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Spatial variation, more than ontogenetic, explains the diet of *Bryconamericus exodon* in two Pantanal rivers

Variação espacial, mais que a ontogenética, explica a dieta de *Bryconamericus exodon* em dois rios do Pantanal

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Abstract: Aim: Studies of natural variations in fish diet allow, in turn, a better understanding of environmental changes along the hydrological cycle that can affect resources and, hence, biodiversity conservation. With this in mind, the present study aimed to understand how spatial and ontogenetic aspects (using Standard Length as proxy) define dietary composition, trophic position and trophic niche breadth for a small characid (*Bryconamericus exodon*) in streams located in two rivers of the Brazilian Pantanal. We also assessed whether spatial differences influence the structuring of trophic networks. **Methods:** Fish were sampled monthly in the rainy season (October/2017 to March/2018) in four tributaries of the Negro and Apa Rivers, using different sampling methods. In the laboratory, fish were measured and weighed, followed by excision of stomach for posterior analysis. **Results:** We analyzed 211 individuals, 126 from the Apa River (Standard $length_{min}$= 11.28mm; Standard $length_{max}$= 43.53mm) and 85 from the Negro River (Standard $length_{min}$= 13.26mm; Standard $length_{max}$= 40.05mm), that consumed mainly aquatic insects (Alimentary $index_{Total}$= 87.97%), followed by terrestrial insects (Alimentary $index_{Total}$= 9.02%). Dietary composition was mainly influenced by spatial variation ($Pseudo\text{-}F_{1,194}$=12.21; p<0.001), followed by ontogenetic variation ($Pseudo\text{-}F_{1,190}$=7.23; p<0.001), however, for trophic niche breadth, we did detect a higher importance of spatial variation (t=4.71; p<0.001) and an absence of ontogenetic variation (t=1.24; p=0.213). No spatial variation was detected for complementary specialization (p=0.998); only connectance showed a significant variation (p=0.047) with higher mean values in the Negro River (C= 0.27 ± 0.016) when compared to those of populations in the Apa River (C=0.22 ± 0.019). In addition, trophic position was not influenced by spatial (t= -1.77; p=0.077) or ontogenetic (t=0.69; p=0.494) variations. **Conclusions:** *B. exodon* is considered an insectivorous species whose dietary composition can be explained more by spatial than ontogenetic variation.

Keywords: trophic niche breadth; trophic ecology; trophic position; complex network.

Resumo: Objetivo: O estudo das variações naturais na dieta dos peixes permite, por sua vez, uma melhor compreensão das alterações ambientais ao longo do ciclo hidrológico que podem afetar os recursos e, consequentemente, a conservação da biodiversidade. Com isso em mente, o presente estudo teve como objetivo compreender como os aspectos espaciais e ontogenéticos (usando o Comprimento padrão como proxy) definem a composição da dieta, posição trófica e amplitude de nicho trófico para um pequeno caracídeo (*Bryconamericus exodon*) em riachos localizados em dois rios do

Pantanal brasileiro. Também avaliamos se as diferenças espaciais influenciam na estruturação das redes tróficas. **Métodos:** Os peixes foram amostrados mensalmente na estação chuvosa (Outubro/2017 a Março/2018) em quatro tributários dos rios Negro e Apa, utilizando diferentes métodos de amostragem. Em laboratório, os peixes foram medidos e pesados, seguido de excisão do estômago para posterior análise. **Resultados:** Foram analisados 211 indivíduos, sendo 126 do Apa (Comprimento $padrão_{min}$= 11,28mm; Comprimento $padrão_{max}$= 43,53mm) e 85 do Negro (Comprimento $padrão_{min}$= 13,26mm; Comprimento $padrão_{max}$= 40,05mm), que consumiram principalmente insetos aquáticos (Índice $alimentar_{Total}$= 87,97%), seguidos de insetos terrestres (Índice $alimentar_{Total}$=9,02%). A composição da dieta foi influenciada principalmente pela variação espacial ($Pseudo\text{-}F_{1,194}$=12,21; p<0,001), seguida da variação ontogenética ($Pseudo\text{-}F_{1,190}$=7,23; p<0,001), no entanto, para amplitude de nicho trófico, detectamos uma maior importância da variação espacial (t=4,71; p<0,001) e ausência de variação ontogenética (t=1,24; p=0,213). Não foi detectada variação espacial para especialização complementar (p=0,998); apenas a conectância obteve uma variação significativa (p=0,047), com valores médios maiores no rio Negro (C= 0,27 ± 0,016) quando comparados aos das populações do rio Apa (C=0,22 ± 0,019). Além disso, a posição trófica não foi influenciada por variações espaciais (t=-1,77; p=0,077) ou ontogenéticas (t=0,69; p=0,494). **Conclusões:** *B. exodon* é considerada uma espécie insetívora, cuja composição da dieta pode ser explicada mais pela variação espacial do que pela variação ontogenética.

Palavras-chave: amplitude de nicho trófico; ecologia trófica; posição trófica; redes complexas.

1. Introduction

Variability in resource use is a typical characteristic in fish species with wide distribution (Neves et al., 2021). Accordingly, environments with higher degree of environmental changes along the hydrological cycle can meet the dietary needs of species that also have wider trophic niche breath (Ríos-Pulgarín et al., 2016). Such variability leads to Neotropical floodplain habitats with many generalist species and greater species diversity with little possibility of trophic niche overlap (Loureiro & Hahn, 1996; Abelha et al., 2001; Neves et al., 2021).

In dynamic and productive environments, such as those found in tropical regions, hydrological variations driven by the seasonality of floods and the resultant connectivity of environments can change the availability and variety of food items (Lowe-McConnell, 1999; Scanferla & Súarez, 2016; Gouveia et al., 2022). During floods, river flow increases, connecting aquatic and terrestrial habitats. This connectivity favors the entry of allochthonous material into the environment, creating micro-habitats for various species and serving as a source of energy and nutrients for a variety of aquatic organisms (Luiz et al., 2018).

Fish feeding is mainly associated with morphological adaptations, behavioral issues, the availability of resources in the environment and the quality of the environment, or, more specifically, the composition of riparian vegetation (Ferreira et al., 2012a). From this perspective, the same species of fish, but sampled in different environments, can show variability in food composition. Thus, the abundance, diversity and spatial distribution of food resources can reflect directly on the trophic niche breadth of ichthyofauna since species with more specialized diets are more likely to be affected by seasonal fluctuations (Abelha et al., 2001).

Apart from spatial variations, ontogenetic variations in dietary composition are common in many animals (Nakazawa, 2015; Sánchez-Hernández et al., 2019), mainly in response to variations in individual characteristics, such as mouth size and energetic need, which are, in turn, important in defining growth rate, fitness and survival (Choi & Suk, 2012). Thus, considering such characteristics, it is common for small fish to limit themselves to catching small prey, while larger fish catch larger prey (Nakazawa, 2017). However, while a more positive relationship is evident between trophic position and body size for aquatic predators (Potapov et al., 2019), this is not a hard-and-fast rule (Layman et al., 2005), as reported by Fernando & Súarez (2021).

Many Neotropical fish species are predominantly planktivorous during juvenile phase (Gerking, 1994; Silva & Bialetzki, 2019), changing diet composition along growth, allowing the consumption of larger prey with higher energetic return (Huss et al., 2013). Such differences in food composition between juvenile and adult fish during ontogenetic development as result from morphological and physiological factors as well as response of different spatial distribution among each size classes.

The relative effects of ontogenetic and environmental variation on dietary composition are, however, less evaluated, except for the work of Wang et al. (2019). In general, only spatiotemporal effects have been evaluated with larger spatial biasing toward the Upper Paraná River Basin, as evidenced by more studies when compared to those reporting on other regions. Here, we are interested in characterizing the dietary composition of a widely distributed small fish species, anticipating that such study will provide more understanding about the role of distribution range, niche breadth and environmental variability along hydrological fluctuation.

The genus *Bryconamericus* is composed of smaller species widely distributed in South America (Mirande, 2019). In particular, *Bryconamericus exodon* and *B. iheringii* are the only such species present in the Paraguay River Basin (Fricke et al., 2023). Of the two, *B. exodon* is the only species registered in the Brazilian portion of the Paraguay Basin. The present study aimed to understand how spatial and ontogenetic aspects (using Standard Length as proxy) define dietary composition, trophic position and trophic niche breadth for the small characid (*Bryconamericus exodon*) in tributaries located in two rivers of the Brazilian Pantanal. We also assessed whether spatial differences influence the structuring of trophic networks.

2. Material and Methods

2.1. Study area

The Paraguay River Basin stretches over a flood plain of nearly 1.300.000 km^2 in which the Brazilian portion represents near 140.000 km^2 with many sub regions, each one with different hydrological and ecological characteristics. In our study, we focused on two subbasins, the Apa and Negro Rivers. The Negro River presents higher vegetative cover when compared to Apa (Riveros et al., 2021), along with differences in mean water conductivity ($Mean_{Negro}$=34.4 µS/cm^{-1}; $Mean_{Apa}$=437.5 µS/cm^{-1}). All sites sampled have sandy soil, little aquatic vegetation and high current velocity ($Mean_{Negro}$=0.42 m/s; $Mean_{Apa}$=0.42 m/s).

2.2. Sampling

Samples were collected in two tributaries each from the Negro and Apa Rivers, Upper Paraguay River, monthly from October/2017 to March/2018 (Figure 1). We used rectangular sieves (0.8×1.2 m) and seine nets (1.5×5 m) with approximately 2 mm mesh. Sampled fish were anesthetized using clove oil and then fixed in formalin (10%) for at least four days. Scientific field sampling was approved by the Ethical Committee of Mato Grosso do Sul State University (#010/2014) and Instituto Chico Mendes de Conservação da Biodiversidade (#13458-1).

2.3. Laboratory analysis

After preservation in 70% alcohol, each individual was measured, and afterwards, the stomach was excised to analyze the contents. Stomach contents were assessed with the aid of an optical microscope and quantified by the volumetric

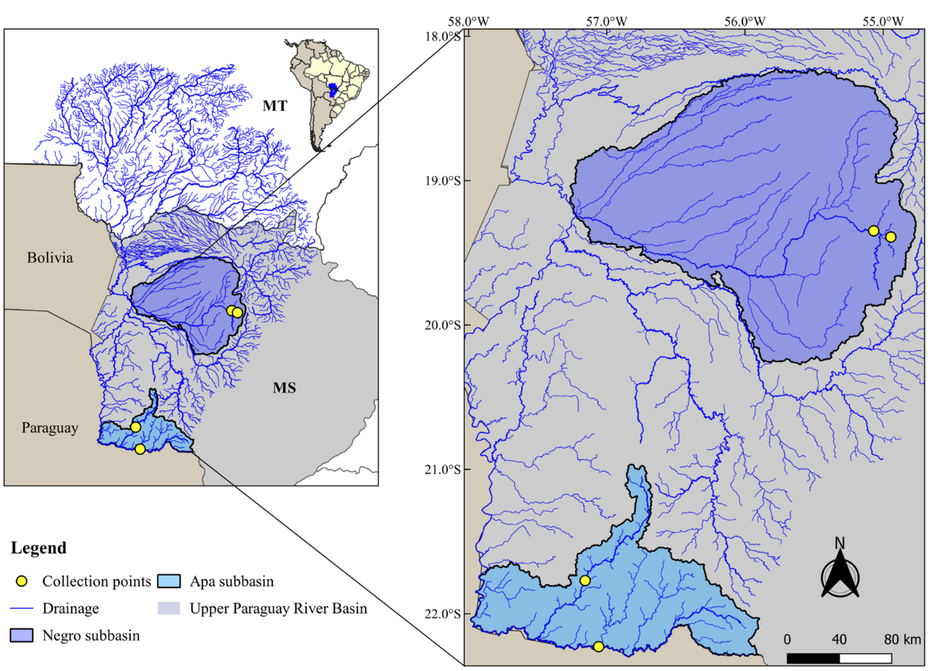

Figure 1. Sampled sites (yellow dots) of *Bryconamericus exodon* in Apa and Negro subbasins in the Upper Paraguay River Basin.

method (Hellawell & Abel, 1971). The volume of each food item was assigned a percentage of the total volume of all stomach contents (Hyslop, 1980), using a glass counting plate. Food item volume was obtained in mm^3 and then converted to ml. The volume and frequency of occurrence of each group of alimentary items were used to estimate the Alimentary Index (IAi), as proposed by Kawakami & Vazzoler (1980), and calculated as Equation 1:

$$IAi = Fi * Vi / \sum_{i=1}^{n}\left(Fi * Vi\right) \quad (1)$$

where *Fi* is food item occurrence frequency (%); and *Vi* is food item volume (%).

2.4. Statistical analysis

Aiming to understand different food items consumed by *B. exodon* in the spatial context, we used binary and quantitative data (relative abundance). For each matrix (binary and quantitative), data were organized in a manner that treated individuals as rows and feeding items as columns to estimate connectance and complementary specialization (H_2') for each network. Connectance is a measure of cohesion, evaluating the observed connections among fish and prey in comparison to possible interactions (Pimm, 1982). On the other hand, complementary specialization (Blüthgen et al., 2007) is a measure of the specialization level of a trophic network wherein higher levels of selectivity of feeding items are correlated with higher H_2'. These estimations were made using the *'bipartite'* package (Dormann et al., 2014; Dormann, 2020), the *'networklevel'* function, *'connectance'* and *'H2'*, respectively.

Since connectance is a network metric, we established a procedure to use 40 random individuals of each population (Apa and Negro) and 1000 permutations. Then, estimates of connectance and H_2' were random or not. Null models were generated using the *'mgen'* and *'r2dtable'* functions to test these variables. The *'mgen'* function is an algorithm based on a probability matrix and a desired number of interactions (Vázquez et al., 2009), while the *'r2dtable'* is used to weight networks (Patefield, 1981).

We also estimated the z-score for each network to determine any statistical differences between obtained values for each metric and expected by simple chance, calculated as *observed – mean (nulls) / standard deviation (nulls)*. Z-score values above 1.96 indicate significant difference (Durán et al., 2019).

To evaluate the role of fish size on trophic network structure for *B. exodon*, we generated size classes of 5mm for each subbasin and weighted the importance of feeding items. The last size class was larger than the others given a 10mm range to avoid a smaller number of individuals. We used a permutational multivariate analysis of variance based on distances (PERMANOVA) with 999 permutations to evaluate whether diet varies spatially (subbasin) and ontogenetically (using Standard Length classes as proxy) with diet converted into Bray-Curtis distance. For this procedure, we used the *'adonis2'* function in the *'vegan'* package (Oksanen et al., 2016).

For each individual, we estimated a trophic niche breadth based on *'Levins'* niche breath index, using the *'niche.breadth'* function in the *'spaa'* package (Zhang et al., 2016). We also estimated trophic niche position of each individual according to the equation proposed by Vander Zanden et al. (1997) and calculated as Equation 2:

$$TP = \sum\left(Vi * TPi\right) + 1 \quad (2)$$

where *TP* = trophic position of each feeding item; and *Vi* = relative volume of each feeding item.

We further realized a permutational analysis of covariance using the *'lmperm'* function from the *'permuco'* package (Frossard & Renaud, 2019) to test the hypothesis that subbasins (factor) and standard length (covariable) explain variation in trophic niche breadth and trophic position for *B. exodon* with 999 permutations to provide a significance estimation. Standard length was previously converted to log_2+0.1. All analyses were made in R environment (R Development Core Team, 2021).

3. Results

We analyzed a total of 211 *B. exodon* individuals, 126 from the Apa River (Ls_{min}= 11.28mm; Ls_{max}= 43.53mm) and 85 from the Negro River (Ls_{min}= 13.26mm; Ls_{max}= 40.05mm). A total of 16 individuals presented empty stomachs and set aside for posterior analysis.

The dietary items we found in both rivers consisted of 26 items classified into 8 food categories to estimate alimentary index and bipartite network. Aquatic insects were the main feeding category (IAi_{Apa}= 94.96% and IAi_{Negro}= 70.45%), followed by terrestrial insects (IAi_{Apa}= 4.70% and IAi_{Negro}= 18.55%). Other items, e.g., detritus, plant remains and others, presented more importance in the Negro River population. Filamentous algae, Arachnida and Annelida represented no more than 2%

(Figure 2). From these results, it can be concluded that *B. exodon* has an insectivorous diet.

Negro and Apa populations have network connectance (C_{Apa}=0.20, z-score$_{Apa}$=19.73, p=0.001 and C_{Negro}=0.24, z-score$_{Negro}$=14.09, p=0.001) and complementary specialization ($H_2'{}_{Apa}$=0.46, z-score$_{Apa}$ =10.6, p=0.001 and $H_2'{}_{Negro}$= 0.42, z-score$_{Negro}$=12.13, p=0.001) that differ from random (Figure 3); however, only connectance showed significant spatial differences (p<0.05).

Interestingly, our PERMANOVA results show that dietary composition mainly changed according to subbasin (Pseudo-$F_{1,194}$=12.21; p<0.001), followed by standard length (Pseudo-$F_{1,190}$=7.23; p<0.001). The bipartite trophic network using relative volume of food categories showed differences in detritus and aquatic insect consumption by each size class in the Apa and Negro Rivers, as evidenced by the width of links (Figure 4). Detritus was consumed in a very proportional way by individuals in the Apa, which was not the case in the Negro, as detritus was not present in the diet of even the smallest individuals (10-15mm) and was consumed in smaller quantities by the 15.1-20mm size classes, compared to the other size classes. Aquatic insects were present in the diet of fish of all sizes; however, their consumption was higher for individuals between 15.1 and 25mm in both subbasins. Smaller size classes mainly consumed terrestrial and aquatic insects when compared to larger fishes that presented higher variability in trophic resource use. This means that larger fish interacted with practically all trophic categories, while smaller fish mainly consumed insects (Figure 4).

Despite differences in dietary composition along the fish length gradient, we did not observe any significant effect of standard length on trophic niche breadth (t=1.24; p=0.213) or trophic position (t=0.69; p=0.494). Trophic niche breadth is different between subbasins (Mean$_{Apa}$= 2.50 ± 0.83 and Mean$_{Negro}$= 3.18 ± 1.06) (t=4.71; p<0.001), but trophic position did not differ according to subbasin (Mean$_{Apa}$= 3.05 ± 0.16 and Mean$_{Negro}$= 3.01 ± 0.17) (t= -1.77; p=0.077) (Figure 5).

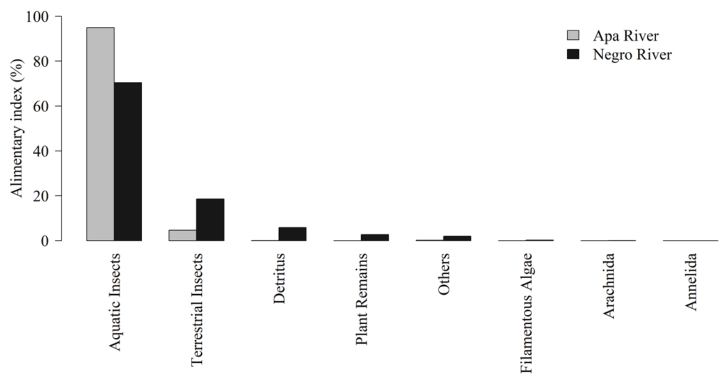

Figure 2. Alimentary index (%) for *Bryconamericus exodon* in the Apa and Negro subbasins, Upper Paraguay River, Brazil.

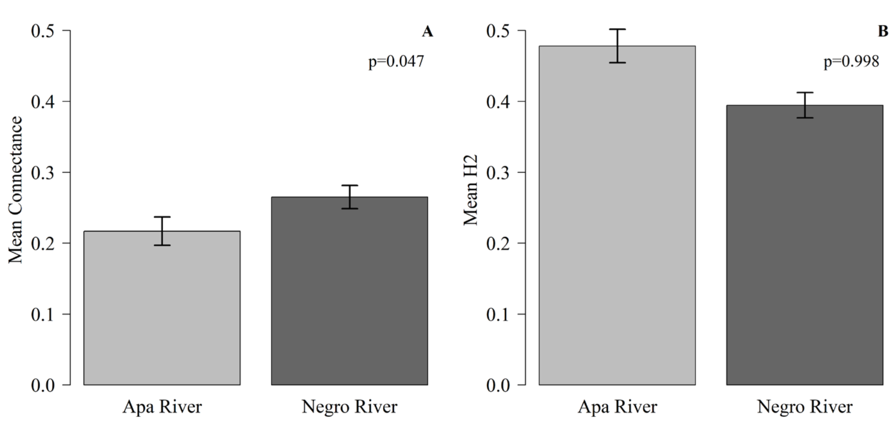

Figure 3. Mean and standard deviation for connectance (A) and complementary specialization (B) for trophic network of analyzed populations of *B. exodon* in the Upper Paraguay River Basin.

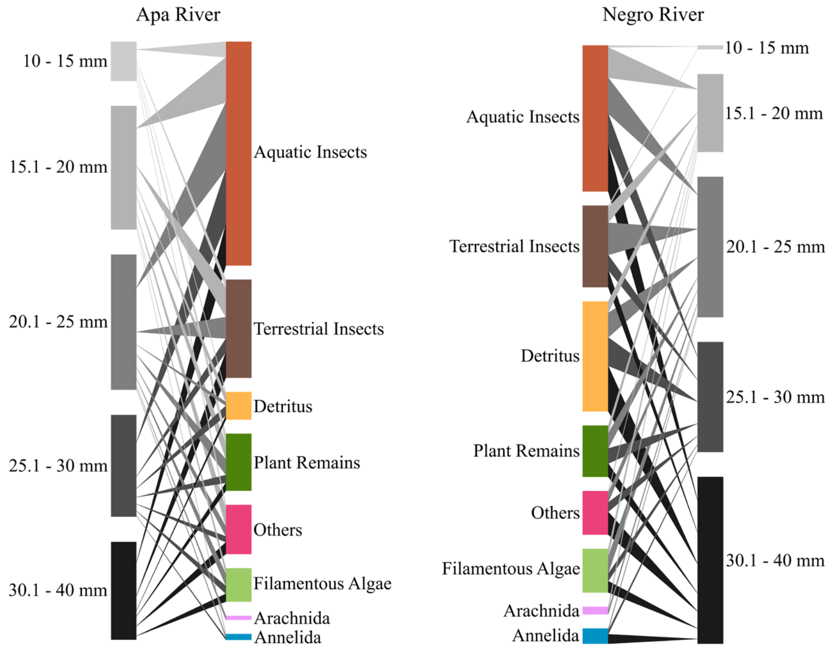

Figure 4. Trophic bipartite network for *B. exodon* in the Apa and Negro subbasins of the Upper Paraguay River Basin. Gray boxes represent size gradient, and other colored boxes represent alimentary items. Link width represents trophic interaction intensity.

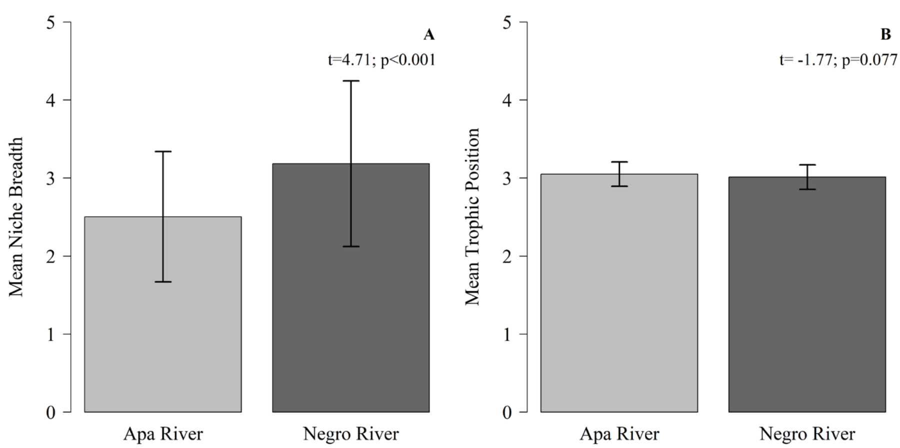

Figure 5. Mean and standard deviation of trophic niche breadth (A) and trophic position (B) between populations of *B. exodon* sampled at two subbasins in the Upper Paraguay River Basin.

4. Discussion

Bryconamericus exodon is usually categorized as insectivorous (Russo et al., 2004; Novakowski et al., 2008), and our data corroborate this classification. Other studies found this species to be predominantly diurnal, occurring mainly in the littoral portion and primarily feeding on autochthonous prey or drifting terrestrial insects (Severo-Neto et al., 2023).

Insects are predominant items in the diet; however, other items, such as filamentous algae and different groups of invertebrates, also occur in the diet of *B. exodon*, showing that this species presents higher feeding plasticity than other Neotropical fish species (Lowe-McConnell, 1999; Abelha et al., 2001), mainly in response to spatiotemporal changes in the availability of trophic items. Despite this higher plasticity, insects remain a staple prey type for *B. exodon*.

Despite the predominance of insects, we still observed spatial and ontogenetic variation in dietary composition which can be (for spatial variation) related to environmental differences between the sampled rivers (Pinto & Uieda, 2007; Neves et al., 2018), as observed in other species that mainly consume insects in their diet (Ferreira et al., 2012b; Astudillo et al., 2016; Virgilio et al., 2018; Fernando & Súarez, 2021) or exhibit variations in prey use corresponding to variation in mouth size or energetic need along fish growth (Abelha et al., 2001; Ramos-Jiliberto et al., 2011).

More specifically, deforested areas, or areas with less vegetative cover, are more affected by habitat degradation (Brejão et al., 2018) in response to erosion, which, in turn, affects trophic network and ecosystem services (Nakano & Murakami, 2001; Zeni et al., 2017). Thus, since the Negro River presents higher riparian cover compared to the Apa River (Riveros et al., 2021), it can also offer a greater availability of allochthonous items to *B. exodon*, resulting in a more complex trophic network and less specialized trophic network when compared to the Apa population.

The effect of riparian cover on fish dietary composition is also seen in *Astyanax lineatus*, which inhabits the headwaters of the Miranda and Apa Rivers, showing that fish in streams with lower riparian cover more frequently consume filamentous algae compared to fish in pristine streams (Fernando & Súarez, 2021), suggesting that more light input alters trophic resource availability in these streams.

Changes in the trophic position of fish are usually driven by abiotic and biotic factors (Sánchez-Hernández & Amundsen, 2018) since habitat heterogeneity offers the availability of more diverse resources to fish, mainly for omnivorous species. In these conditions, predators are typically larger in size than their prey, and this positive relationship is more common for aquatic predators compared to terrestrial predators (Potapov et al., 2019). In fact, changes in diet along fish growth affect the dynamics of aquatic communities, altering intra- or interspecific competition rate (Nakazawa, 2015) as a direct response to prey diversification (Bozza & Hahn, 2010), mainly in Neotropical fishes (e.g., Abilhoa et al., 2009; Fernando & Súarez, 2021; Lampert et al., 2022). However, this is not a hard-and-fast rule, as indicated by Layman et al. (2005).

Ontogenetic variations in fish diet are common (Dias et al., 2017; Sánchez-Hernández et al., 2019), and these were observed in our study. However, the observed changes in dietary composition were not sufficient enough to cause changes in trophic position. If prey occupy the same trophic position as that occupied by the same prey in the past, then trophic position is maintained. Since *B. exodon* changes prey types that occupy the same trophic position along its growth, our results suggest that changes in dietary composition of the species were not caused by changes in trophic position at the evaluated scale (spatial and ontogenetic). Nonetheless, temporal changes still can affect the feeding ecology of *B. exodon*. This result, when accompanied by the absence of changes in trophic niche breadth (Pearson r= 0.14), suggests that larger fish use different prey, but with similar niche position along fish growth. Thus, differences in prey characteristics can be more associated with energetic return or the ability to capture and manage different prey species. On the other hand, the absence of relationship between standard length and trophic niche breadth suggests that intraspecific competition is not important for *B. exodon*.

Trophic niche breadth can also be influenced by environmental differences among habitats since higher net productivity can be created by more specialized populations in response to higher prey availability (Sánchez-Hernández et al., 2021). For our study area, we did not collect information about primary productivity; however, the Apa River does have higher water conductivity compared to the Negro River, suggesting more prey availability in the Apa River. This suggests that the Negro River with its larger riparian cover could offer a higher diversity of allochthonous prey, thus generating higher trophic niche breadth, whereas in the Apa River, higher water conductivity could lead to higher primary productivity, offering larger autochthonous prey to *B. exodon*.

In summary, our results show that *B. exodon* is mainly an insectivorous species with larger spatial differences in dietary composition. Neither ontogenetic nor spatial changes were observed in trophic position while niche breadth vary only in spatial. These results could be caused by changes in the consumption of prey species that occupy the same trophic position. Therefore, studying the ecological traits of widely distributed fish species should lead to a better understanding of how changes in local and regional environments can affect fish biology.

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