The ecomorphological diversity of Amazonian stream fishes is constrained by phylogenetic relationships

Bruno E. Soares[1]; Naraiana L. Benone[2]; Rafael P. Leitão[3]; Cecília G. Leal[4]; Luciana L. Santos[5]; Luciano F. A. Montag[5]; Leandro Duarte[6]; Erica P. Caramaschi[7]

[1] Institute of Environmental Change & Society, University of Regina, Regina, Canada
[2] Universidade do Estado de Minas Gerais, Passos, Brazil
[3] Departamento de Biologia Geral, Universidade Federal de Minas Gerais, Belo Horizonte, Brazil
[4] Lancaster Environment Centre, Lancaster University, Lancaster, UK
[5] Instituto de Ciências Biológicas, Universidade Federal do Pará, Belém, Brazil
[6] Departamento de Ecologia, Universidade Federal do Rio Grande do Sul, Porto Alegre, Brazil
[7] Departamento de Ecologia, Universidade Federal do Rio de Janeiro, Rio de Janeiro, Brazil

Correspondence

Bruno E. Soares
soares.e.bruno@gmail.com

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Conflict of Interest

The authors declare no conflict of interest.

Author contributions

BES designed the study, performed the data analyses, and wrote the first draft of the paper. RPL, CGL, NLB, LLS, and LFAM provided the initial and final datasets that this manuscript explored. LD and EPC supervised the development of the manuscript. All authors discussed results and revised the writing of the manuscript.

Data availability statement

Dataset and coding supporting this manuscript are available at Zenodo (10.5281/zenodo.6329980).

Abstract

Phylogenetic history and environmental conditions determine the trait diversity of species pools. Stream fishes have diversified into a wide range of body and oral shapes that allow a similarly wide range of functional traits, but that can be determined by habitat type and taxon. Herein, we analyzed 16 ecomorphological traits of nearly 400 fishes inhabiting streams distributed across the Brazilian Amazon to (i) describe the main axes of ecomorphological variation of Amazonian stream fishes; (ii) quantify the proportion of the potential combination of traits that is displayed by the regional pool of species; (iii) evaluate the distribution of different taxonomic groups in those axes; (iii) determine the overall contributions of the taxonomic groups to regional ecomorphological diversity. Our results show that Amazonian stream fishes concentrate around multiple combinations of traits defined by five axes of ecomorphological variation. The benthic-nektonic axis segregates fishes with upper-positioned eyes and wide mouth gapes from fishes with lower-positioned eyes and narrow mouth gapes related to narrower body shapes. Benthic fishes further differ in three groups of species depending on ecomorphological traits coupling different strategies for feeding and swimming. Taxonomic order and family constrained species position along these axes of variation and consequently determined their contribution to overall ecomorphological variation. Overall, we show that five axes related to habitat and food partitioning explain most of the ecomorphological diversity of Amazonian stream fishes, but taxonomic identity determines species suite of traits.

Kew words

Regional diversity, Ecomorphology, Ecological niche, Fish assemblages, Functional diversity

Introduction

Ecomorphological traits are widely used to evaluate fish functional diversity (Leitão et al., 2017; Teresa et al., 2015; Toussaint et al., 2016) and are used more often than other biological, physiological or ecological attributes. Describing biological communities through functional traits supposedly allows us to better understand ecological mechanisms behind community patterns, since measures are based on how organisms relate to the environment (Villéger et al. 2017). Therefore, functional traits should predict how organisms change their environment (effect traits) or respond to it (response traits). These traits may compose a multidimensional functional space that relates to the Hutchinsonian *n*-dimensional niche space (Blonder 2018). Identifying major axes of variation in this space is essential for deciphering ecological and evolutionary mechanisms related to species persistence.

Functional traits in animal ecology are often related to five fundamental niche dimensions that encompass the ecological strategies related to species survival: feeding strategy, habitat use, life history, defense, and metabolic type (Winemiller et al. 2015). Particularly for fish, ecomorphological traits have been mostly applied as proxies of feeding strategy and habitat use. For example, both large areas of the pelvic fins and dorsoventrally compressed bodies provide important mechanisms for fishes to maintain themselves in the stream bottom (Oliveira et al., 2010; Soares et al., 2013; Watson & Balon, 1984). Therefore, these traits are linked to ecological strategies and are important tools to understand species relationship with the environment (Santos et al. 2019; Côte, Kuczynski, and Grenouillet 2022). The distribution of the species ecological dissimilarities shapes the ecomorphospace, which is often constrained by life-history and morphophysiological trade-offs because species cannot optimize their performance in all ecological strategies simultaneously (Winemiller 1989; Webb 1984). In addition, ecomorphological patterns of local assemblages are primarily driven by environmental filtering and limiting similarity (Leitão et al. 2017; Mouillot 2007), which are, in turn, constrained by the set of traits of the regional pool of species.

The regional pools of fishes depend on ecological, biogeographic, and evolutionary processes in short and long-term time scales (Cornell and Harrison 2014; Weeks, Claramunt, and Cracraft 2016). They may be constrained by old vicariant processes and barriers to dispersal (Peixoto et al. 2014), but high ecological tolerance and short-termed environmental changes allow recurrent invasions in new habitats, as marine-derived lineages in freshwater systems (Bloom and Lovejoy 2017). Evolutionary history unarguably shapes regional pools of species and, consequently, the set of functional traits on which major ecological processes act up on (Vellend 2010; Kraft et al. 2007). Assessing the phylogenetic structure of fish communities has demonstrated the human impacts in biodiversity (Su et al. 2021; Luo et al. 2022; Qian et al. 2022) and how historical processes determined local pools of species (Aquino and Colli 2017; Abreu et al. 2019; Craig et al. 2020). Despite these advances, fish ecology has been addressing mostly the functional structure of communities rather than the phylogenetic structure (Soares and Nakamura 2021; Teresa, Rodrigues-Filho, and Leitão 2021), which may be partially explained by the relative scarcity of large-scale phylogenies (Nakamura, Richter, and Soares 2021).

Under neutral evolution, the diversification within lineages fills contiguous regions in ecomorphospace, so closely related species tend to be more similar than distantly related species and occupy closer portions in trait space, *i.e.* phylogenetic signal (Losos 2008; Harvey and Rambaut 2000). In such scenarios, clades comprise functionally redundant species, but in niche-mediated evolutionary processes, clades may contain species displaying a large diversity of traits (Deline et al. 2018; Price et al. 2015). Morphological differences among clades occur because of differences in timing, rate, direction or distribution of morphological diversification (Hopkins 2016; Sidlauskas 2008). Neotropical characiforms of the families Prochilodontidae and Curimatidae, for example, exhibit higher morphological similarities in cranium morphology than species of Anostomidae and Chilodontidae due to different constraints in morphological diversification (Sidlauskas 2008).

The Neotropical region harbors over 5,700 valid freshwater fish species (Albert and Reis 2011). Neotropical Freshwater Fishes (NFF) include ancient lineages that originated in Western Gondwana before the separation of South America and Africa and peripheral clades that invaded freshwaters from the sea or other continents during the last 30 Mya (Albert and Reis 2011). Richness is unevenly distributed among higher taxa, as the orders Characiformes or Siluriformes encompass together more than half of all NFF, while the remaining orders may comprise from a few described species to hundreds of species (Albert and Reis 2011; Albert, Tagliacollo, and Dagosta 2020). In addition, NFF comprises the largest fish functional richness among biogeographical realms, driven mainly by some functionally unique clades (Toussaint, Charpin, and Brosse 2016). These lineages are widespread in the Amazon basin, which harbors all the most diverse freshwater fish assemblage in the world, encompassing over 2700 valid species (Dagosta & Pinna, 2019).

Herein, we explore the ecomorphospace of NFF from a large database comprising community-level samples from 405 streams across the Amazon to address four questions. Our dataset includes information on the regional pool of many Amazonian sub-basins and ecomorphological traits related to foraging, habitat use, and locomotion. First, we aimed to determine the major axes of ecomorphological variation of NFF. Space and food are the most important niche dimensions for fishes to compete (Schoener 1974; Ross 1986), thus we expected that ecomorphological traits related to these niche axes would explain most of the differences among species. Second, we aimed to quantify the proportion of potential trait combinations that is realized in Amazonian stream fishes. Not all combinations of traits are equally successful due to physical constraints and ecological trade-offs, *i.e.*, some traits will be strongly correlated with each other, then making some combinations of traits more probable than others (Céréghino et al. 2018; Diaz et al. 2016). We expect that evolutionary history constrain some combinations of traits in Amazonian stream fishes, generating a low occupation of the potential trait space. Third, we aimed to uncover the taxonomic constraints in the observed ecomorphospace. If we consider the common assumption of niche conservatism (Losos 2008) and that NFF encompass a both early-branching and recent clades species (Albert, Tagliacollo, and Dagosta 2020), we expect a mosaic of strongly clustered lineages and more overdispersed lineages across the ecomorphospace. Fourth, we aimed to understand the contribution of different taxonomic orders to the ecomorphospace as the composition of clades might be used to understand ecological patterns (Santos et al. 2022). We expect that (i) Siluriformes will contribute with a large portion of the ecomorphospace as this order is comprised by the highest number of independent lineages occupying the Amazonian region (Albert & Reis, 2011) and that (ii) Gymnotiformes will contribute with the highest ecomorphological specialization as it exhibits a highly specialized morphology for electrocommunication (Albert, 2001).

Material and methods

Study area

The Amazon-Tocantins basin is the largest aquifer in the world, harboring over 8.000.000 km² and 5% of the Earth surface, and it supports the highest biodiversity in the Earth (Barthem and Fabré 2003; Molinier et al. 2009). The Amazon basin has a tropical humid climate of tropical rainy type in Köppen-Geiger classification, where its seasonal pluviometry shapes marked spatiotemporal variation in river levels (Alvares et al. 2013). Despite its great geographical extent, the regional topography sets a low variation in temperature, which ranges between 24 and 26° C (Sioli 1975). The Amazon hydrographic basin is divided in four geomorphological units that determine the physical and chemical parameters of their waterbodies: (i) Andean region; (ii) Guyana Shields; (iii) Brazilian Shield; and (iv) Fluvial Plains (Filizola & Guyot, 2011; Sioli, 1975). We analyzed fish assemblages in 405 cis-Andean Amazonian streams (Figure 1) in a broad geographical range and environmental variation within well-preserved forests. Streams were distributed in four minor basins that drained directly into the Amazon River (n = 128) and other six major drainage basins, namely: Coastal drainage basin (n = 24), Guamá River basin (n = 26), Madeira River basin (n = 48), Negro River basin (n = 74), Tapajós River basin (n = 43), and Xingu River and Paru River basin (n = 62). These basins are broadly distributed in the Brazilian Shields and Fluvial Plains systems.

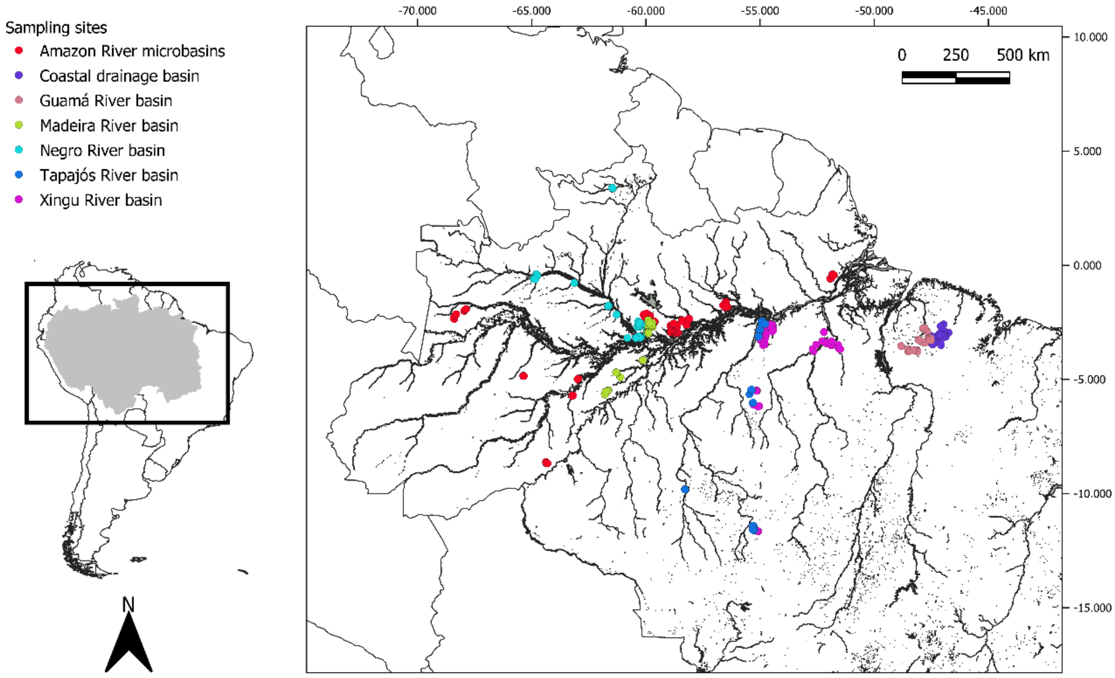

Figure 1 – Study sites sampled for stream fish assemblages in the cis-Andean Amazon.

Fish sampling and composition

The stream fish assemblages were sampled between 2004 and 2012. Sample sites were 50 to 150 m length and comprised different microhabitats, such as sand banks, litter banks, water column, macrophyte banks, crevices, and backwater. Fishes were captured using seines and hand nets during daylight, then euthanized using lethal doses of eugenol, fixed in 10% formalin and preserved in 70% alcohol (see more details in Mendonça *et al.*, 2005). The selected streams displayed small dimensions and marked habitat boundaries harboring small-size species, allowing efficient sampling with the applied protocol (Ribeiro and Zuanon 2006; Anjos and Zuanon 2007; Pompeu et al. 2021). Voucher specimens are deposited in fish collections of Instituto Nacional de Pesquisas da

Amazônia (INPA), Museu Paraense Emílio Goeldi (MPEG), and Universidade Federal de Lavras (UFLA). We identified 395 species, classified in 35 families and eight taxonomic orders (Supplementary Table 1). Characiformes was the most representative order (170 species), followed by Siluriformes (113) and Cichliformes (55). Beloniformes, Gobiiformes, and Synbranchiformes were represented by less than 10 species. Characidae was the most representative family (100 species), followed by Cichlidae (54) and Loricariidae (37). Our dataset covers a wide range of regions in the Amazon basin and represent taxonomic patterns of the fish fauna inhabiting small-order Amazonian streams, in except for the absence of some families with restricted number of species or occurrence, such as Tarumaniidae (De Pinna et al. 2018).

Ecomorphological trait assessment

We calculated 16 ecomorphological traits related to describe the ecomorphological structure in fish assemblages of Amazonian streams (Table 1). Selected traits summarize different morpho-functional attributes of fishes, including: (i) eye, mouth, teeth and gill-rakers attributes related to food acquisition and handling; (ii) body and fins attributes related to swimming capacity and habitat use. Food acquisition and handling traits determine how fishes use food resources by favoring different strategies in prey location, foraging microhabitats, and handling. Swimming capacity and habitat use traits determine how fishes use space by favoring different locomotory strategies and microhabitat choice. A couple of traits exhibited a certain degree of interdependency in their equation. Both the shape and surface of the oral gape, for example, depend on the width and depth of the mouth opening, but the second one is relative to body measurements. Indices summarizing the surface area of pectoral and caudal fins share common variables but highlight different morphological attributes of the species depending on which other variables they are relative to.

Most of the traits were calculated as unitless ratios using morphometric linear measurements, areas and angles taken on up to 12 adult individuals per species, preferably from different river basins to include intraspecific variation. We also included teeth shape as a categorical variable (10 binary variables) and gill-raker shape as a semi-quantitative variable. Linear measurements were taken using digital caliper (0.1 mm) and areas were estimated in digital pictures or drawings of fin outline in the Image J software. Swamp-eels (Synbranchiformes) and electric fish (Gymnotiformes) do not have caudal fins and Synbranchiformes do not have pectoral fins; therefore, a couple of conventions were adopted for representing ecomorphological traits including these fins (Villéger et al. 2010; Brosse et al. 2021). Caudal peduncle throttling was set to one for species with no visible caudal fin, indicating that caudal fin depth and caudal peduncle depth are equal. Pectoral-fin position was fixed to 0 to indicate the lack of pectoral fins. We used average trait values for each species in further analyses.

The variation in body size is a fundamental factor determining body shape variation within (Dunic and Baum 2017; Wainwright, Bellwood, and Westneat 2002; Evans et al. 2019) and between species though evolutionary mechanisms (Bright et al. 2016; Cardini and Polly 2013). For fishes, recent evidence suggests that variation in body length is not as strongly related to body shape as in other clades (Friedman et al. 2019), probably because body size in fishes depend on length, weight, and depth (Alencar et al. 2022). Given the importance of body size to explain variation in body shape, we tested the univariate correlation between each ecomorphological trait with body mass (Supplementary Material). Most of the variables were weakly correlated to body size ($r < 0.3$), but body transversal surface was moderately correlated to it ($r < 0.6$). Since none of the traits were strongly correlated to body size ($r > 0.7$), we performed further analysis without further corrections to body size.

Table 1 - Ecomorphological traits used to describe the use of habitat and prey selection of fish species in Amazonian streams, with their respective formulas, and ecological interpretations. Codes: BDP - Body depth at Pectoral fin insertion; CFA – Caudal fin area; CFD – Caudal fin depth; CPD – Caudal peduncle depth; ED – Eye diameter; HD - Head depth; HE - Height of the eye; HPF - Height of the pectoral fin insertion; MBD – Maximum body depth; MBW – Maximum body width; MD – Mouth depth; MO – Mouth orientation; MW – Mouth width; PFA – Pectoral fin area; PFL – Pectoral fin length; PRT – Protruded snout length; SN – Snout length. A figure representing the taken measurements can be found in the Supplementary Material.

Ecomorphological trait	**Classes/Equation**	**Ecological interpretation**
Teeth shape	Absent Canine Comb-shaped Conic Incisiform Molariform Multicuspid Spoon-shaped	Dentition is related to the type of food items consumed by the fish, as well as to the feeding method they use for handling the item. Variation in teeth shape allow species to food processing and prey type depending on their functionality, such as the use of caniniform or villiform teeth for holding large prey, molariform teeth for crushing hard-shelled prey, and spoon-shaped or absent teeth that facilitates detritivory (Sazima and Caramaschi 1989; Gidmark et al. 2015; Lujan, Winemiller, and Armbruster 2012; Mihalitsis and Bellwood 2019; Delariva and Agostinho 2001).

	Tricuspid Viliform	
Gill-raker shape	0 - Absent 1 - Short/Sparse 2 - Intermediate 3 - Long/Numerous	Gill rakers are related to the type and size of food items by functioning as a crossflow filter. Gill rakers retain prey and food particles depending on their length, width, and density (Sanderson et al. 2001). Variation in gill raker morphology ranges from short, sparser gill rakers in benthivorous or generalist fishes to long, denser gill rakers in planktivorous species (Kahilainen et al. 2011; Spiegel, Quist, and Morris 2011; Sibbing and Nagelkerke 2000).
Mouth-protrusion length	$\frac{PRT}{SN}$	Higher values indicate upper jaws that extend longer. Protrusion of the mouth is related to the type of consumed food and feeding method. The protrusion of the upper jaws approximates predator and prey quickly and creates a suction flow that optimizes uptake. Protrusion can also favor detritivorous fishes by promoting mixing and sorting of the consumed detritus within the expanded oral cavity (Sibbing and Nagelkerke 2000; Bellwood et al. 2015; Waltzek and Wainwright 2003; Konow and Bellwood 2011).
Oral-gape shape	$\frac{MD}{MW}$	Increasing values indicate increasingly narrower oral gapes. The shape of the mouth is related to the type of consumed food item and method for capturing or handling items. The oral-gape shape is one of

		the factors determining force and kinematic efficiencies (Day et al. 2015; Porter and Motta 2004). In addition, it determines foraging behavior and accessibility to prey; for example, tube-snouted fishes use a grasp-suction feeding mode for taking prey from burrows or hidden in interstitial spaces (Marrero and Winemiller 1993) and elongated, slightly curved jaw of the wimple piranha allows it to feed on the scale of other fishes (Janovetz 2005).
Oral-gape surface	$\frac{MW * MD}{MBW * MBD}$	Higher values indicate larger mouths. Gape size is related to the type and size of consumed prey. Species with larger mouths tend to feed on larger prey and display higher trophic levels (Karpouzi and Stergiou 2003; Paul et al. 2017; Dunic and Baum 2017), and variation in gape size and potential prey is observed even within trophic levels (Mihalitsis and Bellwood 2017; Bonato, Burress, and Fialho 2017).
Oral-gape position	$\frac{MO}{HD}$	Higher values indicate upper-turned mouth openings. The position of the mouth opening is related to the method and microhabitat location for capturing food items. Upturned mouth opening favor the capture of prey in the surface or immediately above the water column stratum the predator uses; ventral and subterminal mouth openings favor the capture of prey in bottom of the water column, in the surface

		of substrate or crevices; and terminal mouth opening allow a more generalist approach for capturing prey (Carlson and Wainwright 2010; Ibañez et al. 2007; López-Fernández et al. 2012).
Eye size	$\frac{ED}{HD}$	Higher values indicate larger eyes relatively to the head diameter. The size of the eye is related to the method and capacity for prey detection, which ultimately determine the size and type of consumed prey. Larger eyes are related to increased visual acuity and are related to increasing predation (Caves, Sutton, and Johnsen 2017; Beston et al. 2019; Beston and Walsh 2019).
Eye position	$\frac{HE}{HD}$	Higher values indicate upper-positioned eyes. The position of the eye in the head is related to how the organism perceive the environment and prey, then being related to prey detection. Vertically positioned eyes are mostly related to ambush predators living in the bottom of the water column or to organisms feeding in the surface of the water column (Pouilly et al. 2003; Winemiller 1991)
Compression index of the body	$\frac{MBD}{MBW}$	Higher values are associated with laterally compressed and deep-bodied fishes and lower values are associated with dorsoventrally compressed fishes. Body shape affects how the organism can use the environment by determining the kinematics and hydrodynamics of the body, then being related to its movement in water (Sfakiotakis, Lane, and Davies 1999; Tytell et al. 2010). Generally, laterally compressed bodies provide higher maneuverability and favor the use of pelagic habitats; conversely,

		dorsoventrally compressed bodies reduce streamflow drag and favor the use of high-energy and benthic habitats (Barros, Louvise, and Caramaschi 2019; Larouche et al. 2020).
Aspect ratio of pectoral fin	$\frac{PFL^2}{PFA}$	Higher values indicate longer and narrower pectoral fins. The shape of the pectoral fins determines the propulsion efficiency; long wing-like fins favor flapping movement and continuous swimming, while short paddle-like fins favor rowing movement and maneuverability (Walker and Westneat 2002; Aguilar-Medrano et al. 2013; Wainwright, Bellwood, and Westneat 2002).
Pectoral-fin position	$\frac{HPF}{BDP}$	Higher values indicate pectoral fins positioned higher at the body depth of the fish. Upper-positioned pectoral fins are closer to the center of mass of the organism and favor maneuverability in complex environments (Dumay et al. 2004; Webb 2002; Thorsen and Westneat 2005).
Body transversal surface	$\frac{\ln\left(\frac{\pi}{4} * MBW * MBD\right) + 1}{\ln(Mass + 1)}$	The index summarizes the mass distribution along the body axis (Villéger et al. 2010). Higher values are associated to deep or wide fishes (mass concentrated in specific areas), and lower values are associated to elongated or streamlined fishes (mass distributed along the body axis). Body shape determines locomotion efficiency by determining its kinematics and hydrodynamism (Sfakiotakis, Lane, and Davies 1999; Tytell et al. 2010). Streamlined fishes are adapted for using low-flow pelagic

		habitats or accelerating, while elongation favor the use of undulatory motion of the body or fins for different habitat uses (Webb 1984; Barros, Louvise, and Caramaschi 2019).
Caudal peduncle throttling	$\frac{CFD}{CPD}$	Higher values indicate deep caudal fins compared to caudal peduncle. The depth of the caudal fin is related to its efficiency in producing thrust (Webb 1984; Matta et al. 2019). Deep caudal fins attached to short caudal peduncles increase propulsion and reduce drag force over the body, favoring continuously swimming and sprinting.
Aspect ratio of the caudal fin	$\frac{CFD^2}{CFA}$	Higher values indicate longer and narrower caudal fins, while lower values indicate shorter but deeper caudal fins. The shape of the caudal fin is related to its efficiency in producing thrust (Webb 1984; Matta et al. 2019; Zhong et al. 2022). Short and deep caudal fins favor continuously swimming and sprinting by more efficient propulsion.
Fins surface ratio	$\frac{2 * PFA}{CFA}$	Higher values indicate that pectoral fins are greater than the caudal fin of a given organism. Fishes with large pectoral fins use mostly oscillatory motion of these paired fins for cruising and maneuvering, while fishes with smaller pectoral fins rely in the motion of other fins or the posterior body for locomotion (Webb 1984).

Fins surface to body size ratio	$\frac{(2 * PFA) + CFA}{\frac{\pi}{4} * MBW * MBD}$	Higher values are related to larger surface of pectoral and caudal fins. Larger areas indicate that the organism use a locomotion mode based on their oscillation or undulation (Webb 1984).

Data analysis

Ecomorphological differences among fishes might be phylogenetically constrained to some extent even under neutral evolution (Soares, Ruffeil, and Montag 2013; Roa-Fuentes, Casatti, and Romero 2015), *i.e.*, a portion of the ecomorphological structure of a pool of species might be explained purely by the divergence time among clades. Since phylogenetic signal might affect the position of species across the ecomorphospace and subsequent analyses (Duarte et al. 2018), we followed the Phylogenetic Eigenvectors Regression (PVR) approach (Diniz-Filho et al. 2011; Diniz-Filho, De SanT'Ana, and Bini 1998) for deriving phylogenetically corrected ecomorphological traits. First, we generated a phylogenetic tree for the pool of species using the *FishPhyloMaker* function, which uses a large-scale fish phylogeny (Chang et al. 2019; Rabosky et al. 2018) for grafting species absent in the backbone tree using information on taxonomic hierarchies. Then, we applied the PVR separately for each standardized trait. This approach extracts eigenvectors from the phylogeny and regress them with a given traits, generating a measure of phylogenetic signal (R^2) and phylogenetically corrected traits, the latter being used in subsequent analysis.

To describe the major axes of ecomorphological variation in Amazonian stream fishes, we built an ecomorphospace (*i.e.* multidimensional ecomorphological volume) showing species positions and their distances between each other by running a Principal Coordinates Analyses (PCoA). We generated a dissimilarity matrix between each pair of species using the phylogenetically corrected traits, a weight of 0.1 for each level for each teeth shape level, and the Gower distance available in the *cluster* package (Maechler et al. 2019). Then, we used the function *quality.fspaces* for generating PCoA scores and functional-space quality metrics. The quality assessment of the ecomorphospace followed the mean squared deviation (mSD) approach, in which mSD represents the deviation between the original pairwise distances (in the Gower distance matrix) to pairwise distances in the ecomorphospace (Maire et al. 2015). We selected the minimum number of axes that provided an mSD value up to 0.025. Finally, we analyzed the importance of each trait to the ecomorphological structure using the *envfit* function, in which a series of vectors (the ecomorphological traits, here) are fitted onto an ordination. We interpreted ecomorphological variables with Pearson's correlation coefficient (*r*) equal to or higher than |0.6|.

The distribution of the species in the ecomorphospace may be clumped if evolutionary forces and/or physical constraints select for a single or few combinations of traits. Then, we explored constraints in the ecomorphospace based on the null modelling approach described in (Diaz et al., 2016). We analyzed the convex hull volume occupied by all species in the ecomorphospace and simulated values in four null models to uncover how stream fishes are distributed in the ecomorphospace. Convex hull volume is commonly named as functional richness (FRic) in the functional diversity literature, and it represents the total volume occupied by a set of species in a given *n*-dimensional functional space (Mouchet et al. 2010). Observed and simulated values were calculated based on 95% of species closer to the centroid to control for outliers in the ecomorphospace. Simulated values were calculated by 999 random ecomorphospaces generated from the assumptions of each model. Null Model 1 assumes that ecomorphological traits vary independently from each other following a uniform distribution, thus both central and extreme values are equiprobable. Null Model 2 assumes that traits vary independently from each other, but following a normal distribution, thus central values are more probable than extreme ones. Null model 3 assumes that traits vary independently from each other, and it follows the same data distribution of the observed data. Null model 4 assumes that traits covary and follows a normal distribution.

To better explain results deriving from the null modelling approach, we used two-dimensional Kernel density estimator. This method allows us to estimate the occurrence probability of the trait combinations in the ecomorphospace generated by the PCA. We used unconstrained bandwidth selectors and visualized estimated probabilities in the PCA graph. We built contour plots in the ecomorphospace representing 0.5, 0.95, and 0.99 quantiles of probability distribution that highlighted regions of high and low occurrence probability. We adapted R scripts provided by (Diaz et al., 2016).

Finally, we explored clade constraints in the ecomorphospace. First, we tested if the position in the ecomorphospace is clade-dependent using permutational analyses of variance (PERMANOVA, Gower distance, 9,999 permutations). Two PERMANOVAs were applied; one using the PCoA scores in the relevant axes and taxonomic family information, and another using the PCoA scores in the relevant axes and taxonomic order information. We calculated two indices commonly used in functional diversity studies to describe the ecomorphospace of fish clades inhabiting Amazonian streams: functional richness (FRic) and functional specialization (FSpe). As the convex hull occupied by a set of species in the ecomorphospace, FRic indicates the range of the ecomorphospace occupied by these species (Villéger, Mason, and Mouillot 2008). FSpe is the mean Euclidean distance between a set of species and the centroid of the ecomorphospace, and it indicates the distinctiveness of the ecomorphological traits of the group (Mouillot et al. 2013). Calculated indices are complementary in describing the ecomorphospace. A given clade, for example, may occupy a large portion of the ecomorphospace (high FRic), but placed around the centroid (low FSpe). We presented absolute values for each clade and further compared clades with species richness higher than ten by a null modelling approach. We performed a rarefaction analysis sampling 10 species per clade for comparing FRic and FSpe between random samples. Finally, we calculated the phylogenetic diversity (PD) as the total sum of branch lengths of the random pool of species in the phylogeny. Analyses were performed in R environment (R Core Team 2018) using the packages *FishPhyloMaker* (Nakamura, Richter, and Soares 2021), *geometry* (Roussel et al. 2019), *ks* (Duong et al. 2019), *mFD* (Magneville et al. 2022), *picante* (Kembel et al. 2018), phytools(Revell 2012), *PVR* (Diniz-Filho et al. 2012), , and *vegan* (Oksanen et al. 2016).

Results

Major axes of ecomorphological variation

Five axes summarized a large portion of the variation (82.64%) in the ecomorphospace of Amazonian stream fishes. These axes were related to variation in teeth shape, body shape, fins' area, and gill rakers (Table 2). The first axis separated fishes with wider mouth gapes, longer and narrower pectoral fins, and tricuspid or canine teeth from fishes with narrower mouth gapes, shorter pectoral fins, and other types of teeth. The second axis separated fishes presenting greater oral-protrusion, larger eyes, dorsally-positioned pectoral fins, and conic teeth from fishes with no oral-protrusion, smaller eyes, ventrally-positioned pectoral fins, and other types of teeth. The third axis separated fishes with greater areas of fins, strongly throttled caudal peduncles, and comb- or spoon-shaped teeth from fishes with smaller fins, less caudal peduncle throttling, and other types of teeth. The fourth axis separated short, laterally compressed fishes with protrusible jaws and incisiform or molariform teeth from fishes with deep or wide body shapes having non-protrusible jaws and other types of teeth. The fifth axis separated fishes with long, dense gill rakers, upper-positioned eyes, and larger mouths with villiform teeth from fishes with short, sparse gill rakers, lower-positioned eyes, and multicuspid teeth.

Table 2 – Pearson’s correlation coefficient (*r*) between ecomorphological traits and principal components (PC1 to PC5) of the ecomorphospace of Amazonian stream fishes.

The module of the coefficients higher than 0.6 in each axis are shown in bold type and were used for ecological interpretation.

Ecomorphological traits	PC1	PC2	PC3	PC4	PC5
Mouth-protrusion length	0.15	**-0.75**	0.02	**-0.63**	0.09
Oral-gape surface	-0.35	-0.25	-0.09	**0.62**	**-0.65**
Oral-gape position	-0.42	-0.49	-0.48	0.23	-0.54
Oral-gape shape	**-0.91**	-0.12	-0.04	-0.33	0.24
Eye size	-0.47	**-0.65**	0.48	0.14	0.33
Eye position	0.57	0.39	0	0.25	**-0.68**
Compression index of the body	-0.46	-0.06	-0.5	**-0.72**	-0.12
Body transversal surface	0.05	-0.25	0.11	**0.95**	0.11
Pectoral-fin position	0.49	**-0.61**	-0.3	-0.11	-0.54
Aspect-ratio of the pectoral fin	**-0.66**	0	0.22	0.53	0.49
Caudal peduncle throttling	-0.16	0.44	**0.74**	-0.41	-0.26
Aspect-ratio of the caudal fin	-0.58	0.38	0.53	-0.38	-0.29
Fins surface to body size ratio	0.29	-0.01	**0.87**	-0.32	-0.27
Fins surface ratio	0.18	-0.41	**0.88**	-0.09	-0.13
Gill-raker shape	-0.47	-0.04	0.11	0.24	**-0.84**
Teeth shape: Conic	0.31	**-0.83**	-0.17	-0.07	0.41
Teeth shape: Tricuspid	**-0.84**	0.26	-0.06	-0.05	-0.48
Teeth shape: Multicuspid	-0.31	-0.09	0.06	0.18	**0.93**
Teeth shape: Canine	**-0.71**	0.31	-0.1	-0.41	-0.47
Teeth shape: Comb-shaped	0.22	0.46	**0.83**	0.06	0.22
Teeth shape: Incisiform	-0.19	0.22	-0.21	**-0.76**	0.54
Teeth shape: Molariform	-0.18	0.32	-0.19	**-0.78**	-0.47
Teeth shape: Absent	0.18	0.35	**-0.78**	-0.04	0.49
Teeth shape: Spoon-shaped	0.23	0.43	**0.73**	-0.48	-0.02
Teeth shape: Viliform	0.28	0.15	0	0.36	**-0.88**
Eigenvalue	2.62	1.32	0.91	0.57	0.52
Variance explained (%)	**36.46**	**18.36**	**12.6**	**8.01**	**7.21**

Realized vs. potential trait volume

Species were concentrated in multiple combinations of traits in the first five axes defined by differences in ecomorphological differences. For example, differences in teeth shape, body shape, fins' area, and gill raker shake organize species in three combinations of traits in the first two axes of the ecomorphospace (Figure 2a) and the third axis show a bimodal distribution determined by variation in fin area and teeth shape (Figure 2b). On the other hand, the fourth and fifth axes show a unimodal distribution around combinations of body, teeth, and gill-rakers shape. Given the concentration of species around modal combinations of traits, the ecomorphospace of Amazonian stream fishes is smaller than expected in null scenarios considering independent covariation of traits (observed FRic occupies 8.39% and 47.89% of simulated Fric in Null Models 1 and 3, respectively) and scenarios considering a single modal combination of traits (observed Fric occupies less than 0.1% of simulated Fric in Null Models 2 and 4).

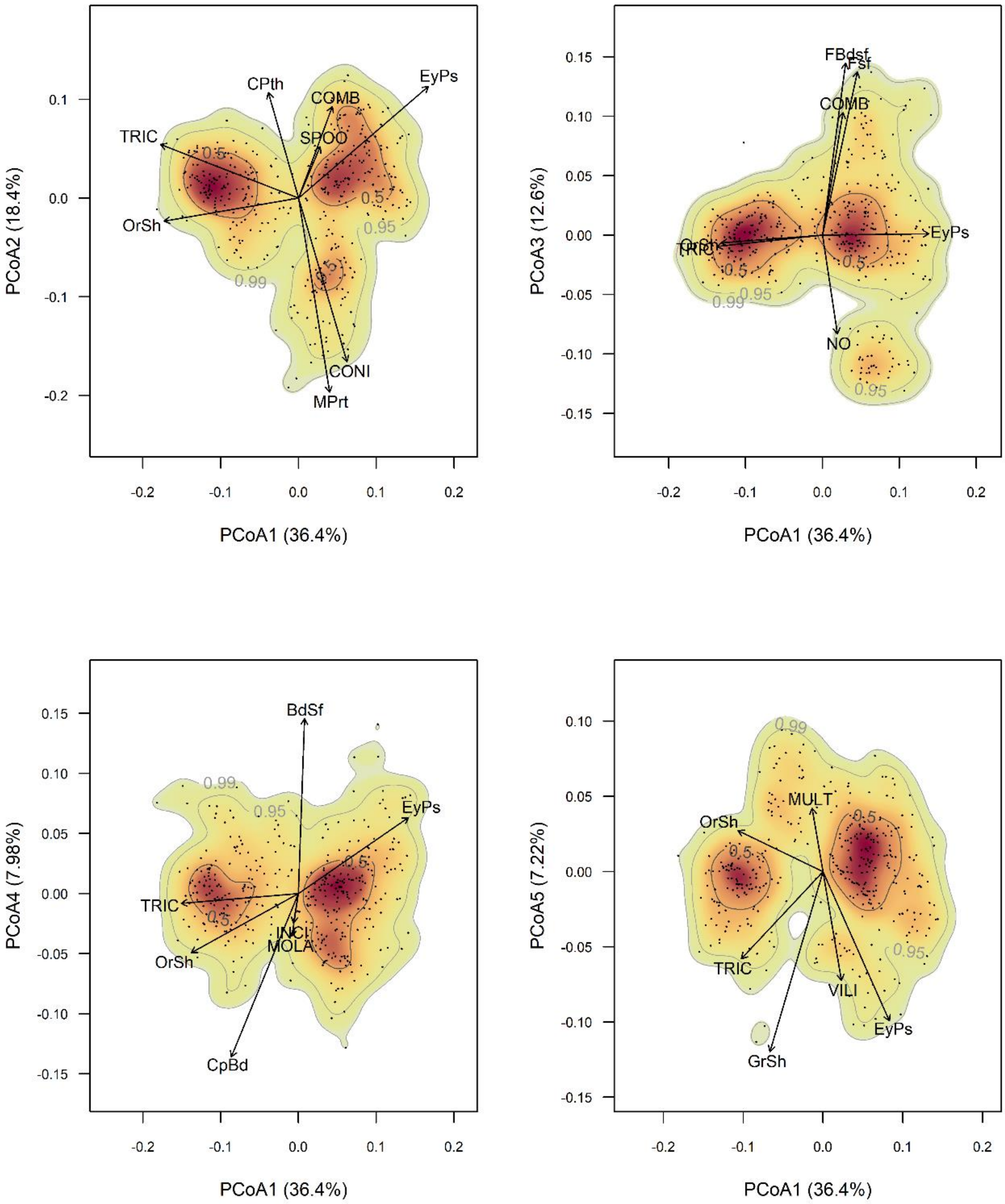

Figure 2 – Kernel density estimation representing the probability of occurrence of combination of ecomorphological traits summarized by five principal components for Amazonian stream fishes. We show the combination from the second to the fifth axis against the first axis. Color gradient represents the highest (red) to the lowest (white) occurrence probability of species in the ecomorphospace. Contour lines indicate 0.5, 0.95

and 0.99 quantiles of occurrence probability. Codes: Bd–f - Body transversal surface; COMB – Teeth Shape: Comb-shaped; CO–I - Teeth Shape: Conic; CpBd – Compression of the Body; CPth – Caudal peduncle throttling; EyPs – Eye position; Fsf – Fin surface ratio; FBdsf – Fin surface to body size ratio; GrSh: Gill-raker shape; INCI – Teeth Shape: Incisiform; MOLA – Teeth Shape: Molariform; MPrt – Mouth protrusion-length; MULT – Teeth Shape: Multicuspid; NO – Teeth Shape: Absent; OrSh – Oral-gape shape; SP–O - Teeth Shape: Spoon-shaped; TR–C - Teeth Shape: Tricuspid; VILI – Teeth Shape: Viliform.

Taxonomic constraints in trait space

Distribution in the ecomorphospace was taxon-dependent, as both taxonomic family (PERMANOVA; df = 34; $R^2 = 0.77$; $p < 0.001$) and order (df = 7; $R^2 = 0.56$; $p = 0.001$) explained the position of the species in the multidimensional space. For example, Characiformes showed the lowest values in PCoA1, differing from almost all other taxonomic orders (Figure 3a). The remaining orders differed in PCoA2, in which Beloniformes, Cichliformes, Cyprinodontiformes, and Gobiiformes showed the lowest values (Figure 3b). Finally, in PCoA3, Gymnotiformes and Synbranchiformes differed from the other clades by displaying the lowest values (Figure 3c). Therefore, the position of fish species in the ecomorphospace is not random, but largely constrained by their order and family, as species belonging to the same clade are often located around the same ecomorphological hotspot. Nevertheless, the pairwise comparison among clades showed that a few overlapped in the ecomorphospace (Supplementary Table 2; Supplementary Table 3), such as Beloniformes vs. Synbranchiformes, Heptapteridae vs. Pseudopimelodidae.

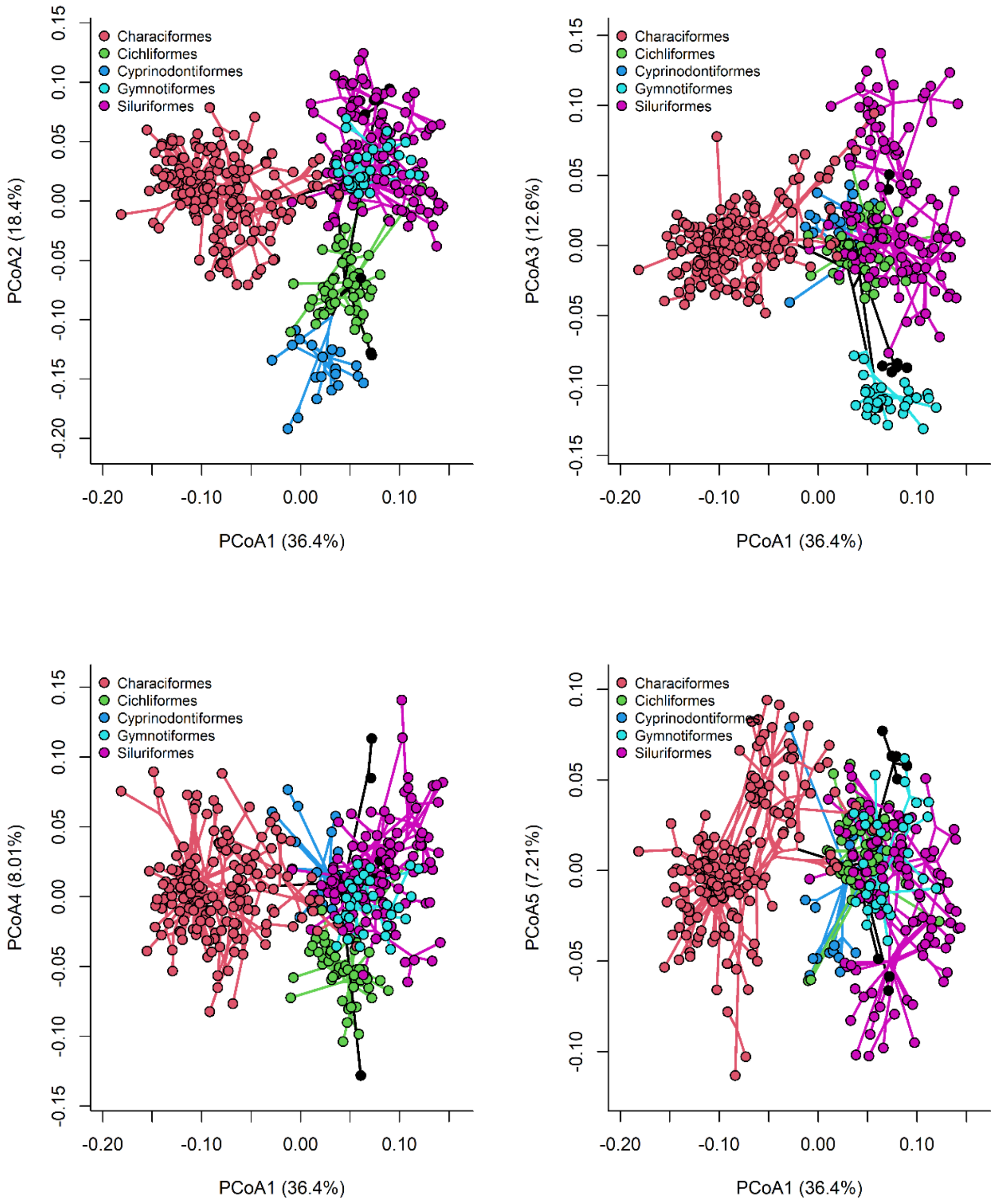

Figure 3 – Phylomorphospace of the most representative taxonomic orders of Amazonian stream fishes across the ecomorphospace shaped by the first five principal components.

Taxonomic order’s contribution to trait space

Siluriformes occupied the highest volume in the ecomorphospace (FRic = 7.63% of total ecomorphospace), followed by Characiformes (7.02%), while the other clades occupied smaller portions (Cichliformes: 0.84%; Cyprinodontiformes: 0.07%; Gymnotiformes: 0.04%). Controlling for the variation in the number of species, Siluriformes still occupied a disproportionally large volume in the ecomorphospace when compared to other clades, in except to Characiformes (Figure 4a). Poorly represented clades exhibited higher values of ecomorphological specialization (Characiformes: 0.52; Cichliformes: 0.52; Cyprinodontiformes: 0.75; Gymnotiformes: 0.67; Siluriformes: 0.58; Synbranchiformes: 0.76; Gobiiformes: 0.93), and null models highlighted the highest ecomorphological specialization of Cyprinodontiformes compared to the remaining analyzed orders, and from Gymnotiformes compared to Characiformes and Cichliformes (Figure 4b). The total phylogenetic diversity was the lowest in less diversified clades (Characiformes: 6,116.58; Cichliformes: 1,756.38; Cyprinodontiformes: 928.17; Gymnotiformes: 1,483.54; Siluriformes: 4,637.56; Synbranchiformes: 105.00; Gobiiformes: 42.54). Controlling for the variation in the number of species, null models highlighted the lower phylogenetic diversity in Cichliformes compared to Characiformes, Cyprinodontiformes, Gymnotiformes, and Characiformes (Figure 4c).

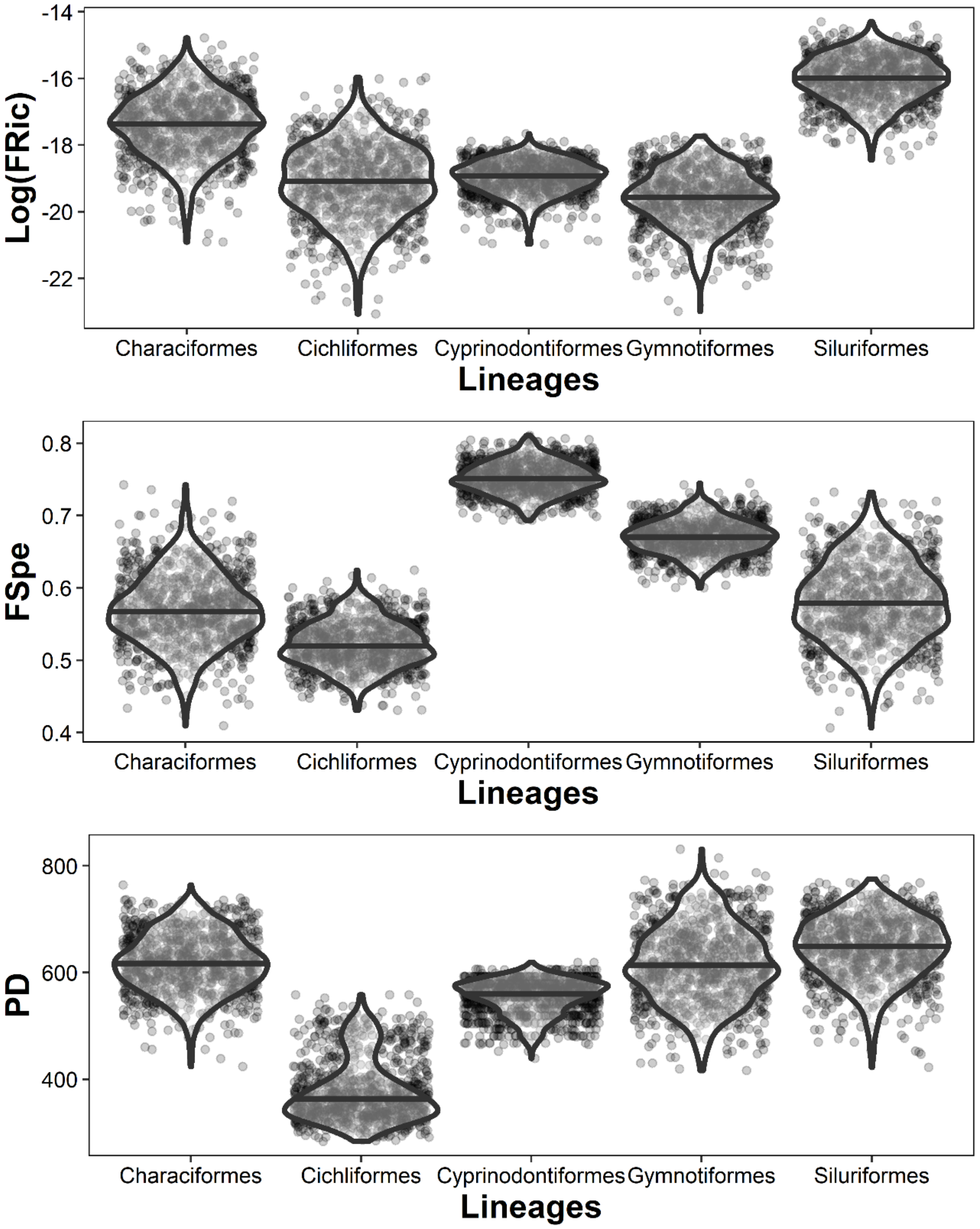

Figure 4 – Estimated functional richness (FRic), functional specialization (FSpe), and phylogenetic diversity (PD) in 1,000 rarefied samples of 10 species for the most representative lineages in Amazonian streams.

Discussion

In this study, we revealed that the axes of variation in the ecomorphospace of Amazonian stream fishes are related to traits representing position in the water column, feeding mode, and swimming mode. Only a small portion of potential trait space is filled if we consider that all trait combinations are equiprobable or that extreme traits are selected against. Therefore, these fishes do not concentrate around a single combination of traits, but rather around different ecomorphological types. The distribution of fish species in these trait constellations is not random: phylogeny play an important role, constraining the position of species in the ecomorphospace by their taxonomic relationships, as well as their contribution to the volume and shape of the ecomorphospace of Amazonian stream fishes.

The ecomorphospace of Amazonian stream fishes is comprised by multiple morphological hotspots that allow fish species to utilize these highly heterogeneous and complex systems. Species' distribution in the ecomorphospace may be an important underlying mechanism for resource partitioning. Dietary and spatial resources are primary drivers of species' coexistence in vertebrates (Schoener 1974) and several studies present evidences of habitat segregation in Neotropical stream fishes (Brejão, Gerhard, and Zuanon 2013; Silva et al. 2016; Soares et al. 2017; Ferreira et al. 2021). On the other hand, Ross (1986) suggested that food partitioning is more important than spatial segregation in fishes, which is supported for some Neotropical fish assemblages (Brazil-Sousa, Marques, and Albrecht 2009; Fernandes et al. 2017; Barili et al. 2011; Correa and Winemiller 2014). Our results highlight that the most important traits favoring spatial and trophic partitioning covary in Amazonian stream fishes, hence being both equally important for potential niche partitioning. In this spatial scale, it highlights that fishes display ecological strategies that merge how they use habitat and food resources. For example, upper-positioned eyes and low caudal peduncle throttling in Cichliformes favor the use of benthic substrata with low flow, and their conic teeth and oral protrusion allow them to capture and hold the prey. Hence, while elongation and laterally-compression are usually important axes in body shape variation in fishes (Price et al. 2019; Claverie and Wainwright 2014), we show coupling in ecomorphological traits determining spatial and trophic resources use.

The benthic-pelagic axis constitutes the first axis of ecomorphological variation, separating a group of species displaying centrally positioned eyes, laterally compressed bodies that use the oscillatory motion of short-based fins to primarily explore the upper layer of the water column (*e.g.*, Characiformes), and multicuspid teeth. The second group comprise species with upper-positioned eyes and larger mouth gaps, which segregates in the subsequent axes of the ecomorphospace, separating a group of species with high maneuverability, low propulsion capacity, and oral protrusion (Cichliformes) in the second axis and fourth axis, and a group comprising species that use the undulation of long-based fins (Gymnotiformes) or body (Synbranchiformes) for high maneuvering in complex environments and burrowing abilities, respectively, in the third axis. Fishes vary from specialist and generalist swimming strategies, and specialists have morphological adaptations to optimize one of three functions: cruising, maneuvering, or accelerating (Webb 1984). Results highlight that Amazonian stream fishes are concentrated around multiple combinations of traits specialized for maneuvering and using the benthic stratum of the water column, and one generalist ecomorphotype adapted for cruising and accelerating but specialized in the use of the upper layer of the water column.

A small portion of the potential trait space was filled when considering that all traits could be equiprobably combined or if extreme traits were selected against. The partial filling of potential niche space is commonly associated with environmental filtering constraints. Céréghino et al. (2018), for example, argued that poorly oxygenated waters exclude some major invertebrate taxa common to other Neotropical habitats (*e.g.*, Ephemeroptera, Plecoptera) to occupy bromeliad tanks, thus excluding some clade-specific combination of traits. A few empty areas in the trait space may be explained by the absence of clades that occur in other Amazonian environments, as rivers or lakes. 1st to 4th order streams differ from other Amazonian freshwater environments mainly due to water volume and surface area. The smaller areas in 1st to 4th order streams limit the occurrence of species that need larger home ranges, as home range and habitat use are strongly dependent on body size (Woolnough, Downing, and Newton 2009), which can exclude species adapted for cruising in those systems. Other empty areas in the trait space may occur due to physical limitations of different strategies in swimming, habitat use, and foraging. For example, a strongly laterally or dorsoventrally compressed body shape would reduce the maneuverability of the undulatory-based swimming of Gymnotiformes in highly complex systems (Lannoo and Lannoo 1993). Another example is the high modularization in body shape in catfishes of the family Loricariidae (Black and Armbruster 2022).

We observed varying levels of phylogenetic signal in the ecomorphological traits of Amazonian stream fishes, corroborating studies that show phylogenetic signal in morphological and ecological traits of Neotropical freshwater fishes (Roa-Fuentes, Casatti, and Romero 2015; Keppeler and Winemiller 2020). Even when phylogenetic signal was controlled, we observed that clades segregated in the ecomorphospace. This highlights the importance of the common ancestry in the ecomorphological attributes of fishes and, therefore, of the evolutionary history of Neotropical fishes on their morphology and ecological roles (Soares and Nakamura 2021). On the other hand, some taxa converged in all selected axes of the ecomorphospace (*e.g.*, Gymnotiformes and Synbranchiformes). Evolutionary history is marked both by niche conservatism and convergence that can structure species in a functional multivariate space (Blonder 2018). Gymnotiformes, for example, exhibit a highly conserved body plan, but it also harbors well-known examples of evolutionary convergence with tube-snouted mormyriforms in their foraging behavior (Marrero and Winemiller 1993; Winemiller and Adite 1997). In addition, (Bower et al., 2021) showed that, world widely, stream fishes occupying high water velocity and low structural complexity microhabitats converged ecomorphologically.

Siluriformes and Characiformes occupied the higher portions of the ecomorphospace, and thus were responsible for a great portion of the trait diversity of Amazonian stream fishes. they encompass the highest number of species in Amazonian streams, which usually lead to increasing functional richness (Mouchet et al. 2010; Nakamura, Vicentin, and Súarez 2018). Nevertheless, they also display high levels of functional richness when controlling for species richness. This may be due to the high phylogenetic diversity these clades encompass and the number of phylogenetically independent lineages that occupied and diversified in Neotropical freshwaters. Following (Albert & Reis, 2011), NFF are comprised by approximately 66 independent lineages. Characiformes is comprised by four independent lineages (*Chalceus*, Characoidea, Ctenolucoidea, and Erythrinoidea), Siluriformes is comprised by five independent lineages (Aspredinidae, Cetopsidae, Doradoidea, Loricarioidea, and Pimelodoidea), while other clades are composed by single monophyletic lineages (*e.g.*, Cichliformes, Gymnotiformes). In addition to clade age and lineages composition, Characiformes displays accelerated diversification in body shape (Melo et al. 2021; Burns and Sidlauskas 2019). Therefore, Siluriformes and Characiformes merge distinct evolutionary histories and high levels of diversification and, consequently, different ecomorphological strategies that allows the large area occupied in the ecomorphospace.

Since clade age is not a strong predictor of the number of species (Rabosky, Slater, and Alfaro 2012), we observed that Gymnotiformes displayed low number of species and the smallest functional richness despite high phylogenetic diversity. The highly conserved body plan of gymnotiforms led to the low observed functional richness and high functional specialization. These fishes are nocturnal, benthic, and usually predate on aquatic invertebrate (Brejão, Gerhard, and Zuanon 2013), which is favored by an electrogenesis and active electroreception system. Gymnotiformes can generate and perceive electric fields that help them to navigate in complex environments, detect prey and to intraspecific communication (Babineau et al., 2007; Nanjappa et al., 2000). This highly specialized behavior requires a highly specialized morphology: the culteriform body plan. This body plan is characterized by a highly elongate body and anal fin, lack of dorsal, adipose and pelvic fins, and it generates a knifelike shape (Albert 2001). The abdominal cavity is limited to the anterior portion of the body and most of the length of the body is invested with numerous tuberous and ampullary electroreceptor organs (Lavoué et al., 2012; MacIver et al., 2010). The culteriform body shape favors the production of a stereotyped three-dimensional electric field (Stoddard and Markham 2008) and the maintenance of a semirigid body surface during swimming allows the electrotopic mapping of electroreceptors to the primary electrosensorial system (Shirgaonkar et al. 2008; Albert 2001). Therefore, their dependence on the electrogenesis and electroreception system for their life history and the specialized morphology necessary for maintaining it determine their contribution to the overall ecomorphological space.

Finally, we observed that Cichliformes and Cyprinodontiformes displayed higher functional richness and specialization, respectively, than Gymnotiformes, despite their more recent occupation of Neotropical freshwaters and markedly low phylogenetic diversity in Cichliformes. The high functional richness of Cichliformes compared to their phylogenetic diversity can be explained by the rapid diversification in cichlids due to ecological opportunity (Arbour 2016), especially related to trophic ecomorphological traits and body size (Arbour and López-Fernández 2014; Steele and López-Fernández 2014). Contrastingly, Cyprinodontiformes occupy a small area in the ecomorphospace of Amazonian stream fishes, but display high functional specialization, which might be related to their amphibious lifestyles demanding specific traits (Turko and Wright 2015).

While our study highlighted ecomorphological differences related to spatial and trophic segregation in Amazonian stream fishes, four shortcomings must be highlighted. First, ecomorphological traits represent morphological adaptations favoring specific ecological strategies (Harmon et al. 2005; Winemiller 1992), which might relate to the potential niche of the species, thus a range of plasticity to the functionality and actual use of morphology is expected. For example, Neotropical fishes exhibit high trophic plasticity (Abelha, Agostinho, and Goulart 2001) and some studies show that phylogenetically-close species use habitat differently, but exhibit moderate to high levels of trophic overlap despite morphological dissimilarity (Soares et al., 2017). Even traits specifically evolved for a function might not limit other uses; for example, oral structures adapted for a specific type of prey might not limit the use of other prey (Bartolette et al. 2018). Second, other traits that we did not include in this study might be equally or more important. For example, the morphology and morphometrics of the digestive tract is an important morphological feature determining the diet composition of fishes (Moraes, Barbola, and Guedes 1997; Wagner et al. 2009; Konow et al. 2017) and its use for air-breathing (Persaud, Ramnarine, and Agard 2006), and gut length is usually important for the ecomorphological structure of fish communities (Soares, Ruffeil, and Montag 2013; Karachle and Stergiou 2011). Third, specific values of a given ecomorphological traits might have different functionalities in different clades. For example, upper-positioned eyes are usually found in benthic species, but the four-eyed fish *Anableps* (Cyprinodontiformes: Anablepiidae) displays upper-positioned eyes that allow it swimming in the waterline where it can see simultaneously below and above water (Perez et al. 2017). Fourth, we used species trait averages, but ecomorphological traits might exhibit high levels of intraspecific variation in response to environmental gradients (Manna et al. 2018; Luiz et al. 2022)

We presented evidence that Amazonian stream fishes are primarily distributed in multiple hotspots in the ecomorphospace that might be linked to their strategies for using food and spatial resources. Further studies may now consider the specific traits defining these hotspots in ecomorphospace to understand the functional diversity of Amazonian fish assemblages. In addition, the evolutionary history of Neotropical fishes greatly shapes their occupation in the ecomorphospace and their contribution to local and regional pool of functional traits. Ecomorphological patterns are tightly linked to functional diversity in fishes (Villéger et al. 2017), thus phylogenetic constraints in trait space implies that phylogenetic history is also linked to functional diversity in fish assemblages. At the local scale, environmental factors could affect the trait distribution of fish assemblages. In larger scales, historical contingency will take a role, as the species distribution in the ecomorphospace is not random but constrained by their taxonomic position and marked by both morphological conservation and convergence. In both cases, understanding the evolution in the ecomorphospace of Amazonian stream fishes and the phylogenetic diversity patterns will help to unveil the role of speciation to community assemblage.

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