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

Running title: Ecomorphology of Amazonian stream fishes

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Abstract

Phylogenetic history and environmental conditions determine 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 that are related to resource use and phylogenetic closeness. 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 displayed by the regional pool of species; (iii) evaluate the distribution of taxonomic orders and families in those axes; (iii) determine the overall contributions of taxonomic orders to the 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 a better understanding of 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 modulate ecosystem processes (effect traits) or respond to environmental gradients (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 involved in 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 depressed bodies favor fishes to maintain themselves in the stream bottom facing strong currents (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 ecomorphospace, *i.e.*, a *n*-dimensional space summarizing species ecomorphological variation, is often constrained by life-history and morphophysiological trade-offs because species cannot optimize their performance in all ecological strategies simultaneously (Webb, 1984; Winemiller, 1989). 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 (Spasojevic et al., 2018).

The regional pools of fishes depend on ecological, biogeographic, and evolutionary processes in short and long-term time scales (Cornell & Harrison, 2014; Weeks et al., 2016). They may be constrained by geological processes posing barriers to dispersal (Peixoto et al., 2014), but high ecological tolerance and short-termed environmental changes allow recurrent invasions in new habitats, such as marine-derived lineages in freshwater systems (Bloom & Lovejoy, 2017). Evolutionary history unarguably shapes regional pools of species and the set of functional traits on which major ecological processes act up on (Kraft et al., 2007; Vellend, 2010). Consequently, phylogenetic diversity might be used to assess anthropogenic impacts on biodiversity (Luo et al., 2022; Qian et al., 2022; Su et al., 2021), the importance of historical processes to community structure (Abreu et al., 2019; Aquino & Colli, 2017; Craig et al., 2020), and prioritize species or areas for conservation (Gumbs et al., 2023; Soares et al., 2023; Strecker et al., 2011).

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

(Harvey & Rambaut, 2000; Losos, 2008). 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 & Reis, 2011). Neotropical Freshwater Fishes (NFF) encompasses 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 & Reis, 2011). Richness is unevenly distributed among higher taxa, as the orders Characiformes and 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 et al., 2020; Albert & Reis, 2011). In addition, NFF comprises the largest fish functional richness among biogeographical realms, driven mainly by some functionally unique clades (Toussaint et al., 2016). These lineages are widespread in the Amazon basin, which harbors the most diverse freshwater fish assemblage in the world, encompassing over 2700 valid species (Dagosta & Pinna, 2019).

Herein, we explore the ecomorphospace of Neotropical stream fishes from a large database comprising community-level samples from 405 streams across the Amazon to understand how these communities are functionally organized. 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 (Ross, 1986; Schoener, 1974), 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 both early-branching and recent clades species (Albert et al., 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 fish orders to the ecomorphospace as the composition of clades might be used to understand ecological patterns (Santos et al., 2022; Silva et al., 2022). We expect that clades with higher number of independent lineages occupying the Amazonian region (e.g., Siluriformes) will contribute with larger portions of the ecomorphospace and clades that exhibit highly specialized traits (such as electrocommunication in Gymnotiformes) will contribute with the highest ecomorphological specialization.

Material and methods

Study area

The Amazon basin is the largest aquifer in the world, harboring over 8.000.000 km² and 5% of the Earth surface, and supporting the highest biodiversity on Earth (Barthem & Fabré, 2003; Molinier et al., 2009). 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 microbasins that drained directly into the Amazon River (n = 128) and other six major drainages, namely: Gurupi River 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 basin (n = 62). These basins are broadly distributed in the Brazilian Shields and Fluvial Plains systems.

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 hours, 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 have small dimensions and marked habitat boundaries harboring small-size species, allowing efficient sampling with the applied protocol (Anjos & Zuanon, 2007; Pompeu et al., 2021; Ribeiro & Zuanon, 2006). 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). Characidae was the most representative family (100 species), followed by Cichlidae (54) and Loricariidae (37).

Ecomorphological trait assessment

To describe the ecomorphological structure of fish assemblages, we calculated 16 traits related to feeding strategy, swimming capacity and habitat use (Table 1). 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. 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 and areas were obtained from digital pictures in the Image J software. A minor set of linear measurements was taken using digital caliper (0.1 mm) (Supplementary Material). Specific conventions were adopted for representing ecomorphological traits in case of absences, such as caudal fin in Swamp-eels (Synbranchiformes) and electric fish (Gymnotiformes) and caudal and paired fins in Synbranchiformes, which were set to zero (Brosse et al., 2021; Villéger et al., 2010). 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. We used average trait values for each species in further analyses.

Body size is a fundamental factor determining body shape variation within (Dunic & Baum, 2017; Evans et al., 2019; Wainwright et al., 2002) and between species though evolutionary mechanisms (Bright et al., 2016; Cardini & 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 corrections to body size.

Data analysis

Ecomorphological differences among fishes might be phylogenetically constrained to some extent even under neutral evolution (Roa-Fuentes et al., 2015; Soares et al., 2013), *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., 1998, 2011) 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 regresses against a series of 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, i.e. most of the species in a given pool of species would exhibit 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 et al., 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 et al., 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.

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 shape 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).

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.

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).

Discussion

We found that the principal 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 et al., 2013; Ferreira et al., 2021; N. C. dos S. Silva et al., 2016; Soares et al., 2017). 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 (Barili et al., 2011; Brazil-Sousa et al., 2009; Correa & Winemiller, 2014; Fernandes et al., 2017). 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 (Claverie & Wainwright, 2014; Price et al., 2019), 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 gapes, 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 et al., 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 & Lannoo, 1993). Another example is the high modularization in body shape in catfishes of the family Loricariidae (Black & 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 (Keppeler & Winemiller, 2020; Roa-Fuentes et al., 2015). 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 & 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 & Winemiller, 1993; Winemiller & 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 et al., 2018). Nevertheless, they also display high levels of functional richness when controlling for species richness, which may be related to the high phylogenetic diversity originating from the 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 (Burns & Sidlauskas, 2019; Melo et al., 2021). 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 species richness (Rabosky et al., 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 et al., 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 & Markham, 2008) and the maintenance of a semirigid body surface during swimming allows the electrotopic mapping of electroreceptors to the primary electrosensorial system (Albert, 2001; Shirgaonkar et al., 2008). 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 & López-Fernández, 2014; Steele & 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 & 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 et al., 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 evolved for a certain 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 (Konow et al., 2017; Moraes et al., 1997; Wagner et al., 2009) and its use for air-breathing (Persaud et al., 2006), and gut length is usually important for the ecomorphological structure of fish communities (Karachle & Stergiou, 2011; Soares et al., 2013). 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 (Luiz et al., 2022; Manna et al., 2018)

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. On the local scale, environmental factors could affect the trait distribution of fish assemblages. Yet at 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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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).

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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 (Delariva & Agostinho, 2001; Gidmark et al., 2015; Lujan et al., 2012; Mihalitsis & Bellwood, 2019; Sazima & Caramaschi, 1989).

	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; Sibbing & Nagelkerke, 2000; Spiegel et al., 2011).
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 (Bellwood et al., 2015; Konow & Bellwood, 2011; Sibbing & Nagelkerke, 2000; Waltzek & Wainwright, 2003).
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 & 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 & 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 (Dunic & Baum, 2017; Karpouzi & Stergiou, 2003; Paul et al., 2017), and variation in gape size and potential prey is observed even within trophic levels (Bonato et al., 2017; Mihalitsis & Bellwood, 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 & 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 (Beston et al., 2019; Beston & Walsh, 2019; Caves et al., 2017).
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 et al., 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 et al., 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 (Aguilar-Medrano et al., 2013; Wainwright et al., 2002; Walker & 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; Thorsen & Westneat, 2005; Webb, 2002).
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 et al., 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 (Barros et al., 2019; Webb, 1984).

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 (Matta et al., 2019; Webb, 1984). 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 (Matta et al., 2019; Webb, 1984; 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).

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**