



Trophic ecology of the vulnerable tetra *Mimagoniates lateral* (Nichols, 1913) in a blackwater stream of the Atlantic Forest

Ecologia trófica do tetra vulnerável *Mimagoniates lateral* (Nichols, 1913) em um riacho de água preta da Mata Atlântica

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Abstract: Aim: Here we investigated the diet of *Mimagoniates lateral* (Nichols, 1913) in a blackwater restinga stream of the Atlantic Forest, aiming to identify the main food sources consumed and to verify if ontogenetic variations occur. **Methods:** Specimens were sampled in January 2024 in the Panema stream, Itanhaém – SP. The diet of 124 individuals was determined through stomach content analysis, and the Feeding Preference Degree (FPD) was used to measure the importance of the consumed items. **Results:** The diet comprised 21 items, among which detritus, plant fragments, and adult Hymenoptera were predominant. Only detritus was classified as a secondary item in terms of feeding preference, while all other items were considered occasional. Larger fish were more likely to consume adult Coleoptera and Hymenoptera, while smaller individuals were more likely to consume items such as Trombidiformes and detritus. **Conclusions:** The results suggest an ontogenetic dietary shift, favoring specific prey and reducing dependence on other food items. The high presence of allochthonous items in the diet of *M. lateral* highlights the crucial role of riparian vegetation as an essential source of food resources. The preservation of riparian forests supports the balance of these ecosystems and is vital for the survival of *M. lateral*, a species vulnerable to extinction, reinforcing the urgency of effective measures of conservation.

Keywords: diet; ontogenetic variation; southeastern Brazil; Itanhaém River Basin.

Resumo: Objetivo: No presente estudo, investigamos o conteúdo estomacal de *Mimagoniates lateral* (Nichols, 1913) em um riacho de restinga de água preta da Mata Atlântica, com o objetivo de identificar as principais fontes alimentares consumidas e verificar se ocorrem variações ontogenéticas. **Métodos:** Os exemplares foram amostrados em janeiro de 2024 no riacho Panema, Itanhaém – SP. A dieta de 124 indivíduos foi determinada por meio da análise do conteúdo estomacal, e o Grau de Preferência Alimentar (GPA) foi utilizado para mensurar a importância dos itens consumidos. **Resultados:** A dieta foi composta por 21 itens, entre os quais detrito, fragmento vegetal e Hymenoptera



adulto foram predominantes. Apenas detrito foi classificado como item secundário, sendo todos os demais itens ocasionais. Os peixes de maior comprimento apresentaram a maior probabilidade de consumir adultos de Coleoptera e Hymenoptera, enquanto indivíduos menores tiveram a maior probabilidade de consumo de itens como Trombidiformes e detrito. **Conclusões:** Os resultados sugerem uma mudança ao longo da ontogenia na dieta, favorecendo presas específicas e reduzindo a dependência de outros itens alimentares. A elevada presença de itens alóctones na dieta de *M. lateralis* ressalta o papel fundamental da vegetação marginal como fonte essencial de recursos alimentares. A preservação da mata ciliar sustenta o equilíbrio desses ecossistemas, e é crucial para a sobrevivência de *M. lateralis*, uma espécie vulnerável à extinção, reforçando a urgência de medidas efetivas de conservação.

Palavras-chave: dieta; variação ontogenética; sudeste do Brasil; Bacia do Rio Itanhaém.

1. Introduction

The Atlantic Forest is recognized as a global biodiversity hotspot, predominantly located along the Brazilian coast (Myers et al., 2000). Due to its environmental heterogeneity, freshwater fish diversity is remarkably high, with a significant proportion of small-sized species (Abilhoa et al., 2011; Marques & Grelle, 2021). In coastal aquatic ecosystems, endemism rates are particularly elevated, primarily due to the presence of numerous independent small river drainages and the unique characteristics of watersheds confined between the Serra do Mar mountain range and the oceanic area (Costa, 2019; Giongo et al., 2023; Costa et al., 2024).

Among coastal aquatic ecosystems, blackwater streams stand out due to their distinct environmental features. These systems are characterized by slow water flow, fine sediment substrates, dark-reddish water coloration, high concentrations of humic acids, elevated acidity, and a distinctive odor (Cardoso & Esteves, 2022). These unique conditions not only define the ecological identity of blackwater streams but are also expected to promote the presence of endemic organisms specially adapted to acidic environments (Por & Lopes, 1994).

Coastal blackwater streams in the Atlantic Forest face severe threats, particularly the loss of riparian vegetation due to urban expansion (Alves & Pereira, 2015; Daunt et al., 2021). Meanwhile, riparian forests play a crucial ecological role, acting as natural filters that reduce sediment and pollutant transport into waterways, while also regulating water temperature through shading (Tolkkinen et al., 2020; Marques et al., 2021). The degradation of these forests directly affects fish-forest interactions, as aquatic food webs and primary production rely heavily on allochthonous inputs such as fruits, seeds, and insects, which constitute essential food resources for fish (Gonçalves et al., 2018; Costa et al., 2021; Pires et al., 2024).

Trophic ecology studies have demonstrated significant dietary plasticity in fish species, often

linked to morphological, physiological, and behavioral adaptations (Abelha et al., 2001; Esteves et al., 2021). Such plasticity may also be expressed throughout ontogeny, with juveniles and adults occupying distinct dietary niches and habitats, potentially reducing intraspecific competition and promoting population stability (Barreto & Aranha, 2006; Manna & Rezende, 2021). Furthermore, habitat modifications have been identified as key drivers of shifts in trophic structure, as changes in environmental conditions may alter food resource availability and consequently species interactions (Carvalho et al., 2019; Kliemann et al., 2019).

Dietary analysis is a fundamental tool to understanding fish biology and ecological requirements, providing essential insights for conservation strategies to mitigate habitat loss and ensure species persistence. This is particularly relevant for *Mimagoniates lateralis* (Nichols, 1913), a small Glandulocaudinae tetra restricted to blackwater streams and coastal floodplains, occurring in remaining areas of the Atlantic Forest from southern São Paulo to northern Santa Catarina (Menezes & Weitzman, 2009). Classified as Vulnerable in Brazil (ICMBio, 2025) and Endangered in the state of São Paulo (Oyakawa et al., 2009; São Paulo, 2014), *M. lateralis* is highly dependent on riparian vegetation for population viability (ICMBio, 2025).

While previous studies have investigated aspects of its reproductive biology (Moraes et al., 2020), systematics and phylogenetics (Menezes & Weitzman, 2009), and behavior (Nelson, 1964b, c; Duboc, 2007), its trophic ecology remains unexplored. In this context, the present study aims to investigate the trophic ecology of *M. lateralis*, by describing and quantifying its diet, and analyzing ontogenetic dietary shifts in a blackwater stream of the Atlantic Forest, within the Itanhaém River Basin, in the coastal region of São Paulo State. Considering the flexibility and tendency to omnivory of tetra species (Souza et al., 2015; Delariva & Neves, 2020; Costa et al., 2021;

Neves et al., 2021), we also assessed whether changes occur along size (ontogeny), concerning the main sources of resources.

2. Material and Methods

2.1. Study area and sampling

The Itanhaém River Basin is the second-largest coastal basin in the state of São Paulo, it retains remaining areas of the original Atlantic Forest and is distinguished by its environmental heterogeneity, ranging from steep mountainous regions to coastal plains (Camargo et al., 1997). The Itanhaém River basin comprises four main tributaries: the Mambu, Aguapeú, Branco, and Preto rivers. The Preto River sub-basin contains streams that originate in steeper regions with clear waters, as well as water bodies that drain low-elevation areas, characterized by dark waters, high acidity, and low oxygen levels (Camargo & Cancian, 2016).

Sampling was conducted in the Panema stream, a blackwater restinga stream (24°11'09.4"S 46°54'42.2"W) within the Preto River sub-basin in Itanhaém, São Paulo (Figure 1). This stream is situated in a densely forested area of the Atlantic Forest; however, it faces significant anthropogenic pressures, including deforestation due to the irregular housing constructions (Camargo & Cancian, 2016). These anthropic pressure developments are often linked to land tenure claims, leading to the degradation of native vegetation.

Fish were sampled in January 2024 and were captured using hand nets, with 50 x 40 cm oval mouth and 1 mm panel mesh size. After collection, the specimens were anesthetized with 1 to 1.5 mL of eugenol per liter of water and kept in 10% formalin for 48 hours, and subsequently preserved in 70% alcohol. All sampling and procedures were carried out under the SISBIO 90241-1 license and CEUA – IB/CLP n° 15/2023. Also, physicochemical parameters (pH, temperature (°C), dissolved oxygen (mg/L), and conductivity (mS/cm)), were assessed using a Horiba U-52 G multiprobe, on the same day as fish sampling, with a measurement every 5m in a 65m stretch (Table 1).

2.2. Laboratory procedures

The sampled individuals were weighed (g) and measured (standard length, mm). After that, they were dissected along the abdominal region to remove the stomachs. Each individual was classified by sex and stomach repletion (SR), being categorized into three levels, empty (SR = 1), partially full (SR = 2) or full (SR = 3) (Braga, 1990). The stomach contents were subsequently examined under a stereomicroscope and identified to the lowest possible taxonomic level according to the literature (Mugnai et al., 2010; Triplehorn & Jonnson, 2011). For dietary analysis, stomachs with food contents (SR = 2 or 3) were considered.

The frequency of occurrence was calculated as the number of stomachs containing a food item and

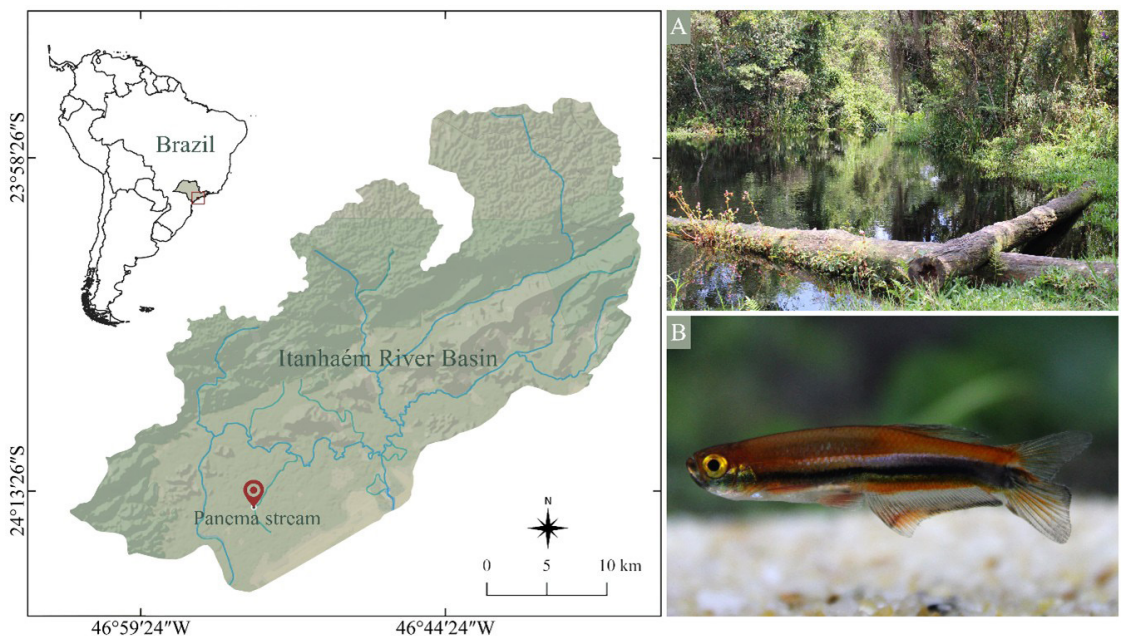


Figure 1. Study area and sampling site in (A) Panema stream, Itanhaém, SP, Brazil, and (B) sampled specimen of *Mimagoniates lateralis*. Photographs: Amanda Selinger.

Table 1. Physicochemical properties of the Panema stream, Itanhaém, São Paulo, sampled in January 2024.

	Minimum	Maximum	Mean \pm standard deviation
pH	3.9	4.9	4.3 \pm 0.3
EC (mS/cm)	0.077	0.087	0.080 \pm 0.003
DO (%)	18.2	29.2	21.3 \pm 3.2
TS (g/L)	0.050	0.056	0.052 \pm 0.002
ORPmV	310.0	364.0	336.4 \pm 18.8
Temperature (°C)	28.6	29.4	28.8 \pm 0.2

pH = hydrogen potential; EC = electrical conductivity; DO = dissolved oxygen; TS = total solids; ORPmV (oxidation-reduction potential in millivolts).

expressed as the percentage of the total number of examined stomachs. To quantify the diet, the Food Preference Degree (FPD) was used, in which items are classified according to their representation in the stomach (Braga, 1999). When registering only one item in the stomach, the value 4 was assigned, with more items being assigned the values 3, 2 and 1, depending on the abundance of the item within that stomach. After that, food preference was calculated by $S_{(i)}/N$, where $S_{(i)}$ is the sum of the values assigned to a certain item i and N is the number of stomachs analyzed, being considered an absolute preferred item when $FPD = 4$, preferential to a high degree, if $3 \leq FPD < 4$, preferential with intake of others if $2 \leq FPD < 3$, secondary when $1 \leq FPD < 2$ and occasional if $FPD < 1$ (Braga, 1999).

2.3. Data analysis

Standard length (mm) and weight (g) values were presented as mean and standard deviation (SD), and compared between sexes using Student's t -test. To evaluate how the number of distinct food items accumulates as more stomachs are analyzed, we used the *iNEXT* package in R (Hsieh et al., 2016). Specifically, we performed interpolation and extrapolation of our incidence data (presence/absence of each item per stomach) up to a total of 200 stomachs. We set $q=0$, which focuses on species (in this case, food items) richness, and employed 999 bootstrap replicates to estimate 95% confidence intervals. In this context, *iNEXT* uses the Chao2 estimator (for incidence data) to account for unseen food items. This extrapolation procedure allowed us to assess how many additional food items might be expected if more stomachs were analyzed beyond our actual sample size.

To evaluate how fish standard length influenced the presence or absence of dietary items, in the analysis of ontogenetic change, we first filtered out all items with a frequency of occurrence below 5% across all analyzed stomachs. This threshold was chosen to remove rare items that might introduce

noise and obscure general dietary patterns. After filtering, we employed the *mvabund* package (Wang et al., 2012) in R to perform a multivariate generalized linear model. Each of the remaining diet items was treated as a binary response variable (0 = absent, 1 = present), while standard length was included as the predictor. A binomial family was specified to model the presence-absence data, and we used 999 bootstrap iterations (via PIT-trap resampling) to account for correlation among the multiple responses. To validate the adequacy of the multivariate generalized linear model, diagnostic plots were generated. These included residuals vs. fitted values and a quantile-quantile (QQ) plot of the residuals, both of which were inspected for patterns or deviations from normality. Model significance was evaluated by comparing the full model to a null model containing only the intercept. All statistical analyses were conducted in R version 4.2.1 (R Core Team, 2023).

4. Results

A total of 163 individuals were sampled and measured, of which 126 were males and 37 were females. The mean standard length of females was 25.70 mm (SD = 2.98), while for males was 25.90 mm (SD = 5.33), with no significant difference between sexes ($t = 0.29$, $p = 0.76$; Figure 2A). Similarly, the mean weight of females was 0.24 g (SD = 0.13 g), compared to 0.27 g (SD = 0.25 g) for males, and this difference was also not significant ($t = 1.26$, $p = 0.20$; Figure 2B). Regarding stomach repletion, 23.92% of the individuals had empty stomachs (SR = 1), 50.31% had partially full stomachs (SR = 2), and 25.77% had full stomachs (SR = 3).

The stomach contents of 124 individuals were analyzed, and the population's diet was composed of 21 items (considering larger taxonomic groups up to order), with seven autochthonous items, 10 allochthonous and four items of unknown origin (Table 2). The items with the highest

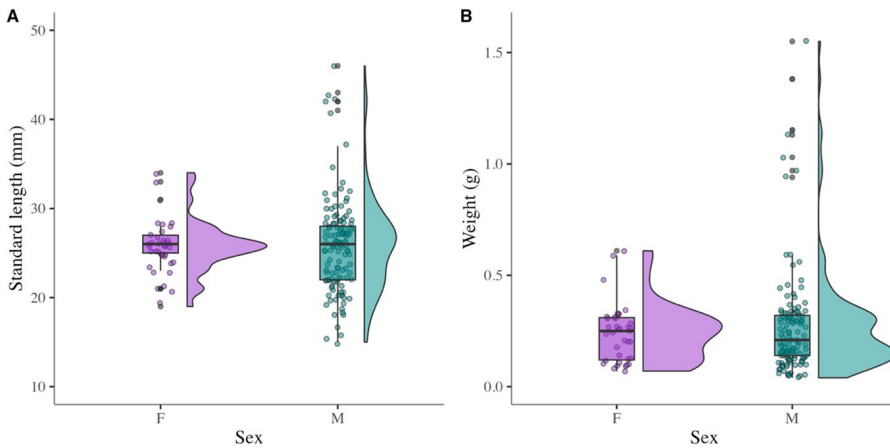


Figure 2. Comparison of (A) standard length (mm) and (B) weight (g) between female (F) and male (M) individuals of *Mimagoniates lateralis*, sampled at the Panema stream, Itanhaém, São Paulo. Each panel shows a combination of a boxplot (left) and a half-violin plot (right), illustrating the data distribution and variability. Points represent individual data observations.

Table 2. Food items found in stomachs of *Mimagoniates lateralis*, sampled at the Panema stream, Itanhaém, São Paulo, with their frequency of occurrence (FO) in percentage and Feeding Preference Degree (FPD) with the respective classification (N = 124 stomachs). FPD was only calculated for larger taxonomic groups.

Items	FO (%)	FPD	Classification
Autochthonous			
Algae	3.22%	0.04	Occasional
Coleoptera (larvae)	1.61%	0.03	Occasional
Diptera (larvae)	23.28%	0.28	Occasional
Ephemeroptera (nymphs)	0.80%	0.01	Occasional
Fragments of aquatic insects	3.22%	0.08	Occasional
Ostracoda	15.32%	0.18	Occasional
Trichoptera (larvae)	0.80%	0.01	Occasional
Allochthonous			
Araneae	12.90%	0.21	Occasional
Bird feather	0.80%	0.01	Occasional
Coleoptera (adults)	11.29%	0.27	Occasional
Collembola	9.67%	0.09	Occasional
Hypogastruridae	8.06%	-	-
Sminthuridae	1.61%	-	-
Diptera (adults)	16.12%	0.31	Occasional
Calliphoridae	0.80%	-	-
Drosophilidae	1.61%	-	-
Muscidae	6.45%	-	-
Syrphidae	4.38%	-	-
Tabanidae	1.61%	-	-
Fragments of terrestrial insects	25.80%	0.52	Occasional
Fruits	12.09%	0.16	Occasional
Hymenoptera (adults)	31.45%	0.60	Occasional
Apidae	1.61%	-	-
Formicidae	23.39%	-	-
Vespidae	7.26%	-	-
Orthoptera (adults)	1.61%	0.04	Occasional
Seeds	12.09%	0.16	Occasional
Unknown origin			
Detritus	70.16%	1.54	Secondary
Trombidiformes	9.67%	0.11	Occasional
Insect eggs	3.22%	0.04	Occasional
Plant fragments	45.16%	0.93	Occasional

frequency of occurrence were, respectively, detritus (70.16%), plant fragments (45.16%) and adults of Hymenoptera (31.45%). Regarding the Feeding Preference Degree, only detritus was classified as secondary, with all other items being classified as occasional (Table 2). The rarefaction and extrapolation curve showing the relationship between the number of stomachs analyzed and the cumulative number of distinct food items observed appears to demonstrate a tendency to still be stabilizing (Figure 3), which demonstrates a great variety in the species' diet even with 124 stomachs analyzed.

The multivariate generalized linear model indicated a significant effect and strong relationship of fish standard length on the probability of consuming some dietary items (Wald = 6.36, $p = 0.001$). Similarly, the Analysis of Deviance showed that adding standard length to the null model reduced deviance by 43.82 ($p = 0.001$), reinforcing the importance of length as an explanatory variable. These results suggest that larger fish are more likely to feed on items such as Coleoptera and Hymenoptera adults, and that smaller fish are more likely to feed on items such as Trombidiformes and detritus (Figure 4).

5. Discussion

Our study provides a detailed analysis of the trophic ecology of *M. lateralis*, a vulnerable tetra species inhabiting blackwater streams of the Atlantic Forest. The species exhibits a diverse omnivore diet, with detritus, plant fragments, and adult Hymenoptera being the most frequently consumed, and differences according to the size of the fish, reflecting the remarkable trophic flexibility of the species. The Food Preference Degree (FPD) analysis identified detritus as a secondary item, while all other items were classified as occasional, indicating a predominantly opportunistic feeding pattern. The rarefaction curve suggests that the richness of dietary items has not yet stabilized, suggesting that the species may exploit an even broader range of food resources than currently recorded, despite the analysis of 124 stomachs. Additionally, a significant relationship between fish standard length and dietary item occurrence demonstrates ontogenetic shifts in feeding patterns, reinforcing the dynamic nature of the trophic behavior of the species.

Historically, Glandulocaudinae have been characterized as surface feeders that primarily consume terrestrial arthropods falling into the water (Nelson, 1964a; Costa, 1987; Dufech et al.,

2003; Gracioli et al., 2003). Our findings on *M. lateralis* largely corroborate this pattern, given the frequent occurrence of items such as adult Diptera, Coleoptera, Hymenoptera (Vespididae, Formicidae, Apidae) and Araneae in its diet. However, the presence of seeds and fruits—items not commonly reported for this subfamily—reveals a broader trophic plasticity than previously recognized, at

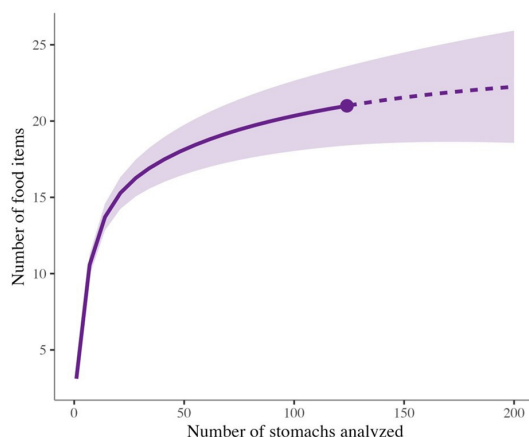


Figure 3. Rarefaction and extrapolation curve showing the relationship between the number of stomachs analyzed and the cumulative number of distinct food items observed for *Mimagoniates lateralis*, sampled at the Panema stream, Itanhaém, São Paulo. Solid lines represent interpolated values, while the dashed lines represent extrapolated estimates up to 200 stomachs. Shaded areas indicate 95% confidence intervals.

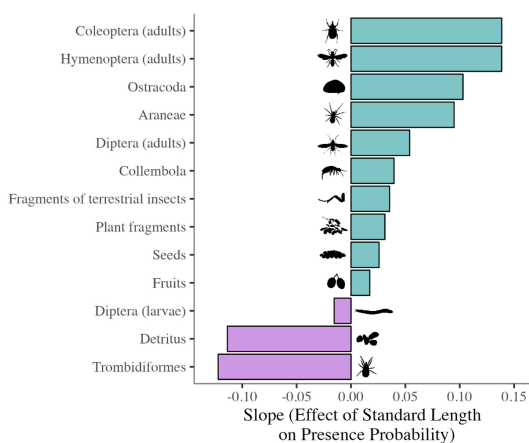


Figure 4. Slopes (coefficients) from the multivariate GLM showing the effect of standard length of *Mimagoniates lateralis* on the probability of occurrence of dietary items. Positive slopes (green bars) indicate that the probability of occurrence increases as fish size increases, while negative slopes (purple bars) indicate a decrease in probability with increasing length. Only dietary items with frequencies of occurrence $\geq 5\%$ were included in the analysis.

least for this species, endemic of blackwater restinga streams. The presence of a bird feather in the stomach content, albeit rare, further demonstrates the opportunistic nature of *M. lateralis*, which appears to consume a wide range of items available on the water surface. Although accidental ingestion cannot be ruled out, this finding contributes to the understanding of trophic dynamics and dietary plasticity in stream-dwelling fishes.

In addition to these items, detritus was also abundant in the diet. Although not exclusively allochthonous, detritus may comprise both organic matter from external sources, such as leaf litter and terrestrial insects, and autochthonous materials, including decaying invertebrates and microbial biofilms (Wallace & Webster, 1996). Therefore, their predominance should be interpreted with caution, given the uncertain origin. Distinguishing between autochthonous and allochthonous detritus poses methodological challenges due to material degradation and morphological similarity. Techniques such as stable isotope analysis and DNA metabarcoding can enhance this identification, allowing for more accurate inferences about resource origins (Whitaker et al., 2019). This distinction is crucial for understanding energy flow and habitat connectivity, providing a more accurate framework for trophic interpretations. As such, it warrants further investigation in future studies on this species.

Comparisons with congeners support the idea of terrestrial insects as key resources: for instance, *Mimagoniates rheocharis* Menezes & Weitzman, 1990, that inhabits fast-flowing streams in southern Brazil, which also have a diet that relies heavily on insects such as Diptera and Hymenoptera, alongside organic matter and microcrustaceans (Dufech et al., 2003). Overall, these findings emphasize the importance of riparian forests, which supply many of the allochthonous items—seeds, fruits, and arthropods—on which *M. lateralis* relies. Moreover, although *M. lateralis* is the most abundant fish in the blackwater streams of this basin (Ferreira et al., 2014), its feeding ecology has been understudied until now, highlighting the need for further research on this vulnerable tetra and its trophic interactions with other species.

Ontogenetic dietary shifts observed in *M. lateralis* are similar to those reported for *M. rheocharis*, where morphological and behavioral changes during growth expand feeding opportunities (Dufech et al., 2003), as well as for *Mimagoniates microlepis* (Steindachner, 1877), in which adults

consumed more allochthonous items than juveniles (Barreto & Aranha, 2006). These patterns suggest that larger individuals can handle bigger prey, while smaller ones presumably focus on smaller food items (Gouveia et al., 2022). In our study, this was evident in the increased consumption of adult insects (e.g., Coleoptera and Hymenoptera) by larger fish—likely facilitated by a larger mouth gape and greater capacity to handle such prey (Truemper & Lauer, 2005; Montaña et al., 2011). A similar trend, though on a smaller scale, was observed for Ostracoda and Araneae. Conversely, smaller individuals consumed higher proportions of detritus and smaller prey (e.g., Trombidiformes), possibly due to their limited mouth size and lower swimming capacity, making benthic feeding grounds a safer and more accessible option than foraging at the surface.

Therefore, our findings have important implications for the conservation of *M. lateralis*. Its reliance on detritus, terrestrial arthropods, and plant material highlights the vital role of riparian zones in supplying key food resources. However, deforestation and the resulting degradation of these habitats can significantly alter prey availability and disrupt the species' trophic structure, ultimately threatening its survival (Effert-Fanta et al., 2023). Therefore, conservation measures should prioritize the protection and restoration of riparian habitats to maintain the ecological integrity of blackwater stream ecosystems. By detailing the diverse diet of this vulnerable tetra, our study helps bridge knowledge gaps on *M. lateralis*, offering guidance for future management and conservation efforts.

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Data availability

All raw data and step-by-step data analysis are available in a GitHub repository (https://github.com/JH-All/Mimagoniates_lateralis_stream) for better reproducibility of the work.

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