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Ecomorphological and behavioral differences mediating resource partitioning among syntopic stream fish species in the Amazon Rainforest

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ABSTRACT

Introduction: Generalist trophic strategies and opportunistic feeding habits of nektonic fish species inhabiting oligotrophic streams in the Amazon Rainforest suggest that minor morphological and niche differences can mediate the occurrence of closely related species in sympatry, alleviating interspecific competition for resources.

Objective: To analyze the ecomorphology, diet composition, vertical and horizontal habitat use, and foraging behavior of four Characiform species in syntopy, to understand resource partitioning and species coexistence.

Methods: From August to October 2011 (dry season), up to 30 specimens of each species were collected from each of eight sampled streams in the Adolpho Ducke Forest Reserve, Amazonas, Brazil, for ecomorphological analyses, with up to 10 of these used for stomach content analysis. Foraging behavior was quantified through underwater observation of vertical and horizontal space use and foraging frequency in the water column. The dietary importance of food items was determined using the Feeding Index (FI_i), and ecomorphological attributes were used to characterize body shape and fin morphology.

Results: Differences were detected in foraging behavior and habitat use. *Hyphessobrycon.* aff. *melazonatus* predominantly occupied the stream margins, and the other species utilized the channel. Additionally, only *H.* aff. *melazonatus* exhibited a difference in stomach content composition. Ecomorphological characteristics showed divergence among species, particularly in body shape, mouth size, and orientation.

Conclusions: The combined analysis demonstrated that differences observed here may mediate syntopic coexistence by alleviating interspecific competition through resource partitioning. The system's sensitivity to anthropogenic impacts and climate change were highlighted on food availability and trophic relations of Amazon stream fishes and underscore the need for headwater stream conservation.

Key words: Amazonian fishes; oligotrophic streams; habitat use; morphology; co-occurrence.

RESUMEN

Diferencias ecomorfológicas y comportamentales que median la repartición de recursos entre especies de peces de arroyos sintópicos en la selva amazónica

Introducción: Las estrategias tróficas generalistas y los hábitos alimenticios oportunistas de las especies de peces nectónicos que habitan en arroyos oligotróficos de la selva amazónica sugieren que pequeñas diferencias morfológicas y de nicho pueden mediar la coexistencia de especies estrechamente relacionadas en simpatría, aliviando la competencia interespecífica por los recursos.

Objetivo: Analizar la ecomorfología, la composición de la dieta, el uso vertical y horizontal del hábitat, y el comportamiento de forrajeo de cuatro especies de Characiformes en sintopía, para comprender la partición de recursos y la coexistencia de especies.

Métodos: Entre agosto y octubre de 2011 (estación seca), se recolectaron hasta 30 especímenes de cada especie en cada uno de los ocho arroyos muestreados en la Reserva Forestal Adolpho Ducke, Amazonas, Brasil, para análisis ecomorfológicos. De estos, hasta 10 fueron utilizados para el análisis de contenido estomacal. El comportamiento de forrajeo se cuantificó mediante observaciones subacuáticas del uso del espacio vertical y horizontal, y la frecuencia de forrajeo en la columna de agua. La importancia dietética de los ítems alimenticios se determinó utilizando el Índice de Alimentación (FI_i), y se caracterizaron atributos ecomorfológicos relacionados con la forma del cuerpo y la morfología de las aletas.

Resultados: Se detectaron diferencias en el comportamiento de forrajeo y el uso del hábitat. *Hyphessobrycon* aff. *melazonatus* ocupó predominantemente las márgenes de los arroyos, mientras que las otras especies utilizaron el canal. Además, solo *H.* aff. *melazonatus* mostró una diferencia en la composición del contenido estomacal. Las características ecomorfológicas mostraron una divergencia entre las especies, particularmente en la forma del cuerpo, el tamaño y la orientación de la boca.

Conclusiones: El análisis combinado demostró que las diferencias observadas pueden mediar la coexistencia sintópica al aliviar la competencia interespecífica mediante la partición de recursos. Se destacó la sensibilidad del sistema a impactos antropogénicos y al cambio climático en la disponibilidad de alimentos y las relaciones tróficas de los peces de arroyos amazónicos, subrayando la necesidad de conservar los arroyos de cabecera.

Palabras clave: peces amazónicos; arroyos oligotróficos; uso del hábitat; morfología; co-ocurrencia.

INTRODUCTION

Understanding the feeding tactics and habitat use of sympatric fish species that are phylogenetically close and show similar habits is crucial for comprehending species coexistence, interspecific ecological interactions and resource partitioning (Lowe-McConnell, 1999). Physical environmental factors can influence habitat use dynamics and feeding behavior among phylogenetically related species (Leitão et al., 2015; Peres-Neto, 2004). Resource partitioning in these environments is an important ecological factor that tends to reduce interspecific competition, thus facilitating coexistence (Aranha et al., 1998; Baldasso et al., 2019; Peres-Neto, 2004). However, there is no consensus on the relative importance of these factors (both physical and intrinsic to the species) in the dynamics of resource partitioning that mediate the coexistence of sympatric species in species-rich Amazonian streams (Baldasso et al., 2024; Delariva & Neves, 2020).

The coexistence of species through resource partitioning can be reflected in patterns of body sizes and/or combinations of morphological traits within communities (Manna et al., 2020; Shukla & Bhat, 2022). Subtle morphological differences can allow the coexistence of closely related species from a same family. For instance, the relationship between body size and shape can indicate how space is utilized by stream fishes (Brejão et al., 2018; Santos et al., 2019; Wolff et al., 2023). These studies emphasize the fine tuning between fish body shape and functional groups with the characteristics of the aquatic environment, and how this can influence swimming performance, particularly regarding foraging behavior, space use, feeding behavior and the structure of fish assemblages. Body shape, fin morphology, and mouth orientation reflect the use of different microhabitats by fish, indicating adaptations to specific conditions of water velocity, depth, and substrate type (Casatti & Castro, 2006; Lamouroux et al., 1999; Langerhans et al., 2003; Teresa et al., 2021). Additionally, the relationship between mouth size and orientation can indicate the type and position of food relative to the fish and the water column stratum in which the fish forages (Casatti & Castro, 2006), as well as the origin (allochthonous or autochthonous) of the consumed food items (Mazzoni et al., 2010).

However, external morphology alone is not always a good predictor of trophic niche (Casatti & Castro, 2006; Manna et al., 2017). In such cases, foraging behavior can provide important complementary explanations for these differences (Ceneviva-Bastos & Casatti, 2007; Costa-Pereira & Severo-Neto, 2012). Direct behavioral observation is generally the most effective method for obtaining such information. The use of diving techniques for direct fish observation is still uncommon in freshwater aquatic environments (Leite et al., 2023) but has proven highly effective in studies aiming to elucidate habitat use and foraging characteristics of species (Brejão et al., 2013; Buck & Sazima, 1995; Casatti, 2002; Nunes et al., 2020; Sabino & Castro, 1990; Sabino & Zuanon, 1998; Sazima, 1986; Zuanon et al., 2006).

Amazonian streams, regionally known as *igarapés*, are small water courses characterized by the presence of discrete habitats and limited space availability, making them ideal for exploring hypotheses about ecological interactions of fish with their environment. Among the species inhabiting these streams, the most diverse and abundant group is Characiformes, especially represented by nektonic fish species (Dagosta & de Pinna, 2019; Toledo-Piza et al., 2024), which have very active individuals, exhibiting pronounced exploratory behavior and diverse and opportunistic feeding strategies (Barros et al., 2017; Carvalho et al., 2007; Lowe-McConnell, 1999; Sabino & Zuanon, 1998; Sazima, 1986). Phylogenetically related species may exhibit more significant morphological similarities and conserved ecological niches (Casatti & Castro, 2006; Peres-Neto, 2004; Wiens et al., 2010; Winemiller, 1991), which, in theory, increases niche overlap and the likelihood of interspecific competition, particularly in oligotrophic environments such as small streams in the Amazon Rainforest (Henderson & Walker, 1986). In the Adolpho Ducke Forest Reserve, previous studies (Barros et al., 2017; Espírito-Santo et al., 2009; Mendonça et al., 2005) have documented the syntopic occurrence (individuals of two or more species sharing the same microhabitat) of various nektonic species in several of these streams, including *Bryconops inpai* Knöppel, Junk & Géry, 1968, *Bryconops giacopinii* (Fernández-Yépez, 1950) and *Iguanodectes geisleri* Géry, 1970 (Iguanodectidae), and *Hyphessobrycon melazonatus* Durbin, 1908 (Characidae). These species exhibit diurnal habits, are considered trophically opportunistic, and are frequently observed sharing the same stream stretches, suggesting potential niche overlap among them. Additionally, the conservation of such streams and species is relevant due to the high sensitivity to anthropogenic pressures (where they can act as bioindicators), the interface of streams with the forest, the maintenance of the watershed integrity, and the potential for ornamental use of the species.

Considering these ecological aspects of oligotrophic streams, this study aimed to analyze ecomorphological characteristics, diet, foraging behaviour, and space use of four phylogenetically close and syntopic nektonic species, investigating whether resource partitioning and morphological dissimilarity act as mediators of their coexistence in Amazonian streams.

MATERIALS AND METHODS

Study area: The study was conducted at the Reserva Florestal Adolpho Ducke (RFAD), a 10 000-ha area of primary lowland tropical rainforest located North of Manaus, Amazonas State, Brazil (02º 55’ and 02º 53’S & 59º 58’W). The study was conducted in the Acará (AC) and Bolivia (BO) sub-basins, both of which draining to the Tarumã-Açu River Basin, a tributary on the left bank of the Negro River. Fish were observed and collected from a 50-meter stretch along the stream banks. Three of these streams were first-order (AC13, BO12, and BO13), four were second-order (AC23, BO20, BO21, and BO22), and one was a third-order stream (AC30), following the Horton-Strahler classification system (Petts, 1994), resulting in a total of 8 sampled streams (SMF 1).

Upland streams (regionally known as “terra firme”) exhibit a meandering streambed and a high interface with the riparian forest. The streambed alternates between riffles, characterized by high water flow, shallow depth, and a substrate predominantly consisting of sand, gravel, and small rocks, and pools, which are deeper and have a substrate mainly composed of coarse particulate organic matter (leaf litter), fine particulate organic matter, small branches, and sand (Fittkau, 1967). The banks are abundant with shrubby plants, leaves, and roots from the riparian vegetation, and submerged trunks create natural barriers that contribute to longitudinal heterogeneity. The water has a pH of approximately 4.5 due to the presence of fulvic and humic acids resulting from the decomposition of plant organic matter. The average water temperature is 25 °C with minimal variation throughout the year. These are oligotrophic streams, where the primary autotrophic productivity is very low, associated with the scarcity of inorganic compounds in the water and dense shading from the riparian forest canopy (Junk & Furch, 1985; Walker, 1995). The studied streams are deeply inserted in the Reserve and are free from direct anthropogenic disturbances.

The streams and species *Bryconops giacopinii* (GIA), *Bryconops inpai* (INP), *Iguanodectes geisleri* (GEI) and *Hyphessobrycon* aff. *melazonatus* (MEL) were selected based on records of species abundance and composition previously conducted by Espírito-Santo et al. (2009) and Mendonça et al. (2005), which provided information on different combinations of species co-occurrence in these streams (SMT 1).

First, a search was carried out in the collection database, and the streams in which the most abundant nektonic species co-occurred were identified. After this step, we returned to these streams to double-check for the presence of the species, to carry out the collections and to make underwater observations of their behavior.

Naturalistic observations: Behavioral data were recorded through direct observation of fish during snorkeling sessions (Sabino, 1999), using a visual scanning method (Altmann, 1974). In this method, a single observation session involved recording the frequency of occurrence (FO %) of foraging events of an individual or a group of the same species over 3 min. The observations included the horizontal space use, distinguishing between the Excavational Margin (EM), identified by bank excavation caused by water flow and velocity; the Depositional Margin (DM), where sediments are deposited due to water flow eddies; and the Channel (C), the central position relative to the stream banks. Vertical space use was categorized into the Upper Third (UT), Middle (MT), and Lower Third (LT) of the water column. Each of these horizontal and vertical segments was considered a distinct microhabitat due to their unique characteristics of water velocity, food availability, and depth, which significantly influence local fish composition and abundance (Barili et al., 2011; Brejão et al., 2013; Leitão et al., 2015).

The underwater observations were conducted in the same streams where the specimens were subsequently collected. The diver surveyed a 50-meter stretch of the stream for two hours (between 11:00 AM and 1:00 PM), a time when the species are more active (Sabino & Castro, 1990; Sabino & Zuanon, 1998; Sazima, 1986). After a 10-minute acclimation period at each site, observation sessions began, consisting of 3 min of recording foraging events and habitat use of individuals (or groups) present at the EM, DM and C, one species at a time, at five observation sites (evenly spaced along the 50-meter stretch of the stream). A single foraging event was defined as any behavior directed to a food item, whether or not followed by manipulation or ingestion of the item. During the direct observation sessions, the following foraging event types were recorded: i) surface food picking (Keenleyside, 1979); ii) drift food picking in the water column (Grant & Noakes, 1987); and iii) bottom substrate food picking (Sazima, 1986).

Stomach contents: Each 50-meter section of the stream was sampled in a standardized manner over two hours by two collectors using a small hand-held seine net (mesh size 5 mm between opposite knots) and dip nets. Block nets were installed at the beginning and end of the section to prevent fish escape and optimize capture (Mendonça et al., 2005). After capture, individuals were immersed in an anesthetic solution, one liter of water and five drops of Eugenol (clove oil). When opercular movement ceased, specimens were fixed in 10 % formalin and subsequently preserved in 70 % ethanol. INPA's Institutional Ethics Committee for Animal Use in Research authorized field and laboratory protocols (permit # 043 / 2012 granted to GGB).

Stomach content analysis was performed on ten specimens of each species from each of the eight streams (10 stomachs/stream/species). Following stomach dissection, the degree of fullness (FD) was determined according to Goulding et al. (1988).

For each species, the frequency of occurrence (F_i) (Hyslop, 1980) of each food item in the stomachs was calculated relative to the total number of stomachs containing food. The relative volume (V_i) of each food item was estimated visually, as the percentage of the total volume of each item in the stomach, with the total volume considered as 100 % (cf. Hynes, 1950, modified by Soares, 1979). The values of V_i were multiplied by their respective FD to correct the relative volumes of different food items present in the stomachs. Food items were identified to the Taxonomical Order (Merritt & Cummins, 1996; Passos et al., 2007; Pes et al., 2005; Salles et al., 2004).

To evaluate the importance of each ingested item for the species, the Food Index (FI_i) (Kawakami & Vazzoler, 1980) was applied using the following formula:

$$FI_i = F_i V_i \,/\, [\Sigma\, (F_i V_i)]^{-1}$$

where FI_i = food index, F_i = frequency of occurrence of item i, and V_i is the relative volume of item i.

Food items were also classified according to their origin (autochthonous or allochthonous). Data analysis was performed for each species, and comparisons among them were made using Pearson's Chi-square test (Pearson, 1900).

Morphological measurements: Morphometric analyses were conducted on 22 specimens of each species from the eight sampled streams, with the following size ranges: GIA (20.6-97.0 mm); MEL (22.7-39.0 mm); INP (36.0-90.6 mm); and GEI (27.8-50.8 mm).

Seventeen linear morphometric measurements based on Gatz (1979) and Watson & Balon (1984) were taken point-to-point using a digital caliper (0.1 mm precision) and related to standard length (SL). Five body and fin area measurements, excluding the anal fin (adapted from Beaumord & Petrere, 1994), were made for each specimen using the projected image on graph paper. Fins were extended on the paper and outlined with a pencil. The fin areas were then related to body area to maintain proportionality, regardless of size variation among specimens. The outlines were scanned, and the pixels representing morphological structures were converted to cm^2 using a known area scale ($273\ px = 1\ cm^2$) with ImageJ.

The morphometric measurements and areas were used to calculate 18 ecomorphological attributes that potentially reflect habitat use and feeding behavior aspects of the species (Gatz, 1979; Watson & Balon, 1984): body compression index (BCI), relative body height (RBH), relative caudal peduncle length (RCPL), caudal peduncle compression index (CPCI), ventral flattening index (VFI), relative dorsal fin area (RDFA), relative pectoral fin area (RPFA), relative pelvic fin area (RPvA), relative caudal fin area (RCFA), pectoral fin configuration ratio (PFCR), caudal fin configuration ratio (CFCR), relative head length (RHL), relative eye position (REP), relative eye size (RES), relative mouth width (RMW), relative mouth height (RMH), mouth configuration ratio (MCR), and mouth orientation (MO).

Data analysis: The Frequency of Occurrence (FO %) data for horizontal and vertical space use were transformed into proportions and tested for differences between strata among species (e.g., 4 species X Channel), and for each species among strata (e.g., GIA X DM/EM/C) using a two-way ANOVA with post-hoc Tukey's test at a significance level of $\alpha = 0.05$. FO % data for foraging events were also tested with a two-way ANOVA, comparing strata among species (e.g., 4 species X mid-water) and for each species among strata (e.g., GIA X mid-water/surface). These analyses were conducted using Statistica 6.0 (Statsoft, 2001).

A non-parametric MANOVA was performed with the Bray-Curtis similarity index using the V_i values for each food item to test the significance of differences in stomach content among species. To compare these differences between species pairs, a MANOVA with the same similarity index was performed, including Holm's correction (Holm, 1979) (as cited in R Development Core Team, 2011), with adjusted significance level ($p < 0.006$) due to multiple pairwise comparisons.

To order the species in the ecomorphological space, a Principal Component Analysis (PCA) was performed using the values of the 18 attributes. The axes with eigenvalues greater than one were retained for interpretation (Motta et al., 1995). This analysis was conducted using the R statistical software (R Development Core Team, 2011).

To test the significance of morphological differences among species, using the eight principal components with the highest eigenvalues from the PCA, a non-parametric MANOVA was applied with the Bray-Curtis similarity index, including Holm's correction (Holm, 1979) for pairwise comparisons (as cited in R Development Core Team, 2011).

RESULTS

Behavior and habitat use: A total of 711 observation sessions of fish behavior and habitat use were conducted, comprising 341 sessions for MEL (2 356 individuals), 218 for GIA (1 998 individuals), 88 for INP (243 individuals), and 64 for GEI (95 individuals), resulting in a total observation time of 35 hours and 55 min.

Bryconops giacopinii, INP, and GEI predominantly used the stream channel, with percentages of 80, 87, and 75 % respectively, while MEL more frequently utilized EM and DM, with individuals observed in 43 % and 24 % of the underwater sessions, respectively (ANOVA, F = 24.5, d.f. = 3 / 707, $p < 0.001$ (SMF 2A).

A similar pattern of vertical use of the water column was observed between the species (ANOVA, F = 0.617, d.f. = 3 / 768, p = 0.415). However, a higher FO % was observed for GEI in the lower third (22 %) compared to INP (14 %), MEL (12 %), and GIA (9 %) (SMF 2B).

Regarding foraging frequency, similar foraging was observed in the water column: surface (52 %) and mid-water (47 %) for GIA (ANOVA, F = 0.625; d.f. = 2 / 180, p = 0.429), as well as for MEL (ANOVA, F = 0.341; d.f. = 2 / 206, p = 0.559) with 51 % and 48 %, respectively. On the other hand, INP exhibited a higher FO % at the surface (66 %) compared to mid-water (34 %) (ANOVA, F = 14.37; d.f. = 2 / 78, $p < 0.001$), while GEI showed a more frequent foraging in mid-water (65 %) than at the surface (35 %) (ANOVA, F = 5.079; d.f. = 2 / 56, p = 0.026; SMF 2C). Foraging events on the substrate were rarely observed (less than 1 % of observations for each species) and thus were not included in the analyses.

Stomach Content Analysis: A total of 170 stomachs were examined, consisting of 70 from MEL (18.6-38.4 mm Standard Length, SL), 60 from GIA (18.5-103.3 mm SL), 30 from GEI (31.1-50.5 mm SL), and 10 from INP (37.7-87.7 mm SL). The degree of stomach fullness indicated that 87.6 % of the examined stomachs (n = 149) were full.

The species exhibited a broad dietary spectrum, with 31 different food categories identified from the stomach contents of the four species. The diet was predominantly composed of items of animal origin, although there was a minor but significant presence of plant-origin items (SMT 2). The analysis revealed that the food categories Insect Fragments, Hymenoptera, Ephemeroptera Larvae, and Plant Fragments were the most important components of the stomach contents across the four fish species, though with varying proportions, and Ephemeroptera Larvae made an important contribution to the difference in the diet between species (SMF 3).

No significant difference was detected among the stomach contents of the four species overall (MANOVA, $F = 3.723$; $r^2 = 0.06$; $p = 0.086$). However, pairwise comparisons revealed significant differences between MEL and GIA, MEL and INP, as well as MEL and GEI (SMT 3). In addition to the high importance of Ephemeroptera Larvae in the diet of MEL, significantly higher values for Diptera Larvae, Coleoptera, and Diptera Pupae were also observed compared to the other species.

The contribution of allochthonous items ($\chi^2 = 4.941$; $p = 0.176$) and autochthonous items ($\chi^2 = 5.396$; $p = 0.144$) to the stomach contents was not significantly different among the four species. Of the four species, only INP exhibited a higher frequency of occurrence (FO %) of allochthonous items compared to autochthonous items ($\chi^2 = 8.100$; $p = 0.004$).

Ecomorphology: Principal Component Analysis (PCA) revealed a distinct morphological pattern among the analyzed species. The first eight PCA axes, with eigenvalues greater than 1, accounted for 70.5 % of the cumulative variance.

The first two components (PC1 and PC2) explained 56.9 % of the total ecomorphological variation. PC1 (33.2 % variance) was mostly influenced by attributes such as BCI, RBH, CPCI, RHL, RES, and RMW. This component effectively differentiated between GIA, INP, and MEL, which possess a higher and more laterally compressed body, a less compressed caudal peduncle, a longer head, larger eyes, and a broader, more terminal mouth compared to GEI. The latter species, in contrast, has a more terminal mouth position, a lower and less compressed body, a more fusiform shape, and relatively smaller eyes and head relative to its body size, with a more compressed caudal peduncle (SMF 4).

In the formation of PC2 (23.7 % of variance), the most important attributes were RCPL, RDFA, RMH, and MCR, which contributed to the discrimination of INP, GIA, and GEI, which share shorter caudal peduncles, smaller dorsal fin areas, narrower mouths with larger openings, from MEL, which has a relatively longer caudal peduncle, larger relative dorsal fin area, and a wider mouth with a smaller opening (SMF 4).

The PC3 of the ordination, representing 13.6 % of the variance, highlighted the importance of the RPFA and RPvA, contributing to the morphological divergence between GIA and its congener INP, as GIA has relatively smaller pectoral and pelvic fins (SMF 5).

Significant morphological differences were detected among the studied species (MANOVA, $F = 45.172$, $r^2 = 0.61$, $p < 0.001$). For pairwise comparisons, the smallest significant morphological difference was found between MEL and INP, followed by GIA and INP. The pairs with the most significant differences were INP and GEI, followed by MEL and GEI (SMT 4).

DISCUSSION

Even though the fact that the nektonic stream fish species are similar in terms of their overall ecology and body shape, the results indicated that there are ecomorphological, stomach contents, and behavioral differences that can act as mediators of the coexistence of individuals of the four syntopic characiform fish species through the sharing of food and spatial resources.

Ecomorphology and habitat use: Despite the overall morphological similarity, opportunistic habits, trophic niche overlap, and phylogenetic proximity among them (Barros et al., 2017; Brejão et al., 2013; Dagosta & de Pinna, 2019; Sabino & Zuanon, 1998; Sabino & Sazima, 1999; Sazima, 1986), interspecific ecomorphological differences appear to be associated with the use of specific microhabitats, as well as the consumption of different combinations of food items and employing slightly different foraging behaviors, which tend to alleviate the potential interspecific competition. The relationship between the observed morphological divergences and ecological patterns supports the ecomorphological hypothesis (Casatti & Castro, 2006; Winemiller, 1992), which posits that morphological characteristics reflect important aspects of the individuals' ecology and, therefore, indicate modes of life and adaptations to different habitats and food resource availability.

The three distinct clusters formed along the first axis of the ecomorphological ordination reflect differences in swimming performance and occupation of distinct microhabitats, as well as preferences for prey size and type, foraging location, and the position of the food relative to the fish (Langerhans et al., 2003; Portella et al., 2017). As a function of movement physics, body shape strongly influences swimming performance, microhabitat preference, foraging frequency, and space sharing (Barros et al., 2019; Dala-Corte & De Fries, 2018; Souza & Pompeu, 2020). Therefore, significantly distinct ecomorphological characteristics are related to the detected horizontal space segregation, evidenced by the higher occurrence of MEL close to the stream margins. This species has a relatively shorter, higher, and laterally compressed body, which possibly provides greater swimming performance in low-flow water environments, such as backwaters or among roots and holes in the margins (Barros et al., 2019). Several species of the same functional group have shown similar space use (Brejão et al., 2013; Teresa et al., 2021), even extending beyond the margins and colonizing temporary pools along the stream margins (Espírito-Santo et al., 2017). The other three species, GIA, INP, and GEI, showed a clear preference for the stream channel, where the water flow is greater and the fusiform body shape of these species is better adapted, being energetically more favorable for maintaining the body in this microhabitat (Barros et al., 2019; Brejão et al., 2013; Langerhans, 2008; Neves & Monteiro, 2003).

Ecomorphological attributes associated with PC2 mainly contributed to the differentiation of MEL. This species had a dorsal fin with a larger relative area, typical of species adapted to lentic or low-flow water environments, where a larger fin can function more effectively (Gosline, 1971; Langerhans et al., 2003), aiding the fish in making short movements and maneuverability.

Bryconops giacopinii had relatively larger pectoral and pelvic fin areas compared to INP. Although GIA showed body shape characteristics that confer greater adaptability to the main channel environment, fish with large pectoral fins are potentially more efficient at maneuvering (Howe et al., 2021). Large pelvic fins are associated with demersal habits (Gatz, 1979), and these characteristics may also make GIA efficient in other microhabitats, such as backwaters and margins. These characteristics help explain the broad distribution of this species in small streams of various hydrographic basins in the Amazon (Dagosta & de Pinna, 2019), suggesting high environmental adaptability.

Foraging: Mouth orientation data are quite revealing regarding the water column stratum in which the fish forages, the origin of the ingested food, and the fish's position relative to the food (Motta et al., 1995; Portella et al., 2017). For example, *Bryconamericus stramineus* Eigenmann, 1908 was observed capturing items at the water surface, explained by the predominance of terrestrial insects in its diet (Casatti & Castro, 1998), as was *Astyanax altiparanae* Garutti & Britski, 2000 (Casatti et al., 2003). Individuals of *Hemigrammus marginatus* Ellis, 1911 are insectivorous but prefer aquatic insects, evidenced by foraging in the mid-water column (Casatti et al., 2003). In the present study, GEI had a terminal mouth position and a higher frequency of observed foraging events at mid-water, collecting items carried downstream. *Bryconops inpai* had a slightly upward positioned mouth compared to the others and foraged mostly at the water surface, which was associated with a higher proportion of allochthonous items found in the stomach. Regarding GIA and MEL, which had intermediate mouth positions compared to GEI and INP, there was no preference for foraging location (surface or mid-water), as well as a similar proportion of allochthonous and autochthonous items in the stomach. The lack of preference for one of the foraging strata can be attributed to opportunistic life history strategies and greater feeding behavioral plasticity in individuals of these species (Aranha et al., 1998; Barros et al., 2017; Brejão et al., 2013; Sabino, 1999; Sabino & Zuanon, 1998; Sazima, 1986). Although less specialization in foraging stratum in the water column may result in lower competitive ability of these species compared to more specialized fish, the use of a greater variety of microhabitats for feeding, on the other hand, increases their versatility and competitive advantage for available trophic resources, allowing them to explore other foraging locations and alternative food items of lower energetic value (but more abundant). These conditions are typical of oligotrophic streams with low carrying capacity, like those studied here, where fish heavily rely on allochthonous resources and are adapted to opportunistically handle high unpredictability in food availability (Barili et al., 2011; Henderson & Walker, 1986; Walker, 1995).

Stomach contents: Greater similarity in ingested food items was observed between GEI, GIA, and INP compared to MEL, as well as similar horizontal space use (GEI, GIA, and INP in the Channel and MEL in the margins). The lower number of analyzed stomachs for INP may have blurred the true diversity of food items ingested by this species because of the lower probability of detecting some rare items in its diet; however, the use of somewhat broad food categories in this study probably attenuated such problem. Moreover, the main differences in the diet of the four species were mainly related to MEL, which also reduces the risk of misinterpretation of the results presented herein.

Dietary differences among ecologically and morphologically similar species are commonly associated with differences in body and mouth shape, size, and feeding behavior among species (Aranha et al., 1998; Barros et al., 2017; Brejão et al., 2013; Esteves et al., 2021; Portella et al., 2017). Gorman & Karr (1978) proposed that food item selection among related species is primarily a consequence of the habitat in which individuals are found, and where they select among available food items. Dala-Corte & De Fries (2018) and Montaña & Winemiller (2010) observed that body size, and to a lesser extent habitat use, are the main factors causing dietary segregation among syntopic congeneric species. In MEL, a higher proportion of Coleoptera, Diptera, and especially Ephemeroptera larvae were detected in the stomach contents, which significantly contributed to the trophic divergence between species. The selection of different food items by MEL compared to other species relates to different patterns of use of margin and channel microhabitats, but also to its smaller body size relative to the others. Barros et al. (2017) attributed the proportional use of different feeding tactics and space use to the narrowing of the feeding niche in MEL when syntopically co-occurring with the same species studied here. The authors suggested this occurred i) due to changes or differences in items collected at the surface or mid-water; ii) through the ingestion of food items of different sizes and origins, mediated by mouth morphology (e.g., mouth size, mouth orientation) and specific behaviors (e.g., ability to locate small food items); iii) and through the use of different microhabitats for foraging (e.g., central channel vs. margins). The results found here support and complement such hypotheses, adequately explaining the margin use segregation by MEL, correlated with functions of specific morphological structures (mouth configuration and size), different feeding tactics employed, and local conditions of microhabitats (low water speed and shelter among roots).

Resource partitioning and competition: Ecological interactions associated with microhabitat heterogeneity can mediate variations in feeding tactics and space use by opportunistic species (Brejão et al., 2013; Casatti & Castro, 1998; Ceneviva-Bastos et al., 2010), and vertical and horizontal partitioning of the water column plays an important role in microhabitat occupation patterns (Leitão et al., 2015; Peres-Neto, 2004; Portella et al., 2017). The high overlap in the use of the middle third of the water column by the four species suggests a reflection of the evolutionary history of this phylogenetically related group, which has retained a generalized body morphology, allowing it to perform similar ecological functions, resulting in similar patterns of vertical water column use. On the other hand, the pressure for channel microhabitat uses by GIA, INP and GEI may be alleviated by the apparent segregation of MEL in the margins, potentially resulting in reduced interspecific competition. Individuals of MEL were only observed continuously occupying the channel in the absence of the other syntopic species in the BO13 stream (channel 56 %, ME 21 %, and MD 23 %). This pattern of space use by MEL and other species suggests the evidence of interference competition (Schoener, 1974), associated with a dynamic mechanism of resource partitioning, where ecomorphological and dietary differences, foraging behavior and space use segregation plays a mediating role, facilitating coexistence (Baldasso et al., 2019; Dala-Corte & De Fries, 2018; da Silva et al., 2017; Delariva & Neves, 2020; Leitão et al., 2015; Manna et al., 2017; Portella et al., 2017; Souza & Pompeu, 2020).

These amazonian nektonic stream fishes here studied are phylogenetically related, morphologically similar, trophic opportunist, with high niche overlap. Several studies have reported minimal niche differentiation in tropical stream fish assemblages (Aranha et al., 1998; Barros et al., 2017; Esteves et al., 2021; Goulding et al., 1988; Herder & Freyhof, 2006; Kliemann et al., 2021; Peres-Neto, 2004; Sabino & Zuanon, 1998), suggesting that the composition of these tropical stream fish assemblages may reflect stochastic processes. However, the combined analysis of direct observation of behavior (foraging and habitat use), stomach contents, and ecomorphological characteristics demonstrated that, despite being seemingly subtle, the significant differences observed here suggest they act as a mechanism for reducing interspecific competition, emphasizing the mediating role of resource sharing and spatial partitioning in the coexistence of these syntopic species in small, oligotrophic upland streams in the Amazon Rainforest.

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See supplementary material
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