Environmental conditions promote local segregation, but functional distinctiveness allow aggregation of catfishes in the Amazonian estuary

Bruno E. Soares[1], Naraiana L. Benone[2], Ronaldo B. Barthem[3], Alexandre P. Marceniuk[3], Luciano F. A. Montag[4]

[1] Laboratório de Limnologia, Instituto de Biologia, Universidade Federal do Rio de Janeiro – UFRJ, Rio de Janeiro – RJ, Brazil

[2] Universidade do Estado de Minas Gerais – UEMG, Unidade Passos, Passos – MG, Brazil

[3] Museu Paraense Emílio Goeldi, Belém – PA, Brazil

[4] Laboratório de Ecologia e Conservação, Instituto de Ciências Biológicas, Universidade Federal do Pará – UFPA, Belém – PA, Brazil

Abstract

Cooccurrence patterns of species can appear through niche-related processes such as (i) environmental filtering matching specific sets of traits to a given environment, and (ii) limiting similarity selecting divergent functional traits to reduce niche overlap. Locally, both processes should act together to shape the distribution of species. We evaluated the importance of environmental variables and functional distinctiveness to the co-occurrence patterns of nine marine catfishes in the inner estuary of the Amazon River mouth. Sampling was carried out in the dry seasons of 1996 and 1997, and the rainy season of 1996 by nearly 120 standardized bottom trawls per expedition. We observed 13 significant pairs of segregated species and two pairs of aggregated species, which sum 41.7% of all combinations. *Amphiarius phrygiatus* and *Sciades couma* segregated from all the remaining marine catfishes by occupying shallower areas with lower salinity levels. Aggregated pairs were strongly associated with higher functional distinctiveness. We concluded that environmental filtering is the main force structuring the co-occurrence patterns by promoting spatial segregation, but functional distinctiveness allowed some species to aggregate.

Keywords: environmental filtering; limiting similarity; ecomorphology; Ariidae, co-occurrence patterns.

Highlights

- Environmental filtering and limiting similarity shape the co-occurrence of species
- We studied the co-occurrence of marine catfishes in the Amazon River estuary
- Marine catfishes exhibited a high rate of non-random co-occurrence structure
- Non-random pairs were mostly segregated due to differences in salinity and depth
- Aggregated pairs exhibited high functional distinctiveness

Introduction

Community structure is shaped by many processes from which environmental filtering and limiting similarity are usually highlighted. Environmental filtering favors the survival of species exhibiting suitable traits given regional or local abiotic variables (Kraft *et al.* 2015). Limiting similarity inhibits species' coexistence with an overlapping niche in scenarios of limited resources and unequal competitive ability (Meszéna *et al.* 2006, Violle *et al.* 2011). These processes have contrasting effects on the structure of ecological communities (Mouillot *et al.* 2007) but are not mutually exclusive (Boet *et al.* 2020, Várbíró *et al.* 2020).

In general, environmental filtering is the first process that acts upon the regional pool of species by selecting those that may survive locally (Kraft *et al.* 2015). Limiting similarity may have a strong role in the local community structure by eliminating poor competitors (Huston 1999). The relative importance of environmental filtering and limiting similarity depends on multiple factors, such as environmental context (Echevarria & Rodriguez 2017, Álvarez-Grzybowska *et al.* 2020) and spatial scale (Araújo & Rozenfeld 2014, Boet *et al.* 2020). For example, environmental conditions may filter most of the functional traits of fish communities, while limiting similarity may be stronger on traits related to trophic partitioning if the competition for trophic resources is important (Ford & Roberts 2020). The debate on the relative importance of environmental filtering and limiting similarity is often addressed by analyzing diversity measures, but species within communities may be affected differently by assembly rules (*e.g.*, dominant and rare species; Benone *et al.* 2020). Pairwise co-occurrence patterns offer fine-scale information on how and why species occupy a given site (Echevarria & Rodriguez 2017).

Pairwise co-occurrence tests return pairs of spatially segregated (species that often do not co-occur) and aggregated (species that often co-occur) species. Regionally, segregated pairs are more common than aggregated pairs in plant and animal communities (Gotelli & McCabe 2002). Species segregations were initially associated with competitive exclusion (Diamond 1975), but other processes promote species' segregations, such as environmental specialization to microhabitats (Guterres *et al.* 2020) or historical contingencies (Germain *et al.* 2016). Conversely, species aggregation arises if species have similar niche requirements or positive species interactions (Peoples & Frimpong 2016, Cordero & Jackson 2019). Co-occurrence patterns are not direct measures of species' interactions, but they may strongly shape it in some circumstances (Blanchet *et al.* 2020). Nonetheless, the signal of these assembly processes in the pairwise associations may be intricate: environmental tracking, for example, may lead to both segregated and aggregated pairs in the same environment (D'Amen *et al.* 2018).

The Amazon River estuary provides suitable conditions to test co-occurrence because it encompasses some marked environmental variation and highly diversified fauna. The area is dominated by the Amazon River's influence, which carries one-fifth of the global freshwater discharge and 40% of the Atlantic Ocean's sediment flux (Armijos *et al.* 2020). This discharge interacts with the tides and creates a marked gradient in salinity, organic matter, and sediment deposition that strongly affects species distribution and population dynamics (Martins *et al.* 2015, Lobato *et al.* 2018, Neumann-Leitão *et al.* 2018). Such spatial heterogeneity and high biological productivity support high endemism and fisheries activities (MPA 2012, Aguilera & Marceniuk 2018, Marceniuk *et al.* 2020). Marine catfishes (Siluriformes: Ariidae) are important components of the regional fauna as they exhibit high biomass (Barletta *et al.* 2005) and taxonomic diversity (13 species divided into five genera; Marceniuk & Menezes 2007). Marine catfishes have an overall conserved body plan and similar ecological strategies but display differences in body size (Soares *et al.* 2016), diet composition (Mishima & Tanji 1982, Mendes & Barthem 2010), habitat use, and freshwater affinity (Barletta *et al.* 2008, Dantas *et al.* 2010).

Here, we evaluated the relative role of environmental filtering and limiting similarity on the local distribution of marine catfishes in the shallow and muddy bottom of the inner Amazonian estuary. We disentangled the co-occurrence patterns of marine catfishes by identifying segregated and aggregated species pairs. Then we analyzed how non-random patterns were related to environmental variation and functional distinctiveness. Given the marked variation in salinity, we expected that environmental filtering would promote species' segregation or aggregation by their freshwater affinity. As we characterized species by functional traits related to habitat use and feeding, we considered two competing hypotheses: (i) environmental filtering could select similar functional traits, then aggregated species would be ecologically redundant; or (ii) functional distinctiveness would allow the use of different resources within sites and, consequently, would promote aggregation.

Material and methods

Study area and fieldwork

This study was conducted in the inner estuary of the Amazon River mouth between the latitude 2º 30'N to 0º 05'N and by the longitude 47º 50'W to 50º 30'W (Figure 1), and the isobaths 5 - 50 m classified into three strata: 5-10 m, 10-20 m, and 20-50 m. The climate is tropical, characterized by high temperature and precipitation throughout the year, with relative humidity above 80% and an average atmospheric temperature of 25 ºC. The area is characterized by a shallow muddy substrate and the dynamism of the mixture of the Amazon River's freshwater discharge and the marine water (Eisma & Van der Marel 1971, Curtin & Legeckis 1986). The annual cycle of the Amazon River discharge is the most important force acting in the salinity structure because it determines the displacement of the salty wedge along the shelf of the Amazon River mouth (Geyer *et al.* 1996). The dry period is marked by the brackish waters to the coast from May to November, and the rainy period by the predominance of fresh waters from December to April (Barthem & Schwassmann 1994).

Data were obtained during the sea-borne survey of the project executed in the Amazon River Mouth by Japan International Cooperation Agency (JICA), Museu Paraense Emílio Goeldi (MPEG), and Instituto Brasileiro do Meio Ambiente e dos Recursos Naturais Renováveis (IBAMA) between 1996-1997. The sampling area was divided into 1,330 blocks of 3' latitude by 3' longitude each and nearly nine nautical miles of area. Samplings were carried out during three trawling expeditions during the dry period of 1996 (August to September of 1996), the rainy period of 1997 (March to April of 1997), and the dry period of 1997 (August to September of 1997). Each seasonal survey comprised 120 trawling stations distributed randomly and proportionally to the area of each isobath stratum. In each station, fishes were sampled by bottom trawling conducted by a pair of vessels operating for 30 minutes along the current direction at a constant 2-3 knots speed. Standardized trawls were carried out at daytime by trawlers equipped with bottom-trawl nets of 58.2 meters length and 14 cm between opposite knots (JICA 1998).

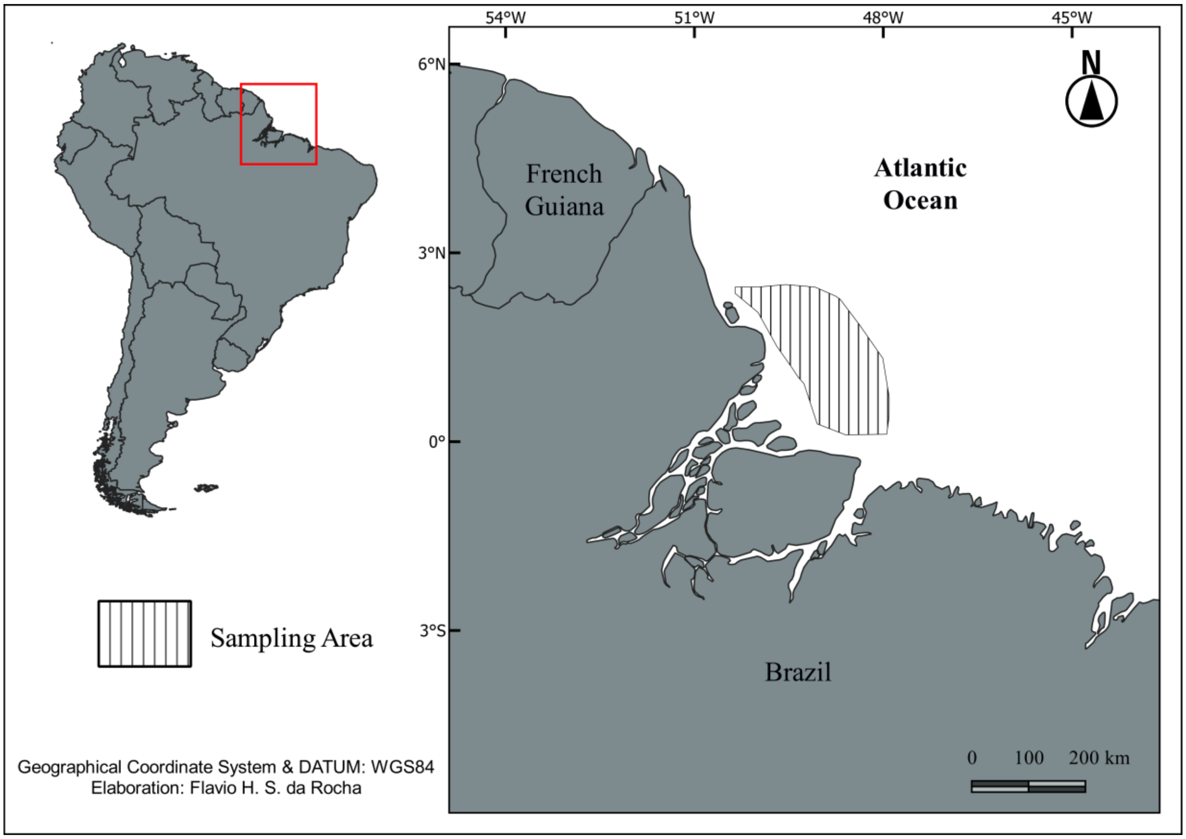


Figure 1 – Area in the inner estuary of the Amazon River mouth where marine catfishes were sampled in the dry season of 1996 and 1997, and during the rainy season of 1996.

Environmental variables

We recorded measured salinity and temperature at the bottom of the water column for each site to describe the environmental conditions in which species occurred by using a multiparameter. We characterized the environmental conditions in which species occurred based on the average of the salinity and temperature taken at the 5 m near the bottom, which correspond to the trawl net mouth height, using a salinity/temperature/depth instrument (temperature measuring capability 5–40ºC, precision 0.02ºC, salinity measuring capability 0–40 ‰, depth range 0–200 m, measurement distance 0.2 m). Environmental variation was spatially constrained by the linear distance among sampled stations (Mantel test; $r = 0.66$; $p = 0.001$). We summarized the environmental variation by applying a Principal Component Analysis (PCA). We selected only the first axis of the PCA, which explained ~53% of the total variation and was strongly related to depth and salinity (Supporting Information). We used values in the first axis of the PCA to represent the environmental variation in further analysis.

Functional distinctiveness

We used nine ecomorphological indices describing the species based on body size, the shape of the caudal peduncle, the size of the eyes, barbels, and mouth width (Supporting Information). These indices are related to food acquisition and mobility of fishes and are often used as functional traits in fish ecology (Villéger *et al.* 2017). For example, the shape of the teeth is related to the type of consumed items. Long, recurved teeth indicate ariid catfishes with stronger piscivorous habits, while small, conical teeth are more associated with polychaete-eaters (Blaber *et al.* 1994). Regarding body size, larger fish are expected to be faster swimmers and better at avoiding predation than small fish (Villéger *et al.* 2017).

We built a dissimilarity matrix based on the functional traits using the Gower distance. Then, we calculated the average functional distinctiveness (D_i; Violle *et al.* 2017) for the species captured in each trawl. D_i is the average distance of each species to the remaining species in the site; therefore, average D_i represents the site's average functional originality. We built the dissimilarity matrix and calculated D_i by using the *cluster* (Maechler *et al.* 2019) and *funrar* (Grenié *et al.* 2017) packages in R environment (R Core Team 2018).

Co-occurrence patterns

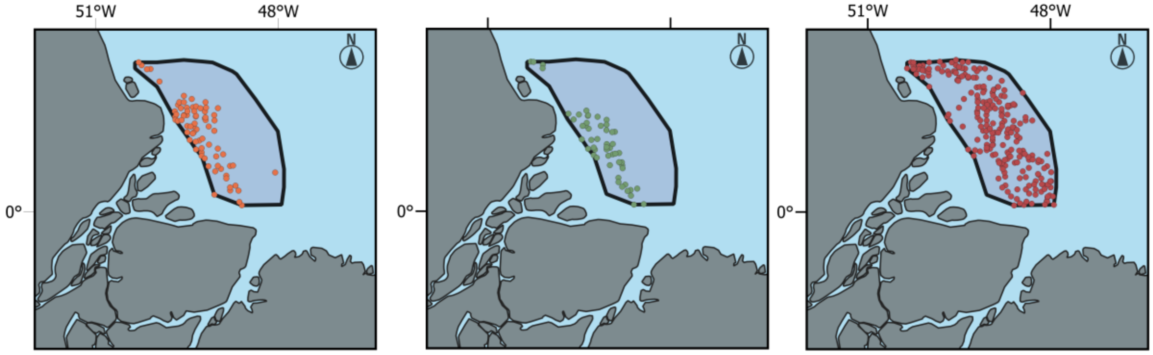
We identified species co-occurrence patterns by quantifying the strength and significance of pairwise associations between species against null probabilities (Gotelli & Ulrich 2010). We quantified the strength of the association between species pairs by calculating the C-score index (Stone & Roberts 1990) rescaled from 0 (maximum aggregation) to 1 (maximum segregation). We established the significance of aggregation or segregation patterns by comparing observed values to 10,000 null communities' values. Null communities were generated by a 'fixed-equiprobable' algorithm that preserves species' frequency in the samples but randomizes equiprobably the richness per sample (Gotelli 2000). Then, we reduced the rate of type I error by applying the empirical Bayes approach. In this approach, pairwise C-scores were grouped in 22, evenly spaced bins. Significant C-scores are those whose values per bin are higher than the average number of values per bin drawn from a null distribution. Non-random C-scores were standardized to Z-scores by the null mean and standard deviation to compare different pairs of species and classify between aggregation (positive values) or segregation (negative values).

Finally, we compared differences in the environmental variables (first axis of the environmental PCA) and in the functional distinctiveness (D_i) between sets of sites to infer the processes shaping the observed patterns of co-occurrence, following the framework from Blois *et al.* (2014). Sites were categorized in four occupancy classes depending on the presence/absence of the species from an associated pair: (1,0) and (0,1) if the site contains only species *a* or *b*, respectively; (1,1) and (0,0) if the site includes both or neither species, respectively. Tests referring to segregated pairs compare the average differences in the dependent variables between classes (1,0) and (0,1), while tests referring to aggregated pairs compare the average differences in the dependent variables between classes (1,1) and (0,0). We applied a Multivariate Analysis of Variance (MANOVA) in the distance tests and Analyses of Variance (ANOVA) for the environmental and functional tests. Additionally, we applied Chi-squared tests to evaluate if the relative number of segregations [(1,0) and (0,1)] and aggregations (1,1) were different between rainy and dry seasons. All co-occurrence analyses were based on the classic framework available in D'Amen *et al.* (2018). Our dataset and R coding are available at Zenodo (https://doi.org/10.5281/zenodo.4118631).

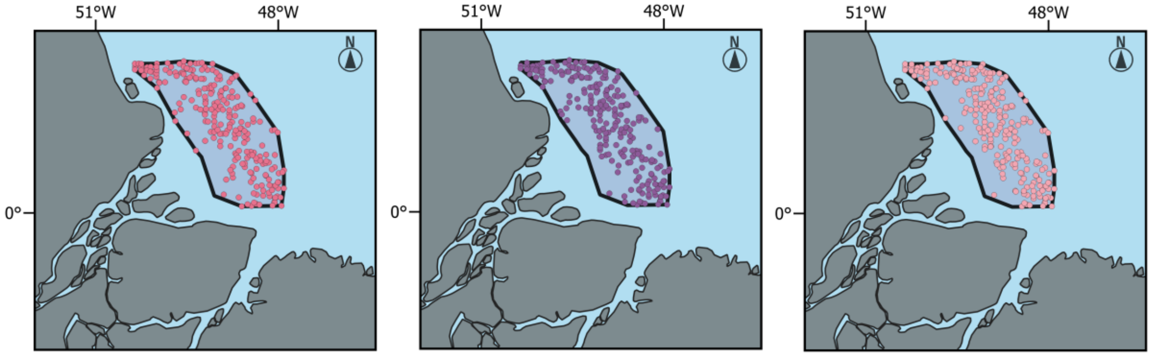
Results

Catfishes differed in the ecomorphological space and local occupancy. Ecomorphologically, species varied primarily by body size, the shape of the caudal peduncle, the size of the eyes, and length of the mentonian barbel (Supporting Information). In regional occupancy, *Sciades couma* was the rarest species, while *Bagre bagre*, *Notarius grandicassis,* and *Cathorops arenatus* were the most frequent ones (Figure 2). We observed 15 non-random pairs of species (41.7% of all possible combinations). Among them, 13 showed segregated patterns, and 2 showed aggregated patterns (Table 1). Patterns were related to environmental variation and functional distinctiveness and did not shift between seasons (Supplementary Table 1).

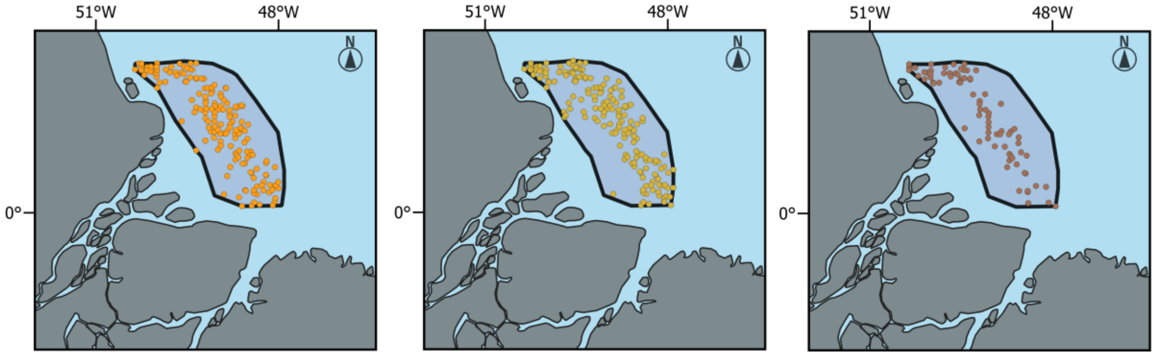
Amphiarius phrygiatus and *S. couma* were generally segregated from all the remaining ariids due to differences in environmental conditions. *A. phrygiatus* and *S. couma* occupied shallower areas with lower salinity levels and D_i than other species (Figure 3; ANOVA; $p < 0.001$). Aggregation was primarily related to functional distinctiveness. Assemblages encompassing aggregated species exhibited higher D_i than those that neither occurred (Figure 4; ANOVA; $p < 0.001$). Aggregated pairs exhibit marked differences in the body size and relative size of the mouth (*A. quadriscutis* and *S. parkeri*) or the relative size of eyes and depth of the caudal peduncle (*A. rugispinis* and *C. arenatus*). Nonetheless, other pairs displaying opposite ecomorphological patterns did not exhibit strong association (*e.g., C. arenatus* and *N. grandicassis*). Environmental conditions poorly explained the co-occurrence of aggregated pairs (low R^2).



Amphiarius phrygiatus (n = 76) *Sciades couma* (n = 53) *Aspistor quadriscutis* (n = 226)



Bagre bagre (n = 241) *Cathorops arenatus* (n = 234) *Notarius grandicassis* (n = 238)



Amphiarius rugispinis (n = 166) *Sciades parkeri* (n = 172) *Sciades proops* (n = 77)

Figure 2 – Occupancy patterns of marine catfishes (Ariidae) in the studied area of the inner estuary of the Amazon River mouth.

Table 1 – Association of environment and functional distinctiveness with the co-occurrence patterns of marine catfishes in the inner estuary of the Amazon River mouth. The coefficients of explanation (R²) of the linear models indicate the strength of the association.

Associated pairs	Environmental test (R²)	Environmental test (p-value)	Functional test (R²)	Functional test (p-value)
Segregated pairs				
Amphiarius phrygiatus - *Aspistor quadriscutis*	0.372	< 0.001	0.510	< 0.001
Amphiarius phrygiatus - *Amphiarius rugispinis*	0.586	< 0.001	0.744	< 0.001
Amphiarius phrygiatus - *Bagre bagre*	0.406	< 0.001	0.468	< 0.001
Amphiarius phrygiatus - *Cathorops arenatus*	0.409	< 0.001	0.502	< 0.001
Amphiarius phrygiatus - *Notarius grandicassis*	0.391	< 0.001	0.439	< 0.001
Amphiarius phrygiatus - *Sciades parkeri*	0.583	< 0.001	0.746	< 0.001
Amphiarius phrygiatus - *Sciades proops*	0.648	< 0.001	0.612	< 0.001
Amphiarius rugispinis - *Sciades couma*	0.509	< 0.001	0.688	< 0.001
Bagre bagre - *Sciades couma*	0.303	< 0.001	0.272	< 0.001
Cathorops arenatus - *Sciades couma*	0.302	< 0.001	0.289	< 0.001
Notarius grandicassis - *Sciades couma*	0.302	< 0.001	0.259	< 0.001
Sciades couma - *Sciades parkeri*	0.472	< 0.001	0.672	< 0.001
Sciades couma - *Sciades proops*	0.656	< 0.001	0.622	< 0.001
Aggregated pairs				
Aspistor quadriscutis - *Sciades parkeri*	0.022	0.021	0.869	< 0.001
Amphiarius rugispinis - *Cathorops arenatus*	0.086	< 0.001	0.864	< 0.001

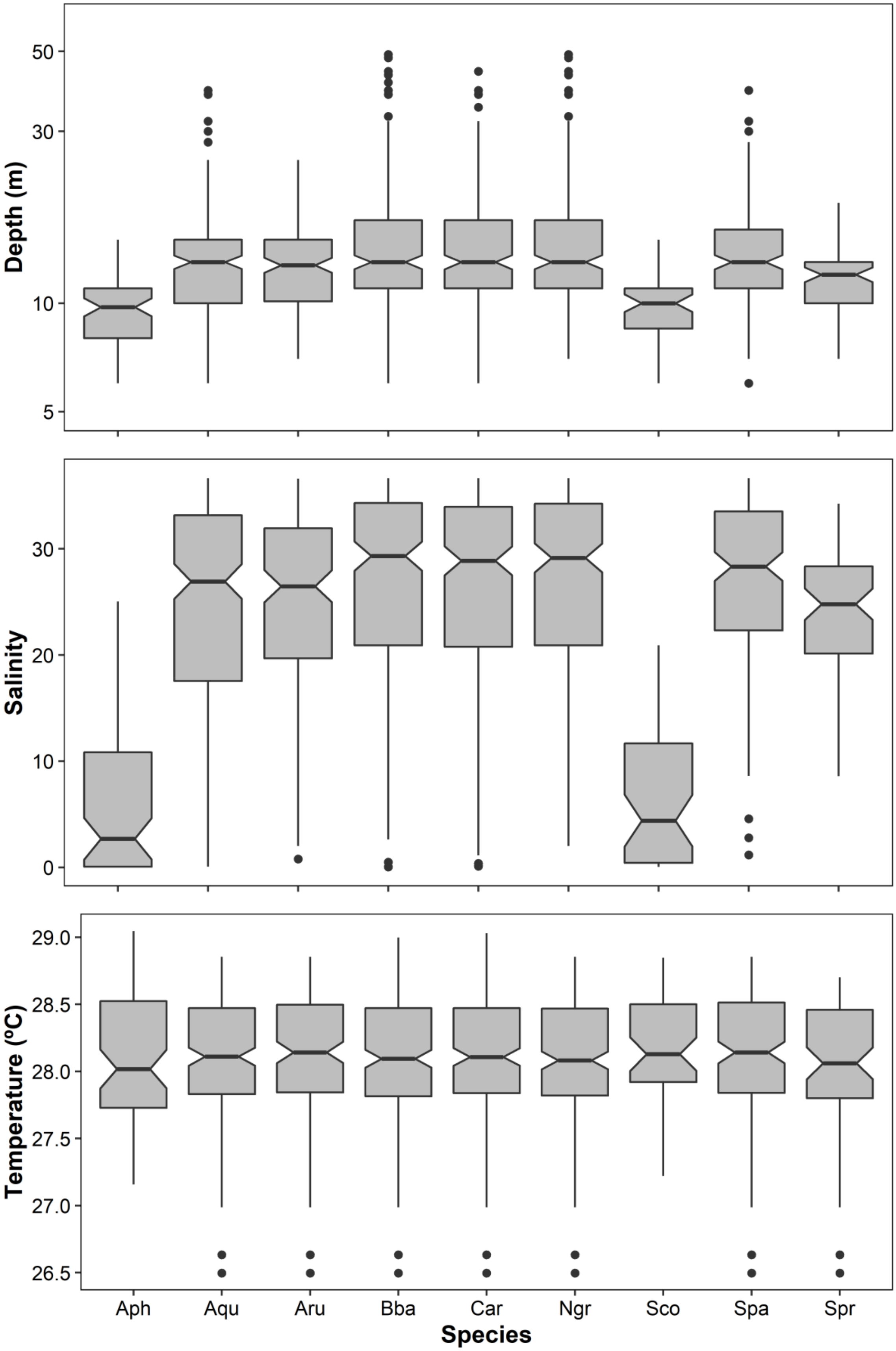

50
30
10
5
Depth (m)
30
20
10
0
Salinity
29.0
28.5
28.0
27.5
27.0
26.5
Temperature (ºC)
Aph
Aqu
Aru
Bba
Car
Ngr
Sco
Spa
Spr
Species

Figure 3 – Depth (m), salinity (‰), and temperature (ºC) in the sites where each species occurred. Codes: Aph – *Amphiarius phrygiatus*; Aqu – *Aspistor quadriscutis*; Aru – *Amphiarius rugispinis*; Bba – *Bagre bagre*; Car – *Cathorops arenatus*; Ngr – *Notarius grandicassis*; Spa – *Sciades parkeri*; Spr – *Sciades proops*; Sco – *Sciades couma*.

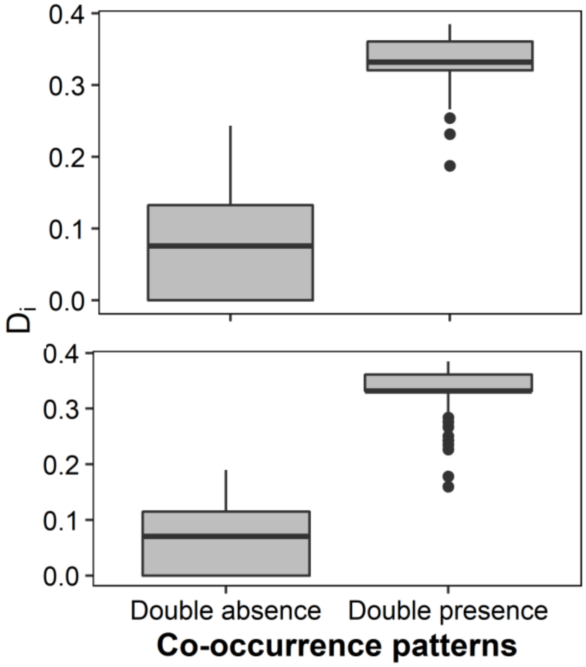


Figure 4 – Functional distinctiveness (D_i) of the assemblages in which aggregated pairs were both absent or both present: *Aspistor quadriscutis* and *Sciades parkeri* (above); *Amphiarius rugispinis* and *Cathorops arenatus* (below).

Discussion

Environmental conditions favor the occurrence of some species but hinder the occurrence of others, thus promoting aggregation and segregation patterns. If environmental filtering constrains functional traits, aggregated species should promote low functional distinctiveness. In contrast, these features may allow habitat partitioning and favor species aggregation; then, aggregated species would display higher functional distinctiveness. We showed that depth and salinity heterogeneity promote spatial segregation but not the aggregation of marine catfishes in the inner estuary of the Amazon River mouth. Aggregation only occurred in two species pairs and were strongly linked to high functional distinctiveness. Therefore, both environmental filtering and habitat partitioning are shaping the occupancy patterns of species in estuaries.

Estuarine fishes are known to track optimal conditions in the face of salinity variation (Barletta *et al.* 2005, 2008) or to use areas where environmental conditions are stable (Vendel *et al.* 2010). The Ariidae family comprises euryhaline fishes that inhabit both freshwater and marine systems (Schmidt *et al.* 2008, Pusey *et al.* 2020). Juvenile and adult fish usually exhibit marked segregation in habitat use juveniles and spawning adults usually occupy shallower and less saline areas (Mishima & Tanji 1981, Dantas *et al.* 2010). Because of the wide range of salinity and depth that ariid catfishes occur, depth and salinity should be less critical to shape adult distribution in the inner estuary. Therefore, despite the overall capacity to use freshwater and marine environments during their life cycle, these catfishes exhibited differences in environmental affinities and tracked favorable conditions in the inner estuary as *A. phrygiatus* and *S. couma* segregated from the remaining species by occupying less saline and shallower areas.

The marine catfishes were divided into two groups in the inner Amazonian estuary: (i) two species occupying shallower, less saline areas, and (ii) seven species inhabiting deeper, more saline areas. Most of the species with similar environmental affinities co-occurred randomly, and two pairs of species in the deepest area were aggregated. Therefore, negative interactions do not seem to be a major determinant in structuring the co-occurrence patterns of these catfishes. Aggregated species greatly varied in niche axes that promote shared use of space and food: (i) *S. parkeri* is a large species with caniniform teeth, while *A. quadriscutis* is a small species with molariform teeth; and (ii) *A. rugispinis* and *C. arenatus* are small-sized species that differ in traits related to habitat use, such as eye size and depth of the caudal peduncle. In fishes, ecomorphological differences between phylogenetically close species facilitate coexistence either by trophic (Portella *et al.* 2016, Silva *et al.* 2016) or microhabitat partitioning (Manna *et al.* 2017, 2020). Trophic partitioning may be an important factor underpinning the observed co-occurrence patterns because marine catfishes display high interspecific trophic variation (Mishima & Tanji 1982, Dantas *et al.* 2013), and syntopic species may exhibit trophic specialization (Maitra *et al.* 2020). If food resources are limiting and homogeneously distributed, trophic partitioning would inhibit competition and spatial segregation. Indeed, marine catfishes in the Amazonian estuary exhibit marked differences in the main prey type: *S. parkeri* and *S. couma* feed primarily on benthonic fishes, *C. arenatus* feed primarily on copepods, and the remaining species feed primarily on other crustaceans (Mendes & Barthem 2010, Soares *et al.* 2020).

Nonetheless, trophic and ecomorphological dissimilarity do not promptly determine species aggregation separately, as some pairs that exhibit marked functional and trophic differences do not aggregate. For example, *C. arenatus* is markedly different from *A. phrygiatus* and *N. grandicassis* in the ecomorphospace, but they do not aggregate. Different affinities to salinity and depth segregate the first pair (*C. arenatus* and *A. phrygiatus*), but the second pair (*C. arenatus* and *N. grandicassis*) inhabited sites with similar environmental conditions and co-occurred randomly. Several reasons may hinder the identification of non-random co-occurrence structure. First, temporal variation in the movement and distribution of the species may be a confounding factor. Marine catfishes usually move to less saline habitats for spawning (Dantas *et al.* 2010, 2012) and exhibit markedly seasonal distribution in the Amazonian estuary (Barletta *et al.* 2005). These seasonal movements should decrease local occupancy and abundance in the sampling area and do not change the pairwise co-occurrence patterns. Second, the adequate sampling size to identify co-occurrence patterns with a 95% confidence interval is over 500 samples (Blanchet *et al.* 2020), often unachievable in ecological studies. Third, the higher the number of non-random patterns within a community, the weaker and more undetectable the remaining ones are (Cazelles *et al.* 2016, Blanchet *et al.* 2020).

We recovered nearly half of the total number of species pairs as non-random associations, a high proportion compared to studies applying similar methods (Blois *et al.* 2014, Lyons *et al.* 2016). The explanation is threefold. First, we used a less conservative method to build the pairwise null models (fixed-equiprobable algorithm) than the one applied in other studies (fixed-fixed algorithm). This may only slightly affect overall results as they return similar results (Gotelli 2000). Second, this method is sensitive to species rarity and may not detect a significant pairwise structure when analyzing two rare species (D'Amen *et al.* 2018). We included species with at least 50 occurrences, thus diminishing issues related to low detectability of non-random associations in rare/rare species pairs. Third, we analyzed the co-occurrence patterns of species within a single taxonomic family, thus encompassing less phylogenetic diversity than assemblages investigated in other studies (*e.g.*, Cordero & Jackson 2019, Guterres *et al.* 2020). Phylogenetic proximity constrains ecological diversification and species interactions (Peralta 2016, Laigle *et al.* 2018), which drive some co-occurrence patterns (Freilich *et al.* 2018) and may have contributed to the high proportion of non-random patterns observed herein.

We can draw meaningful conclusions from these data. The environmental heterogeneity in the inner estuary of the Amazon River mouth sets boundaries to the local distribution and co-occurrence patterns despite the temporal dynamics in the species' movements. This suggests that regional variation in the environmental conditions promote spatial segregation even in closely related species inhabiting an environment with a homogenous shallow muddy substrate and that could be similarly important in other marine systems. We also showed that functional differences related to habitat use allow species aggregation. Therefore, both environmental filtering and limiting similarity play a role in shaping species' distribution and co-occurrence. Future research may better disentangle the relative roles of environmental filtering and competition by evaluating species affinities in a phylogenetic and historical context or determining the behavioral and physiological traits underpinning species' co-occurrence.

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Author statement

Soares BE: Writing – Original Draft; **Soares BE, Benone NL**: Conceptualization, Methodology, Formal analysis. **Barthem RB, Marceniuk AP**: Data curation, Project administration, Funding acquisition. **Benone NL, Barthem RB, Marceniuk AP, Montag LFA**: Writing – Review & Editing.

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