RESEARCH ARTICLE

Feeding habits influence species habitat associations at the landscape scale in a diverse clade of Neotropical fishes

Karold Viviana Coronado-Franco[1] | Pablo A. Tedesco[2] | Matthew A. Kolmann[3] |
Samuel R. Borstein[4] | Kristine O. Evans[1] | Sandra Bibiana Correa[1]

[1]Department of Wildlife, Fisheries, and Aquaculture, Mississippi State University, Mississippi State, Mississippi, USA

[2]Laboratoire Evolution et Diversité Biologique (EDB), UMR5174, CNRS, Institut de Recherche pour le Développement (IRD), Université Toulouse 3 Paul Sabatier, Toulouse, France

[3]Museum of Paleontology, University of Michigan, Ann Arbor, Michigan, USA

[4]Department of Ecology and Evolutionary Biology, University of Michigan, Ann Arbor, Michigan, USA

Correspondence
Sandra Bibiana Correa, Department of Wildlife, Fisheries, and Aquaculture, Mississippi State University, Box 9690, Mississippi State, MS 39762, USA.
Email: sbc257@msstate.edu

Funding information
Centre d'Etude de la biodiversité Amazonienne; Joint Programming Initiative Water challenges for a changing world; McIntire-Stennis Cooperative Forestry Program

Handling Editor: Ana Filipa Palmeirim

Abstract

Aim: A primary goal of community ecology is to understand the mechanisms that drive species' spatial distribution and habitat associations. Species' geographic distribution can be influenced by the distribution of their prey partly because consumers' behaviour is oriented to optimal energy use during foraging. We analysed how differences in dietary preferences influence the spatial distribution and habitat associations of species at the landscape scale. We hypothesized that differences in feeding guilds will lead to divergent habitat association patterns among species.

Location: Amazon River drainage basin.

Taxon: Characiform fishes in the family Serrasalmidae (piranhas and pacus).

Methods: We used diet data to classify species into feeding guilds (frugivores, herbivores, piscivores, fin and scale feeders and planktivores). We used three proxies of habitat association derived from satellite products: floodplain extent, landscape heterogeneity and flood duration, in three distance buffers. We implemented phylogenetic generalized least squares models to evaluate the relationship between habitat association and feeding guilds.

Results: Frugivores, piscivores and fin and scale feeders presented similar patterns of habitat associations, with frugivores occupying wider areas of floodplain and greater landscape heterogeneity. Herbivores and planktivores were associated with smaller floodplain extents and lower landscape heterogeneity. All feeding guilds were associated with similar levels of flood duration.

Main conclusions: Differences in resource distribution (assessed through feeding guilds) can influence habitat association. Considering the hydrological variability (i.e. floodplain extent) and landscape heterogeneity that characterize floodplains, the patterns of habitat association vary with the spatial scale considered. This work highlights the importance of understanding species habitat associations by fish as well as food resource dynamics and floodplain dependence. This realization is critical for assessing the impact of anthropogenic activities on freshwater ecosystems.

KEYWORDS
Amazon River basin, feeding guilds, floodplain, habitat heterogeneity, macroecology, Serrasalmidae

1 | INTRODUCTION

Elucidating the mechanisms that drive species' spatial distribution and habitat associations is a primary goal of community ecology (Heino et al., 2015; Jackson et al., 2001; King et al., 2021; Mittelbach & McGill, 2019). Strong relationships between species' geographic distribution and the distribution of their prey demonstrate the influence of food availability in shaping the habitat association of consumers (Doublet et al., 2019; Johnson & Sherry, 2001; Tableau et al., 2016). Consumer behaviours that seek to optimize energy use relative to foraging could explain part of this influence on spatial patterns (Tableau et al., 2016). According to optimal foraging theory, to enhance fitness, animals favour foraging strategies that provide the most benefit for the least cost, thus maximizing the net energy gained by individuals (Perry & Pianka, 1997). This implies that animal diets will adapt to fluctuations in food resource accessibility. For instance, in the Amazon, the diet breadth of frugivore fish species changes according to seasonal variation in food availability, consuming a higher amount of fruits during the flooding season (Correa & Winemiller, 2014). Similarly, mammals like northern Australian quolls exhibit plasticity in diet according to variations in the landscape and habitat around them (Dunlop et al., 2017).

Food resource use, one of the axes of the multidimensional niche of a species, plays a fundamental role in the relationship between species and their use of the environment (Pianka, 2000). Divergent use of food resources usually leads to niche partitioning among species, allowing them to coexist in a shared niche space; however, niche overlap can also occur along other niche axes (i.e. space and time; Chesson, 2000; Kraft et al., 2015; Mittelbach & Schemske, 2015; Pianka, 1973, 2000). Environmental characteristics associated with resource availability, such as landscape heterogeneity, can significantly influence the partitioning of resources among species for different stages in a species' life cycle (Pérez-Crespo et al., 2013).

Although different definitions have been used to talk about environmental heterogeneity, referring to measures of diversity and structure of the environment (Ben-Hur & Kadmon, 2020; Stein et al., 2014), in the context of this study, we refer to landscape heterogeneity as areas containing several dissimilar habitat types or land cover types. Areas with higher levels of landscape heterogeneity are expected to contain more species and individuals than more homogeneous areas of the same habitat type (Turner & Gardner, 2015). Variability in environmental conditions, like topography and microclimate, increases with patch size and offers more opportunities for organisms with different preferences and tolerances to find optimal conditions within the patch (Turner & Garner, 2015). Landscape variability, for instance, has been shown to be important in determining the distribution, abundance and diversity of several mammal, bird and fish species (Arantes et al., 2019; Lee & Martin, 2017; Thornton et al., 2011). For instance, differences in avian diversity were found when comparing landscapes dominated by agriculture versus non-crop vegetation cover, showing that species richness was lower when there were more agricultural fields in a landscape (Lee & Martin, 2017).

The Neotropical fish family Serrasalmidae (pacus and piranhas) offers an ideal model for studying the influence of feeding specialization on species habitat associations, given that dietary composition and level of specialization vary considerably within clades. This family is composed of c. 100 species and has developed trophically specialized clades ranging from frugivory to piscivory (Correa et al., 2007). Rheophilic species (e.g. *Ossubtus xinguense*, *Tometes ancylorhynchus* and *Mylesinus paucisquamatus*) specialize in periphytic bryophytes and vascularized plants (e.g. Podostemaceae) that grow on rocks in rapids (Andrade et al., 2019; Vitorino et al., 2016). Other species of the genera *Colossoma*, *Piaractus*, *Myloplus* and *Myleus* feed heavily on fruits and seeds and inhabit flooded forests where they serve as seed dispersers (Correa et al., 2007, 2015). Some more ectoparasitic or omnivorous taxa, like *Catoprion mento* and *Acnodon normani*, feed on scales or fins (Janovetz, 2005; Leite & Jégu, 1990), whereas larger piranhas like *Serrasalmus* spp. and *Pygocentrus* spp. are piscivorous and feed mainly from biting off pieces of flesh from other fishes (Goulding, 1980; Nico & Taphorn, 1988).

The diversity of feeding habits within Serrasalmidae is related to morphological traits for food acquisition (Huby et al., 2019). The species that feed on fruits and seeds have molariform teeth, while species that graze on leaves or stems have high-crowned incisiform-like teeth (Huie et al., 2020). In contrast, predators like piranhas that feed on other fishes have sharp, multicuspid, blade-like teeth. Lastly, scale-feeders have specialized stouter, conical or spatulate dentitions (Correa et al., 2007; Goulding, 1980; Kolmann et al., 2018). Other characteristics that differentiate clades within this family are bite force and digestive tract length. Carnivorous species deliver more forceful bites than their herbivorous counterparts (Huby et al., 2019). Herbivorous species have longer guts than carnivorous and omnivorous relatives to cope with less digestible plant material (Pelster et al., 2015). Independent of family, planktivorous fishes have long and thin gill rakers for filter feeding so they are considered a specialized group (Burton & Burton, 2017). The morphological characteristics of the alimentary tract are thus helpful to infer trophic guild and level of specialization of fish taxa.

The geographic distribution of the Serrasalmidae family is restricted to tropical South America, mainly in the lowland (i.e. <500 m above sea level) areas of the Amazon drainage basin (Dagosta & de Pinna, 2017; Jézéquel et al., 2020). Amazon lowlands are characterized by a mosaic of habitats composed of evergreen forests, periodically flooded forests (e.g. várzea or igapó), savannas, lakes and extensive floodplains (Junk et al., 2010). The flooding dynamic is an essential ecological driver in floodplain ecosystems. According to the Flood Pulse Concept (FPC), the flood pulse influences the presence and distribution of organisms, determines life-history traits, affects primary and secondary production and influences decomposition and nutrient recycling (Junk & Wantzen, 2004). This is particularly important for fish species because the flood pulse enhances lateral connectivity between the river channel and floodplain, thereby enlarging aquatic habitats and allowing access to different feeding resources not available in the main channel (Junk, 1997).

The high landscape heterogeneity present in the Amazon lowlands and the role of the flood pulse in the expansion and connectivity of aquatic habitats are related to the distribution and availability of food resources for fish. They, therefore, are expected to influence fish abundance and distribution. For example, frugivorous fish species feed mainly on fruits from the flooded forest (Correa et al., 2007). The access and permanence of frugivorous fishes in the flooded forest depend on the flood pulse and the flood duration (Correa et al., 2015). The extent and diversity of floodplain habitats also are flood-pulse dependent. Wider floodplains will likely include more diverse habitats such as oxbow lakes. In these lentic systems, low water velocity enhances sedimentation and thereby present higher sunlight penetration. Such conditions support plankton growth (Bogotá-Gregory et al., 2020) which provides food for planktivorous species (e.g. *Metynnis*) and juvenile frugivores (e.g. *Colossoma*; Oliveira et al., 2006). Areas with a greater flooding magnitude would likely inundate more extensive floodplains and thereby increase food resource availability for flooded forest-dependent species, like frugivores.

Here, we used geospatially explicit fish occurrences from the most comprehensive dataset available (the AmazonFish project database, Jézéquel et al., 2020), diet data and satellite-derived landscape variables to explore how differences in feeding guilds influence the habitat association of serrasalmid species in the Amazon basin. We tested the hypothesis that serrasalmid species specializing in different food resources will use different habitat types. If serrasalmids optimize their foraging, as predicted by theory (Perry & Pianka, 1997), then the most specialized species should have distributions that closely track the habitats harbouring their preferred food resource. In the case of frugivores, for instance, their primary food source is restricted to floodplain forests (Correa & Winemiller, 2014; Goulding, 1980) and thus are expected to inhabit areas with a broad floodplain extent and long inundation time but low habitat heterogeneity (mostly forest). Likewise, planktivores follow the distribution of plankton, which in Amazonia is restricted to floodplain lakes because slow-moving and less turbid waters promote plankton production (Bogotá-Gregory et al., 2020; Forsberg et al., 2017) and thus are expected to inhabit areas with a broad floodplain extent

and long inundation time but low habitat heterogeneity (mostly open-water floodplain lakes). In contrast, herbivores feed on a wide range of plant material (leaves, stems, flowers) and the distributions of those food types are spatially broad (Arantes et al., 2019; Silva et al., 2021). Thus, herbivores are expected to inhabit areas with high floodplain extent and landscape heterogeneity irrespective of flood duration. Lastly, for piscivores and species feeding on flesh, scales or fins of other fishes, their food base is broadly distributed (Martelo et al., 2008; Siqueira-Souza et al., 2016). Thus, these species are expected to inhabit areas with high landscape heterogeneity irrespective of floodplain extent and flood duration given that consumers can track prey movement into the floodplain for short or long periods of time (Table 1).

2 | MATERIALS AND METHODS

2.1 | Study area

This study focused on the Amazon drainage basin, where most of the species of the Serrasalmidae family occur (Figure 1; Dagosta & de Pinna, 2017; Jézéquel et al., 2020). Some serrasalmid species have a restricted distribution, including *O. xinguense* that is endemic to the rapids of the Xingu River (Andrade et al., 2016) and *M. paucisquamatus*, endemic to the rapids of the Tocantins River (Vitorino et al., 2016). Others are broadly distributed, such as *Colossoma macropomum* and *Serrasalmus rhombeus* (Dagosta & de Pinna, 2017).

Area estimations based on satellite imagery show that at least $8.4 \times 10^5 \, km^2$ of the Amazon lowlands are occupied by wetlands, representing 14% of the total basin area ($5.83 \times 10^6 \, km^2$; Hess et al., 2015). Basin-wide, about three-quarters of these wetlands, are covered by forest, woodland or shrubland (Hess et al., 2015). The flooding regime for the Amazon River and its tributaries presents a monomodal flood pulse related to dry and rainy seasons (Junk & Wantzen, 2004). Therefore, these area estimates can change with the flooding regime; for instance, the flooded portion of the wetland area can vary from 34% to 75% from the dry to the flood season (Hess et al., 2015).

TABLE 1 Predicted habitat associations for Serrasalmidae feeding guilds in the Amazon basin

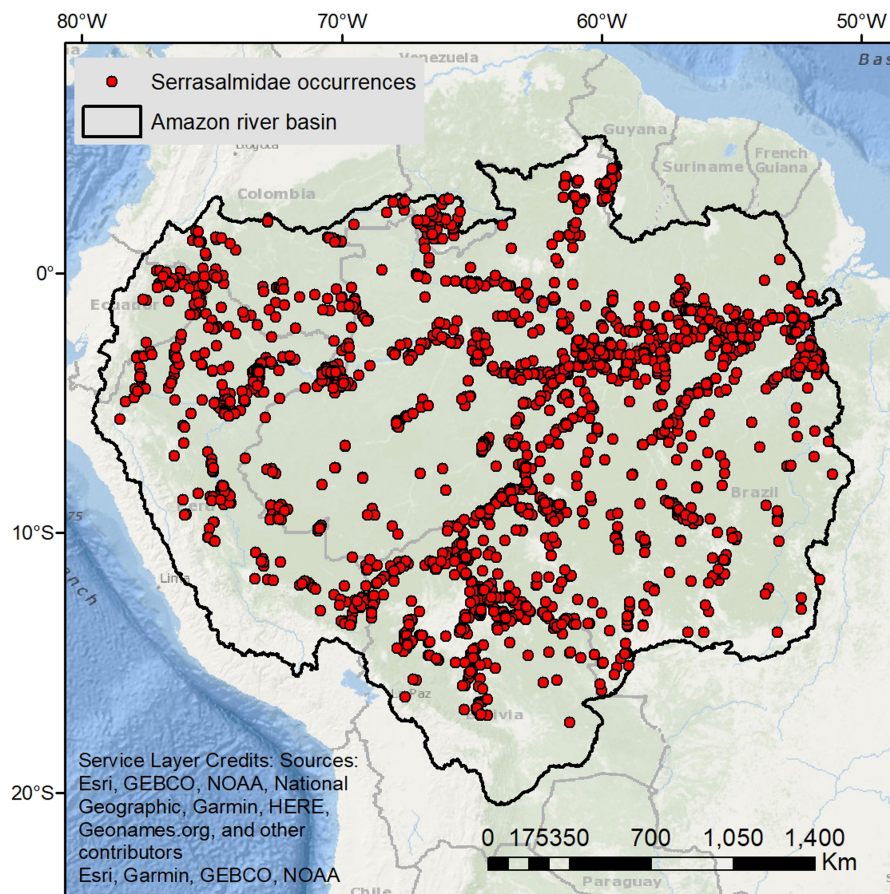| Predictor		Floodplain extent	Landscape heterogeneity	Flood duration
		Response variables		
Feeding guilds	Herbivores	⬆ High	⬆ High	⬇⬆ Variable
	Piscivores Fin and scale feeders	⬇⬆ Variable	⬆ High	⬇⬆ Variable
	Frugivores Planktivores	⬆ High	⬇ Low	⬆ High

FIGURE 1 Spatial distribution of occurrence data in the Amazon River basin for the fish family Serrasalmidae retrieved from the Amazon fish project (Jézéquel et al., 2020)

2.2 | Habitat association proxies

We used occurrence data, from the AmazonFish project database (Jézéquel et al., 2020), covering all the major sub-basins within the Amazon drainage basin such as Xingú, Tapajós, Madeira, Purus, Juruá, Uacayali, Putumayo, Japurá, and Negro (Figure 1). This database contains the most complete information currently available on freshwater fish species distribution for the Amazon drainage basin. For the Serrasalmidae family, there are 14,269 occurrences of 81 species available, representing 83% of the valid species in the family. We, however, selected a subset of species based on the availability of diet data and phylogenetic information, yielding a final number of 61 species with 13,667 occurrences (i.e. 62.24% of the valid species in the family; Table S1). We assumed that all the occurrences corresponded to adults with complete ontogeny.

Considering the relevance of scale on habitat association studies (Jackson et al., 2001), we used a multiscale approach meaning that our response variables are landscape characteristics measured at different extents. We analysed three habitat association proxies (i.e. floodplain extent, landscape heterogeneity and flood duration) with three different buffer sizes around each species occurrence: (1) small scale: 5 km for floodplain extent and 300 m for landscape heterogeneity and flood duration; (2) intermediate scale: 10 km for floodplain extent and 5 km for

landscape heterogeneity and flood duration; and (3) large scale: 25 km for floodplain extent, landscape heterogeneity and flood duration. We used different small and intermediate scales for floodplain extent considering the natural variation in floodplain width (Cauduro et al., 2013).

The chosen small buffer sizes represent the characteristics of the immediate surrounding habitats around occurrence points while the intermediate and large buffer sizes include the habitats that the species are associated with peripherally, considering the mobility of the fishes. The dispersal ability was deemed to be equal for all species. The 300 m buffer size for landscape heterogeneity was selected to account for the habitats in the immediate surrounding of fish occurrence points. The additional buffer size for heterogeneity (5 km) considers the potential foraging area of fish at an intermediate scale. The radius of the intermediate and large buffer sizes was selected based on lateral migration distances (between the main channel and the floodplain) performed by Characiformes (the order that Serrasalmidae family belongs to) in the Amazon basin (Duponchelle et al., 2021). For instance, Anderson et al. (2011) reported an average daily movement of 1.22 ± 0.641 km for serrasalmid frugivorous fishes foraging within flooded forests. These scales do not account for longitudinal migrations that can extend thousands of kilometres; however, only three serrasalmid species have been documented to engage in long (>1000 km) longitudinal migrations (i.e.

C. macropomum, *Piaractus brachypomus* and *Mylossoma duriventre*; Duponchelle et al., 2021).

2.3 | Floodplain extent

To assess the floodplain extent, we subtracted the area of the main channel of rivers from the database GFPLAIN250m, a global high-resolution dataset of Earth's floodplains. This dataset provides information about the delineation of floodplains worldwide with 250 m of spatial resolution (Nardi et al., 2019). We estimated the mean floodplain extent considering the number of pixels pertaining to floodplain inside buffers of 5, 10 and 25 km of distance around the occurrence points. The values of the first quartile (i.e. 25%) of floodplain extent were calculated per species, and we used this variable to explore which feeding guilds were associated with even low values of floodplain extent, suggesting floodplain dependence.

2.4 | Landscape heterogeneity

The habitat types in the Amazon drainage basin were obtained from the satellite-derived product LBA-ECO LC-07 Wetland Extent, Vegetation and Inundation: Lowland Amazon Basin (Hess et al., 2015). This dataset provides a map of wetland extent, vegetation type and dual-season flooding state of the entire lowland Amazon basin and is derived from mosaics of Japanese Earth Resources Satellite 1 (JERS-1) imagery acquired during October–November 1995 and May–June 1996 (Hess et al., 2015). Land cover classes in the high-water season include aquatic macrophytes, flooded forest, flooded shrub and flooded woodland. Aquatic macrophytes include emergent flooded herbaceous plants and floating beds of herbaceous aquatic vegetation, but omit submerged aquatic plants, as these are undetectable with Synthetic Aperture Radar (SAR). Shrub represents woody vegetation that is partitioned between tree and shrub using a height limit of 5m. Woodland represents areas with 20%–70% of tree canopy cover. Forest represents areas with tree canopy cover >70% (Hess et al., 2015). To maintain standardized buffer areas, we considered all pixels falling within the buffer areas.

We calculated the number of occurrences per dominant land cover type (land cover type with higher proportion) within three buffer distances (300 m, 5 km and 25km). A diversity index for the landscape was calculated within the three buffers, considering the proportional abundance of each land cover type, based on the Shannon's diversity index:

$$\text{SHDI} = -\sum_{i=1}^{m} (Pi \times \ln Pi)$$

where *Pi* is the proportion of class *i*. The values of this index range from SHDI = 0 when the landscape contains only one land cover type (i.e. no diversity) to SHDI >0, without limit; SHDI increases as the number of different land cover types (i.e. land cover richness) increases and/or the proportional distribution of area among land cover types becomes more equitable (McGarigal et al., 2012).

2.5 | Flood duration

We calculated the average flood duration (in number of months) in buffers of 300 m, 5 km and 25km around occurrence points per species. We used the GIS product Surface WAter Fraction High Resolution (SWAF-HR) for 2021 (Parrens et al., 2019) which was the only publicly available dataset. This database contains monthly inundation areas at a high spatial resolution (1 km). Average flood duration represents the mean of the number of months each 1 km pixel, within each buffer, was flooded in 2012.

2.6 | Dietary classification

We used diet data from analyses of stomach contents to group species according to feeding habits. Diet data were compiled through a literature review (Kolmann et al., 2021) and include 62.24% of serrasalmid species (i.e. 61 species). In most cases, our diet database contains multiple records/references per species and references that used qualitative (i.e. presence/absence of prey items) or quantitative methods, the latter being either singular (i.e. volume, weight occurrence) or composite (i.e. Alimentary Importance Index, IAI; Index of Relative Importance, IRI) metrics for representing diet composition. Because our dataset contained qualitative and quantitative data, we used a quartiles system to assess the specialization degree per species. For instance, if a species had >75% of fish remains in the reported stomach contents, the species was classified as a highly specialized piscivore and a species with <25% of any food item was classified as a low specialized species (Table S1). In addition, because fish frugivory is a unique feeding habit and fruit has a restricted distribution (fruits mainly occur in forested areas; Correa & Winemiller, 2014), we classified all species according to their level of frugivory, considering the presence and proportion of fruits and seeds in the stomach contents, using the rule described above (Table S1).

For species where different references used the same method to estimate diet composition, the records were averaged, and then, the quartile rule was applied. In cases where different methods were used, we could not calculate an average but considered the highest value from each reference. Based on food items consumed (Table S2), species were grouped into five functional feeding guilds: frugivores, herbivores, planktivores, piscivores and fin & scale feeders (Table S3). Note that insects were not reported in serrasalmid diets.

2.7 | Data analysis

First, we used principal component analysis (PCA) to visually explore spatial associations among species and land cover types based on their feeding guilds. We created buffers of 300 m, 5 km and 25km, per occurrence record, to characterize the surrounding

landscape. We conducted a covariance-based PCA of dominant land cover types within buffers (i.e. land cover type with the highest proportion) around each occurrence record and classified species according to their feeding guilds. The percentage of variance explained was used to inform the number of axes retained for interpretation (Jackson, 1993). PCAs were implemented in R 4.1.1 (R Core Team, 2021) and visualized using the package 'ggbiplot' (Vu, 2011).

Next, we used phylogenetic generalized least squares (PGLS) regressions to test for relationships between each habitat association response variables (i.e. floodplain extent, landscape heterogeneity and flood duration) and feeding guild predictor variables (i.e. frugivore, herbivore, planktivore, piscivore, fin and scale feeder) in a phylogenetic context. Given that closely related species are assumed to have more similar traits because of their shared ancestry, they are expected to produce more similar residuals from the least square's regression line than distantly related species. PGLS accounts for the interspecific autocorrelation due to phylogenic relatedness (Garamszegi, 2014; Martins & Hansen, 1997). PGLS models were implemented in R (R Core Team, 2021) using the function 'gls' from the package 'nmle' (Pinheiro et al., 2021) with the maximum-likelihood transformation of branch length optimized for the data ('method = ML'). We used a phylogenetic tree that includes 61 species (62.24% of the species in the family; Table S1). The tree was generated by increasing the taxon sampling of the most recent comprehensive phylogeny for serrasalmids (i.e. containing 36 species for which we have diet and occurrence data; Kolmann et al., 2021) with representatives from all recognized serrasalmid genera (See Appendix S1 for method details, Appendix S2 for accessions used for the legacy markers, Appendix S3 for the phylogeny). Previous to model implementation, we tested the assumption of homogeneity of variances which was met by all except one of the models (Landscape heterogeneity at 5 km). Given the closeness of the significance value to 0.05 alpha level, we decided not to change the model or transform the

data to make all models comparable (Table S4 provides the values from Levene's tests). We calculated a pseudo-R^2 by comparing the log-likelihood of the full (actual) and reduced (intercept only) models using the function 'R2.lik' from the package 'rr2' (Ives, 2019; Ives & Li, 2018). Finally, we performed a Tukey HSD post hoc pairwise comparison analysis per PGLS model using the package and function 'emmeans' in R (R Core Team, 2021). The Tukey's HSD tests all pairwise differences while controlling the probability of making one or more Type I errors (Lenth, 2021).

3 | RESULTS

Habitat association proxies were correlated. The mean Pearson's R values for the pairwise correlation between the habitat association proxies are as follows: floodplain extent/landscape heterogeneity = 0.66; floodplain extent/flood duration = 0.37; and flood duration/landscape heterogeneity = 0.52.

3.1 | Land cover types

Irrespective of the buffer size (i.e. 300 m, 5 km or 25 km) around the occurrence record, ordination analyses failed to detect clear associations among feeding guilds and the dominant land cover type within buffers (Figure 2). The degree of feeding guild overlap was buffer size dependent, from complete overlap at 300 m to partial overlap at the largest scales (Figure 2).

3.2 | Floodplain extent

Our PGLS models revealed that feeding guild influences habitat association (Table 2). Pairwise comparisons showed that frugivorous,
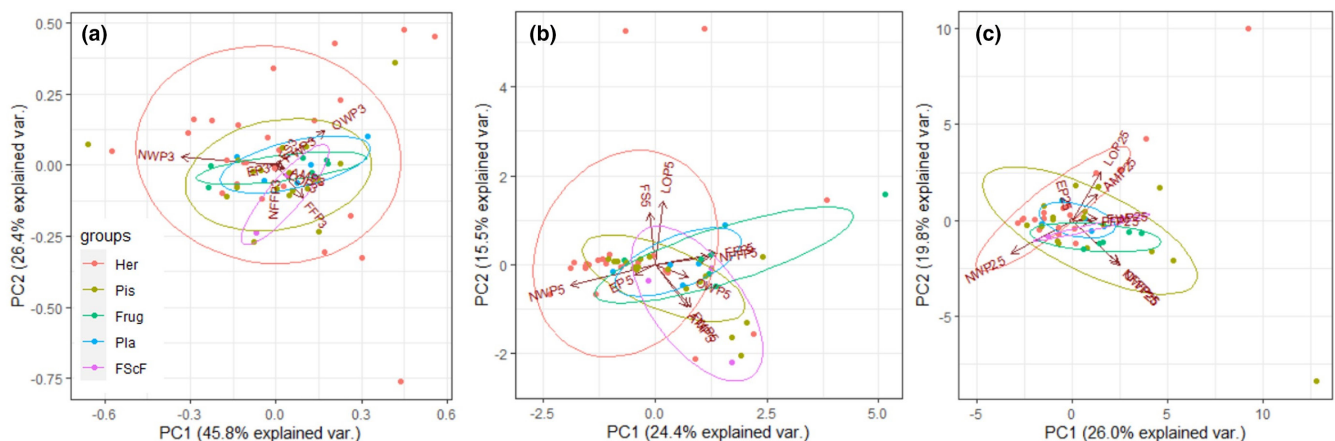

FIGURE 2 Principal components analysis (PCA) representing feeding guilds of the fish family Serrasalmidae in each dominant land cover type at buffers of (a) 300 m, (b) 5 km and (c) 25 km in the Amazon River basin. Concentric ellipses represent a 95% confidence ellipse interval. Arrows represent the main land cover types within each buffer. Abbreviated labels on arrows correspond to land covers: AMP, aquatic macrophyte; EP, elevation above 500 masl; FFP, flooded forest; FWP, flooded woodland; NFFP, no flooded forest; NWP, no wetland within Amazon Basin; OWP, open water. Numbers next to abbreviated labels represent the buffer size 3=300 m, 5=5 km, 25=25 km

TABLE 2 Results of PGLS for the response variables mean floodplain extent at the scales of 5 km, 10 km and 25 km and landscape heterogeneity (Shannon diversity index) and flood duration at the scales of 300 m, 5 km and 25 km

Predictors	Estimates	CI	p	Estimates	CI	p	Estimates	CI	p
Floodplain extent	5 km			10 km			25 km		
(Intercept)	0.35	−0.21 to 0.91	0.223	0.27	−0.34 to 0.88	0.394	0.18	−0.39 to 0.74	0.542
Piscivores	0.27	0.11–0.43	**0.002**	0.33	0.16–0.51	**<0.001**	0.35	0.18–0.51	**<0.001**
Frugivores	0.29	0.13–0.44	**0.001**	0.33	0.16–0.50	**<0.001**	0.34	0.18–0.50	**<0.001**
Planktivores	−0.06	−0.22 to 0.09	0.411	−0.07	−0.23 to 0.10	0.439	−0.06	−0.22 to 0.09	0.423
FScF	0.24	0.03–0.45	**0.032**	0.26	0.03–0.50	**0.03**	0.28	0.07–0.50	**0.012**
AIC	−5.608			6.017			−3.538		
Landscape heterogeneity	300 m			5 km			25 km		
(Intercept)	1.01	−0.75 to 2.76	0.265	1.36	−0.15 to 2.87	0.084	0.91	−0.35 to 2.18	0.163
Piscivores	−0.14	−0.64 to 0.37	0.594	0.59	0.15–1.02	**0.011**	0.92	0.55–1.28	**<0.001**
Frugivores	0.31	−0.18 to 0.80	0.219	0.41	−0.01 to 0.83	0.062	0.68	0.33–1.03	**<0.001**
Planktivores	−0.26	−0.74 to 0.22	0.291	−0.25	−0.66 to 0.17	0.245	−0.07	−0.41 to 0.28	0.705
FScF	−0.26	−0.93 to 0.41	0.451	0.62	−0.05 to 1.20	**0.039**	0.85	0.37–1.34	**0.001**
AIC	134.338			116.234			94.749		
Flood duration	300 m			5 km			25 km		
(Intercept)	6.15	−0.75 to 13.06	0.087	7.25	2.22–12.29	**0.007**	7.28	2.17–12.39	**0.007**
Piscivores	2.43	0.44–4.43	**0.02**	0.48	−0.98 to 1.93	0.522	0.8	−0.67 to 2.28	0.291
Frugivores	1.37	−0.57 - 3.30	0.171	0.51	−0.89 to 1.92	0.477	0.18	−1.25 to 1.61	0.801
Planktivores	−1.15	−3.04 to 0.73	0.235	0.9	−0.47 to 2.28	0.204	0.73	−0.66 to 2.13	0.306
FScF	2.56	−0.07 to 5.20	0.061	0.13	−1.78 to 2.05	0.892	0.37	−1.58 to 2.31	0.713
AIC	301.789			263.246			265.032		

Note: Herbivory is the reference feeding guild. The number of observations is 61 species. Values in bold represent *p*-values significant at alpha level = 0.05. Abbreviations, Feeding guild abbreviations: AIC, Akaike Information Criteria; FScF, Fin and scale feeder.

piscivorous and fin and scale feeders species use habitats associated with a broader mean floodplain extent than herbivores and planktivores at all spatial scales studied (Table 3; Figure S1). However, frugivorous species' associations with floodplain extent were held even when there were small floodplain areas inside the buffers (represented by the first quartile values) (Table S5). Unexpectedly, piscivores and frugivores are not different in terms of floodplain mean extent (Table 3). Based on the Pseudo R^2, feeding guilds explained more mean floodplain extent used at all buffers' radius than landscape heterogeneity and flood duration (Table S6). When considering the frugivory level of all species, our analyses failed to detect habitat association patterns related to floodplain extent (Table S7).

3.3 | Landscape heterogeneity

At all scales, some feeding guilds inhabit areas with greater landscape heterogeneity than others (based on the Shannon diversity index for buffers 5 and 25 km, Tables 2 and 3, Figure S1). At small buffer scales, frugivores are different from planktivores, piscivores and fin and scale feeders by inhabiting areas with greater landscape heterogeneity (Table 3, Figure S1). Frugivores, piscivores and fin and scale feeders are associated with areas with greater landscape heterogeneity than herbivores and planktivores at the largest scale (25 km, Table 2). With the

increase in buffer scale, the number of feeding guild pairs that exhibit significant differences also increased (Table 3). This trend is unexpected as one expects that the higher the scale, the higher the homogenization, so the feeding guilds should be more similar in their habitat associations. In terms of frugivory level, mid-low frugivores were related to lower levels of landscape heterogeneity at the 25 km buffer size (Table S8).

3.4 | Flood duration

Only at the smallest scale (300 m), some feeding guilds are influenced by flood duration in the areas they inhabit (Table 2). Specifically, fin and scale feeders, piscivores and frugivores are associated with areas of longer flood duration than planktivores (Table 3, Figure S1).

4 | DISCUSSION

Our results indicated that the distribution of preferred food resources on habitats influences habitat association by consumers (i.e. feeding guilds) at the landscape scale in the Amazon River basin. This pattern was mainly supported when considering the variation in floodplain extent and landscape heterogeneity that characterizes large rivers and their floodplains. Moreover, our results

TABLE 3 Pairwise comparison results for three habitat association proxy variables at three spatial scales

Contrast	Flood extent 5 km	Flood extent 10 km	Flood extent 25 km	Landsc. Heterog. 300 m	Landsc. Heterog. 5 km	Landsc. Heterog. 25 km	Flood duration 300 m	Flood duration 5 km	Flood duration 25 km
Her—Pis	**0.015**	**0.004**	**0.001**	0.983	0.078	**<0.001**	0.132	0.967	0.823
Her—Frug	**0.006**	**0.003**	**0.001**	0.726	0.328	**0.004**	0.640	0.952	0.999
Her—Pla	0.921	0.936	0.928	0.823	0.765	0.995	0.751	0.701	0.839
Her—FScF	0.194	0.185	0.088	0.941	0.229	**0.009**	0.325	1.000	0.996
Pis—Frug	0.997	1.000	1.000	**0.031**	0.656	0.193	0.378	1.000	0.621
Pis—Pla	**<0.001**	**<0.001**	**<0.001**	0.957	**<0.001**	**<0.001**	**<0.001**	0.917	1.000
Pis—FScF	0.994	0.921	0.926	0.986	1.000	0.996	1.000	0.987	0.970
Frug—Pla	**<0.001**	**<0.001**	**<0.001**	**0.004**	**<0.001**	**<0.001**	**0.001**	0.906	0.739
Frug—FScF	0.980	0.947	0.964	0.206	0.884	0.889	0.776	0.987	0.999
Pla—FScF	**0.012**	**0.012**	**0.003**	1.000	**0.007**	**<0.001**	**0.013**	0.879	0.992

Note: Values in bold represent *p*-values significant at alpha level = 0.05 adjust for multiple comparisons within phylogenetic generalized least squares models via Tukey honest significant difference tests.

Abbreviations, Feeding guild abbreviations: Her, Herbivore; Pis, Piscivore; Frug, Frugivore; Pla, Planktivore; FScF, Fin and scale feeder. Landsc. Heterog, Landscape heterogeneity.

demonstrated how patterns of habitat association with landscape heterogeneity are extent-dependent (i.e. buffer size).

Taken together, our results suggest that feeding guilds do influence species habitat associations. Our predictions, however, were only partially supported. We expected that herbivores would be associated with high floodplain extent and landscape heterogeneity, irrespective of flood duration. Results contradicted this expectation concerning habitat heterogeneity, showing associations between herbivores and low floodplain extent and low landscape heterogeneity at a large scale only. The primary food resource of herbivores, plants, are not mobile but are widely distributed and abundant (Silva et al., 2021), being present in different habitats like flooded forest, flooded shrub and flooded woodland, as well as along the river margin. Our unexpected results may be related to foraging specialization by some herbivorous fish species. For example, aquatic macrophytes of the rheophilic family Podostemaceae are restricted to areas of rapids and therefore limit the number of habitat associations for specialized herbivorous fishes (Andrade et al., 2019).

For piscivores and fin/scale feeders, we predicted associations with high landscape heterogeneity irrespective of floodplain extent and flood duration levels. Our results supported the prediction that piscivores and fin/scale feeders use areas with high landscape heterogeneity. However, these feeding guilds explore areas with high floodplain extent (similar to frugivores) and intermediate flood duration. These results reflect the spatial distribution of fish prey for piscivores and fin/scale feeders, which are widely distributed in the main channel of rivers and streams, as well as within floodplain habitats since fish perform lateral migrations during the flood season (Rodrigues et al., 2018). Also, piscivorous' diet composition is affected by hydrological change, including the opportunistic consumption of plant material by some species (e.g. *Serrasalmus* spp.) during the flooding season due to the high availability of these food types (Prudente et al., 2016).

This implies associations with various habitat types, supporting the observed high landscape heterogeneity of piscivores and fin/scale feeders.

Due to their dependence on floodplain forests to access fruits and lakes to access plankton, we expected that frugivores and planktivores would inhabit areas with low landscape heterogeneity (i.e. forest or open water dominated, respectively), but broader floodplain extent and longer flood duration than other guilds. Unexpectedly, frugivores and planktivores presented contrasting patterns. Frugivores tended to explore broader floodplain extents but similar or even higher landscape heterogeneity than other guilds. The results confirmed the expectation of low landscape heterogeneity for planktivores. However, other results for planktivores contradicted the expectation for the two other habitat association proxies (i.e. planktivores were associated with areas with low floodplain extent and flood duration). Other studies conducted in the Amazon do not show any relationship between planktivores and forest cover (another measure of heterogeneity), possibly because the production of phytoplankton and zooplankton is limited under the forest canopy (Arantes et al., 2019). In terms of floodplain extent, we expected more expansive floodplains to be more likely to contain floodplain lakes. Perhaps that is not always the case, as lake formation is influenced by meandering and channel migration. Lastly, floodplain lakes are annually connected to river channels by the annual flood cycle. Thus, flood duration may not affect whether they remain as open water bodies capable of supporting plankton and planktivores during the dry season. However, changes in hydrology induced by dams and climate change may reduce flow and turn floodplain lakes ephemeral in the future (Correa et al., 2022). Frugivores and piscivores appear to be similar in terms of how much floodplain extent they occupy but are different when we consider the landscape heterogeneity, with frugivores occupying areas with higher levels of heterogeneity at the smallest buffer size (300 m). For frugivores, the observed association with a wider floodplain

extent is supported by the fact that they feed primarily on fruits from the flooded forest and serve as seed dispersers for numerous plant species (Correa et al., 2007, 2015). Regarding the observed high landscape heterogeneity, frugivorous species like *C. macropomum* use different habitats during their life cycle; while adults and large juveniles are associated with flooded forests, small juveniles usually are associated with aquatic macrophytes (Carvalho de Lima & Araujo-Lima, 2004). However, the occurrence database used does not provide information about the development stage of the individuals caught. Also, this pattern could be explained by a higher plant species diversity associated with higher levels of habitat heterogeneity (Corro et al., 2019; Gastauer et al., 2021), potentially offering a greater variety of food items for frugivores.

Landscape heterogeneity is essential for the maintenance of biodiversity. Recent evidence demonstrated higher biomass in catchments with greater forest cover, particularly for piscivores, as well as other feeding guilds (Arantes et al., 2019). Forest cover and other landscape-level features such as open water and aquatic macrophytes have been proven to influence fish richness and biomass in Amazonian floodplains (Arantes et al., 2018). Moreover, land cover types such as wetlands and shrubs greatly influence fish assemblages diversity in Amazonian floodplain lakes (Freitas et al., 2018). However, the relationship between land cover and fish assemblage structure seems to be scale-dependent, with stronger landscape effects at larger spatial scales (Freitas et al., 2018; Lobón-Cerviá et al., 2015). Our results show that habitat associations per feeding guilds are scale-dependent (i.e. buffer size) in landscape heterogeneity and flood duration, but not floodplain extent. We observed a trend of more feeding guilds occupying areas with similar heterogeneity at the small buffer size, but divergent heterogeneity at intermediate and large buffer sizes. This could be explained because a small buffer size includes fewer pixels, so the landscape heterogeneity is lower than the intermediate buffer size (5 km) and large buffer size (25 km), where more habitat types are likely included. This also implies that species feeding on different resources require different levels of landscape heterogeneity.

Our study provides insights on patterns of species habitat associations at a large scale. This is possible because we used data for the entire Amazon River basin and focused on perhaps one of the most trophically diverse fish families within the Amazon region. Previous studies relating landscape variables and patterns of freshwater fish diversity are mainly localized to central Amazonia (Arantes et al., 2018, 2019; Castello et al., 2018; Lobón-Cerviá et al., 2015). An important caveat is that the microhabitat variability that influences species habitat use, and associations is not detectable with the land cover types and occurrence data that we used due to limitations on spatial resolution. However, our study provides a valuable first step towards assessing general relationships among species that use similar resources (i.e. feeding guilds) and their surrounding environment at the scale of the entire Amazon basin. High-resolution land cover data are available for Brazil (Mapbiomas https://mapbiomas.org) (Souza et al., 2020); however, the rest of the Amazon region lacks this type of information, making it challenging to conduct high-resolution regional assessments and preventing us from providing a more detailed regional assessment.

Understanding species habitat associations by fish, through food resource dynamics and floodplain dependence, is pivotal to assessing the impact of anthropogenic activities, such as water regulation projects, pollution and climate change, on the processes that affect ecological patterns. Species in feeding guilds that are associated with wider extensions of floodplain and that depend on allochthonous food resources provided by floodplain habitats (i.e. frugivores) are very likely to be affected by the modification of the flow regime due to hydropower damming of large rivers (Arantes et al., 2019; Correa et al., 2022; de Bem et al., 2021) and climate change (Herrera-R et al., 2020). That is due to the disruption of the connectivity between the river and floodplains, which impedes the lateral exchange of nutrients and organisms. The homogenization caused by the land-use change in the Amazon (Souza et al., 2020) can affect species that require different levels of landscape heterogeneity (Tuomisto et al., 2003) because they need different habitats during their life cycle. Ultimately, our results can be useful to identify which guilds and species could be more sensitive to anthropogenic impacts affecting Amazonian freshwater ecosystems. Examples are frugivorous, piscivorous and fin and scale feeder fishes that seem largely dependent on extensive floodplain habitat.

CONFLICT OF INTEREST

We do not have any conflict of interest.

DATA AVAILABILITY STATEMENT

The data that supports the findings of this study are available in the supplementary material of this article.

ORCID

Karold Viviana Coronado-Franco https://orcid.org/0000-0002-5691-1714

Pablo A. Tedesco https://orcid.org/0000-0001-5972-5928

Matthew A. Kolmann https://orcid.org/0000-0001-9748-2066

Samuel R. Borstein https://orcid.org/0000-0002-7258-141X

Kristine O. Evans https://orcid.org/0000-0001-6815-2383

Sandra Bibiana Correa https://orcid.org/0000-0003-4466-6923

REFERENCES

Anderson, J. T., Nuttle, T., Rojas, J. S. S., Pendergast, T. H., & Flecker, A. S. (2011). Extremely long-distance seed dispersal by an over-fished amazonian frugivore. *Proceedings of the Royal Society B: Biological Sciences*, 278(1723), 3329–3335. https://doi.org/10.1098/rspb.2011.0155

Andrade, M. C., Fitzgerald, D. B., Winemiller, K. O., Barbosa, P. S., & Giarrizzo, T. (2019). Trophic niche segregation among herbivorous serrasalmids from rapids of the lower Xingu River, Brazilian Amazon. *Hydrobiologia*, 829(1), 265–280. https://doi.org/10.1007/s10750-018-3838-y

Andrade, M. C., Sousa, L. M., Ota, R. P., Jégu, M., & Giarrizzo, T. (2016). Redescription and geographical distribution of the endangered fish *Ossubtus xinguense* Jégu 1992 (Characiformes, Serrasalmidae) with comments on conservation of the rheophilic fauna of the Xingu River. *PLoS One*, 11(9), 1–29. https://doi.org/10.1371/journal.pone.0161398

Arantes, C. C., Winemiller, K. O., Asher, A., Castello, L., Hess, L. L., Petrere, M., & Freitas, C. E. C. (2019). Floodplain land cover affects biomass distribution of fish functional diversity in the Amazon River. *Scientific Reports*, 9(1), 13. https://doi.org/10.1038/s41598-019-52243-0

Arantes, C. C., Winemiller, K. O., Petrere, M., Castello, L., Hess, L. L., & Freitas, C. E. C. (2018). Relationships between forest cover and fish diversity in the Amazon River floodplain. *Journal of Applied Ecology*, 55(1), 386–395. https://doi.org/10.1111/1365-2664.12967

Ben-Hur, E., & Kadmon, R. (2020). Heterogeneity–diversity relationships in sessile organisms: A unified framework. *Ecology Letters*, 23(1), 193–207. https://doi.org/10.1111/ele.13418

Bogotá-Gregory, J. D., Lima, F. C. T., Correa, S. B., Silva-Oliveira, C., Jenkins, D. G., Ribeiro, F. R., Lovejoy, N. R., Reis, R. E., & Crampton, W. G. R. (2020). Biogeochemical water type influences community composition, species richness, and biomass in megadiverse Amazonian fish assemblages. *Scientific Reports*, 10(1), 1–15. https://doi.org/10.1038/s41598-020-72349-0

Burton, D., & Burton, M. (2017). Food procurement and processing. In *Essential fish biology: Diversity, structure, and function* (p. 400). Oxford University Press.

Castello, L., Hess, L. L., Thapa, R., McGrath, D. G., Arantes, C. C., Renó, V. F., & Isaac, V. J. (2018). Fishery yields vary with land cover on the Amazon River floodplain. *Fish and Fisheries*, 19(3), 431–440. https://doi.org/10.1111/faf.12261

Cauduro, R., De Paiva, D., Buarque, D. C., Collischonn, W., & Bonnet, M. (2013). Large-scale hydrologic and hydrodynamic modeling of the Amazon River basin. *Water Resources Research*, 49, 1226–1243. https://doi.org/10.1002/wrcr.20067

Chesson, P. (2000). Mechanisms of maintenance of species diversity. *Annual Review of Ecology and Systematics*, 31(1), 343–366. https://doi.org/10.1146/annurev.ecolsys.31.1.343

Correa, S. B., Costa-Pereira, R., Fleming, T., Goulding, M., & Anderson, J. T. (2015). Neotropical fish-fruit interactions: Eco-evolutionary dynamics and conservation. *Biological Reviews*, 90(4), 1263–1278. https://doi.org/10.1111/brv.12153

Correa, S. B., van der Sleen, P., Siddiqui, S. F., Bogotá-Gregory, J. D., Arantes, C. C., Barnett, A. A., Couto, T. B. A., Goulding, M., & Anderson, E. P. (2022). Biotic indicators for ecological state change in Amazonian floodplains. *Bioscience*, 72, 1–16. https://doi.org/10.1093/biosci/biac038

Correa, S. B., & Winemiller, K. O. (2014). Niche partitioning among frugivorous fishes in response to fluctuating resources in the Amazonian floodplain forest. *Ecology*, 95(1), 210–224. https://doi.org/10.1890/13-0393.1

Correa, S. B., Winemiller, K. O., LóPez-Fernández, H., & Galetti, M. (2007). Evolutionary perspectives on seed consumption and dispersal by fishes. *Bioscience*, 57(9), 748–756. https://doi.org/10.1641/b570907

Corro, E. J., Ahuatzin, D. A., Aguirre, A., Favila, M. E., Cezar, M., Juan, R., & Da, W. (2019). Forest cover and landscape heterogeneity shape ant – Plant co-occurrence networks in human-dominated tropical rainforests. *Landscape Ecology*, 4, 93–104. https://doi.org/10.1007/s10980-018-0747-4

Dagosta, F. C. P., & de Pinna, M. (2017). Biogeography of Amazonian fishes: Deconstructing river basins as biogeographic units. *Neotropical Ichthyology*, 15(3), 1–24. https://doi.org/10.1590/1982-0224-20170034

de Bem, J., Ribolli, J., Röpke, C., Winemiller, K. O., & Zaniboni-Filho, E. (2021). A cascade of dams affects fish spatial distributions and functional groups of local assemblages in a subtropical river. *Neotropical Ichthyology*, 19(3), 1–18. https://doi.org/10.1590/1982-0224-2020-0133

De Lima, Á. C., & Araujo-Lima, C. A. R. M. (2004). The distributions of larval and juvenile fishes in Amazonian rivers of different nutrient status. *Freshwater Biology*, 49(6), 787–800. https://doi.org/10.1111/j.1365-2427.2004.01228.x

Doublet, V., Gidoin, C., Lefèvre, F., & Boivin, T. (2019). Spatial and temporal patterns of a pulsed resource dynamically drive the distribution of specialist herbivores. *Scientific Reports*, 9(1), 17787. https://doi.org/10.1038/s41598-019-54297-6

Dunlop, J. A., Rayner, K., & Doherty, T. S. (2017). Dietary flexibility in small carnivores: A case study on the endangered northern quoll, *Dasyurus hallucatus*. *Journal of Mammalogy*, 98(3), 858–866. https://doi.org/10.1093/jmammal/gyx015

Duponchelle, F., Isaac, V. J., Rodrigues Da Costa, C., Doria, C., Van Damme, P. A., Herrera-R, G. A., Anderson, E. P., Cruz, R. E. A., Hauser, M., Hermann, T. W., Agudelo, E., Bonilla-Castillo, C., Barthem, R., Freitas, C. E. C., García-Dávila, C., García-Vasquez, A., Renno, J. F., & Castello, L. (2021). Conservation of migratory fishes in the Amazon basin. *Aquatic Conservation: Marine and Freshwater Ecosystems*, 31(5), 1087–1105. https://doi.org/10.1002/aqc.3550

Forsberg, B. R., Melack, J. M., Richey, J. E., & Pimentel, T. P. (2017). Regional and seasonal variability in planktonic photosynthesis and planktonic community respiration in Amazon floodplain lakes. *Hydrobiologia*, 800(1), 187–206. https://doi.org/10.1007/s10750-017-3222-3

Freitas, C. E. C., Laurenson, L., Yamamoto, K. C., Forsberg, B. R., Jr., Petrere, M., Jr., Arantes, C., & Siqueira-Souza, F. K. (2018). Fish species richness is associated with the availability of landscape components across seasons in the Amazonian floodplain. *PeerJ*, 2018(6), 1–16. https://doi.org/10.7717/peerj.5080

Garamszegi, L. Z. (2014). Modern phylogenetic comparative methods and their application in evolutionary biology, 2014, 1–552. https://doi.org/10.1007/978-3-662-43550-2

Gastauer, M., Kuster, S., & Carolina, M. (2021). Landscape heterogeneity and habitat amount drive plant diversity in Amazonian canga ecosystems. *Landscape Ecology*, 36, 393–406. https://doi.org/10.1007/s10980-020-01151-0

Goulding, M. (1980). *The fishes and the forest: Explorations in the Amazonian natural history*. University of California Press.

Heino, J., Melo, A. S., Siqueira, T., Soininen, J., Valanko, S., & Bini, L. M. (2015). Metacommunity organisation, spatial extent and Dispersal

in aquatic systems: Patterns, processes and prospects. *Freshwater Biology*, 60(5), 845–869. https://doi.org/10.1111/fwb.12533

Herrera-R, G. A., Oberdorff, T., Anderson, E. P., Brosse, S., Carvajal-Vallejos, F. M., Frederico, R. G., Hidalgo, M., Jézéquel, C., Maldonado, M., Maldonado-Ocampo, J. A., Ortega, H., Radinger, J., Torrente-Vilara, G., Zuanon, J., & Tedesco, P. A. (2020). The combined effects of climate change and river fragmentation on the distribution of Andean Amazon fishes. *Global Change Biology*, 26(10), 5509–5523. https://doi.org/10.1111/gcb.15285

Hess, L. L., Melack, J. M., Affonso, A. G., Barbosa, C., Gastil-Buhl, M., & Novo, E. M. L. M. (2015). Wetlands of the lowland Amazon Basin: Extent, vegetative cover, and dual-season inundated area as mapped with JERS-1 synthetic aperture radar. *Wetlands*, 35(4), 745–756. https://doi.org/10.1007/s13157-015-0666-y

Huby, A., Lowie, A., Herrel, A., Vigouroux, R., FrÉDÉRich, B., Raick, X., Kurchevski, G., Godinho, A. L., & Parmentier, E. (2019). Functional diversity in biters: The evolutionary morphology of the oral jaw system in pacus, piranhas and relatives (Teleostei: Serrasalmidae). *Biological Journal of the Linnean Society*, 127(4), 722–741. https://doi.org/10.1093/biolinnean/blz048/5486927

Huie, J. M., Summers, A. P., & Kolmann, M. A. (2020). Body shape separates guilds of rheophilic herbivores (Myleinae: Serrasalmidae) better than feeding morphology. *Proceedings of the Academy of Natural Sciences of Philadelphia*, 166(1), 1–15. https://doi.org/10.1635/053.166.0116

Ives, A. R. (2019). R 2 s for correlated data: Phylogenetic models, LMMs, and GLMMs. *Systematic Biology*, 68(2), 234–251. https://doi.org/10.1093/sysbio/syy060

Ives, A. R., & Li, D. (2018). rr2: An R package to calculate R^2s for regression models. *The Journal of Open Source Software*, 3(30), 1028. https://doi.org/10.21105/joss.01028

Jackson, D. A. (1993). Stopping rules in principal components analysis: A comparison of Heuristical and statistical approaches. *Ecology*, 74, 2204–2214. https://doi.org/10.2307/1939574

Jackson, D. A., Peres-Neto, P. R., & Olden, J. D. (2001). What controls who is where in freshwater fish communities – The roles of biotic, abiotic, and spatial factors. *Canadian Journal of Fisheries and Aquatic Sciences*, 58(1), 157–170. https://doi.org/10.1139/cjfas-58-1-157

Janovetz, J. (2005). Functional morphology of feeding in the scale-eating specialist *Catoprion mento*. *Journal of Experimental Biology*, 208(24), 4757–4768. https://doi.org/10.1242/jeb.01938

Jézéquel, C., Tedesco, P. A., Bigorne, R., Maldonado-Ocampo, J. A., Ortega, H., Hidalgo, M., Martens, K., Torrente-Vilara, G., Zuanon, J., Acosta, A., Agudelo, E., Barrera Maure, S., Bastos, D. A., Bogotá Gregory, J., Cabeceira, F. G., Canto, A. L. C., Carvajal-Vallejos, F. M., Carvalho, L. N., Cella-Ribeiro, A., … Oberdorff, T. (2020). A database of freshwater fish species of the Amazon Basin. *Scientific Data*, 7(1), 96. https://doi.org/10.1038/s41597-020-0436-4

Johnson, M. D., & Sherry, T. W. (2001). Effects of food availability on the distribution of migratory warblers among habitats in Jamaica. *Journal of Animal Ecology*, 70(4), 546–560. https://doi.org/10.1046/j.1365-2656.2001.00522.x

Junk, W. J., Piedade, M. T. F., Wittmann, F., Schöngart, J., & Parolin, P. (2010). *Amazonian Floodplain Forests. Ecophysiology, Biodiversity and Sustainable Management*. https://doi.org/10.1007/978-90-481-8725-6

Junk, W.J., & Wantzen, K. M. (2004). The flood pulse concept: New aspects, approaches and applications – An update. *Proceedings of the Second International symposium on the Management of Large Rivers for fisheries*, May, 117–149. Food and Agriculture Organization and Mekong River Commission, FAO Regional Office for Asia and the Pacific.

Junk, Wolfgang J. (1997). *The Central Amazon floodplain. Ecology of a pulsing system*. Springer Berlin Heidelberg. 10.978-3-642-08214-6

King, T. W., Vynne, C., Miller, D., Fisher, S., Fitkin, S., Rohrer, J., Ransom, J. I., & Thornton, D. H. (2021). The influence of spatial and temporal scale on the relative importance of biotic vs. abiotic factors for species distributions. *Diversity and Distributions*, 27(2), 327–343. https://doi.org/10.1111/ddi.13182

Kolmann, M. A., Hughes, L. C., Hernandez, L. P., Arcila, D., Betancur, R. R., Sabaj, M. H., López-Fernández, H., & Ortí, G. (2021). Phylogenomics of piranhas and Pacus (Serrasalmidae) uncovers how dietary convergence and parallelism obfuscate traditional morphological taxonomy. *Systematic Biology*, 70(3), 576–592. https://doi.org/10.1093/sysbio/syaa065

Kolmann, M. A., Huie, J. M., Evans, K., & Summers, A. P. (2018). Specialized specialists and the narrow niche fallacy: A tale of scale-feeding fishes. *Royal Society Open Science*, 5(1), 1–14. https://doi.org/10.1098/rsos.171581

Kraft, N. J. B., Godoy, O., & Levine, J. M. (2015). Plant functional traits and the multidimensional nature of species coexistence. *Proceedings of the National Academy of Sciences of the USA*, 112(3), 797–802. https://doi.org/10.1073/pnas.1413650112

Lee, M. B., & Martin, J. A. (2017). Avian species and functional diversity in agricultural landscapes: Does landscape heterogeneity matter? *PLoS One*, 12(1), 1–21. https://doi.org/10.1371/journal.pone.0170540

Leite, R., & Jégu, M. (1990). Régime alimentaire de deux espèces d'Acnodon (Characiformes, Serrasalmidae) et habitudes lepidophages de *A. normani*. *Cybium*, 14, 353–359.

Lenth, R. (2021). emmeans: Estimated Marginal Means, aka Least-Squares Means (R package version 1.5.5–1.). https://cran.r-project.org/package=emmeans

Lobón-Cerviá, J., Hess, L. L., Melack, J. M., & Araujo-Lima, C. A. R. M. (2015). The importance of forest cover for fish richness and abundance on the Amazon floodplain. *Hydrobiologia*, 750(1), 245–255. https://doi.org/10.1007/s10750-014-2040-0

Martelo, J., Lorenzen, K. A. I., Crossa, M., & Mcgrath, D. G. (2008). *Habitat associations of exploited fish species in the Lower Amazon river – floodplain system*. 2455–2464. https://doi.org/10.1111/j.1365-2427.2008.02065.x

Martins, E. P., & Hansen, T. F. (1997). Phylogenies and the comparative method: a general approach to incorporating phylogenetic information into the analysis of interspecific data. *The American Naturalist*, 149(4), 646–667.

McGarigal, K., Cushman, S. A., & Ene, E. (2012). FRAGSTATS v4: Spatial pattern analysis program for categorical and continuous maps. Computer software program produced by the authors at the University of Massachusetts, Amherst. http://www.umass.edu/landeco/research/fragstats/fragstats.html

Mittelbach, G. G., & McGill, B. J. (2019). *Community ecology* (2nd ed.). Oxford University Press. https://doi.org/10.1093/oso/9780198835851.001.0001

Mittelbach, G. G., & Schemske, D. W. (2015). Ecological and evolutionary perspectives on community assembly. *Trends in Ecology and Evolution*, 30(5), 241–247. https://doi.org/10.1016/j.tree.2015.02.008

Nardi, F., Annis, A., Di Baldassarre, G., Vivoni, E. R., & Grimaldi, S. (2019). GFPLAIN250m, a global high-resolution dataset of earth's floodplains. *Scientific Data*, 6, 1–6. https://doi.org/10.1038/sdata.2018.309

Nico, L., & Taphorn, D. (1988). Food habits of piranhas in the Low Llanos of Venezuela. *Biotropica*, 20(4), 311–321.

Oliveira, A. C., Martinelli, M., Moreira, M., Soares, M., & Cyrino, J. E. (2006). Seasonality of energy sources of *Colossoma macropomum* in a floodplain lake in the Amazon: Lake Camaleao, Amazonas, Brazil. *Fisheries Management and Ecology*, 13, 135–142.

Parrens, M., Al Bitar, A., Frappart, F., Paiva, R., Wongchuig, S., Papa, F., Yamasaki, D., & Kerr, Y. (2019). High resolution mapping of inundation area in the Amazon basin from a combination of L-band passive microwave, optical and radar datasets. *International Journal of Applied Earth Observation and Geoinformation*, 81(August 2018), 58–71. https://doi.org/10.1016/j.jag.2019.04.011

Pelster, B., Wood, C. M., Speers-Roesch, B., Driedzic, W. R., Almeida-Val, V., & Val, A. (2015). Gut transport characteristics in herbivorous and carnivorous serrasalmid fish from ion-poor Rio Negro water.

Journal of Comparative Physiology B: Biochemical, Systemic, and Environmental Physiology, 185(2), 225–241. https://doi.org/10.1007/s00360-014-0879-z

Pérez-Crespo, M. J., Fonseca, J., Pineda-López, R., Palacios, E., & Lara, C. (2013). Foraging guild structure and niche characteristics of waterbirds in an epicontinental lake in Mexico. *Zoological Studies*, 52(1), 1–17. https://doi.org/10.1186/1810-522X-52-54

Perry, G., & Pianka, E. (1997). Animal foraging: Past, present and future. *Trends in Ecology and Evolution*, 12, 360–384.

Pianka, E. R. (1973). The structure of lizard communities. *Annual Review of Ecology and Systematics*, 4(1), 53–74. https://doi.org/10.1146/annurev.es.04.110173.000413

Pianka, E. R. (2000). *Evolutionary ecology* (6th ed.). Benjamin Cummings.

Pinheiro, J., Bates, D., DebRoy, S., & Sarkar, D. (2021). _nlme: Linear and Nonlinear Mixed Effects Models_. (R package version 3.1–152). https://cran.r-project.org/package=nlme

Prudente, B. S., Carneiro-Marinho, P., Valente, R. M., & Montag, L. F. A. (2016). Ecologia alimentar de *Serrasalmus gouldingi* (Characiformes: Serrasalmidae) na região do baixo Rio Anapu, Amazônia Oriental, Brasil. *Acta Amazonica*, 46(3), 259–270. https://doi.org/10.1590/1809-4392201600123

R Core Team. (2021). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing.

Rodrigues, A. C., de Santana, H. S., Baumgartner, M. T., & Gomes, L. C. (2018). Coexistence between native and nonnative species: The invasion process and adjustments in distribution through time for congeneric piranhas in a neotropical floodplain. *Hydrobiologia*, 817(1), 279–291. https://doi.org/10.1007/s10750-018-3541-z

Silva, P. B., Arantes, C. C., Freitas, C. E. C., Petrere, M., Jr., & Ribeiro, F. R. V. (2021). Seasonal hydrology and fish assemblage structure in the floodplain of the lower Amazon River. *Ecology of Freshwater Fish*, 30(2), 162–173. https://doi.org/10.1111/eff.12572

Siqueira-Souza, K., Freitas, C. E. L., & Petrere, M. (2016). *Amazon floodplain fish diversity at different scales: Do time and place really matter?* (Vol. 776, pp. 99–110). https://doi.org/10.1007/s10750-016-2738-2

Souza, C. M., Shimbo, J. Z., Rosa, M. R., Parente, L. L., Alencar, A. A., Rudorff, B. F. T., Hasenack, H., Matsumoto, M., Ferreira, L. G., Souza-Filho, P. W. M., de Oliveira, S. W., Rocha, W. F., Fonseca, A. V., Marques, C. B., Diniz, C. G., Costa, D., Monteiro, D., Rosa, E. R., Vélez-Martin, E., ... Azevedo, T. (2020). Reconstructing three decades of land use and land cover changes in brazilian biomes with landsat archive and earth engine. *Remote Sensing*, 12(17), 1–27. https://doi.org/10.3390/RS12172735

Stein, A., Gerstner, K., & Kreft, H. (2014). Environmental heterogeneity as a universal driver of species richness across taxa, biomes and spatial scales. *Ecology Letters*, 17(7), 866–880. https://doi.org/10.1111/ele.12277

Tableau, A., Brind'Amour, A., Woillez, M., & Le Bris, H. (2016). Influence of food availability on the spatial distribution of juvenile fish within soft sediment nursery habitats. *Journal of Sea Research*, 111, 76–87. https://doi.org/10.1016/j.seares.2015.12.004

Thornton, D. H., Branch, L. C., & Sunquist, M. E. (2011). The influence of landscape, patch, and within-patch factors on species presence and abundance: A review of focal patch studies. *Landscape Ecology*, 26(1), 7–18. https://doi.org/10.1007/s10980-010-9549-z

Tuomisto, H., Ruokolainen, K., & Yli-halla, M. (2003). Floristic variation of Western Amazonian forests. *Sience*, 299(January), 241–245.

Turner, M., & Gardner, R. (2015). *Landscape ecology in theory and practice*. Springer.

Vitorino, O. B., Agostinho, C. S., & Pelicice, F. M. (2016). Ecology of *Mylesinus paucisquamatus* Jegu & Santos, 1988, an endangered fish species from the rio Tocantins basin. *Neotropical Ichthyology*, 14(2), 1–8. https://doi.org/10.1590/1982-0224-20150124

Vu, V. (2011). *ggbiplot: A ggplot2 based biplot. R package version 0.55*. http://github.com/vqv/ggbiplot

BIOSKETCHES

Karold Viviana Coronado-Franco is broadly interested in landscape ecology of aquatic ecosystems. This work represents a component of her PhD work at Mississippi State University on macroecology of frugivorous fishes in the Amazon River drainage basin. Her current collaborative research focuses on understanding patterns of Amazonian fish diversity (see Correa River Ecology Lab, http://www.riverecologylab.org).

Author contributions: KVCF, SBC and PAT conceived the ideas; KVCF collected the data with additional material from collaborators; SRB constructed the phylogenetic tree, KVCF analysed the data; and KVCF led the writing with assistance from SBC, PAT, MAK, SRB and KOE.

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.