#### **RESEARCH ARTICLE**



## Influence of environmental conditions and the fragmented landscape on the co-occurrence patterns of the ichthyofauna of a stream in southwestern Brazilian Amazon

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#### Abstract

We assessed the spatiotemporal co-occurrence patterns of a fish assemblage in the watershed of a stream in the western Amazon basin, and verified the influence of abiotic factors (physicochemical variables and the hydrological phase) on these patterns. We also examined whether species that were more similar in their tolerance of physicochemical variables tended to co-occur more frequently. The structure of the assemblage was evaluated using the standardized effect size (SES) of the C-score index and null models, with the SES being used as an indicator of the organization of the assemblage. We employed linear regression models to investigate the influence of precipitation levels and physicochemical variables on the SES. We calculated the outlying mean index and ran a Mantel test on the checkerboard unit matrix of the C-score and tolerance values to assess the influence of species tolerance on co-occurrence patterns. Finally, we examined the correlations between species pairs and both physicochemical variables and adjacent land use. We observed patterns of aggregation or randomness in varying degrees at different scales. Increased precipitation influenced the establishment of random patterns, while species pairs correlated primarily with the degree of preservation of the local habitat at each study site. During the dry season, species that were more similar to each other in their environmental tolerance tended to co-occur more systematically. If the current levels of change in land use in the study area continue, the fish assemblage investigated here may suffer a significant loss of diversity, as well as destabilization of its structure, with a high possibility of local extinction of the most sensitive species.

Keywords Community assembly · Ichthyofauna · Null models · Landscape

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### Introduction

The structure of an ecological community may be influenced by either deterministic, stochastic processes, or a combination of the two (Zhou et al. 2020). Deterministic ecological processes include non-random, niche-oriented mechanisms, while stochastic processes result in species composition, abundance, and diversity patterns that are indistinguishable from those established by chance (Chase and Myers 2011). Environmental filtering (e.g., due to climatic variables, pH, nutrients, and oxygen concentrations) and biotic interactions are examples of deterministic processes, which include niche-based ecological mechanisms that underpin the configuration of a community (Leibold and Mikkelson 2002; Peres-Neto 2004). By contrast, stochastic processes that involve neutral mechanisms, in which a pool of ecologically identical species may cooccur (or not) as a result of the process, as well as provoking the random extinction of some species or the colonization of the environment by others (Leibold and Mikkelson 2002). Given this, the ecological investigation of species co-occurrence patterns at different spatiotemporal scales can contribute important insights for the understanding of how the various deterministic and stochastic processes influence the species composition, distribution, and structure of ecological communities. In a set of communities influenced by deterministic processes, microhabitats with ideal conditions and resources for the establishment and growth of the populations of a given species will tend to drive patterns of aggregation and segregation between species pairs (D'Amen et al. 2018). When aggregated, individuals or species will co-occur at specific spatiotemporal scales (Surendran et al. 2020), but when segregated, these species will tend not to co-occur spatiotemporally (Surendran et al. 2020). Stochastic processes introduce random patterns in the co-occurrence of species in a community, with individuals or species occurring at random (Ortega et al. 2015), which results in unpredictable variations in species composition among communities, given that they are not subject to systematic community structuring mechanisms (Rosindell et al. 2012).

In freshwater ecosystems, predation patterns, environmental filtering (Giam and Olden 2016), the hydrological regime (Fernandes et al. 2009; Ortega et al. 2015), and dispersal patterns (Gatto and Trexler 2020) are the main ecological factors determining the spatiotemporal patterns of community organization. For example, trophic parameters may have a direct influence on species composition by eliminating or reducing the abundance of one or more prey species (Sharpe et al. 2017), while they may also lead, indirectly, to shifts in habitat preferences and foraging patterns (Oliveira et al. 2005). Environmental filtering is a deterministic process in which abiotic and/or biotic environmental "filters" exclude either individuals or species that have inadequate phenotypic or functional characteristics from a given patch of habitat (Mittelbach and Schemske 2015; Giam and Olden 2016). In this scenario, species that are highly specialized in ecological terms will be found only in areas that contain a narrow range of environmental conditions, while generalists will tolerate a diversity of environmental conditions and tend to be more widely distributed (Ducatez et al. 2014). Given this, fish species with similar environmental requirements will tend to co-occur in communities that have similar biological conditions and resources (Mittelbach and Schemske 2015; Giam and Olden 2016). The environmental tolerance of any given species in an assemblage will thus reflect the position and amplitude of its niche, and will be linked intrinsically to the co-existence of specialists and generalists in the wild, where the species adopt varying adaptive strategies in response to shifts in environmental conditions at different scales (Dolédec et al. 2000; Ducatez et al. 2014; Granot et al. 2017; Carscadden et al. 2020). Therefore, it is necessary to understand how the niche breadths of the species interact with environmental heterogeneity to determine patterns of species co-occurrence, and to verify how the degree of habitat specialization causes interspecific variations due to the varying sensitivity of the different species to environmental changes (Ducatez et al. 2014; Bar-Massada 2015).

One factor that can cause significant changes throughout the entire aquatic community is the hydrological cycle (ebb and flood), which can determine the species composition of a fish assemblage (Fernandes et al. 2009; Ortega et al. 2015). During the ebb and low water periods, some stretches of water become isolated, with direct effects on local biological interactions, which influence the organization of the assemblage, generating patterns of segregation (Fernandes et al. 2009). During rainy periods, when the water level rises, there is a larger area for species to disperse across, which may result in more random patterns of co-occurrence (Fernandes et al. 2009; Ortega et al. 2015). Most physicochemical characteristics vary substantially across the hydrological cycle in aquatic ecosystems such as Amazonian streams, with electrical conductivity and dissolved oxygen concentrations (DOs) typically increasing during the rainy period, while the pH decreases (Winemiller et al. 2008; Figueiredo et al. 2010).

In addition to the intrinsic characteristics of these types of streams, the surrounding landscape exerts an important influence on the organization and species composition of their fish assemblages. The preservation of the riparian forest is fundamental to stream function, given that the forest canopy will reduce autotrophic production in the stream by shading it from the sun, while also contributing large amounts of allochthonous organic material through falling debris, such as twigs, leaves, and fruit (Vannote and Sweeney 1980). The shading effect of the riparian forest also favors a reduction in the temperature of the water, and contributes to an increase in DOs, creating conditions that are favorable to certain fish species (Teresa and Casatti 2010). Given the combined influence of all these factors, the variation in the composition of freshwater fish assemblages provides important insights for the identification of the impacts of shifting land use, given that these assemblages have been found to be characterized by high levels of species diversity (Lévêque et al. 2008; Albert et al. 2020), as well as marked morphological and functional variability (Winemiller 1991; Toussaint et al. 2016), and distinct trophic groups (Valverde et al. 2020).

In the present study, we evaluated the spatiotemporal patterns of co-occurrence of the fish assemblages of an Amazonian sub-basin, with the aim of evaluating the main factors that underpin these patterns. We used the data to test the following hypotheses: (1) the spatiotemporal structure of the fish assemblage is non-random, with co-occurrence patterns being influenced by hydrological conditions, physicochemical variables, and land use and cover, reflecting the ecosystem factors that determine the configuration of the assemblage; and (2) the co-occurrence of species that are less similar to each other in terms of their tolerance of environmental conditions is reduced during the dry season, given that the environmental conditions of this period are more stressful for stream-dwelling fish.

### Materials and methods

#### Study area

The micro-watershed of the Quinoá Stream (MWQS), a right-bank tributary of the Acre River, is located approximately 25 km from the city of Rio Branco, in the



**Fig. 1** Map showing the location of the Brazilian Amazon (**a**), the state of Acre (**b**) and the sampling points in the micro-watershed of the Quinoá Stream (MWQS), numbered from the headwaters to the

mouth in ascending order (c). Data on the forest and farmland cover for 2018 were obtained from collection 7 of the MapBiomas Project (Souza et al. 2020)

municipality of Senador Guiomard, in the Brazilian state of Acre (10°06'03.33" S, 67°40'11.50" W; Fig. 1). The landscape of the MWQS features first-, second-, and third-order streams surrounded primarily by cattle ranches and forest fragments with varying degrees of conservation. The local anthropogenic environments include dams and reservoirs, and the degradation of riparian forest for the establishment of pasture, with an accumulation of solid waste and the discharge of untreated domestic effluents into local bodies of water (Corrêa et al. 2018). The local climate is divided into a rainy season, between November and April, and a drier period between May and October, when the mean precipitation is much lower (Acre 2012).

# Collection of fish specimens and measurement of environmental variables

We collected fish specimens every 2 months at five sampling points (Fig. 1) over a 2-year period, between August 2016 and July 2018. We collected the specimens under Sistema de Autorização e Informação em Biodiversidade—SIS-Bio/Instituto Chico Mendes de Conservação da Biodiversidade—ICMBio, permit number 11.778, with the aim of sampling the different species present in the first-, second-, and third-order streams of the MWQS, which were classified based on the system of Vannote and Sweeney (1980).

We collected the fish specimens using three different methods (Corrêa et al. 2015): a seine net (5 m long, 2.25 m high, 5-mm mesh), which we deployed three times at each sampling site during each bimonthly visit; two dip nets (50 cm long, 30 cm wide, 5-mm mesh), which we deployed

for 30 min at each site; and two sieves (80 cm long, 50 cm wide, 5-mm mesh), which we also deployed for 30 min during each visit.

After each sampling session, we euthanized all the captured individuals with eugenol, and then placed them in individually labeled plastic bags with 5% formalin for transportation to the laboratory, where we identified them using the appropriate species keys. We consulted taxonomic experts, whenever necessary, to determine inconclusive taxa. We then placed the specimens in 70% alcohol, and deposited voucher specimens in the fish collection of the Universidade Federal do Acre in Rio Branco.

Concurrently with the collection of fish specimens, we obtained data on the electrical conductivity, DO), potential of hydrogen (pH), and temperature of the water (Table 1) of each stream using a Sanxin SX751A multiparameter apparatus. We obtained data on precipitation from the meteorological database of the Instituto Nacional de Meteorologia (2023).

We also obtained data on land use and cover, as classified by the MapBiomas project (Souza et al. 2020). This project has compiled annual Landsat satellite images of Brazil from 1985 through 2021 (collection 7), and has classified the land use and cover of each pixel ( $30\text{-m} \times 30\text{-m}$  resolution) using a random forest algorithm (Souza et al. 2020). We created a 100-m buffer around the site coordinates of each MWQS sampling point. Based on the available categories, we used a forest classification map to quantify the forest cover at each of the five MWQS sampling points between 2016 and 2018 (see Supplementary 1).

Table 1	Mean values $(\pm SD)$ of
the phys	sicochemical variables
recorde	d in the micro-watershed
of the Q	uinoá Stream (MWQS)
betweer	1 2016 and 2018

Period (month and year)	Electrical conductivity (µS cm <sup>-1</sup> )	Dissolved oxygen (mg/L)	рН	Temperature (°C)	Precipitation (mm/month)
Flood					
December 2016	$6.62 \pm 5.2$	$4.35 \pm 1.9$	$6.27\pm0.6$	$30.55 \pm 2.6$	219.30
February 2017	$0.09 \pm 0$	$4.88 \pm 0.3$	$6.1 \pm 0.9$	$28.43 \pm 0.8$	236.50
April 2017	$8.42 \pm 2.6$	$5.44 \pm 1.3$	$5.84 \pm 0.2$	26.39±1.6	205.30
December 2017	$12.2 \pm 4.2$	$3.51 \pm 2.4$	$6.7 \pm 0.3$	$28.62 \pm 1.1$	354.20
February 2018	$12.53 \pm 2.6$	$8 \pm 1$	$6.01 \pm 0.3$	$26.41 \pm 0.5$	467.70
April 2018	$8.3 \pm 1.5$	$5.82 \pm 1$	$6.06 \pm 1.1$	$28.87 \pm 1.1$	359.20
Dry					
August 2016	$10.17 \pm 2$	$5.26 \pm 1.2$	$5.88 \pm 1.9$	$29.01 \pm 1.6$	30.60
October 2016	$12.77 \pm 2$	$6.59 \pm 1$	$5.77 \pm 2.9$	$28.96 \pm 1.6$	211.30
June 2017	$9.23 \pm 2.8$	$7 \pm 1.9$	$5.89 \pm 0.2$	$28.79 \pm 0.9$	25.40
August 2017	$6.83 \pm 1.8$	$5.81 \pm 1.3$	$6.05\pm0.4$	$27.16 \pm 1.4$	63.40
October 2017	$10.78 \pm 2.4$	$5.77 \pm 2.3$	$6.82\pm0.6$	$30.72 \pm 1.8$	110.90
June 2018	$13.93 \pm 3.8$	$8.33 \pm 1.2$	$6.2\pm0.5$	$28.09 \pm 1.5$	26.70

#### **Data analysis**

#### Co-occurrence patterns of the fish assemblage

To analyze patterns of species co-occurrence, we organized the data in a presence-absence matrix, with the species in rows and the samples in columns. We assessed the spatiotemporal organization of the fish assemblage using the C-score co-occurrence index (Stone and Roberts 1990). The C-score represents the mean co-occurrence of each pair of species in the community (Gotelli and McCabe 2002) and is given by:

$$CScore = \sum_{i} \sum_{j} \frac{Cij}{(M(M-1)/2)}$$

$$Cij = (ri - Sij)(rj - Sij)$$

where Cij = the checkerboard unit for species pair ij; ri = total number of occurrences of species i in the matrix (sum of presences in row i); rj = total number of occurrences of species j in the matrix (sum of presences in row j); Sij = the number of co-occurrences of species i and j (both present in the same column); and M = the total number of species in the matrix.

We subsequently ran null models to determine whether the observed pattern was significantly different from patterns generated at random (Gotelli and McCabe 2002). This is a statistical approach that tests whether the spatiotemporal patterns found in a community are similar to a pattern that occurs at random, or whether there is a systematic spatial or temporal structure of species aggregation or segregation (Gotelli and McCabe 2002). To achieve this, we sequentially randomized the occurrence data in the matrices, using a fixed equiprobable algorithm with 9999 randomizations (Gotelli 2000). In this algorithm, the frequency of occurrence of the species was maintained (fixed columns), while the species richness varied among the MWQS sampling points (equiprobable rows).

We compared the degree of organization of the fish assemblage by calculating the standardized effect size (SES) of the C-score (Gotelli and Rohde 2002) for the whole MWQS dataset. This index estimates the deviation of the observed co-occurrence from the mean simulated co-occurrence, in units of SD from the observed variance, calculated as follows: SES = (Cobs-Csim)/Ssim, where Cobs = the observed C-score, Csim = the mean value of the simulated C-scores, and Ssim = the SD of the simulated C-scores. The higher the value of the SES, the greater the likelihood that the organization of the assemblage is significantly different from random (Gotelli 2000). We considered SES values of at least 11.961 to be significant. A large difference (SES > 1.96) between sites in relation to a specific environmental variable indicates

habitat segregation, whereas small differences (SES <-1.96) indicate habitat filtering (Ulrich 2004; Sawilowsky 2009).

To verify whether pairs of species co-occurred more, or less, frequently than expected at random, we analyzed pair associations following Veech (2013), using the coocur package in R (Griffith et al. 2016). We removed pairs of species with an expected co-occurrence of <1 from the analysis, as recommended by Veech (2013). We conducted this analysis with the data of the dry and rainy seasons separately to determine whether seasonality influenced the formation of non-random pairs. We also assessed spatiotemporal patterns, using non-random pairs in a redundancy analysis (RDA), as described below.

#### Simple and multiple regression models

We ran a principal components analysis (PCA) using a correlation matrix to summarize the variation in the physicochemical parameters of the MWQS during the study period. The axes with eigenvalues of over 1 were retained for analysis. To assess the potential relationship between environmental heterogeneity and co-occurrence patterns, we conducted multiple linear regressions between the SES values representing the temporal scale (response variable) and the scores of the PCA axes retained for the physicochemical variables (predictor variables). We ran this analysis to test the hypothesis that the physicochemical variables influence species co-occurrence patterns. We also evaluated the influence of precipitation on co-occurrence patterns at the temporal scale, based on simple linear regressions between the SES values for each month (response variable) and mean monthly precipitation (predictor variable). We ran this analysis to test the hypothesis that the hydrological conditions influence species co-occurrence patterns. We examined three assumptions before implementing the regression models, to ensure an adequate distribution, i.e., normality, outliers, and overdispersion, using the simulate residuals function of the DHARMa package (Hartig and Lohse 2022). We would like to further emphasize here that the environmental differences between the sampling points and the distances between them were taken into account in the analyses to guarantee the validity of the samples. This assessment highlighted the suitability of the samples as representative replicates of the study basin.

#### Relationship between non-random co-occurring pairs and environmental variables

We applied a RDA (Borcard et al. 2011) to assess the degree of relationship between the species that formed non-random pairs in the null model and the environmental variables. We ran this analysis to verify the relationship between the environmental variables (physicochemical variables and land use and cover) and the co-occurring pairs. For this analysis, we square root transformed the matrix of the fish species composition, and used a dissimilarity matrix of proportional differences (Borcard et al. 2011). We tested the significance of the RDA axes using the Monte Carlo test with 9999 permutations (Borcard et al. 2011). We used the envfit routine of the vegan package (Oksanen et al. 2022) to determine the contribution of the fish species and environmental variables to the dissimilarity identified by the RDA. Once again, we evaluated the significance of the associations between species and environmental variables based on 9999 permutations (Borcard et al. 2011), with a significance level of 5% (p < 0.05), in the R program (R Core Team 2023).

# Correlation between co-occurrence patterns and environmental niche breadth

We employed the outlying mean index (OMI) (Dolédec et al. 2000) to estimate species tolerance (TOL) as a physicochemical niche. This approach is an ordination technique that considers the ecological niche of each species (the abundance of the species was used here) within a community through combinations of environmental variables (in the present case, electrical conductivity, DO, pH, and temperature). In this approach, the tolerance of a species refers to the extent of its environmental niche, which reflects the amplitude of its distribution along the environmental gradient found in the study area. A low OMI value indicates that the distribution of a species is restricted by environmental conditions (specialist species), whereas a high value implies that the species has a broader distribution in habitats with more variable environmental conditions (generalist species). We used the subniche package for this analysis (Karasiewicz 2022). Then, to evaluate whether species co-occurrence was correlation by fish TOL in relation to spatiotemporal and seasonal environmental factors, we applied the Mantel test between the checkerboard unit matrix of the C-scores (the number of times a species did not form a species pair) and the TOL values from the OMI. The TOL values were transformed into the Euclidean distance that separated each species pair, while rare species were removed, and the environmental variables (except pH) were standardized by log10 transformation. We ran this analysis to test hypothesis 2.

### Results

#### Co-occurrence patterns of the fish assemblage

We collected a total of 8187 individual fish during the study period, representing 75 species, 25 families, and seven orders. The most prominent orders were the Characiformes, with 5794 specimens, followed by the Cichliformes (1777 specimens) and the Gymnotiformes (387 specimens). The most abundant families were the Characidae, with 4544 specimens collected, the Cichlidae (1777 specimens), and the Iguanodectidae (418 specimens). *Serrapinnus micro-don* (Eigenmann, 1915) was the most common species, with 1335 specimens collected, followed by *Serrapinnus micropterus* (Eigenmann 1907) with 1051 specimens, and *Apistogramma acrensis* Staeck, 2003, with 847 specimens.

We recorded a species richness of nine species (n = 1417)specimens) at site P1, 33 at P2 (n = 506), 24 (n = 867) at P3, 50 (n = 2956) at P4, and 42 (n = 2441) at P5 (see Supplementary 2). We tested 32 null models, of which 18 (56.25%) returned patterns significantly different from random, while 14 (43.75%) presented a random pattern (Table 2). These 18 non-random models all revealed positive associations, i.e., an aggregated pattern among the species (SES < -1.96). While other models were significantly different from random, they did not have SES values of greater than 1.96 or less than -1.96, which means that they were random. At a larger scale (spatiotemporal or seasonal), random patterns were only found for the flood period, while the other patterns were aggregated (Table 2). At a more restricted scale (sampling points and months), seven samples were aggregated, while eight were random.

At the spatiotemporal scale, the application of Veech's (2013) analytical approach permitted the removal of 1933 (73.55%) of the 2628 possible species pairs from the analysis because the expected co-occurrence was < 1, leaving 695 pairs for analysis. Almost a quarter (24.7%) of these pairs were non-random, with 130 positive (aggregated) and 42 negative (segregated) pairs, while the remaining 523 (75.3%) pairs were random. During the dry season, there were 1540 possible species pairs, of which we removed 938 (60.91%) due to them having an expected co-occurrence of less than 1. One hundred (16.6%) of the remaining 602 pairs were non-random, including 80 positive and 20 negative pairs, while the other 502 pairs (83.4%) were random. In the rainy season, we removed 1222 (76.57%) of the 1596 possible species pairs from the analysis due to their expected co-occurrence being less than 1, which left 374 pairs for analysis. Only 15.2% of these pairs were non-random, consisting of 32 positive (aggregated) and 25 negative pairs (segregated), while the other 317 (84.8%) were random.

#### Simple and multiple regression models

The first two axes of the PCA presented eigenvalues greater than 1, and explained approximately 76.05% of the total variance in the physicochemical data (Table 3). The first axis was correlated positively with DO and negatively with the pH and temperature of the water. The second axis was related positively, primarily, to conductivity. The SES was not related to any of the PCA axes ( $F_{2,9}$ =1.44,

Table 2	Null models	for the fish	assemblage o	of the micro-v	vatershed
of the Q	uinoá Stream	(MWQS) sa	ampled betwee	en 2016 and 2	2018

**Table 3** Results of the principal components (PC) analysis applied to the physicochemical variables measured bimonthly during the present study, over a 12-month period

Null models	n	Observed index	Mean of simulated indi- ces±SD	SES
Spatiotemporal			,	
Sites and months	60	28.01	$30.58 \pm 0.14$	- 6.69*
Sites	5	0.54	$0.96 \pm 0.00$	- 19.12*
Months	12	2.29	$2.42 \pm 0.02$	- 2.20*
Spatial scale				
Site 1	12	0.33	$0.87 \pm 0.092$	- 1.35
Site 2	12	2.85	$3.34 \pm 0.01$	- 3.54*
Site 3	12	1.00	$1.22 \pm 0.01$	- 1.89
Site 4	12	2.69	$3.01 \pm 0.007$	- 3.76*
Site 5	12	3.64	$3.95 \pm 0.01$	- 2.71*
Seasonal scale				
Dry	30	12.34	$14.43 \pm 0.06$	- 8.73*
Flood	30	10.89	$10.83 \pm 0.045$	0.25
Dry season				
Site 1	6	0.13	$0.42 \pm 0.022$	- 1.93
Site 2	6	0.88	$1.11 \pm 0.004$	- 3.29*
Site 3	6	0.61	$0.6 \pm 0.006$	0.17
Site 4	6	1.15	$1.22 \pm 0.003$	- 1.26
Site 5	6	1.13	$1.11 \pm 0.002$	0.30
Flood season				
Site 1	6	0.07	$0.29 \pm 0.029$	- 1.53
Site 2	6	1.31	$1.42 \pm 0.009$	- 1.23
Site 3	6	0.85	$0.99 \pm 0.005$	- 3.33*
Site 4	6	0.84	$0.955 \pm 0.007$	- 3.34*
Site 5	6	1.05	$1.187 \pm 0.002$	- 2.73*
Temporal scale				
August 2016	5	0.68	$1.00 \pm 0.001$	- 7.70*
October 2016	5	0.00	$0.731 \pm 0.007$	- 8.20*
December 2016	5	0.91	$1.01 \pm 0.002$	- 1.88
February 1207	5	0.92	$0.93 \pm 0.004$	- 0.10
April 2017	5	0.87	$0.98 \pm 0.001$	- 2.70*
June 2017	5	0.84	$0.98 \pm 0.001$	- 3.50*
August 2017	5	0.71	$0.90 \pm 0.002$	- 3.60*
October 2017	5	0.99	$1.15 \pm 0.002$	- 2.90*
December 2017	5	1.26	$1.18 \pm 0.003$	1.38
February 2018	5	1.24	$1.27 \pm 0.005$	- 0.40
April 2018	5	1.26	$1.31 \pm 0.005$	- 0.70
June 2018	5	0.85	$1.19 \pm 0.002$	- 6.40*

SES Standardized effect size

\* Model is significantly different from random

adjusted  $r^2 = 0.07$ , p = 0.28), although there was a positive relationship between the SES values and precipitation, with significant SES values being recorded during periods of reduced precipitation ( $F_{1,10} = 7.42$ , adjusted  $r^2 = 0.37$ , p = 0.02; Fig. 2).

Variables	PC1	PC2
Water temperature	- 0.77	0.27
Conductivity	0.21	0.91
Dissolved oxygen concentration	0.76	0.38
pH	- 0.82	0.33
Eigenvalue	1.89	1.16
Percent of variability explained	47.19	28.88



Fig. 2 Simple linear regression between the standardized C-scores (*SES*) of the fish assemblage and mean monthly precipitation (millimeters) on a  $\log 10$  scale

# Relationship between non-random co-occurring pairs and environmental variables

In the RDA, axes 1 and 2 together explained 24.5% of the total variance in the spatiotemporal data from the MWQS (Table 4). The temperature of the water, DO, pH, forest cover, and pasture were all correlated significantly (p < 0.05) with the RDA axes. DO (0.33), pH (0.37), and forest cover (0.64) contributed positively to RDA1, while the other variables had a negative contribution, i.e., water temperature (-0.40) and pasture (-0.73). While DO (0.23) and forest

 Table 4 Loadings of the redundancy analysis (RDA) between species that formed non-random pairs and the abiotic variables measured in the micro-watershed of the Quinoá Stream (MWQS)

Variable	RDA1	RDA2
Water temperature	0.40	0.19
pH	- 0.37	0.22
Dissolved oxygen concentration	- 0.34	- 0.23
Forest cover	- 0.64	- 0.43
Pasture	0.73	0.33
F (ANOVA)	12.64	6.47
Eigenvalue	0.09	0.04
Proportion explained	0.16	0.08

cover (0.44) also contributed positively to RDA2, water temperature (-0.20), pH (-0.22), and pasture (-0.34) all contributed negatively.

In the RDA, 29 of the 40 species that formed non-random pairs were related significantly to environmental variables (Supplementary 3). The electric fish *Gymnorhamphichthys rondoni*, the armored catfish *Rineloricaria lanceolata* and *Ancistrus* spp., the leaf fish *Helogenes marmoratus*, and the tetra *Hemigrammus ocellifer*, were all associated positively with forest cover and DOs, and negatively with pasture and water temperature. On the other hand, *Bryconops* cf. *caudomaculatus*, *S. microdon*, and *Triportheus angulatus* were associated negatively with pH, occurring typically in areas with reduced forest cover. The cichlids *Apistogramma acrensis*, *Aequidens tetramerus*, and *Crenicichla semicincta*, as well as the wolf fish *Hoplias malabaricus* (Bloch, 1794), also occurred in less forested areas (Fig. 3).

# Correlation between co-occurrence patterns and environmental niche breadth

At a spatiotemporal scale, we found no significant correlation between the C-score chessboard units and either the tolerance of the species to environmental conditions (r=-0.05; p=0.82; Supplementary 4) or the flood period (r=-0.06; p=0.73). We did, however, find a low, but significant, correlation for the dry period (r=0.14; p=0.002; Fig. 4).

### Discussion

We observed aggregated and random co-occurrence patterns in the fish assemblage of the MWQS at both regional and local scales. Precipitation significantly influenced the randomness of species co-occurrence patterns, while species pairs were correlated with the varying degrees of habitat preservation at the different study sites. During dry periods, the physicochemical conditions of the environment also played a fundamental role, driving down the co-occurrence of species with dissimilar environmental requirements.

# Co-occurrence patterns of the fish assemblage and simple and multiple regression models

At a spatiotemporal scale, the fish assemblages of the MWQS presented patterns of aggregation, being influenced by both month and sampling point, which underscores the importance of assessing the characteristics of a community at multiple scales (Denny et al. 2004; Mouchet et al. 2013; Ortega et al. 2015). Williams et al. (2022) demonstrated how certain resources are ephemeral and vary considerably over time, while habitat preferences shift over a much bigger scale. Given this, co-occurrence approaches that do not incorporate a temporal dimension may fail to detect which resources affect ecological processes. In the present study, we found that different types of co-occurrence pattern were influenced by the scale of analysis. Thus, important aspects

Fig. 3 Redundancy analysis (RDA) between the species that formed non-random pairs and the abiotic factors recorded in the micro-watershed of the Quinoá Stream (MWQS). The longer arrows indicate higher levels of correlation with the axes, while the green shading of the circles indicates the forest cover of each sampling point. AEQTET Aequidens tetramerus, APIACR Apistogramma acrensis. BRYCAU Bryconops caudomaculatus, CRESEM Crenicichla semicincta, EIGVIR Eigenmannia virescens, GYM-RON Gymnorhamphichthys rondoni, HELMAR Helogenes marmoratus, HEMOCE Hemigrammus ocellifer, HOPMAL Hoplias malabaricus, PHEPEC Phenacogaster pectinata, SERMIC Serrapinnus microdon, TRIANG Triportheus angulatus





Fig. 4 Correlation between the checkerboard units and the tolerance levels of environmental conditions in the fish assemblage sampled between 2016 and 2018 in the micro-watershed of the Quinoá Stream (MWQS)

of the patterns of variation may go undetected when the spatial and temporal dimensions of species co-occurrence are analyzed separately.

Spatially, the fish assemblage presented an aggregated pattern at sites with minimal impacts from land use, while patterns were random in the more impacted areas. Site P2 was the most preserved location in the study area, e.g., with total forest cover, sandy substrates, and a continuous flow of water. By contrast, P1 lacked any forest cover whatsoever, and was dominated by macrophytes, which had created a lentic environment with low fish species richness, composed predominantly of species adapted to environments with high levels of anthropogenic impact. Similarly, P3, despite having some forest cover, was affected by a culvert that was undersized, which had resulted in the formation of a lentic environment dominated by macrophytes, which had also led to a reduction in species richness. Site P4 was located near a road with an undersized culvert, while P5 had been dammed to supply farmland with water. However, both of these sites had retained their lotic characteristics, which contributed to a more preserved environment than those found at sites P1 and P3.

Overall, our findings indicate that environmental degradation has had a negative impact on the fish assemblage of the MWQS, which has led to a reduction in species richness and the destabilization of local fish co-occurrence patterns. This is consistent with the expectation that non-random cooccurrence patterns are driven by common species-habitat relationships in the study system (Peres-Neto 2004). Seasonal variation also played a significant role in shaping cooccurrence patterns, with aggregated patterns arising during the dry months and practically random patterns during the rainy season. There were also more positive associations between pairs of species during the dry season than during the rainy season. The linear regression between the SES and precipitation revealed that the influence of the latter on co-occurrence patterns differed according to season. The increased precipitation during the rainy season led to the randomization of co-occurrence patterns, due primarily to a lack of organization at points 1 and 2. During periods of lower precipitation, during the dry season, by contrast, the fish fauna presented marked aggregation, influenced primarily by the organization of the community at point 2. Based on these findings, we can partially accept our first hypothesis, i.e., that seasonal variation had a significant influence on patterns of species co-occurrence, even though the physicochemical variables had no clear effects.

The natural hydrological regime is considered to be the most important source of variation in fluvial systems, as observed by Jackson et al. (2001). In the MWQS, monthly precipitation varied greatly over the course of the 2 years of the study period, ranging from 25 to 467 mm. In lotic systems, the flood pulse can lead to a segregation of the fish assemblage, whereas in lentic systems, it tends to result in a random distribution. Fitzgerald et al. (2017) found that during the rainy season, the fish assemblages of tropical streams are highly structured through environmental filtering, as they disperse and select habitats across the expansive areas inundated on the floodplain, which are not available to them during the dry season. In the dry season, the reduction in the area of aquatic habitat available to fish leads to decreased dispersal and an increase in interspecific competition for habitat. As a consequence, the increase in the water level in Amazonian streams during the flood period allows for a greater diversity of habitats and access to larger quantities of feeding resources. These findings underscore the importance of using a seasonal approach for research in the Amazon region.

The numerous anthropogenic impacts observed within the MWQS, such as the construction of dams and roads, and shifts in land use for agriculture, account for the large numbers of random species pairs identified at all scales in the present study. Anthropogenic events, and even natural impoundment, can randomize co-occurrence patterns within an assemblage, as the resulting changes in habitat conditions disrupt the fish assemblage. One other determining factor may be the extreme environmental heterogeneity of the study ecosystem, given that Amazonian stream species do not typically rely on each other, but rather respond collectively to the availability of resources and habitat heterogeneity. In the only previous study, to the best of our knowledge, of species co-occurrence patterns in Amazonian stream fish, Lobato et al. (2022) also documented a large number of random species pairs, and concluded that the highly diverse and heterogeneous environments of Amazonian streams may favor these random associations.

# Relationship between non-random co-occurring pairs and environmental variables

We found that a combination of forest cover and DO influenced certain, more specialized species. Differences in the percentage of forest cover among the sampling points filtered species, with generalists occurring in degraded environments, from which the more specialized species tended to be absent. Deforestation can lead to an increase in the total abundance of some fish species, due to the proliferation of generalists, while species associated with riparian vegetation tend to disappear (Casatti et al. 2015; Brejão et al. 2018; Ilha et al. 2019).

Based on these findings, we can accept our hypothesis the spatiotemporal structure of the fish assemblage is nonrandom, and that the species co-occurrence patterns are influenced by land use and cover. Indeed, the influence of the local landscape tends to be more significant in streams with degraded watersheds (Daniel et al. 2015). Local environmental variables are also important predictors of the structure of fish assemblages (Barbosa et al. 2019; Montag et al. 2019), and an increasing number of studies have shown that stream fish assemblages in Amazonian environments are influenced by both variables, in addition to other, interacting factors (Arantes et al. 2018).

In the present study, more sensitive fish species such as *G. rondoni*, *H. marmoratus*, and *Tyttocharax madeirae* occurred exclusively in the stream with total forest cover, i.e., in highly preserved areas. For example, the psammophile *G. rondoni* inhabits sandy bottoms with either high or low flow rates, using sandbanks to shelter and feed, and this specialized species is highly dependent on the availability of a well-structured environment (Soares et al. 2017). Similarly, *H. marmoratus* inhabits entangled roots with leaf litter, and is dependent on the availability of allochthonous materials (Ferreira et al. 2018). This species is considered to be a crucial bioindicator of the ecological integrity of Amazonian streams. Species of the genus *Tyttocharax* inhabit streams with relatively fast flowing water, associated with marginal roots and stems (Brejão et al. 2018), which accounts for the co-occurrence of these species in environments with total forest cover, continuous water flow, and sandy substrates.

The suckerfish *Ancistrus* spp., and *R. lanceolata*, were also more common in streams with total forest cover, and were rare in areas with reduced forest cover. Casatti et al. (2005) noted that species of the family Loricariidae are grazers that rest on logs and rocks to feed on periphytic matter, which makes them dependent on riparian vegetation. The cardinal tetra *H. ocellifer* was associated primarily with well-forested streams, but was common in all areas, reflecting its tolerance of varying conditions.

In contrast with these more specialized fish, species more tolerant of environmental change tended to persist, and even increase in numbers, in degraded areas. These species often have a generalist diet (Casatti et al. 2012; Benone et al. 2022), as seen in the omnivorous *Triportheus angulatus*, or feed primarily on autochthonous resources, such as *Bryconops* cf. *caudomaculatus* and *S. microdon*. Many of these species are also tolerant of extreme conditions, with high trophic plasticity, such as *A. acrensis*, *A. tetramerus*, and *C. semicincta*, and the wolf fish *H. malabaricus*.

We also observed that the presence of *B*. cf. *caudomaculatus*, *S*. *microdon*, and *T*. *angulatus* correlated negatively with pH, which reflects their tolerance of more acid environments. Indeed, some species are able to maintain control of their gill permeability even in environments with a low pH, which makes them more acid tolerant. By contrast, species of the genus *Hemigrammus* have reduced control of their gill permeability in low-pH environments, and are thus less tolerant of acidic conditions. The importance of the pH of the water, especially in lower-order streams, has been well documented in previous studies. The decomposition of organic matter from the riparian vegetation also releases substances, such as humic and fulvic acids, into the water, causing it to become more acidic. This favors species that are more specialized and better adapted to these conditions.

### Correlation between co-occurrence patterns and environmental niche breadth

During the dry season, different species with varying levels of environmental tolerance tended to expand their physicochemical niches, thus avoiding co-occurrence. In a general spatiotemporal context, however, and during the rainy season, species co-occurrence was not correlated with these distinct levels of environmental tolerance. Based on these findings, we can accept our second hypothesis, i.e., that the dry season reduces the co-occurrence of species that are less similar to each other in their tolerance of environmental conditions. In the present study, species from different families, such as the Cichlidae (A. tetramerus, A. acrensis, and Satanoperca jurupari), Characidae (Astyanax bimaculatus and Moenkhausia oligolepis), Crenuchidae (Characidium sp.), Hypopomidae (Brachyhypopomus sullivani), Loricariidae (Farlowella smithi and Rineloricaria castroi), and Serrasalmidae (Serrasalmus rhombeus), all had a broader niche during the dry season, in comparison with the rainy season. These findings reflect how lower water levels forced certain species to expand their niches, resulting in a reduced co-occurrence of species with dissimilar tolerance levels.

During the dry season, the quality of the aquatic habitats and, in particular, the water typically deteriorates, with low concentrations of dissolved oxygen and increased levels of hydrogen sulphide. This leads to an increase in fish mortality, although species with accessory respiratory adaptations are best able to persist under such conditions (Winemiller et al. 2008). In this context, environmental filtering removes species that lack the evolutionary traits that enable them to persist under specific environmental conditions (Keddy 1992). Overall, then, our findings highlight how environmental factors influence fish co-occurrence patterns in Amazonian streams (Peres-Neto 2004; Hoeinghaus et al. 2007; Giam and Olden 2016; Hubbell et al. 2020; Cordero and Jackson 2021).

### Conclusions

To the best of our knowledge, this is the first study to assess the importance of both temporal and seasonal factors in the co-occurrence patterns of Amazonian stream fish assemblages, and, in fact, is one of the few studies of its type to be conducted anywhere in the world. The large numbers of random pairs and the predominance of aggregated pairs, in comparison with segregated pairs, may be the typical pattern in Amazonian streams affected by forest fragmentation. As far as we know, this is also the first study to show that the dry season provokes a broadening of the niches of streamdwelling Amazonian fish species which, in turn, reduces the co-occurrence of these species. Nevertheless, this pattern can only be confirmed by further research that uses a similar approach to that adopted here, and, in particular, by expanding the spatiotemporal scales investigated. Finally, if the current shifts in land use in the study area continue, the fish assemblage investigated here will likely suffer a significant loss of diversity and the destabilization of its community structure, including the probable extinction of the most sensitive species.

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Author contributions LPO, FC and JCGO designed the study, performed the data analyses, and wrote the main text. RSS, EFO and LJSV supervised the development of the manuscript. All authors discussed the results and revised the manuscript.

**Data availability statement** The authors declare that the data supporting the findings of this study are available within the paper and its Supplementary Information files. Should any raw data files be needed in another format, they are available from the corresponding author upon request.

#### Declarations

**Conflict of interest** The authors have no conflicts of interest to declare that are relevant to the content of this article.

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