ AIC indicates the difference between the selected model from the model containing all chemical traits.

Variable	Coefficient	Std Error	t value	p value	R^2 (%)	AIC	Δ AIC
Model - Richness							
<i>($R^2 = 0.311$; Adj $R^2 = 0.253$; $F(4, 48) = 5.406$; $p = 0.0011$)</i>						64.68	58.32
C	-0.201	0.089	-2.25	0.029	2.3 (7.37)		
Na	-2.768	1.673	-1.654	0.105	3.3 (10.68)		
K	5.422	2.189	2.477	0.017	5.1 (16.3)		
Lignin	-0.250	0.066	-3.767	< 0.001	20.4 (65.64)		
Intercept	26.575	6.090	4.364	< 0.001			
Model - Abundance							
<i>($R^2 = 0.054$; Adj $R^2 = 0.035$; $F(1, 51) = 2.901$; $p = 0.095$)</i>						274.94	266.54
Na	-19.24	11.29	-1.703	0.0946	5.38 (100)		
Intercept	9.6249	0.5874	16.387	< 0.001			
Model - Diversity							
<i>($R^2 = 0.253$; Adj $R^2 = 0.207$; $F(3, 49) = 5.537$; $p = 0.002$)</i>						-183.82	-192.87
C	-0.019	0.008	-2.255	0.029	3.52 (13.9)		
K	0.604	0.200	3.021	0.004	8.97 (35.4)		
Lignin	-0.018	0.006	-2.902	0.006	12.8 (50.7)		
Intercept	2.218	0.545	4.069	< 0.001			
Model - Evenness							
<i>($R^2 = 0.0822$; Adj $R^2 = 0.045$; $F(2, 50) = 2.238$; $p = 0.117$)</i>						-176.69	-187.87
Na	0.267	0.159	1.685	0.098	3.24 (39.3)		
Lignin	0.011	0.006	1.647	0.106	4.98 (60.6)		
Intercept	-0.011	0.311	-0.037	0.971			

benthic invertebrates community, assessed by RDA analyses (Figure 3a-b), indicates that most taxa are not associated with litter chemical traits. Only the most abundant groups (Chironominae n.i. and *H. australis*) tend to be positively associated with litter C and K, and N and Na, respectively, if considering the initial litter characterization (Figure 3a). If final characterization is considered, their association are more related to N, P and cellulose (Chironominae n.i.) and to C and K (*H. australis*, Figure 3b). However, the eigenvalues of constrained axes 1 and 2 of the RDA analysis for taxa distribution corresponded to 74.3% and 14.7%, and to 77.5% and 17.9% for initial and final experimental data sets, respectively (Figure 3a-b). But constrained axes were not significant and contributed to less than 16% of the total model variance in both cases (Table 4). On the other hand,

the first unconstrained axis (PC1) contributed to 71.3% and 70.7% out of 86.1% and 84.6% of the total model variance, for initial and final experimental data sets, respectively, which is much more than the variance explained by all constrained explanatory variables together, on both data sets. Similar trends also hold for the most dominant benthic taxa (Supplementary Figure S.1 and S.2, and Table S.2).

Concerning FFGs, some segregation tended to occur only for gathering collectors associated with Ca, and scrapers associated with N and polyphenols according to initial characterization, or to N, and P, polyphenols and lignin, according to final characterization, respectively (Figure 3c-d). However, constrained axes were also not significant and accounted for only a small fraction of total model variance, in both cases (Table 4).

Table 3. Results of multiple regression analysis for predicting final litter quality effects on invertebrate structure (richness, abundance, diversity and evenness). Only selected variables are depicted in the table. R^2 (%) indicates the contribution (and percent contribution) of each selected variable to model R^2 . AIC indicates the Akaike's Information Criterion value for the selected model, while Δ AIC indicates the difference between the selected model from the model containing all chemical traits.

Variable	Coefficient	Std Error	t value	p value	R^2 (%)	AIC	Δ AIC
Model - Richness							
<i>($R^2 = 0.039$; Adj $R^2 = 0.019$; $F(1, 48) = 1.96$; $p = 0.168$)</i>						80.1	66.82
K	26.881	19.200	1.400	0.168	3.9 (100)		
Intercept	4.388	0.478	9.173	< 0.001			
Model - Abundance							
<i>($R^2 = 0.1483$; Adj $R^2 = 0.112$; $F(2, 47) = 4.09$; $p = 0.023$)</i>						261.79	250.63
N	5.958	3.426	1.739	0.0885	5.01 (33.8)		
K	278.383	119.594	2.328	0.0243	9.82 (66.2)		
Intercept	12.04	5.627	2.14	0.0376			
Model - Diversity							
<i>($R^2 = 0.0$)</i>						-162.23	-173.01
Intercept	0.547	0.025	22.03	< 0.001			
Model - Evenness							
<i>($R^2 = 0.093$; Adj $R^2 = 0.074$; $F(1, 48) = 4.941$; $p = 0.031$)</i>						-168.81	-178.86
K	-3.658	1.646	-2.223	0.031	9.32 (100)		
Intercept	0.624	0.041	15.228	< 0.001			

In all these analyses, neither RDA models nor independent constrained axes were statistically significant related to benthic community or FFGs distribution (data not shown).

FRic, a proxy for litter quality based on chemical trait values, reduced from 0.034 at the beginning to 0.014 at the end of the experiment, indicating that litter species in decomposition tended to have a more similar quality at the end of the experiment (Figure 4).

DISCUSSION

To our knowledge, this is the first study that evaluated *restinga* litter quality and benthic invertebrates associations in coastal aquatic ecosystems to date. On our experiment, *restinga* leaf litter species degradability reached not more than 30% mass loss after 123 days at Jurubatiba lagoon. It indicates that the decomposition process was on the initial phase for the species considered, even after all that time. Such rates are considerably lower compared to the decomposition of terrestrial or riparian

vegetation on other tropical lotic (Ferreira *et al.* 2012) or lentic aquatic ecosystems (Anbalagan *et al.* 2014), considering a similar time interval, but are comparable to decay rates on other tropical ecosystems which undergoes low nutrient soil conditions, such as peat swamp forests (Yule & Gomez 2009). Litter decomposition in lentic environments tends to be considerably slower compared to lotic ones, because of the limited physical action of water flux, an important factor for litter degradation (Hepp *et al.* 2008). *Restinga* vegetation also usually produces a low-quality litter, that is among the most refractory substrates for decomposition (Gripp *et al.* 2018, Villela *et al.* 2020), and take considerably more time to be degraded than litter from other neotropical terrestrial ecosystems (Castanho & Oliveira 2008).

Despite a considerable variability on initial litter quality, the segregation of litter species along chemical functional space tended to reduce after four months decomposing at Jurubatiba lagoon (Figure 4). These results indicate that litter quality differences reduced and litter species became more similar in chemical quality at the end of the

experiment. This convergence in quality along decomposition has been widely described in the literature for tropical terrestrial ecosystems (Parsons *et al.* 2014, Sarker *et al.* 2018) and may be associated with the fact that most litter species are at the initial stages of the decomposition process. In this phase, biotic drivers, such as decomposers and detritivores activity tend to be more important to this quality convergence due to organisms selection for labile substrates or labile components within substrates (García-Palacios *et al.* 2016). This preferential feeding by detritivores and associated organisms possibly makes these substrates become more similar along initial

phase of decomposition, reducing litter species chemical functional space.

Based on this and previous findings (Gonçalves Jr. *et al.* 2004), we would expect an association between litter quality and invertebrates community structure and feeding groups at Jurubatiba lagoon. We hypothesized that litter species with higher amounts of organic matter and nutrients would present a higher diversity of taxa. In fact, the initial litter K concentrations improved invertebrate richness and diversity, whereas initial lignin and C availability reduced both. These results are particularly interesting because C and lignin are extremely available

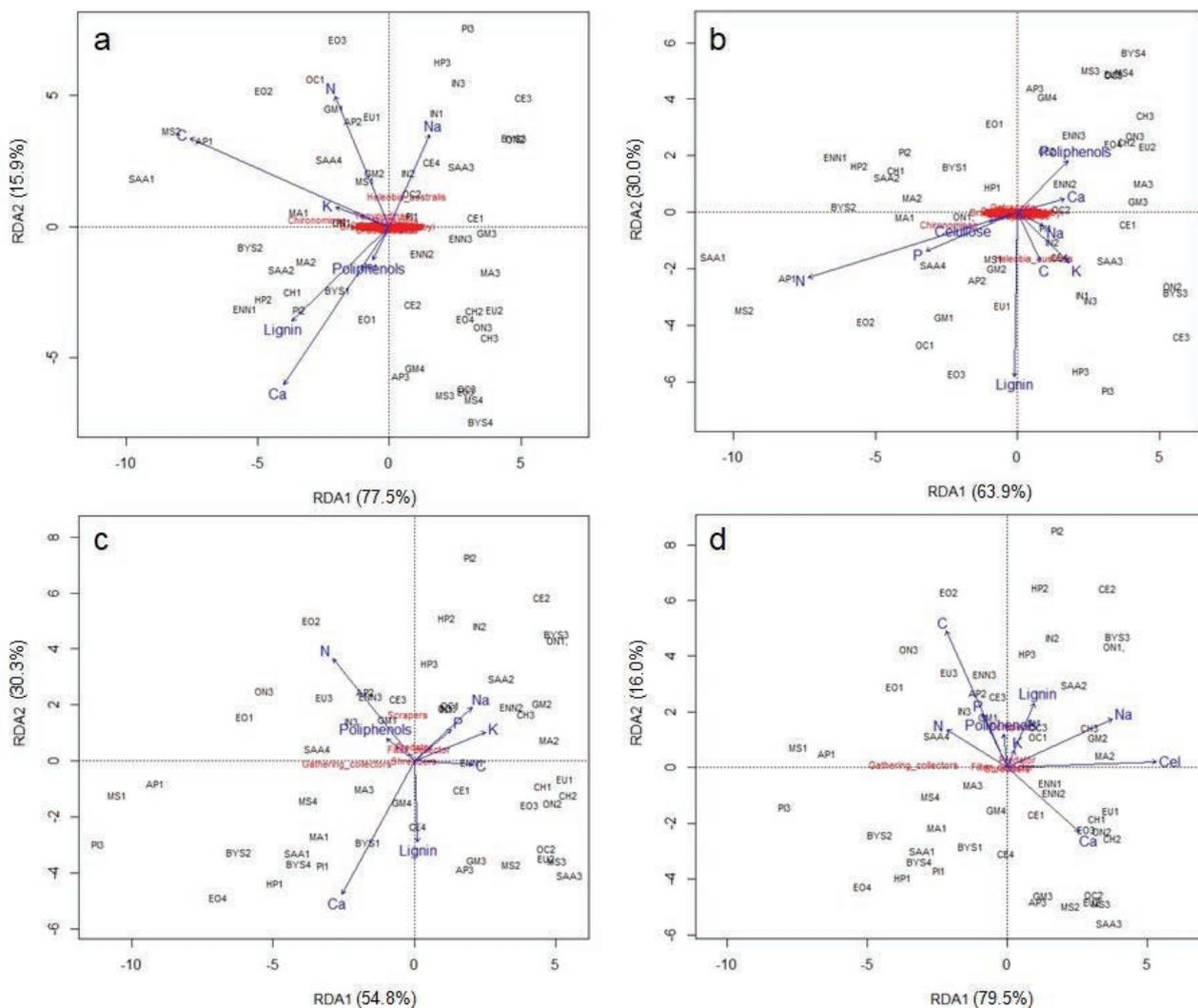


Figure 3. Redundancy analysis (RDA) evaluating the relationship between litter quality and benthic macroinvertebrates community (a-b) and functional feeding groups (FFGs) distribution (c-d), considering initial (a, c) and final (b, d; after 123 days decomposing) chemical characteristics of *restinga* litter species. Chemical variables considered on the analyses were C (Carbon), N (Nitrogen), P (Phosphorus), Ca (Calcium), K (Potassium), Na (Sodium), Lignin, Poliphenols and Celulose (Cel; only at Figures b and d). Litter species acronyms are as described on methods and Figure 2 legend.

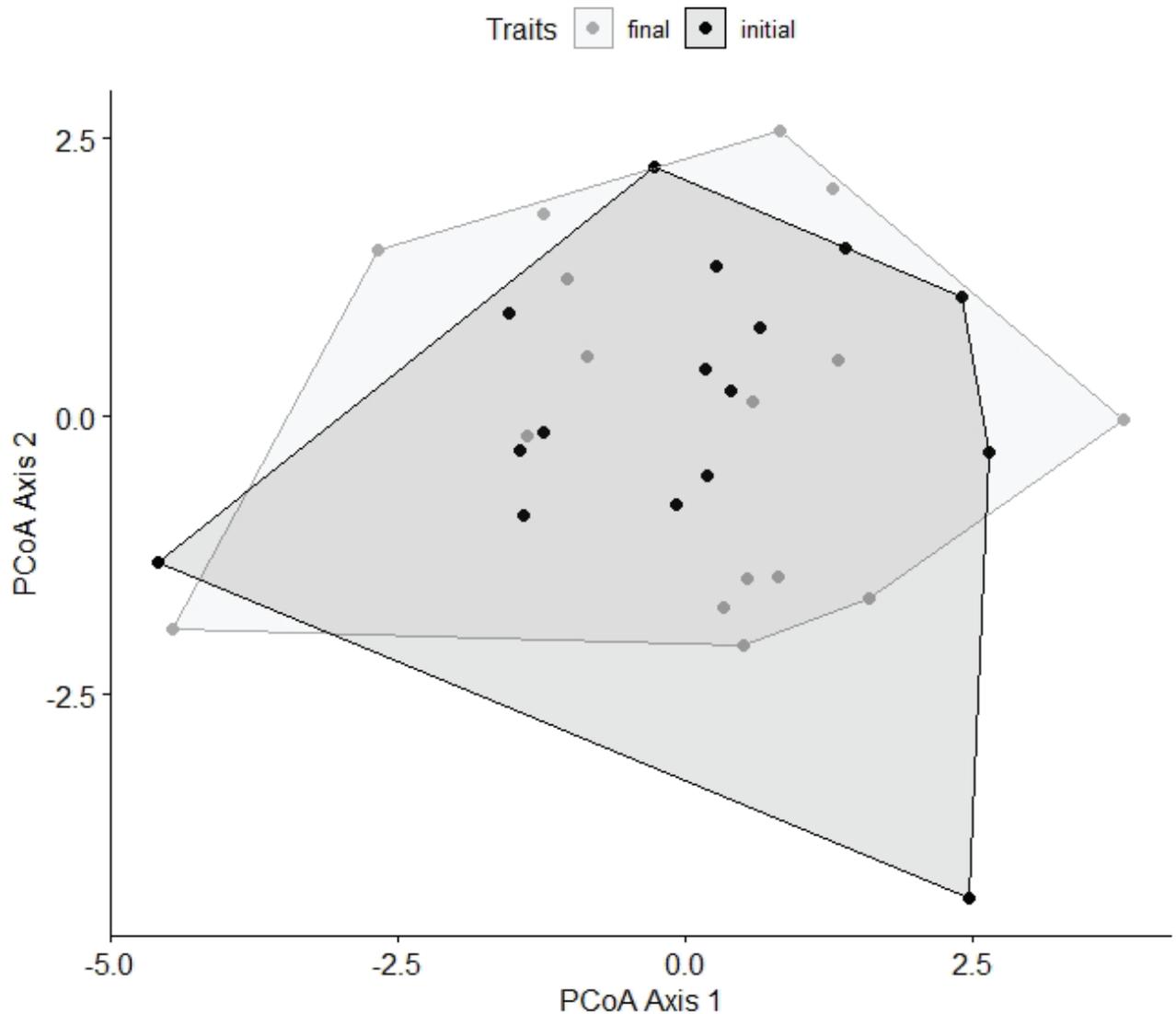


Figure 4. Litter functional space (convex hull volume) based on chemical trait values weighted by litter mass present at initial and final experimental conditions.

at most *restinga* litter species and drastically affect their decay rates (Gripp 2018, Castanho & Oliveira 2008). Lignin constitutes a defense mechanism of terrestrial plants, and high lignin contents makes leaves less palatable to herbivorous (on green leaves) and detritivores (on senescent leaves) (Wainhouse *et al.* 1990, Pooter *et al.* 2004). The preference for poor-C and lignin detritus is a ubiquitous characteristic of detritivore communities, both in terrestrial and aquatic *restinga* ecosystems (Gripp 2018). On the other hand, Potassium is a limiting nutrient for decomposition in tropical ecosystems, and its availability improve microbial colonization and attract more and distinct invertebrates (Chellaiah & Yule 2018).

We also hypothesized that litter containing

higher amounts of organic matter and nutrients would present a greater amount of collector-filterer and collector-gatherers, whereas litter with higher amounts of lignin and cellulose would present a greater amount of scrapers and shredders. However, these hypotheses could not be fully evaluated because most species registered on our experiment had only a few organisms, and collector-filterer and shredders were extremely rare. For example, we registered only five individuals belonging to two shredder species on our study site, what reinforces the low importance of shredders on decomposition process at coastal lagoons (Gonçalves Jr. *et al.* 2004) and corroborates the hypothesis that in tropical aquatic ecosystems, the decomposition is mostly driven by microbial activity and not by the action of shredders (Irons

Table 4. Model parameters of ANOVA, for the biotic (constrained axes) and abiotic matrices considered on the RDA analysis, for benthic community composition and feeding functional groups (FFGs). DF = degrees of freedom; Variance = total variance explained by each component of the model; F = F value; and p = significance level.

Model	DF	Variance	F	p
RDA Composition - Initial				
Constrained	8	21.778	0.9562	0.509
Residual	45	128.116		
RDA Composition - Final				
Constrained	9	16.299	0.5964	0.903
Residual	44	133.595		
RDA FFGs - Initial				
Constrained	9	22.616	0.8053	0.666
Residual	44	137.3		
RDA FFGs - Final				
Constrained	9	24.716	0.8937	0.592
Residual	44	135.2		

et al. 1994, Gonçalves Jr. *et al.* 2004, Ferreira *et al.* 2012). But concerning the dominant taxa (*Heleobia australis* and Chironominae n.i.), they tended to be positively associated mainly with litter C, nutrients (K, N, Na and/or P), lignin and/or cellulose concentrations, depending on the initial or final litter chemical characterization. Those same litter chemical traits are the main characteristics explaining the distribution of collector-gatherers and scrapers at Jurubatiba lagoon, because Chironominae and *H. australis* are representative organisms of these respective groups. Both *H. australis* and Chironomidae have been broadly recorded associated with organic substrates on Restinga de Jurubatiba coastal lagoons (Gonçalves Jr. *et al.* 2004, Figueiredo-Barros *et al.* 2006).

The Chironomidae family is often the most abundant group of macroinvertebrates in both lotic and lentic environments of most neotropical aquatic ecosystems, including the study area (Gonçalves Jr. *et al.* 2004, Figueiredo-Barros *et al.* 2006). Their association to initial C and K and/or final N, P and cellulose concentrations corroborates our predictions about the association of collectors-gatherers with litter quality. Collectors-gatherers distribution tends to be affected by organic matter and nutrients since they get most of their food resources from microbial community that colonizes fine particulate organic matter (FPOM) (König *et al.*

2014). But although Chironomidae is generally placed in the gathering-collectors functional group, studies show that individuals in this group also fragment and even scrape leaf litter (Moretti *et al.* 2007). *Heleobia australis* is common on tropical coastal lagoons and tends to be dominant, even representing up to 80% of the benthic fauna in these systems (Figueiredo-Barros *et al.* 2006). Their association to initial N and Na and/or final C and K concentrations are probably more related to the effects of nutrients availability on the facilitation of periphytic colonization in these ecosystems (Brum & Esteves 2001a, b) than to stability conferred by the low breakdown rate due to the high C concentration (Gonçalves Jr. *et al.* 2004). Despite these trends, the RDA analyses indicated that there was no significant association between benthic invertebrates composition nor FFG distribution and litter quality, what suggest that litter chemical variables do not contribute considerably to explain the distribution of benthic taxa nor FFG on Jurubatiba lagoon.

Despite the great variability on *restinga* litter quality and breakdown rates at Jurubatiba lagoon, the benthic community composition and FFG seems to be randomly distributed among litter substrates, or may be better explained by some other aspect(s) different from those considered in this study. For example, habitat complexity provided by substrate three-dimensionality can determine the composition of local communities,

such that diversity should increase on more complex sites, due to the availability of shelter and refuge against predators, protection against physical disturbances, which support survival, recovery, and persistence of the organisms (Dias *et al.* 2017). It is also well documented that litter colonization by macroinvertebrates is a dynamic and continuous process, and substrate exposure time and sampling intervals are relevant aspects for benthic and substrate associations, sometimes, even more important than other factors, such as litter species properties (Silveira *et al.* 2006). Furthermore, despite allochthonous litter may be an abundant C source for Jurubatiba lagoon, macrophytes derived litter is a greater and much more common substrate available for benthic invertebrates at this ecosystem (Marinho *et al.* 2010), what may restrict strong association patterns between invertebrates and *restinga* litter too. Finally, our results reinforce that invertebrates distribution is primarily influenced by hydrodynamic (lotic or lentic), and general physical (consolidated or unconsolidated) and chemical (organic or inorganic) aspects of the substrate, regardless of its chemical quality (Silveira *et al.* 2006).

Therefore, we may conclude that litter quality affect benthic invertebrates' richness and diversity at Jurubatiba lagoon, but not community composition and FFG distribution. However, we may recognize that the absence of clear trends on the association between benthic composition and FFG with litter quality may be because the community was only sampled once (after four months) and litter structural aspects were not considered in this study. We may also not ignore sampling artefacts and the limitations associated to the use of litterbags on benthic invertebrates and litter colonization studies. For example, it is not uncommon that invertebrates select artificial structures (such as litterbags) as shelter or food source, preferably if it contains organic material (Gonçalves Jr. *et al.* 2012, Dangles *et al.* 2001). Also, the litterbag mesh-size considered in our study, although appropriate to allow the colonization of organisms from a great array of body-sizes, may also affect invertebrates preference and habitat selection, facilitating the colonization of taxa that becomes dominant, and limiting others (*i.e.* macroconsumers; Moulton *et al.* 2019). Future

studies evaluating the relationship between litter traits and colonizers may also consider temporal variations on litter characteristics and benthic community samplings to better elucidate their relationship.

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