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Plant species is more important than urbanization for leaf litter breakdown in a semi-arid river

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ABSTRACT

Plant species is more important than urbanization for leaf litter breakdown in a semi-arid river.

Leaf litter breakdown plays a crucial role in detrital-based ecosystems, and understanding the factors that influence this process is essential, particularly in data-poor semi-arid riparian zones. This study investigated the influence of land use (upstream and downstream of an urban area) on the decomposition of leaf material from common species in the area (*Erythrina velutina*, *Anacardium occidentale*, *Tabebuia aurea*, *Croton sonderianus*, and *Hymenaea courbaril*). Litter bags (single-species, fine and coarse mesh) containing senescent leaves were used to evaluate invertebrate density and richness, shredder and scraper abundance, and litter mass loss after oven drying. Leaf litter with high nutrient content and a low C:N ratio decomposed significantly faster than more recalcitrant litter, likely due to enhanced microbial and invertebrate colonization. Also, litter breakdown was higher when invertebrates had access to leaf material. The effect of invertebrate exclusion was pronounced for high-quality litter, where invertebrate scrapers (Thiaridae, Lymnaeidae, and Planorbiidae) seemed to play a central role in litter fragmentation. Urbanization significantly influenced breakdown rates, but its effects were contingent on litter quality and invertebrate access. Litter breakdown was higher at location under the influence of urbanization, likely due to increased nutrient availability and microbial activity. Ultimately, strong interactions were observed between litter quality, invertebrate access, and urbanization, with the urban effect being most pronounced for high-quality litter, while invertebrate-mediated effects were also stronger for high-quality litter, creating a complex and dynamic ecological condition in the studied semi-arid river.

KEY WORDS: microbial decomposition; shredders and scrapers; leaf decomposition; context dependent, diversity effects.

RESUMO

Espécies vegetais são mais importantes que a urbanização para a decomposição de serapilheira em um rio semiárido.

*LA decomposição da serapilheira desempenha um papel crucial nos processos ecossistêmicos, e entender os fatores que influenciam esse processo é essencial, particularmente em zonas riparias em região semiáridas. Investigamos a influência de cinco espécies de plantas (*Erythrina velutina*,* Anacardium occidentale*,* Tabebuia aurea*,* Croton sonderianus *e* Hymenaea courbaril*) e tipos de uso do solo (a montante e a jusante de uma área urbana) na perda de massa de serapilheira. Utilizamos sacos de serapilheira contendo folhas senescentes para avaliar a densidade e a riqueza de invertebrados, abundância de trituradores e raspadores e medirmos a perda de massa foliar após a secagem em estufa. A serapilheira com alto teor de nutrientes e baixa razão C:N decompôs-se significativamente mais rápido do que a serapilheira mais recalcitrante, provavelmente devido ao aumento da colonização microbiana e de invertebrados. Além disso, a decomposição foi maior quando os invertebrados tiveram acesso ao material foliar. O efeito da exclusão de invertebrados foi mais pronunciado na serapilheira de alta qualidade, onde raspadores (Thiaridae, Lymnaeidae e Planorbidae) desempenharam um papel central na fragmentação da serapilheira. A urbanização influenciou significativamente as taxas de decomposição, mas seus efeitos dependeram da qualidade da serapilheira e da presença de invertebrados. A decomposição foi maior nos locais urbanos, provavelmente devido ao aumento da disponibilidade de nutrientes e da atividade microbiana. No entanto, a urbanização também levou à homogeneização das assembleias de invertebrados, com a dominância de Thiaridae e Chironomidae, substituindo táxons mais sensíveis, como Leptophlebiidae. Isso sugere que, embora a eutrofização induzida pela urbanização possa acelerar a decomposição microbiana, também pode reduzir a diversidade da fauna decompositora. Por fim, observamos fortes interações entre a qualidade da serapilheira, a presença de invertebrados e a urbanização, criando condições ecológicas complexas e dinâmicas em riachos de ambientes semiáridos.*

PALAVRAS-CHAVE: *decomposição microbiana; fragmentadores e raspadores; decomposição foliar; contexto dependente, efeitos de diversidade.*

INTRODUCTION

Leaf litter breakdown is a fundamental process in freshwater ecosystems as it regulates nutrient cycling and energy transfer between terrestrial and aquatic environments (Tank et al., 2010; Graça et al., 2015). This process is mainly influenced by leaf litter quality (Arias-Real et al., 2018; Sena et al., 2020), microbial (Medeiros et al., 2015; Barreto et al., 2023) and invertebrate decomposers (Graça, 2001; Rezende et al., 2018), and environmental conditions such as water chemistry and flow dynamics (Ferreira et al., 2021; Brosed et al., 2022). Understanding the relative importance of these factors across different ecological contexts is essential for predicting organic matter breakdown and its broader implications for ecosystem functioning (Graça et al., 2015; Chauvet et al., 2016; Rezende et al., 2021; Borges et al., 2024).

Plant species influences litter breakdown rates through differences in leaf chemical composition and structural traits (Cornwell et al., 2008; Cararo & Rezende, 2024). Leaves with high nitrogen and phosphorus concentrations decompose more rapidly than those with higher lignin, cellulose, and secondary compounds (Li et al., 2009; Cararo et al., 2023), which inhibit microbial and invertebrate colonization (Graça et al., 2015; Rezende et al., 2019). In semi-arid regions, where riparian vegetation is adapted to drought-prone conditions and exhibits naturally low productivity (Barbosa et al., 2012), leaf litter often exhibits high carbon-to-nitrogen (C:N) ratios and thick cuticles with xeromorphic characteristics (Barbosa et al., 2012; Baradwal et al., 2023), which can slow breakdown rates (Rezende et al., 2018). However, when nutrient-rich litter is introduced (e.g., by urbanization land uses), breakdown rates may increase due to enhanced microbial and invertebrate activity (Tank et al., 2010; Cararo et al., 2023).

While the effects of plant species on litter breakdown have been well-documented in temperate and tropical streams (Boyero et al., 2021), they remain poorly understood for semi-arid rivers (Abelho, 2001; Ferreira et al., 2023). Semi-arid rivers naturally show low nutrient availability and intermittent flow regimes may amplify plant species-specific differences and decomposer community dynamics (Barbosa et al., 2012; Ferreira et al., 2023). In semi-arid environments, where shredders are often scarce, scraper-grazers such as gastropods may dominate the litter breakdown process by consuming biofilms and indirectly fragmenting litter (Rezende et al., 2018). Whether invertebrate exclusion significantly reduces mass loss in semi-arid rivers remains unclear, although it would be expected (Rezende et al., 2019), as microbial decomposition may be the primary pathway in these systems (Rezende et al., 2018; Ferreira et al., 2023).

Urbanization alters river conditions by increasing nutrient loads, modifying hydrology, and degrading water quality (Keinath et al., 2023). Urban streams typically exhibit elevated electrical conductivity, turbidity, and water temperature, coupled with lower dissolved oxygen due to organic pollution (Montebelo et al., 2002; Booth et al., 2004; Tagliaferro et al., 2022). These changes can accelerate microbial decomposition (Quintão et al., 2013; Medeiros et al., 2015) while simultaneously reducing invertebrate diversity (Classen-Rodríguez et al., 2019), particularly among sensitive taxa such as shredders (Del Arco et al., 2012; Akamagwuna et al., 2022). In semi-arid rivers, where water scarcity already imposes physiological stress on aquatic communities (Barbosa et al., 2012), anthropogenic disturbances may further shift litter breakdown pathways (Rezende et al., 2018). Although leaf litter breakdown has been shown to respond to urbanization in temperate and tropical streams (Classen-Rodríguez et al., 2019; Tagliaferro et al., 2022), its effects in Neotropical semi-arid ecosystems remain poorly quantified (Ferreira et al., 2023), particularly concerning interactions between urbanization, litter quality, and invertebrate-mediated breakdown.

Despite increasing recognition of these factors, few studies have evaluated their combined effects on litter breakdown in semi-arid rivers, where naturally low water availability may modify expected patterns. To address this knowledge gap, this study examined how urbanization, leaf species identity and invertebrate exclusion (via mesh size) influence litter breakdown rates and associated invertebrate communities in a Neotropical semi-arid river. Thus, the present study aimed to: i) assess how urbanization and the presence of leaves from five plant species (*Erythrina velutina*, *Anacardium occidentale*, *Tabebuia aurea*, *Croton sonderianus*, and *Hymenaea courbaril*) affect leaf litter mass loss and invertebrate community composition; and ii) determine which factor is most influential in driving the leaf litter breakdown process (by mass loss) in a semi-arid river.

We hypothesized that: i) the location under the influence of urbanization will exhibit higher litter breakdown rates than he location not under the influence of urbanization due to increased nutrient availability, but this effect may be counteracted by reduced invertebrate shredder diversity in degraded habitats; ii) litter quality is the primary driver of litter breakdown rates, with nutrient-rich, low-C:N litter decomposing more rapidly than recalcitrant litter due to enhanced microbial and invertebrate colonization; iii) invertebrate presence (in coarse-mesh bags) will exhibit higher mass loss than invertebrate absence, particularly for the highest abundance of invertebrate scrapers, as microbial decomposition alone is expected to be slower; and iv) interactions between factors will emerge, with urbanization accelerating litter breakdown primarily for high-quality litter, while invertebrate-mediated effects will be more pronounced for palatable litter types.

MATERIALS AND METHODS

Study Area

The study was conducted at six sections of the Apodi-Mossoró River, with three located upstream (spaced at 200-meter intervals) and three downstream (spaced at 200-meter intervals) of Mossoró City, Northeast Brazil (Fig. 1). Thus, the three sites for each location (upstream and downstream) were used as replicates. Mossoró, located in the state of Rio Grande do Norte, is the second most populous municipality in the state, covering an area of approximately 2110 km² with an estimated population of over 300 thousand inhabitants at a density of 126 inhabitants/km² (Silva, 2022). The region is characterized by an average annual rainfall between 550 and 800 mm, an aridity index below 0.5 and an annual probability of drought of over 60% (Barbosa et al., 2012).

The Apodi-Mossoró River is one of the main watercourses in the semi-arid region of Northeast Brazil, extending approximately 210 km and draining a 14 276 km² basin in the state of Rio Grande do Norte (30% of the area of the state). Land use along the watershed is predominantly agricultural, with extensive irrigated fruit farming and pasturelands, alongside urban and industrial expansion near the urban center of the municipality of Mossoró (Silva, 2022). The river's width typically ranges 10 – 50 meters. The substrate is primarily sand and clay, with localized deposits of organic material (Silva, 2022). The Apodi-Mos-

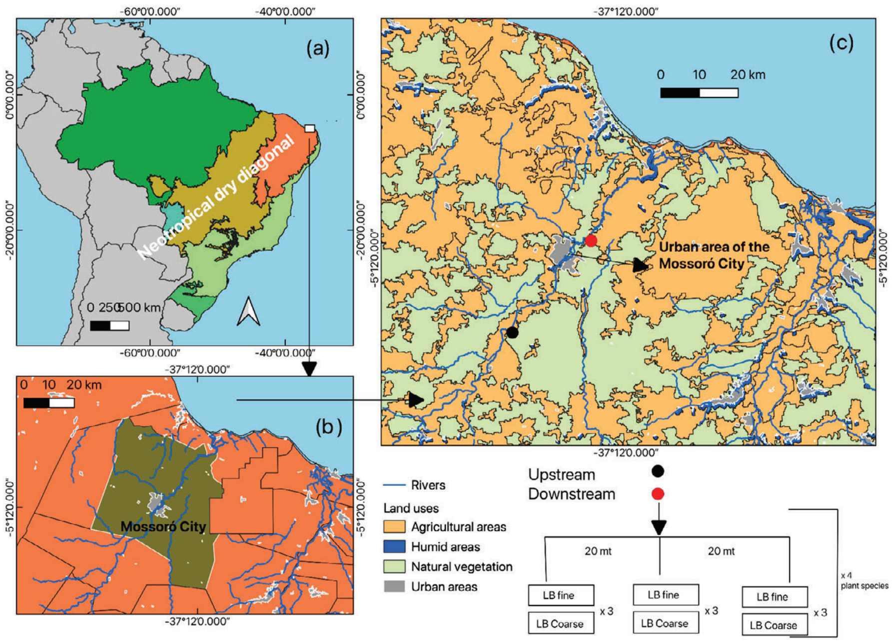

Figure 1. Geographic location of the study sampling area in Brazil (a), the city of Mossoró (b), and urban center of Mossoró (c). Sampling design at each collection point. LB = Litter Bag. *Localização geográfica da área de amostragem do estudo no Brasil (a), na cidade de Mossoró (b) e no centro urbano de Mossoró (c). Desenho amostral em cada ponto de coleta. LB = Litter Bag.*

soró River was perennial but became intermittent with the construction of dams in the urbanized section, within the urban center of the municipality of limits of Mossoró. For more details see also Silva (2022).

The upstream sites are situated approximately 20 km from the city (closest site: 5°24'45.0"S; 37°29'40.6"W) and are characterized by relatively well-preserved environmental conditions (Fig. 1). These sites exhibit approximately 60% canopy cover, primarily composed of riparian vegetation remnants interspersed with agricultural lands. The river in this section has an average width of 8 meters and a depth of approximately 2 meters, with a sandy and clayey substrate and moderate organic matter deposition. Human influence is limited, with low population density and minimal direct anthropogenic impacts, apart from small-scale agriculture and livestock activities.

In contrast, the downstream sites are located approximately 10 km from the city (closest site: 5°09'12.8"S; 37°17'18.9"W) and exhibit pronounced anthropogenic degradation (Fig. 1). These sites have complete canopy openness (~100%), with no significant riparian vegetation, exposing the river to direct sunlight and increasing thermal fluctuations. The river's width is increased, to an average of 20 meters, with depths reaching 5 meters. The substrate is primarily composed of fine sediments, with localized accumulations of organic debris and pollutant loads from urban runoff. These sites are significantly impacted by domestic and industrial effluents, with frequent occurrences of solid waste, including plastic materials and construction debris, along the riverbanks. The presence of wastewater discharge points further exacerbates water quality degradation.

Leaf Litter and Water Physicochemical Characteristics

Senescent leaves of the species *Erythrina velutina* (mulungu tree), *Anacardium occidentale* (cashew tree), *Tabebuia aurea* (yellow ipê tree), *Croton sonderianus* (croton shrubs), and *Hymenaea courbaril* (jatobá tree), were collected using 1-m² nets with a mesh size of 0.5 mm, positioned 1 m above the ground in riparian vegetation of upstream sites. The leaves were air-dried and stored in plastic bags until the start of the experiment. Leaves were then dried at room temperature until a constant weight was achieved. These species were chosen to represent the predominant vegetation found in these riparian ecosystems and all are native to the Caatinga in the São Francisco Valley.

The initial chemical composition of leaf litter was evaluated by analyzing carbon (C), nitrogen (N), and total protein concentrations (in %), and the C:N ratio. Five-leaf pools, one for each species, were randomly collected, washed with distilled water, air-dried, and pulverized for subsequent chemical analyses. Total C concentration was determined using the Combustion Method (Flindt et al., 2020), while N concentration was determined using the Kjeldahl method as described by Cantarella and Trivelin (2001). Total protein concentration was determined using the spectrophotometric analysis described by Baerlocher (Baerlocher, 2020).

The physical and chemical characteristics of the water at each sampling site were measured at the beginning and end of the experiment, in the morning. Electrical conductivity, pH, Nephelometric Turbidity Units (NTU), and dissolved oxygen saturation were measured using a Horiba multiparameter probe, while water temperature was continuously monitored using data loggers (reference) attached to each kit.

Leaf Litter Decomposition

Litter bags were prepared by placing 1.25 g of air-dried leaf litter of each species in separate litter bags with mesh openings of 0.5 mm (fine mesh to exclude invertebrates) and 10 mm (coarse mesh). One litter bag of each type (coarse and fine) and plant species (five species) were distributed at each of the three upstream and downstream sites (2 locations x 3 sites x 5 plant species x 2 mesh types = 60 litter bags). The bags were tied and wholly submerged along the river margins at approximately 30 cm depth between September and October (dry season) of 2019. After 30 days, the samples were retrieved and placed individually in plastic bags and transported in thermal containers to the laboratory, where they were stored in a refrigerator (4°C) until processing (a few minutes or hours until processing).

Leaf litter from all coarse mesh individual litter bags was washed with distilled water on top of a 120-µm mesh sieve in the laboratory. The invertebrates that remained on the sieve were preserved in 70% alcohol for subsequent identification and counting (Cummins et al., 2005; Hamada & Ferreira-Keppler, 2012; Hamada et al., 2014; Merritt et al., 2017). The invertebrates were collected from only one mesh type (coarse mesh). Results were expressed as taxa richness and individual abundance per sample, and the invertebrate's density was determined per gram of remaining litter mass. The invertebrates were categorized into the following five feeding groups (Cummins et al., 2005; Hamada & Ferreira-Keppler, 2012; Hamada et al., 2014; Merritt et al., 2017): collector-gatherers, collector-filterers, shredders, scrapers, and predators. However, only the frequencies of shredders and scrapers were considered to assess the direct effects on leaf litter decomposition.

A disk (1.2 cm diameter) was cut from leaves selected randomly from each litter bag. These disks were used to determine ash-free dry mass (AFDM), calculated after incineration in a muffle furnace at 550°C for 4 hours. The remaining material was oven-dried at 60°C for 72 hours to determine dry weight for use in determining leaf mass loss (ML). ML was calculated as the remaining weight (Wt) divided by the initial weight (W0) multiplied by 100 (Mass loss = (W0 * 100) / Wt) following Bärlocher (2005). The mass of the cut disks was added to the remaining mass.

Data Analysis

An initial linear model was fitted with plant species as the explanatory variable and litter chemical characteristics as the dependent variable. Another linear model was used to test the effects of mesh type, location, and plant species, along with their interactions, on litter mass loss. Similarly, an additional linear model evaluated the effects of location, plant species, and their interaction on invertebrate richness, invertebrate density, and the abundance of shredders and scrapers. Finally, water physicochemical characteristics were compared between sampling locations. Comparisons of sum of squares in the linear model analyses were used to assess the relative contribution of explanatory variables. For all models, analysis of variance (ANOVA; "aov" function from the "vegan" package) was performed to test the significance of variation sources, followed by Tukey's honest significant difference (HSD) test for pairwise comparisons. The distribution and dispersion of residuals of all models were inspected using the "hnp" function to ensure model assumptions were met, and when necessary, data were transformed using the natural logarithm ("decostand" function in "vegan" package).

Differences among categorical variables were evaluated using orthogonal contrast analysis. In this analysis, the dependent variables for different categories were ranked in increasing order and tested pairwise (with the closest values) and sequentially by adding values to the model that showed no differences, then testing with the following model in a stepwise simplification process. We also employed Tukey's test for pairwise comparisons of interactions ("lsmeans" function and package).

An indicator species analysis ("indval" function in "labdsv" package) was performed to identify the invertebrate taxa most clearly responding to urbanization. This method combines the occurrence and frequency of each species at each location with each factor during the study to yield indicator values (IV) (Dufrêne & Legendre, 1997). The significance was tested using a Monte Carlo technique with 1000 permutations. All analyses were performed using R software (R Core Team, 2024).

RESULTS

Leaf Litter Chemical Characteristics and Water Parameters

Carbon concentration was significantly higher for *Hymenaea courbaril* and *Anacardium occidentale* compared to *Croton sonderianus*, *Tabebuia aurea* and *Erythrina velutina* (Table 1). Protein and N concentrations were significantly higher for *E. velutina* compared to *H. courbaril* and *C. sonderianus*, while *T. aurea* and *A. occidentale* had the lowest levels (Table 1). The C:N ratio was significantly higher for *A. occidentale*, followed by *T. aurea*, with intermediate values for *H. courbaril* and *C. sonderianus*, and the lowest for *E. velutina* (Table 1).

Electrical conductivity, pH, turbidity and tem-

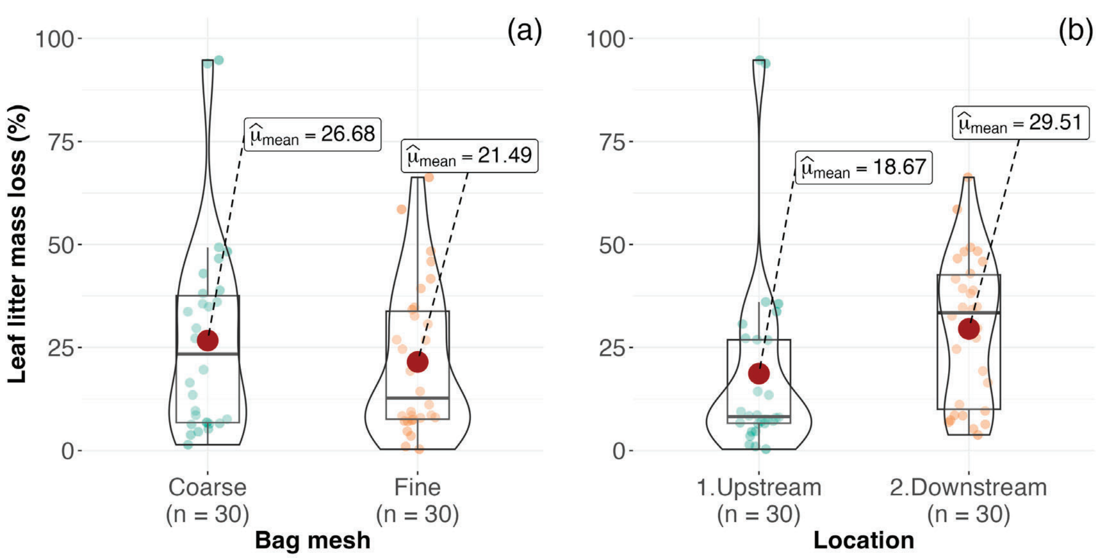

Figure 2. The violin and a box plot of leaf litter mass loss in the two mesh sizes (a), and sampling locations (b) after 30 days incubation. The boxes represent the quartiles, the black line in the horizontal represent the median, and the red circles represent the average. *Gráfico de violino e boxplot da perda de massa da serapilheira nas duas malhas (a) e nos locais de amostragem (b) após 30 dias de incubação. As caixas representam os quartis, a linha preta horizontal representa a mediana e os círculos vermelhos representam a média.*

perature were higher for the sampling location downstream of the urban area (Table 2), while dissolved oxygen was higher for the upstream sampling location (Table 2).

Leaf Litter Decomposition

There was greater litter mass loss over the 30-day study period for the coarse mesh bags (26%) compared to the fine mesh bags (21%) (Table 3a; Fig. 2a). There was also greater mass loss for the downstream location (29%) compared to the upstream location (18%) (Table 3a; Fig. 2b). The plant species with the greatest litter mass loss were *E. velutina* (42%) and *T. aurea* (38%), followed by *C. sonderianus* (22%), *A. occidentale* (10%) and *H. courbaril* (7%) (Table 3a; Fig. 3). There was a significant interaction between the factors (Table S1; supplementary information, available at https://www.limnetica.net/en/limnetica). The percentages of the sum of squares in the linear model indicated that plant species was by far the most important factor controlling leaf litter decomposition (Table 3).

The multiple comparisons analysis (Tukey test; Table S1 and Fig. S1; supplementary information, available at https://www.limnetica.net/en/limnetica) revealed significant differences in leaf mass loss among species, sampling locations, and mesh sizes. Decomposition rates for *E. velutina* and *T. aurea* differed significantly from those for the other species, particularly when comparing upstream and downstream location. Leaf breakdown was significantly higher for *E. velutina* upstream compared to *H. courbaril* and C sonderianus downstream ($p < 0.0001$; Table S1 and Fig. S1). Additionally, *T. aurea* exhibited significantly lower leaf mass loss than *E. velutina* and *A. occidentale* in downstream location ($p < 0.05$; Table S1 and Fig. S1).

There was a significant interaction between location and species, indicating that the effects of urbanization on decomposition were not homogeneous across species (Table S1 and Fig. S1). Leaf mass loss for *E. velutina* (litter with high nitrogen and protein concentrations) was drastically reduced for urban downstream location compared to preserved sites (upstream location) for coarse mesh ($p < 0.0001$), while *H. courbaril* (litter with high carbon concentrations) and *C. sonderianus* (litter with intermediate concentrations for all compounds) showed less variation between lo-

Table 1. Characterization of leaf litter by C:N ratio (%), and protein, nitrogen and carbon concentrations (%). *Caracterização da serapilheira pela razão C:N (%) e pelas concentrações de proteína, nitrogênio e carbono (%).*

	C:N ratio			Nitrogen			Protein			Carbon		
A. occidentale	103.29	±	2.94	0.48	±	0.01	2.99	±	0.09	49.47	±	0.15
C. sonderianus	54.50	±	0.31	0.83	±	0.00	5.19	±	0.01	45.29	±	0.24
E. velutina	22.25	±	0.17	2.01	±	0.01	12.56	±	0.06	44.73	±	0.13
H. courbaril	59.84	±	3.86	0.86	±	0.06	5.38	±	0.35	51.37	±	0.17
T. aurea	88.28	±	1.83	0.51	±	0.01	3.18	±	0.06	44.91	±	0.16
Total mean	65.63	±	1.82	0.94	±	0.02	5.86	±	0.11	47.15	±	0.17
ANOVA	$F_{4,10} = 550$; $p < 0.001$			$F_{4,10} = 1652$; $p < 0.001$			$F_{4,10} = 456$; $p < 0.001$			$F_{4,10} = 937$; $p < 0.001$		

Table 2. Mean values (± standard deviation) of pH, electrical conductivity (mS/cm), turbidity (NTU), water temperature (°C), and dissolved oxygen (mg/L) in the upstream and downstream sections of the Apodi-Mossoró River, near Mossoró City. *Valores médios (± desvio padrão) de pH, condutividade elétrica (mS/cm), turbidez (NTU), temperatura da água (°C) e oxigênio dissolvido (mg/L) nos trechos a montante e a jusante do rio Apodi-Mossoró, próximo à cidade de Mossoró.*

	pH			Electric conductivity mS/cm			Turbidity NTU			Temperature °C			Dissolved oxygen mg/L		
Upstream	7.98	±	0.033	0.60	±	0.003	0.41	±	0.002	27.00	±	0.500	8.18	±	0.458
Downstream	8.47	±	0.071	20.60	±	0.037	2.96	±	0.051	30.00	±	0.530	5.01	±	0.077
Total mean	8.23	±	0.052	10.60	±	0.020	1.69	±	0.026	28.50		0.515	6.59		0.267
ANOVA	$F_{1,10} = 45.5$; $p = 0.006$			$F_{1,10} = 14692.1$; $p = 0.046$			$F_{1,10} = 3196.2$; $p = 0.043$			$F_{1,10} = 56.4$; $p = 0.033$			$F_{1,10} = 1035.8$; $p < 0.001$		

Table 3. Factorial ANOVA performed on mass loss (a; in %), invertebrate richness (b; by number of taxa), invertebrate density (c; in ind.g–1), shredder relative abundance (d; in %) and scraper relative abundance (e; in %) to compare mesh size (fine vs coarse), sampling location (upstream vs downstream urban), plant species (*Erythrina velutina* = E, *Anacardium occidentale* = A, *Tabebuia aurea* = T, *Croton sonderianus* = C, and *Hymenaea courbaril* = H). Degrees of freedom (Df), sum of squares (total and %), test F values and significance by Pr(>F). *ANOVA fatorial realizada para perda de massa (a; em %), riqueza de invertebrados (b; pelo número de táxons), densidade de invertebrados (c; em ind.g^{-1}), abundância relativa de fragmentadores (d; em %) e abundância relativa de raspadores (e; em %) para comparar o tamanho da malha (fina vs grossa), o local de amostragem (a montante vs a jusante da área urbana) e as espécies de plantas (*Erythrina velutina *= E,* Anacardium occidentale *= A,* Tabebuia aurea *= T,* Croton sonderianus *= C e* Hymenaea courbaril *= H). Graus de liberdade (Df), soma dos quadrados (total e %), valores do teste F e significância por Pr(>F).*

	Sum Sq %	Num. DF	Den. DF	F	Pr(>F)	Contrast analysis
a. Mass loss						
Mesh	1.9	1	36	5.11	0.030	Fine < Coarse
Location	1.7	1	4	4.42	< 0.001	Upstream < Downstream
Plant species	58.2	4	36	38.38	< 0.001	H = A < C < T = E
Mesh:Location	7.6	1	36	20.15	< 0.001	Table S1 and Fig. S2
Mesh:Plant species	12.8	4	36	8.40	< 0.001	Table S1 and Fig. S2
Location:Plant species	10.1	4	36	6.65	< 0.001	Table S1 and Fig. S2
Mesh:Location:Plant species	7.7	4	36	5.04	0.002	Table S1 and Fig. S2
b. Richness						
Location	37.1	1	4	1.98	0.232	
Plant species	12.6	4	46	0.17	0.954	
Location:Plant species	50.3	4	46	0.67	0.616	
c. Density						
Location	4.3	1	4	1.11	0.351	
Plant species	65.6	4	46	4.25	0.005	H < A = C = T < E
Location:Plant species	30.1	4	46	1.96	0.117	
d. Shredder						
Location	40.8	1	4	1.25	0.327	
Plant species	29.6	4	46	0.23	0.922	
Location:Plant species	29.6	4	46	0.23	0.922	
e. Scraper						
Location	20.0	1	4	4.76	0.004	Upstream < Downstream
Plant species	76.9	4	46	4.58	0.003	H < A < C = T < E
Location:Plant species	3.1	4	46	0.18	0.945	

cations for both meshes (Table S1 and Fig. S1). Furthermore, there was a significant three-way interaction (Location × Species × Mesh size), revealing that the effects of urbanization on decomposition were modulated by the presence of shredding invertebrates. Species such as *T. aurea* exhibited significant differences in mass loss between fine- and coarse-mesh bags in the urban location ($p < 0.01$; Table S1 and Fig. S1).

Invertebrate Community

The most abundant taxa associated with leaf litter were thiarid snails (25%) followed by baetid mayflies (19%), lymnaeid snails (16%) and chironomid midges (13%) (Table 4). The mean den-

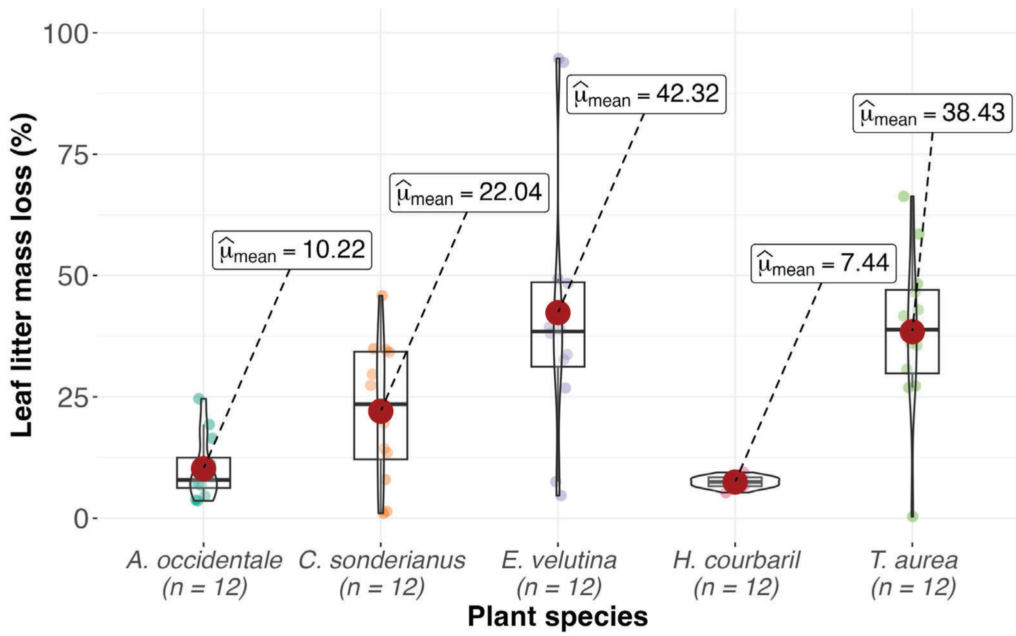

Figure 3. The violin and a box plot of leaf litter mass loss in the five plant species (*Erythrina velutina*, *Anacardium occidentale*, *Tabebuia aurea*, *Croton sonderianus*, and *Hymenaea courbaril*) after 30 days incubation. The boxes represent the quartiles, the black line in the horizontal represent the median, and the red circles represent the average. *Gráfico de violino e boxplot da perda de massa da serapilheira nas cinco espécies de plantas (*Erythrina velutina, Anacardium occidentale, Tabebuia aurea, Croton sonderianus *e* Hymenaea courbaril*) após 30 dias de incubação. As caixas representam os quartis, a linha preta horizontal representa a mediana e os círculos vermelhos representam a média.*

sity of leaf-associated invertebrates ranged from 0.4 to 4.3 individuals/g (Table 4). Invertebrate richness did not differ among treatments (Table 3b; Fig. 4a and Fig. 5a). Total invertebrate density did not differ between locations (Table 3c; Fig. 4b); however, it did differ among plant species, with the highest values for *E. velutina*, followed by *T. aurea*, *C. sonderianus*, *A. occidentale*, and *H. courbaril* (Table 3c; Fig. 5b). Shredder abundance did not differ among treatments (Table 3d; Fig. 4c and Fig. 5c) but scraper abundance differed between locations, being higher upstream compared to downstream (Table 3e; Fig. 4d). The abundance of scrapers also differed among plant species, with the highest abundances in the litter of *E. velutina*, followed by *T. aurea*, *C. sonderianus*, *A. occidentale*, and *H. courbaril* (Table 3e; Fig. 5d). There was no significant interaction between species and location in all cases. The percentage of the sum of squares in the linear model indicated that plant species (58.2%) was the most important factor controlling invertebrate density (65.6%) and scraper abundance (76.9%). Sampling location had a stronger influence on species richness (37.1%) and shredder abundance (40.8%) than did plant species.

Indicator species analysis showed that lymnaeid snails (indval = 70 %; *p* value = 0.001), libellulid dragonflies (indval = 46 %; *p* value = 0.005), planorbiid snails (indval = 43 %; *p* value = 0.001), baetid mayflies (indval = 40 %; *p* value = 0.001), sphaeriid clams (indval = 29 %; *p* value = 0.004), hydropsychid caddisflies (indval = 24 %; *p* value = 0.018), and leptophlebiid mayflies (indval = 22 %; *p* value = 0.014) were indicators of the upstream location while thiarid snails (indval = 69 %; *p* value = 0.001) and chironomid midges (indval = 55 %; *p* value = 0.001) were indicators of the downstream location.

DISCUSSION

The results of the present study highlight the dominant role of plant species identity in controlling leaf litter breakdown, invertebrate density, and scraper abundance in a semi-arid river, compared

Table 4. Mean values of invertebrate community density (individuals per leaf litter g) in different leaf litter species between upstream and downstream sections of the Apodi-Mossoró River, near Mossoró City. *Valores médios da densidade (indivíduos por grama de serrapilheira) da comunidade de invertebrados nas diferentes espécies de serapilheira entre os trechos a montante e a jusante do rio Apodi-Mossoró, próximo à cidade de Mossoró.*

Taxon	Upstream					Downstream					
	A. occidentale	*C. sonderianus*	*E. velutina*	*H. courbaril*	*T. aurea*	*A. occidentale*	*C. sonderianus*	*E. velutina*	*H. courbaril*	*T. aurea*	Total mean
Nematoda											
Annelida											
Hirudinea	0.14	0.16	0.15	0.19	0.17	0.20	0.31	0.32	0.19	0.49	0.23
Arthropoda											
Arachnida											
Hydracarina	0.30	0.29	0.42	0.00	0.38	0.00	0.00	0.00	0.00	0.00	0.14
Insecta											
Ephemeroptera											
Baetidae	5.14	6.07	32.57	0.00	7.61	0.00	0.00	0.00	0.00	0.00	5.14
Lephelbiidae	3.47	3.29	3.23	0.28	4.62	0.00	0.00	0.00	0.05	0.00	1.49
Odonata											
Libellulidae	1.49	1.55	6.30	0.47	2.09	0.36	0.43	0.50	0.00	0.57	1.38
Trichoptera											
Polycentropodidae	0.00	0.00	0.00	0.05	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Hydropsychidae	0.70	0.66	3.17	0.00	0.95	0.00	0.00	0.00	0.09	0.00	0.56
Diptera											
Chironomidae	1.00	1.04	3.23	0.47	1.39	4.39	6.14	6.59	3.09	8.82	3.61
Mollusca											
Thiaridae	1.07	1.06	3.87	1.08	1.38	11.10	13.53	15.21	0.74	18.61	6.76
Planorbiidae	5.03	5.75	8.59	0.05	7.24	0.00	0.00	0.00	0.00	0.00	2.67
Sphaeriidae	0.47	0.54	0.60	0.14	0.68	0.00	0.00	0.00	0.05	0.00	0.25
Lymnaeidae	6.47	7.35	17.90	1.50	9.34	0.00	0.00	0.00	0.19	0.00	4.28

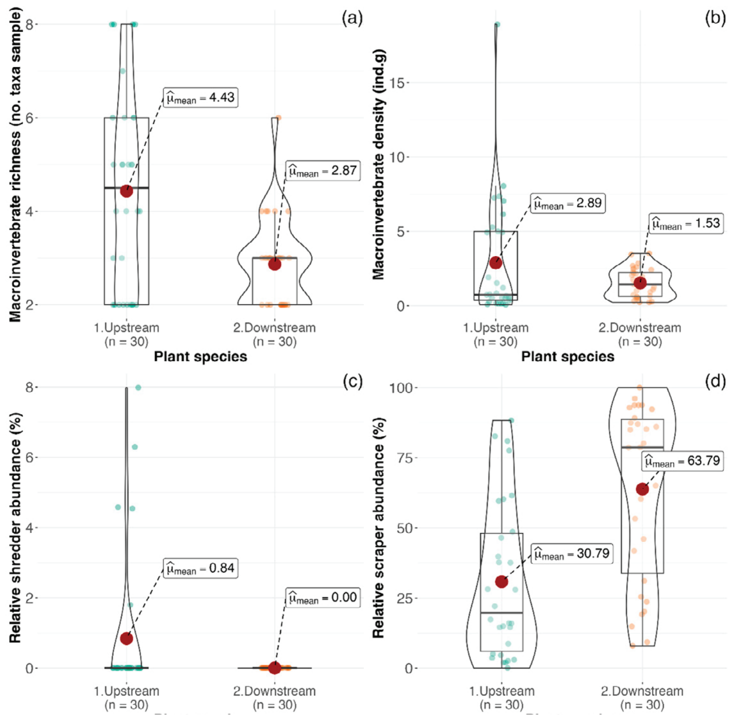

Figure 4. The violin and a box plot of invertebrate richness (a), and density (b), relative shredder (c) and scraper abundance (d) in the two mesh sizes (a), and sampling locations (b) after 30 days incubation. The boxes represent the quartiles, the black line in the horizontal represent the median, and the red circles represent the average. *Gráfico de violino e boxplot da riqueza de invertebrados (a), densidade (b), abundância relativa de fragmentadores (c) e raspadores (d) nas duas malhas (a) e nos locais de amostragem (b) após 30 dias de incubação. As caixas representam os quartis, a linha preta horizontal representa a mediana e os círculos vermelhos representam a média.*

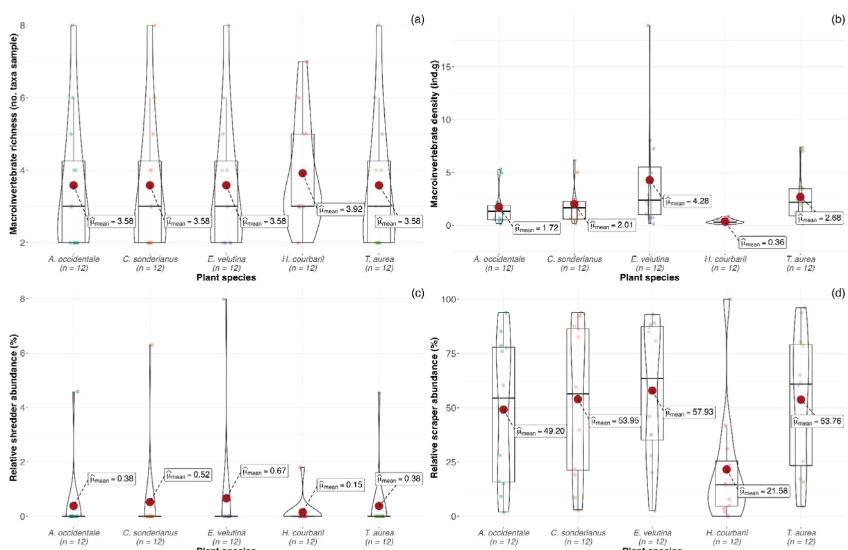

Figure 5. The violin and a box plot of invertebrate richness (a), and density (b), relative shredder (c) and scraper abundance (d) for the five plant species (*Erythrina velutina*, *Anacardium occidentale*, *Tabebuia aurea*, *Croton sonderianus*, and *Hymenaea courbaril*) after 30 days incubation. The boxes represent the quartiles, the black line in the horizontal represent the median, and the black circles represent the average. *Gráfico de violino e boxplot da riqueza de invertebrados (a), densidade (b), abundância relativa de fragmentadores (c) e raspadores (d) para as cinco espécies de plantas (*Erythrina velutina, Anacardium occidentale, Tabebuia aurea, Croton sonderianus *e* Hymenaea courbaril*) após 30 dias de incubação. As caixas representam os quartis, a linha preta horizontal representa a mediana e os círculos pretos representam a média.*

to sampling location and invertebrate access (by mesh size). These results are particularly interesting, as in many experiments in extreme anthropogenic systems, such as urban areas, environmental conditions are often the most important factor (Torres & Ramírez, 2014; Classen-Rodríguez et al., 2019; Wymore et al., 2021). Leaf litter with higher nitrogen and protein content or C:N ratio (e.g., *Erythrina velutina* and *Tabebuia aurea*) exhibited significantly greater mass loss compared to more recalcitrant (highest carbon content) species (*Anacardium occidentale* and *Hymenaea courbaril*). This pattern aligns with previous studies demonstrating that high-quality litter enhances microbial and invertebrate-mediated decomposition (Rezende et al., 2014a; Arias-Real et al., 2018; Sena et al., 2020; Da Silva et al., 2024). However, the breakdown process was also significantly affected by interactions among plant species, invertebrate access (by mesh size), and urbanization, suggesting that these factors jointly influence leaf breakdown dynamics. These findings support the intimate connection between terrestrial and aquatic ecosystems (Rezende et al., 2019; Da Silva et al., 2024), especially in the less structured riparian vegetation of semi-arid regions (Rezende et al., 2018). They also emphasize the crucial role of riparian vegetation in ecosystem processes (Inhamuns et al., 2021).

The present results also emphasize that leaf litter breakdown in semi-arid rivers is shaped by strong interactions between plant species identity, invertebrate access, and urbanization. The hierarchical importance of these factors (by percentage of the sum of squares in the linear model) suggests that: i) plant species identity (with 58.2% of model explanation) is the strongest determinant of breakdown rates, with high-nutrient litter decomposing faster than recalcitrant species; ii) invertebrate access enhances mass loss, particularly for palatable litter types (with 12.8% for the interaction between bag mesh size and plant species), supporting the role of scraper-mediated decomposition; and iii) urbanization amplifies litter breakdown rates, especially for high-quality litter (interaction between location and plant species explains 10.1%), but also alters invertebrate community composition, potentially leading to ecosystem-level changes in organic matter processing. These findings highlight the complexity of decomposition dynamics in semi-arid streams and suggest that both biotic (e.g. litter traits and invertebrate composition) and abiotic (e.g. nutrients and temperature) factors interact to regulate the leaf litter breakdown process. Future studies should explore whether these interactions remain consistent across different hydrological regimes, particularly given the increasing anthropogenic pressures on semi-arid freshwater systems.

Higher mass loss was observed downstream than upstream of the urban area, which may be related to the higher specific conductivity and turbidity observed for the water downstream (Rezende et al., 2014a). These parameters are often associated with effluent discharge, which results in increased nutrient concentrations in the water (Montebelo et al., 2002; Rezende et al., 2014b). Elevated nutrient levels in the water, indicated by higher specific conductivity (a rough proxy for nutrients and pollution), along with increased turbidity (Montebelo et al., 2002; Rezende et al., 2014b), may accelerate the litter breakdown process (Quintão et al., 2013; Rezende et al., 2014a). However, this apparent positive effect could be attributed to several negative factors: i) an increase in nutrient availability for the decomposer community by pollution discharge (Tagliaferro et al., 2022); ii) the selection of larger-bodied scraper species (Thiaridae) due to invertebrate community homogenization, as indicated by the presence of only species of Thiaridae and Chironomidae (Rezende et al., 2018) at the downstream location; and iii) an increase in the metabolic activity of decomposers due to higher water temperatures in river sections downstream of urban areas (Follstad et al., 2017).

Interactions Between Plant Species And Invertebrate Access

The effect of mesh size was significant, with higher mass loss for coarse-mesh bags, whereby invertebrates had access to the litter. However, this effect was strongly modulated by plant species identity. High-nutrient leaves (e.g., *E. velutina* and *T. aurea*) exhibited larger differences in mass loss between coarse- and fine-mesh bags, indicating that invertebrates played a greater role in the decomposition of these palatable species (Sena et al., 2020; Cararo et al., 2023). In contrast, microbial decomposition dominated for more recalcitrant species (*A. occidentale* and *H. courbaril*), as evidenced by the relatively small difference in mass loss between mesh sizes (Alvim et al., 2015; Rezende et al., 2021). This supports the assumption that invertebrate-mediated breakdown is more efficient in high-quality litter, while microbial decomposition is the primary pathway for nutrient-poor, lignin-rich leaves (Tank et al., 2010; Rezende et al., 2018).

In the present study, the prevalence of larger-bodied scraper species could explain the higher mass loss observed for the coarse mesh bags compared to the fine mesh bags. This may indicate how specific traits of species, such as body size and metabolic capacity, can play a crucial role in driving ecological processes at local scales (Chauvet et al., 2016). On the other hand, while our initial interpretation emphasized the contribution of larger-bodied scraper species, it is important to recognize that the exclusion of invertebrates affects individuals across a broad size spectrum, including both large-bodied and smaller-bodied (e.g., Baetidae, Chironomidae, Hydropsychidae) taxa. While shredders are typically the key players in leaf litter breakdown processes (Graça et al., 2015), we noted a low density and richness of these organisms compared to temperate systems, as expected based on previous research (Gonçalves et al., 2006; Rezende et al., 2018). Instead, gastropod scrapers (e.g., Thiaridae, Lymnaeidae, Planorbiidae, and others observed in this study) seemed to fill the ecological niche of shredders in the studied system (Rezende et al., 2018). These scrapers use their radulae to scrape leaf surfaces, enhancing litter breakdown rates (Rezende et al., 2010, 2018).

The abundance of scrapers (e.g., Thiaridae and Lymnaeidae) followed a similar trend, being significantly higher for coarse-mesh bags with *E. velutina* and *T. aurea*. These species are known to facilitate leaf breakdown in tropical systems by grazing biofilms and indirectly fragmenting litter surfaces (Rezende et al., 2010, 2023). The interaction between plant species and invertebrate access suggests that litter quality mediates the relative importance of microbial vs. invertebrate-driven breakdown processes (Graça et al., 2015; Rezende et al., 2019), a pattern consistent with other studies in nutrient-limited ecosystems (Medeiros et al., 2015; Rezende et al., 2018).

Additionally, the leaf litters with the highest mass loss (*E. velutina* and *T. aurea*), which had high N and protein concentrations, a low C:N ratio, and reduced levels of C, are also species known for having high levels of compounds that easily leach into water, such as terpenes, tannins, and phenols (Santos et al., 2013; Mahmoud et al., 2022). A mass loss of around 40% for both of these litter types in 30 days is a relevant result that supports this inference. After leaching (usually anti-herbivory compounds), the litter becomes less toxic and more palatable (Marsaro et al., 2023), allowing for the colonization of the decomposer community (Biasi et al., 2016). This also justifies the higher invertebrate density for *E. velutina* and *T. aurea* (by increase of N and protein concentrations or C:N ratio) compared to litter of other plant species and, consequently, higher leaf litter breakdown (Rezende et al., 2018, 2014b; Brandão et al., 2022).

Interactions Between Urbanization and Plant Species

The effect of urbanization on mass loss was also modulated by plant species identity. While the downstream location exhibited higher litter breakdown rates overall, the difference was most pronounced for high-quality litter. Mass loss for *E. velutina* and *T. aurea* increased by nearly 10% in urban downstream location compared to the upstream location, likely due to enhanced microbial activity driven by nutrient enrichment (Medeiros et al., 2015; Tagliaferro et al., 2022). Conversely, the litter breakdown process for *A. occidentale* and *H. courbaril* remained low for both locations, suggesting that the structural properties of these litters limit degradation regardless of environmental conditions (Torres & Ramírez, 2014; Rezende et al., 2023). This pattern contrasts with what is typically observed in most systems, where decomposition rates are more strongly influenced by site-specific factors.

This pattern suggests that urbanization amplifies differences in the leaf litter breakdown process across litter types, favoring species that are already prone to rapid breakdown (Rezende et al., 2014a). While increased nutrient availability can stimulate microbial activity (Wymore et al., 2021; Tagliaferro et al., 2022), the present results also indicate that urbanization homogenized the invertebrate community, with a higher dominance of pollution-tolerant taxa (e.g., Thiaridae and Chironomidae), as expected (Classen-Rodríguez et al., 2019; Keinath et al., 2023). These organisms may further enhance the breakdown process by fragmenting leaves and altering microbial colonization (Rezende et al., 2018, 2019).

Additionally, the leaf litters with the highest mass loss (*E. velutina* and *T. aurea*) that had high N and protein concentration, or C:N ratio, and reduced levels of C, also are species known for having high levels of compounds that easily leach into water, such as terpenes, tannins, and phenols (Santos et al., 2013; Mahmoud et al., 2022). A mass loss of around 40% for both litter types in 30 days is a relevant result that supports this inference. After leaching (usually compounds against herbivory), the litter becomes less toxic and more palatable (Marsaro et al., 2023), allowing for the colonization of the decomposer community (Biasi et al., 2016), also justifying the higher invertebrate density on *E. velutina* and *T. aurea* (by increase of N and protein concentration, or C:N ratio) compared to other plant species litter, and consequently, its leaf litter breakdown (Rezende et al., 2018, 2014b; Brandão et al., 2022).

Interactions Between Urbanization and Invertebrate Access

The influence of urbanization was also dependent on invertebrate exclusion. Decomposition rates for coarse-mesh bags were higher in urban downstream location, likely due to the increased metabolic activity of decomposers in response to elevated nutrients and temperature (Follstad et al., 2017). However, for fine-mesh bags, where microbial activity was isolated, mass loss did not differ significantly between urban downstream location and urban upstream locations. This may suggest that urbanization primarily accelerates litter breakdown by stimulating invertebrate and fungal activity rather than through direct chemical breakdown (Torres & Ramírez, 2014; Classen-Rodríguez et al., 2019).

The abundance of scrapers was also higher in urban downstream location, further supporting the role of invertebrate-driven litter breakdown in this environment. However, urban streams often experience reduced biodiversity, and the dominance of Thiaridae and Chironomidae suggests potential ecological imbalances that could alter organic matter processing (Rezende et al., 2018). The homogenization of the downstream invertebrate community, with the loss of sensitive taxa (e.g., Leptophlebiidae) (Classen-Rodríguez et al., 2019), may result in a functional shift whereby scraper-mediated leaf litter breakdown replaces that of shredders as the primary pathway (Rezende et al., 2010, 2018).

CONCLUSION

Leaf litter (primary driver) with high nutrient content or C:N ratio decomposed significantly faster than more recalcitrant (high carbon content) litter, likely due to enhanced microbial and invertebrate colonization, corroborating our hypothesis. The effect of invertebrate exclusion was particularly pronounced for high-quality litter, where invertebrate scrapers (Thiaridae, Lymnaeidae, and Planorbiidae) played a central role in litter fragmentation and biofilm removal. Also, litter breakdown was higher for the urban downstream location, but led to a homogenization of invertebrate assemblages, confirming our hypotheses. Strong interactions were observed between litter quality, invertebrate access, and urbanization. The urban effect was most pronounced for high-quality litter, suggesting that microbial activity in nutrient-rich environments selectively enhances decomposition of palatable detritus. Likewise, invertebrate-mediated effects were stronger for high-quality litter, emphasizing that detritivore activity is largely dependent on litter palatability.

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AUTHOR CONTRIBUTIONS

C.Q.A. and R.S.R.: conceived the study; W.F.S, J.S.C. and J.L.C.N.: collected field data; R.S.R.: managed and analyzed the data. W.F.S. and R.S.R.: wrote the manuscript with feedback from J.L.C.N., C.Q.A., J.S.C., J.F.G.Jr. and A.T.

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