

NON-STATIONARY IN DISTRIBUTION OF FISH SPECIES RICHNESS IN TROPICAL STREAMS

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Abstract

Diversity gradients are observed in various groups of organisms. For fishes in streams, the Water-Energy, Productivity and Temporal Heterogeneity hypotheses are considered the best combination to explain richness patterns. The relationship between species diversity and the variables that represent the hypotheses are generally considered linear and stationary, that is, there is equal relation of cause and effect along an entire geographical extension. The assumption of stationarity has not been tested or even observed in diversity gradients, thus producing imprecise models. Therefore, our goal is to quantify stationarity in the existing relationships between the ichthyofauna of streams and the Water-Energy, Productivity and Temporal Heterogeneity hypotheses using a Geographically Weighted Regression – GWR. In the proposed model, there is conspicuous absence of stationarity between fish species richness and the tested hypotheses. Furthermore, water-energy dynamics were observed as a

possible metabolic restriction mechanism acting on the community structuring of stream fishes. This mechanism divides the fish fauna from the studied Brazilian watercourses in two regions: i) Amazonian, characterized by a stable climate and populations with little resistance to thermal variation; and ii) Central, featured by greater ranges of temperature and fish populations resistant to thermal variation.

Introduction

The existence of a diversity gradient, where the maximums are present in equatorial regions and the minimums in polar regions, is observed in many groups of organisms (Willig, Kaufman, and Stevens 2003; Hawkins et al. 2003). This gradient seems to be explained by the Energetic, Water-Energy, Altitude, Climatic Heterogeneity, Primary Productivity, and Metabolic hypotheses (Wright 1983; Hawkins and Porter 2003a; Colwell and Lees 2000). The Water-Energy hypothesis presents the greatest causal effect on species richness distribution (Hawkins et al. 2003) and predicts richness as a product of evapotranspiration and quantity of water available on the considered place (O'Brien and Road 1998).

The relationship between species richness and the variables that represent each of these hypotheses is considered linear and stationary (Angermeier and Schlosser 1989; Wylie and Currie 1993; Tedesco et al. 2005). Stationary relationships are characterized by an equal relation of cause and effect throughout the whole geographical extension of the data considered (Osborne et al. 2007). In this way, the global model (obtained utilizing all the data) is the same as local models (obtained from a subgroup of the data). In fact, stationarity is an assumption for the application of global models (Zar 2010). In many cases this assumption is neither tested nor observed in diversity gradients (Foody 2004; Cassemiro et al. 2007), consequently producing imprecise global models with few representatives of local estimates (Foody 2004).

An example of a non-stationary relationship is assumed by the Water-Energy hypothesis, that is, in lower latitudes the quantity of water available in the system is the limiting factor of diversity, whereas in higher ones, energy (evapotranspiration) determines the richness gradient (Gaston 2000; Hawkins and Porter 2003b; Eiserhardt et al. 2011). This occurs because areas of low latitudes suffer little influence from Earth's precession movements, because of they are located near the equator. Consequently, the energy input (from the Sun) occurs in a uniform way throughout the year, making water the limiting factor of diversity. On the other hand, areas located at high latitudes suffer greater influence from Earth's precession, so there are periods of the year when the hemispheres receive greater or smaller amounts of energy.

Non-stationarity is the main cause of non-significative relationships (Osborne et al. 2007), since the variation of regression's coefficients is ignored and the relationships are described by their average along the geographic space (Foody 2004). Morphological terrain variations and environmental heterogeneity conditions, at the spatial or temporal level, are the main causes of non-stationarity in the relationships of diversity with the environmental variables considered by each hypothesis (O'Brien and Road 1998; Bickford and Laffan 2006). Modifications of the topographical relief can isolate or connect isolated populations, promoting or even avoiding speciation. Heterogeneity of environmental conditions also creates an environment with high habitat diversity, allowing the coexistence of species (Bickford and Laffan 2006). Therefore, a non-stationarity relationship between species richness and environment is a characteristic that cannot be overlooked in studies about diversity gradients (Foody 2004).

For tropical stream fishes it was shown that diversity distribution is a product of the interactions of three hypotheses: (i) Water-Energy; (ii) Terrestrial Primary Productivity and (iii) Climatic Temporal Heterogeneity (Vieira et al. 2018). Despite this, the Brazilian geographical area presents high morphologic and climatic heterogeneity, possessing regions with elevated temperatures and pluviosity (north/northeast regions), regions with low temperatures and high pluviosity (south and part of the southeast regions) and regions with elevated temperatures and long dry periods (midwest and northeast regions (Marengo and Valverde 2007)). Therefore, our objective is to quantify the stationarity of the relationship between stream fish richness and the following hypotheses: (i) Water-Energy; (ii) Terrestrial Primary Productivity and (iii) Climatic Temporal Heterogeneity.

Material and Methods

The database and the macroecological variables used for the analyses were the same considered in Vieira et al (Vieira et al. 2018), January evapotranspiration (ETJan), June evapotranspiration (ETJune); annual rainfall variation (ARV), primary productivity (PP), annual temperature variation (TempVar) and annual rainfall variation (ARV) and can be accessed by <https://doi.org/10.1371/journal.pone.0204114.s005>. The stationarity's quantification of the fish richness-macroecological variables relationship was done using a Geographically Weighted Regression (GWR) following the protocol indicated in Figure 1. This analysis establishes local estimates of adjustments and regression coefficients using subsets of the database considered and defined according to a Spatial Weighting Function. This function attributes a weight (or importance) to each site, which will be used in the coefficient estimates of a focal point. Thus, sites close to each other (given a connectivity criterion) will have greater importance than sites further away from the focal point, considering the close and far threshold defined by the chosen bandwidth, which in our case is represented by the connectivity between sites. This allows the specification of heterogeneity in relationships and identify regions where the model is more robust, as well as which variables are more important to explain the observed pattern. In this study, connectivity between sampling sites was defined in three ways: i) Euclidian distance between all sites; ii) Euclidian distance between all sites (W Global) present in a same hydrographic basin (W Basin), so the sites located in different basins have a connectivity of zero; and iii) Euclidian distance between all sites present in the same ecoregion (W FEOW), thus the sites in different ecoregions have a connectivity of zero. The number of sites used in local estimates was defined as fixed and the radius (664.05 km to Global; 403.14 km to Basin and 486.706 km to FEOW) that minimized spatial self-correlation was chosen (Figure 1). Ecoregions were considered as defined by Abell et al. (2008).

A way to quantify non-stationarity is using local estimate techniques such as the Geographically Weighted Regression – GWR. It calculates all regression coefficients for each point present in a database, contrasting from the Ordinate Least Square – OLS, which calculates the average parameters for the entire database considered in the analysis. The calculation is done by partitioning the data set into subsets, given a connectivity criterion between points (C. Brunsdon, Fotheringham, and Charlton 1998; Chris Brunsdon et al. 1998). A way of quantifying stationarity level is by using local estimate techniques such as Geographically Weighted Regression – GWR, which calculates and adjusts the coefficients of determination for each data point in the database. If the relationship is stationary, the GWR presents the same coefficients throughout the entire geographical extension. Although GWR presents advantages over OLS regression models, it should not be used as an alternative, but as a supplement to OLS (Osborne et al. 2007). While OLS offers an average global estimate of the relationships, GWR shows the peculiarities present in the database, therefore improving the power to predict and explain mechanisms and processes (Osborne et al. 2007).

To quantify spatial autocorrelation, there was considered the W Global matrix (connectivity criterion) and 17 distance classes (each composed by an equal number of sites). For the W Basin and W FEOW matrices, classes that maintained equal distances between the classes' centroids were defined. Afterwards, a GWR was generated for each class (using its respective W matrix as the sites' connectivity criterion) and the Akaike Information Criterion (AIC) was calculated for each model. The Moran's I and AIC distance class values were plotted on a graph, and the classes with the lowest value for the AIC and Moran's I equal or close to zero were selected. This procedure was performed for each W matrix, allowing the selection of three GWR models, one W Global model, one W Basin model, and one W FEOW model (Figure 1). The autocorrelation of each model was evaluated with a Moran's scatterplot. For the best GWR, the global adjustment for the model (r^2) was calculated, the spatial autocorrelation of the residuals was measured, and the variable determination coefficients were specified. The GWR was run on the program Spatial Analysis for Macroecology (SAM (Rangel, Diniz-Filho, and Bini 2010)) using the Gaussian Spatial Weighting Function, all models present the Moran's I value and the Akaike Information Criterion.

Results

For the three matrices, 17 distance classes were defined. In the first distance class, the W Global, W Basin and the W FEOW matrix presented an autocorrelation of 0.459 (Moran's I = 0.459, $p=0.005$; Table 1), 0.495

(Moran's I = 0.495, $p=0.005$; Table 2) and 0.569 (Moran's I = 0.569, $p=0.005$; Table 3), respectively. The Moran's I index considering the W Global matrix presented a positive autocorrelation pattern in the first distance classes, no autocorrelation in the intermediate classes and a negative autocorrelation in the last few classes (Table 1, Figure 2a).

The GWR's considering the distance classes of the: i) W Global matrix displayed a R^2 between 0.095 and 0.677 (Table 2) and a maximum [?]AIC equal to 1,782.488 (Table 2, Figure 2a). Considering the relationship between the Moran's I index and the AIC (Table 2, Figure 2a) a fourth distance class was selected as the optimum radius to investigate the spatial heterogeneity in relationships; ii) W Basin matrix presented R -squared varying from 0.195 to 0.376 (Table 3) and a maximum [?]AIC equal to 119.107 (Table 3, Figure 2b), the fourth distance class was also selected as the optimum radius for the GWR, based on the relationship between Moran's I index and AIC (Table 3, Figure 2b); and iii) When considering the W FEOW matrix (Table 4, Figure 2c), the Moran's I index presented positive autocorrelation for the first distance class and an absence of autocorrelation in classes two to four, reaching negative values in the following classes and a sinusoid behavior in the last few classes (Table 4, Figure 2c). W FEOW matrix distance classes presented a R^2 varying from 0.180 to 0.250 (Table 4) and a maximum [?]AIC equal to 59.112 (Table 4, Figure 2c), the sixth distance class was selected after observing the existing relationship between the Moran's I index and AIC (Table 4, Figure 2c). The three GWR models selected as the optimum model in each connectivity matrix do not present spatial autocorrelation in the selected distance classes (Figure 3).

The comparison between the three best GWR models (according to the relationship of AIC and Moran's I index; Table 4) presented a W Global matrix associated to a radius of 664.053 km as the best way to verify the spatial heterogeneity present in the relationships (Table 5). The GWR of the W Global matrix shows an absence of spatial autocorrelation in all distance classes (Figure 4) as well as presenting a prediction power of 40% ($r^2 = 0.400$; $p = 0.000$) for observed richness (Figure 5a). When we consider each of the hydrographic units separately, most basins show a correlation greater than the global (Amazonian basin, 45.6%, $r^2 = 0.456$, $p = 0.000$, Figure 5b; Tocantins, 59.4%, $r^2 = 0.594$, $p = 0.000$, Figure 5d; Sao Francisco, 72.9%, $r^2 = 0.729$, $p = 0.000$, Figure 5e; east transect of the Atlantic basin, 59.6%, $r^2 = 0.596$, $p < 0.001$, Figure 5f; Parana, 56.8%, $r^2 = 0.568$, $p = 0.000$, Figure 5g; Southeast transect of the Atlantic basin, 87.3%, $r^2 = 0.873$, $p = 0.000$, Figure 5h) except for the North/Northeast transect of the Atlantic basin, which presented a prediction pattern of 21.2% ($r^2 = 0.212$; $p = 0.005$; Figure 5c).

The model revealed an absence of stationarity in the relationships between the ichthyofauna and the tested hypotheses (Water-Energy, Terrestrial Primary Productivity and Climatic Temporal Heterogeneity; Figure 6). The GWR showed that stream ichthyofauna richness was mainly related to annual temperature oscillation (Figure 6a), June's evapotranspiration (Figure 6b) and terrestrial primary productivity (Figure 6c). The average precipitation (Figure 6d), precipitation variation (Figure 6e) and the evapotranspiration of January (Figure 6f) show weak relationships with the richness.

The temperature oscillation-fish richness relationship displayed two gradients: i) from east (positive values) to west (negative values); and ii) from northwest (negative) to southeast (positive; Figure 6a). The June's evapotranspiration also presented a northwest-southeast (positive) gradient, with neutral relationships in the coastal area, Amazonian-Tocantins transition and the northwestern extreme of the Amazonian region (Figure 6b). The terrestrial primary production displayed the inverse gradient of June's evapotranspiration, with positive values in the Amazon basin, north/northeastern transect of the Atlantic region and the Tocantins region, with neutral values in the Parana hydrographic basin, Sao Francisco and Southeast transect of the Atlantic region, and negative values in the east and southeast transect of the Atlantic basin, demonstrating a north-south gradient, where the northern portion (closer to the equator) is more associated to the quantity of water (average annual precipitation; Figure 6c). The precipitation oscillation (Figure 6e) showed positive values in the Amazon basin and the extreme West of the north/northeast transect on the Atlantic basin. January's evapotranspiration (Figure 6f) presented some positive values in the Amazon and the north/northeast transect of the Atlantic basin.

Three regions with distinct characteristics were determined by the analysis: i) the Amazonian region formed

by sites located in the central and the extreme western border of the Amazon basin; ii) the transition one composed by the sites situated in the eastern border of the Amazon basin; and iii) the central region formed by sites from the Tocantins, Sao Francisco and Parana River basin (Figure 6). All regions are organized in a gradient, with the transition region displaying an absence of fish richness-environmental variables relationship (Figure 6). The Amazonian region presented a negative relationship of fish richness with the temperature oscillation (Figure 6a) and June's evapotranspiration (Figure 6b), and a positive one with terrestrial primary productivity (Figure 6c), average precipitation (Figure 6d) and precipitation variation (Figure 6e). The Brazilian central region presented inverse relationship compared with the Amazonian one, that is, a positive relationship of the fish richness with temperature oscillation (Figure 6a) and June's evapotranspiration (Figure 6b) and a negative one with terrestrial primary productivity (Figure 6c). The average precipitation (Figure 6d) presented positive correlation to fish richness in the Tocantins basin and no correlation in the Sao Francisco and Parana basins. The precipitation variation (Figure 6e) did not present any relationship with the fish richness in the Brazilian central region. This suggests that higher fish richness in streams of the Amazonian region is associated to areas that present constant temperature and energy input, with abundant rain homogeneously distributed throughout the year in areas with denser vegetation (greater terrestrial primary productivity). In contrast, for Brazilian central region the greatest fish richness is in areas where temperature and water input are more heterogeneous, with abundant rain and less dense vegetation (less terrestrial primary production).

Discussion

A conspicuous absence of stationarity between fish species richness and the tested hypotheses was determined, but climate was observed to contribute the most to the richness distribution of stream fishes. The water-energy dynamics were the most probable metabolic restriction mechanism acting on the community structuring of stream fishes. Regarding species richness distribution at a macro scale, two characteristics must be considered: i) spatial data autocorrelation and ii) stationarity in fish richness-macroecological variables relationship. Autocorrelation of data modifies both the relationship and the significance of the relationship between the variable of interest and the predictor(s) (BINI et al. 2009). In the present study, the spatial autocorrelation was controlled when the GWR radius that had a Moran's I index close to zero was chosen, isolating the second characteristic (stationarity) and facilitating its analysis.

The absence of stationarity relationship found can be derived from environmental heterogeneity, usually associated to altitude variation that causes climatic anomalies and modifications of local conditions (Kerr and Packer 1997; O'Brien et al. 2000; Rahbek and Graves 2001). Depending on the location and altitude variation, this landscape heterogeneity can increase or decrease diversity. The presence of mountain ranges, like Serra do Mar (southwest) in this study, results in an increased humidity on its windward side and the formation of drier and warmer areas on its leeward side, since the wind and humidity are blocked by the windward side. Local variation of temperature, precipitation and wind regimen influence on microclimate, which consequently change habitat availability and quality. As a result, sites favored by the windward effect can display greater species richness whereas those under the leeward influence could show less species richness, as predicted for all models. The topography gradient was observed as a functional factor structuring fish assemblages in streams of the Tocantins-Araguaia basin, (lower altitudes in the Araguaia (lower) and elevated ones in the Tocantins basin (Carvalho and Tejerina-Garro 2015)). Additionally, geographic heterogeneity increases geographic area (O'Brien, Field, and Whittaker 2000) and allows events of allopatric speciation to occur by interrupting geneflow between populations due to physical discontinuities in the riverbed (waterfalls and dams) or physiochemical changes (pH, temperature (Rahbek and Graves 2001)). An increase of available area favors more individuals and species that can occupy a region. In regions with high elevation, such as Serra do Mar (2,366 m) and Espinhaco (2,072 m), it is common to observe low temperatures and, in lower elevations (near the ocean), higher temperatures. This thermal difference can make species diversity smaller than what was predicted for the region, due to local extinction of species less tolerant to cold weather (Girard et al. 2015; Mas-Marti et al. 2014). This mechanism could occur in regions that have an elevated altitude, such as observed in the Brazilian central region in this study. On the other hand, geographic heterogeneity (quantified by the topography) can create more complex habitats, and allow the coexistence of more species,

than regions with not so conspicuous elevations(Bickford and Laffan 2006).

Regarding the macroecological variables, climate was observed to be what most influences richness distribution of stream fishes. Sixty percent of the diversity gradients had their observed patterns explained by climatic factors, some of them with R-squared close to 90%(Hawkins et al. 2003). In this case, the most important factors for determining species richness are water availability and energy input (Hawkins et al. 2003). The non-stationarity in the relationship between richness and climate was also studied by Hawkins et al.(Hawkins et al. 2003), who observed temperature as more important in high latitudes (colder places) than in low ones (tropical regions). In this study, the variation of temperature was observed as the factor of greatest influence on fish richness, presenting positive relationships in the Brazilian central region and negative in the Amazonian one. The non-stationarity of the relationship between stream fish richness and temperature oscillation can be explained by the climatic heterogeneity of the study area and the climate influence on the taxonomic diversification of the fish. Fish populations found in the Brazilian central region are inserted in a savannah landscape characterized by a tropical climate, with a well-defined dry season and rainfall concentrated in only one period of the year(Marengo and Valverde 2007). This climate type is characterized by seasons with 250 mm or <10 mm of precipitation per month and soil temperature varying between 20 and 40degC(N. B. F. dos Santos, Junior, and Ferreira 2011). Fishes from the Amazonian region are located in areas with equatorial climate, where annual precipitation is 2,000 mm distributed equally throughout the months of the year, presenting an average soil temperature of 27degC varying less than 3degC(S. R. Q. dos Santos et al. 2011). Therefore, fish populations present in savannah areas predominant in the Brazilian central region sampling sites are exposed to a greater range of temperature variation, thus eliminating the occurrence of species with a small thermal range. On the other hand, in Amazonian areas, where the thermal variation is lower, tolerance to changes in temperature should not be a key factor in species selection. This could explain why we observed both tolerant and intolerant species to temperature variation in this region. Consequently, a negative correlation pattern is observed between temperature variation and stream fish richness.

The non-stationary relationship between temperature oscillation and fish richness found in this paper was also observed in snakes (Elapidae) and attributed to historical factors of the group's recent diversification(Braga et al. 2014). The influence of temperature (as well as precipitation) driven diversification in recent taxonomic groups and favoring diversity gradients has ample acceptance in recent literature (Hawkins and Porter 2003b; Rodriguez et al. 2005; e.g.: Hawkins et al. 2003) Two mechanisms, the trophic cascade (greater amount of energy available in the system results in an increase of primary productivity) and the metabolic requirements (different species with different temperature tolerances) are proposed to explain the influence of temperature over the richness gradient(Hawkins et al. 2003).

The results presented here, suggest the relation between the stream fish sampled, the trophic cascade and the metabolic requirements mechanisms. The annual estimate evapotranspiration (AET) in June, which represents the measurement of energy input to the system, is the variable with the second greatest magnitude in determining the observed richness pattern. This variable had a negative relationship with stream fish in the Amazonian region and a positive one in the Brazilian Central region, therefore supporting the idea of physiological restriction. This result strengthens the hypothesis that Amazonian fish have low tolerance to thermal variation, the inverse occurring in fish from the central regions. Additionally, terrestrial primary production predicted fish richness, suggesting the influence of the trophic cascade mechanism. High terrestrial primary productivity is associated with areas that have dense vegetation coverage (England and Rosemond 2004). Forested riparian zones make available large inputs of leaves and terrestrial insects to the instream environment(Meyer et al. 2007), as is the case with the sampled streams (1st and 3rd order). The input of resources from terrestrial vegetation occurs in two ways; i) vertically – leaves, fruits, seeds and plant parts directly falling into the streams; and ii) horizontally – lixiviation of these resources from adjacent areas into the waterbody during the rainy season and/or pulses of inundation(Junk W., Bayley E.P. 1989; Junk and Wantzen 2004). With the entry of allochthonous resources, there is an increased resource availability for primary consumers, thus supporting a richer and more abundant food web.

A particularity of terrestrial primary production observed in this study is its negative effect on fish richness. It suggests that the metabolic restriction mechanism is more important than the trophic cascade mechanism. Organisms in this region, including aquatic ones, are exposed to a greater thermal amplitude (Marengo and Valverde 2007), which, together with increased terrestrial primary productivity, limits species richness. This effect possibly occurs due to increased surface shading of the streams' main channel caused by dense riparian vegetation, since a greater primary productivity is related to areas with denser vegetation (England and Rosemond 2004). The dense vegetation stabilizes local microclimate (Monadjem and Reside 2008; Vieira, Dias-Silva, and Pacifico 2013) reducing climatic heterogeneity (cold water) and consequently species richness, possibly due to local extinction of fishes that had a higher optimum temperature.

The Water-Energy hypothesis is the main predictor of species richness considering the physiological mechanism². This hypothesis predicts a positive relationship between species richness and water quantity in lower latitudes and energy in places of higher latitudes². This relationship was observed in the present study for fish richness in Brazilian streams, where portions located close to the equator (Amazonian region) had a positive relationship to water quantity (average annual precipitation) and negative to energy input (AET in June). Portions with higher latitudes (Brazilian Central region) had a positive relationship with fish richness, while water had no relationship. The tradeoff between water and energy and diversity seems to be more dependent on water scarcity than energy restriction. Hawkins et al.² found that annual precipitation is the variable that determines diversity patterns in birds from the Australian continent, challenging what was expected by the literature, since the region is in an area of high latitude. In another study, Kessler (Kessler 2001) found that pteridophyte richness was a function of precipitation. This relationship was observed in Andean regions, where the expected would be energy (temperature, AET) acting as the limiting factor². These two relationships demonstrate that geographic and climatic heterogeneity generate non-stationary relationships, supporting the hypothesis stated in this paper, that is, the metabolic mechanism acts in a more deterministic way than the food web mechanism, although both are not mutually exclusive².

In conclusion, the diversity pattern of fishes in streams is a function of climatic variables and terrestrial primary production, where both the Water-Energy dynamic and metabolic restriction mechanism are more evident. The metabolic restriction mechanism divides Brazil in two regions: i) Amazonian, with a more stable climate and populations with low tolerance to thermal variation; and ii) Central, with greater temperature amplitude and populations more resistant to thermal variation.

Data accessibility statement

Available in the Title Page.

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Table 1 – Distribution of sampled streams by biome, Brazilian hydrographic region and freshwater Ecoregion (FEOW; Abell et al. 2008).

| Biome | Hydrographic region | FEOW | N |
|-----------------|-----------------------------------|---|-----|
| Amazonia | Amazonian | Amazonian estuary and costal drainages | 27 |
| | | Guiana Amazonian Shield | 7 |
| | | Amazonian lowlands | 138 |
| | | Madeira Brazilian Shield | 21 |
| | | Rio Negro | 70 |
| | | Tapajós Juruena | 26 |
| | | Xingu | 7 |
| Caatinga | Atlantic North/Northeast transect | Amazonian estuary and costal drainages | 17 |
| | Atlantic North/Northeast transect | Northeast Caatinga and costal drainages | 17 |
| | | São Francisco | 1 |
| Cerrado | São Francisco | São Francisco | 1 |
| | Paraná | Paraguay | 6 |
| | | Tocantins-Araguaia | 2 |
| | | Upper Paraná | 100 |
| | São Francisco | São Francisco | 26 |
| | Tocantins | Tocantins-Araguaia | 54 |
| Atlantic Forest | Atlantic East Transect | Upper Paraná | 2 |
| | | Fluminense | 15 |
| | Atlantic Southeast Transect | Paraíba do Sul | 6 |
| | | Laguna dos Patos | 5 |
| | | Ribeira de Iguape | 11 |
| | Paraná | Paraíba do Sul | 1 |
| | | Ribeira de Iguape | 6 |
| | Upper Paraná | 87 | |
| Total | | | 653 |

Table 2 – Spatial autocorrelation and GWR values considering the Global connectivity (W Global) matrix. Values in bold indicate the best model determined by the Akaike information criterion – AIC.

| Spatial structure | Spatial structure | Spatial structure | Spatial structure | Spatial structure | Spatial structure | Spatial structure |
|-------------------|-------------------|---------------------|-------------------|-------------------|-------------------|-------------------|
| Classes | Count | Centroid Degrees | Centroid Km | Moran's I | p | I (max) |
| 1 | 25044 | 0.599 | 66.561 | 0.459 | 0.005 | 1.138 |
| 2 | 25042 | 2.330 | 258.910 | -0.008 | 0.053 | 0.689 |
| 3 | 25040 | 4.275 | 475.038 | 0.220 | 0.005 | 0.891 |
| 4 | 25042 | 5.976 | 664.053 | -0.017 | 0.011 | 1.050 |
| 5 | 25044 | 7.368 | 818.732 | 0.190 | 0.005 | 0.859 |
| 6 | 25046 | 8.386 | 931.852 | 0.026 | 0.010 | 1.221 |
| 7 | 25040 | 9.444 | 1049.417 | -0.047 | 0.005 | 1.431 |
| 8 | 25046 | 11.010 | 1223.431 | 0.031 | 0.005 | 0.638 |
| 9 | 25042 | 13.073 | 1452.672 | 0.113 | 0.005 | 0.654 |
| 10 | 25036 | 14.884 | 1653.910 | -0.114 | 0.005 | 0.701 |
| 11 | 25042 | 16.414 | 1823.924 | -0.090 | 0.005 | 0.577 |
| 12 | 25042 | 17.771 | 1974.714 | -0.036 | 0.005 | 0.361 |
| 13 | 25044 | 19.364 | 2151.728 | -0.027 | 0.005 | 0.658 |
| 14 | 25042 | 20.994 | 2332.853 | -0.265 | 0.005 | 0.800 |
| 15 | 25038 | 22.416 | 2490.866 | -0.140 | 0.005 | 0.593 |
| 16 | 25042 | 24.124 | 2680.659 | -0.095 | 0.005 | 0.531 |
| 17 | 25044 | 29.731 | 3303.709 | -0.227 | 0.005 | 1.178 |

Table 3 – Spatial autocorrelation and GWR values considering the Basin connectivity (W Basin) matrix. Values in bold indicate the best model determined by the Akaike information criterion – AIC.

| Spatial structure | Spatial structure | Spatial structure | Spatial structure | Spatial structure | Spatial structure | Spatial structure |
|-------------------|-------------------|---------------------|-------------------|-------------------|-------------------|-------------------|
| Classes | Count | Centroid Degrees | Centroid Km | Moran's I | p | I (max) |
| 1 | 19134 | 0.518 | 57.560 | 0.495 | 0.005 | 1.135 |
| 2 | 9282 | 1.555 | 172.792 | 0.007 | 0.568 | 0.432 |
| 3 | 6450 | 2.592 | 288.023 | 0.067 | 0.005 | 0.954 |
| 4 | 10778 | 3.628 | 403.143 | 0.128 | 0.005 | 1.073 |
| 5 | 7618 | 4.665 | 518.375 | 0.173 | 0.005 | 1.360 |
| 6 | 12698 | 5.702 | 633.606 | 0.019 | 0.095 | 1.654 |
| 7 | 11982 | 6.739 | 748.838 | 0.144 | 0.005 | 0.967 |
| 8 | 19400 | 7.775 | 863.958 | 0.128 | 0.005 | 1.091 |
| 9 | 13806 | 8.812 | 979.189 | -0.045 | 0.005 | 1.558 |
| 10 | 11400 | 9.849 | 1094.421 | 0.167 | 0.005 | 2.013 |
| 11 | 3462 | 10.885 | 1209.541 | 0.410 | 0.005 | 2.310 |
| 12 | 1342 | 11.922 | 1324.773 | 0.096 | 0.025 | 2.152 |
| 13 | 2548 | 12.959 | 1440.004 | 0.451 | 0.005 | 1.755 |
| 14 | 1682 | 13.996 | 1555.236 | 0.566 | 0.005 | 4.701 |
| 15 | 874 | 15.032 | 1670.356 | 0.647 | 0.005 | 3.786 |
| 16 | 206 | 16.069 | 1785.587 | 0.036 | 0.633 | 0.387 |
| 17 | 590 | 17.106 | 1900.819 | 0.391 | 0.005 | 3.447 |

Table 4 – Spatial autocorrelation and GWR values considering the Ecoregion connectivity (W FEOW)

matrix. Values in bold indicate the best model determined by the Akaike information criterion – AIC.

| Spatial structure | Spatial structure | Spatial structure | Spatial structure | Spatial structure | Spatial structure | Spatial structure |
|-------------------|-------------------|---------------------|-------------------|-------------------|-------------------|-------------------|
| Classes | Count | Centroid Degrees | Centroid Km | Moran's I | p | I (max) |
| 1 | 15942 | 0.398 | 44.226 | 0.569 | 0.005 | 1.351 |
| 2 | 4568 | 1.194 | 132.677 | 0.103 | 0.005 | 0.841 |
| 3 | 4146 | 1.991 | 221.240 | 0.079 | 0.010 | 1.116 |
| 4 | 2532 | 2.787 | 309.691 | 0.015 | 0.533 | 1.568 |
| 5 | 4912 | 3.583 | 398.143 | 0.127 | 0.005 | 1.807 |
| 6 | 2512 | 4.380 | 486.706 | 0.024 | 0.357 | 2.083 |
| 7 | 3602 | 5.176 | 575.157 | -0.256 | 0.005 | 2.614 |
| 8 | 3246 | 5.972 | 663.609 | -0.261 | 0.005 | 3.495 |
| 9 | 2138 | 6.769 | 752.171 | 0.090 | 0.005 | 3.926 |
| 10 | 7150 | 7.565 | 840.623 | 0.466 | 0.005 | 1.811 |
| 11 | 5276 | 8.361 | 929.074 | 0.067 | 0.010 | 3.192 |
| 12 | 4618 | 9.157 | 1017.526 | -0.291 | 0.005 | 3.483 |
| 13 | 4804 | 9.954 | 1106.088 | 0.210 | 0.005 | 3.858 |
| 14 | 410 | 10.750 | 1194.540 | -0.371 | 0.005 | 10.667 |
| 15 | 450 | 11.546 | 1282.992 | -0.094 | 0.136 | 1.143 |
| 16 | 86 | 12.343 | 1371.554 | 0.013 | 0.915 | 2.418 |
| 17 | 302 | 13.139 | 1460.006 | -0.116 | 0.111 | 4.144 |

Table 5 – Results of spatial autocorrelation and GWR between the three connectivity models used. Values in bold indicate the best model determined by the Akaike information criterion – AIC.

| W Model | Spatial structure | Spatial structure | Spatial structure | Spatial structure | Spatial structure | Spatial structure |
|---------------|-------------------|-------------------|---------------------|-------------------|-------------------|-------------------|
| | Classes | Count | Centroid Degrees | Centroid km | Moran's I | p |
| Global | 4 | 25042 | 5.976 | 664.053 | -0.017 | 0.011 |
| Basin | 4 | 10778 | 3.628 | 403.143 | 0.128 | 0.005 |
| FEOW | 6 | 2512 | 4.380 | 486.706 | 0.024 | 0.357 |

Figure 1 – Flowchart of procedures used for selecting the best Geographically Weighted Regression (GWR) model. W Global - connectivity between sampling sites defined as Euclidian distance between all sites; W Basin - connectivity between sampling sites defined as Euclidian distance between all sites present in a same hydrographic basin and W FEOW - connectivity between sampling sites defined as Euclidian distance between all sites present in the same ecoregion. AIC - Akaike Information Criterion.

Figure 2 – Graph of the AIC and spatial autocorrelation by distance class for the a) Global, b) Basin and c) FEOW matrix.

Figure 3 – Moran scatterplot for the a) Global, b) Basin (b) and c) FEOW matrix.

Figure 4 – Autocorrelation values of fish richness and GWR residuals using the global connectivity (W Global) matrix.

Figure 5 – Global adjustment of the GWR model done using a W Global matrix considering a) total, b) Amazonian, c) Atlantic North/Northeast transect, d) Tocantins, e) São Francisco, f) Atlantic east transect, g) Paraná and h) Atlantic southeast transect data.

Figure 6 – Spatialization of the GWR regression coefficients and classification of sites according to the hydrographic basin. a) Annual Temperature Variation, b) Evapotranspiration in June, c) Terrestrial Primary Production, d) Average Annual Precipitation, e) Annual Precipitation Variation and f) Evapotranspiration in January.

Data accessibility statement

The database and the macroecological variables used for the analyses were the same considered in Vieira et al (Vieira et al. 2018) and can be accessed by <https://doi.org/10.1371/journal.pone.0204114.s005>

Competing Interests Statement

There is no conflict of interest.

Author contributions

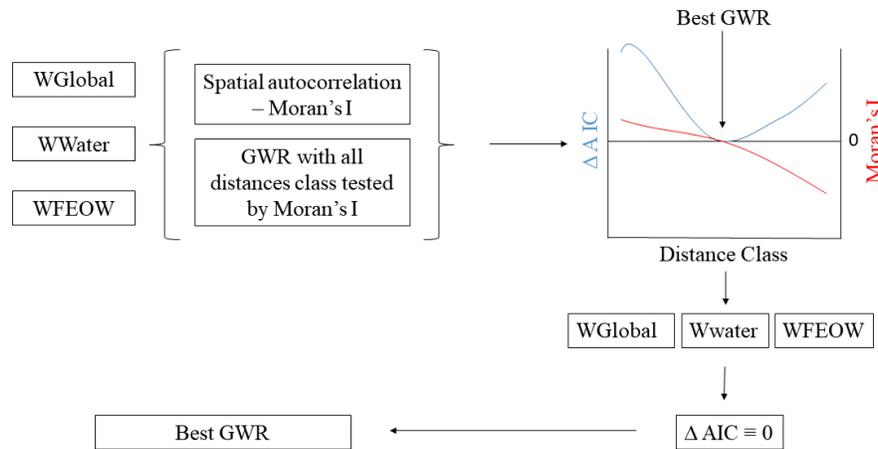
Thiago Bernardi Vieira Formal analysis-Lead, Writing-original draft-Lead Paulo De Marco Supervision-Lead

All of others authors

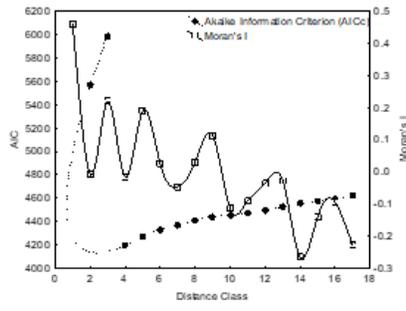
Writing-review & editing-Equal

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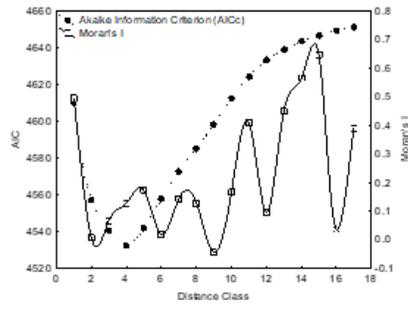
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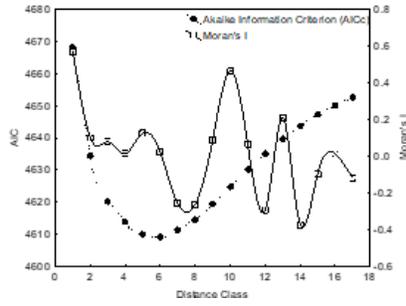
a)



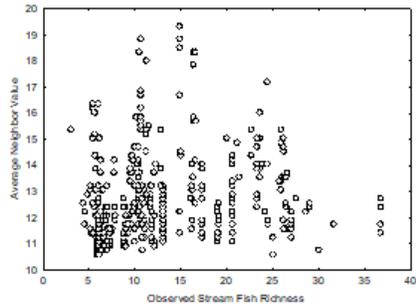
b)



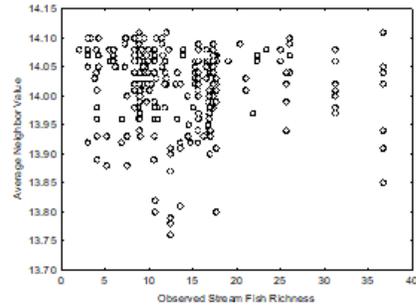
c)



a)



b)



c)

