



Spatial non-stationarity in the distribution of fish species richness of tropical streams

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Abstract

Diversity gradients are observed for various groups of organisms. For fishes in streams, the water-energy, productivity, and temporal heterogeneity hypotheses can explain richness patterns. The relationship between species diversity and the variables that represent these hypotheses is generally linear and stationary, that is, the effect of each of those variables is constant throughout a geographically defined area. But the assumption of spatial stationarity has not yet been tested on a great number of diversity gradients. Therefore, we aimed to quantify the spatial stationarity in the relationships between fish species richness in small stream (653 streams) located throughout Brazil, and the water-energy, productivity, and temporal heterogeneity hypotheses using a geographically weighted regression—GWR. There was a conspicuous absence of spatial stationarity in fish species richness. Furthermore, water-energy dynamics represented a possible metabolic restriction acting on the community structuring of fish species richness in streams. This mechanism separated the fish fauna into two regions: (i) The Amazonian region, characterized by a stable climate and populations that are less resistant to climatic variation; and (ii) The central region, featured by greater ranges of temperature and fish populations that are resistant to climatic variation.

Keywords Climatic temporal heterogeneity · Freshwater ecoregions · GWR · Primary productivity · Water-energy

Introduction

Many groups of organisms exhibit a diversity gradient where the maximum species richness occurs in equatorial regions, and the minimum in polar ones (Hawkins et al., 2003; Willig et al., 2003). From an ecological point of view, this gradient seems to be explained by the energetic, water-energy, altitude, climatic heterogeneity, primary productivity, and metabolic hypotheses (Colwell & Lees, 2000; Hawkins & Porter, 2003a; Wright, 1983). The water-energy hypothesis has the greatest causal effect on richness distributions (Hawkins et al., 2003). It predicts species richness as a product of evapotranspiration and the amount of water available

in a given locality (O'Brien & Road, 1998). More recently, speciation and/or extinction rates have recently received the most attention (Gaston, 2000) and some studies point out to higher speciation rates at low latitudes, but higher rates of recent speciation at high latitudes (Brown, 2014; Fine, 2015; Hanly et al., 2017; Mittelbach et al., 2007). However, estimating and measuring the variation in speciation and extinction rates from phylogenetic data is still a great challenge (Hanly et al., 2017; Morlon, 2014; Rabosky et al., 2015), despite newly developed methods (Hanly et al., 2017).

In most studies, the relationship between species richness and the variables that represent each of the hypotheses mentioned is considered linear or stationary (Angermeier & Schlosser, 1989; Tedesco et al., 2005; Wylie & Currie, 1993). Stationary relationships, in the view of ecology, are characterized by an equal relationship throughout the entirety of a study area (Osborne et al., 2007). In general,

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ecological studies consider solely an ordinary least square (OLS) analysis, called the global model in this paper, including all the points present in a dataset. In studies where the goals include the study of stationarity (like this paper), several models, called local models, are performed. Local models are obtained from a subgroup of data points, where the number of points is defined by the spatial bandwidth. In this way, if stationarity is present in the dataset, all local models would show the same parameters (linear and angular coefficients) and adjustment (R^2) along the whole geographic extension of the analyzed relationship. In fact, this view of stationarity is an assumption for the application of global models (Zar, 2010). In many cases, this assumption is not tested in diversity gradients (Cassemiro et al., 2007; Foody, 2004), consequently producing imprecise or non-significant (global) models (Foody, 2004).

An example of a non-stationary relationship is assumed by the water-energy hypothesis where the amount of water available in the system is the limiting factor for diversity in lower latitudes, whereas the total amount of energy (expressed by the evapotranspiration) is what determines it in higher latitudes (Eiserhardt et al., 2011; Gaston, 2000; Hawkins & Porter, 2003b). This occurs because areas of low latitudes suffer little influence from the Earth's precession, since they are located near the equator. Consequently, the energy input (from the Sun) occurs uniformly throughout the year in those latitudes, making water the limiting factor of diversity. On the other hand, areas located at high latitudes suffer greater influence from the Earth's precession, thus they experience periods of greater or smaller amounts of energy input throughout the year.

Non-stationarity is the main cause of failed attempts to establish the above-mentioned relationships (Osborne et al., 2007) since the variation of the regression coefficients is ignored and the relationships are described by their average along with the geographic space (Foody, 2004). Environmental heterogeneity at spatial or temporal scales is the main cause of non-stationarity in each of the above-mentioned hypotheses (Bickford & Laffan, 2006; O'Brien & Road, 1998). One of the causes of heterogeneity is geographic variation in topography and connectivity. Variations in the altitudinal gradient could lead to changes in environmental conditions, increasing habitat diversity and allowing for the coexistence of a greater number of species (Bickford & Laffan, 2006). Additionally, geographic variation (mountains, canyons, and valleys) can isolate or connect populations, promoting or preventing speciation.

It has been shown that the diversity distribution of tropical stream fishes is a product of the interaction of three hypotheses: (i) water-energy; (ii) terrestrial primary productivity and (iii) climatic temporal heterogeneity (See Table S1 to definitions and variables included in all hypothesis) (Vieira et al., 2018). Despite this, the Brazilian geographical area

presents high morphologic and climatic heterogeneity, harboring regions with both high temperatures and intense rainfall (north/northeast regions), regions with low temperatures and intense rainfall (south and part of the southeast regions), and regions with high temperatures and long dry periods (midwest and northeast regions (Marengo & Valverde, 2007)). Therefore, our aim here is to identify and quantify the spatial stationarity of the relationship between stream fish richness and water-energy, terrestrial primary productivity, and climatic temporal heterogeneity. Additionally, we made a comparison among three ways to quantify the connectivity among streams. We expected that grouping streams by hydrological basins would provide the best geographic structure for explaining stream connectivity because basin divides represent real barriers for fish dispersal. We expected non-stationary relationships because the Brazilian territory is a continental country with regions close to the equator (where water is more important) and regions far from it (where energy is more important than water).

Material and methods

Database

The database harbors data obtained from field surveys carried out by the authors following the criteria: (i) survey carried out in first- to third-order streams; (ii) georeferenced streams; (iii) sampling of ichthyofauna carried out by electric fishing, trawl net, and/or hand net; (iv) a minimum of a 50-m stretch of stream sampled by site; (v) a single sample site by stream; (vi) species identified by experienced researchers according to the taxonomic literature; (vii) list of species per sampled site; and (viii) surveys carried out in locations with the lowest possible human impact. Additionally, in July 2014 we carried out literature searches on scientific studies published in journals, monographs, and dissertations in the CAPES journals website (<https://goo.gl/D2gE54>) using the keywords 'peixe', 'fish', 'riacho', 'stream', 'lista', and 'checklist'. In all cases, only the studies that met the criteria previously determined were included in the database. At the end of the search, 18 studies addressing 89 streams were included in the database (S1 Table). The streams from the literature search were compiled in a database with 564 streams, totaling 653 streams (Fig. 1 and S2 Table). Fish species richness was determined for each of the streams in the database.

Macroecological variables

The macroecological variables used to test our hypotheses were evapotranspiration in January (AETJan) and June (AETJune), with both months representing, respectively, the

Fig. 1 The spatial location of the streams sampled (black dots) in Brazil, South America



warmest and coldest periods of the year; primary productivity (PP); annual temperature variation (TempVar); annual rainfall variation (ARV). AET and PP are items of MODIS (Moderate Resolution Imaging Spectroradiometer) satellite images with information available from 2000 to 2012 on the website of the Laboratory for Image Processing and Geoprocessing of the Federal University of Goiás—LAPIG UFG (<https://goo.gl/FliWvy>). We used the average rates of these variables in the analyses and obtained the spatialized information (raster archives) of AET (available monthly) from January and June, and PP (available annually), both from 2000 to 2012. The raster archives of the different years were added and divided by 12, composing a new raster that represents the 12-year average value of the variable. This procedure was repeated for AETJan, AETJune, and PP data. TempVar and ARV were taken from the IPCC climate scenario A1, available at WORLDCLIM (<http://www.worldclim.org>). These variables are a result of interpolation models built with data collected from 1950 to 2000 by the Global Historical Climate Network Dataset (GHCN). Since the resolution (pixel size) of all the raster archives were originally

1×1 km, they were adjusted to 15×15 km. This way, the information for each site was an average value, product of 225 pixels, and not just the value of one pixel (See Vieira et al., 2018).

Statistical analyses

The quantification of stationarity in the relationship between fish richness and macroecological variables was done using a geographically weighted regression (GWR). The GWR analysis establishes local estimates of regression coefficients using subsets of the database considered and defined according to a Spatial Weighting Function (Austin, 2007; Wheeler, 2014). This function attributes a weight— W (or importance) to each site, which is later used to estimate the coefficient of a focal point, adding a few near points to perform the regression, this procedure depends on the bandwidth, which is what defines which points are considered near or far. Thus, the GWR performs as many regressions as the number of sites (streams) in the database and the number of sites

included in each of the analyses can be different. Sites that are close to each other (given a connectivity criterion) will have a greater impact than sites that are further away from the focal point, considering the distance threshold defined by the chosen bandwidth (Wheeler, 2014). In this study, the connectivity between sampling sites was defined in three ways: (i) The Euclidian distance between all sites; (ii) The Euclidian distance between all sites (W Global) present in the same hydrographic basin (W Basin), where the sites located in different basins have no connectivity; and (iii) The Euclidian distance between all sites present in the same ecoregion (W FEOW), where the sites in different ecoregions have no connectivity. 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. In fact, the ecoregions are a subset of the hydrographic basins and were defined by the historical/phylogenetic relationship among the species occurring in the geographic unit (Abell et al., 2008). The GWR splits the data set into subsets, given a connectivity criterion among points (Brunsdon et al., 1998a, 1998b). If the relationship is stationary, the GWR results in the same coefficients throughout the entire geographical extension. Although the GWR has advantages over OLS regression models, it should not be used as an alternative, but as a complement to OLS (Osborne et al., 2007). While OLS offers an average global estimate of the relationships, the GWR shows the idiosyncrasies that are present in the database, therefore improving the power to predict and explain mechanisms and processes (Osborne et al., 2007).

We used the W Global matrix (connectivity criterion) and 17 distance classes (each composed by an equal number of sites) to quantify spatial autocorrelation. For the W Basin and W FEOW matrices, classes that maintained equal distances between the classes' centroids were defined. Afterward, a GWR was generated for each of those classes (using its respective W matrix as the sites' connectivity criterion) and we calculated the Akaike information criterion (AIC) for each model. The Moran's I and AIC distance class values were plotted on a graph where the classes with the lowest value of AIC and Moran's I equal or close to zero were selected. This procedure was performed for each of the W matrices allowing for the selection of three GWR models, one W Global model, one W Basin model, and one W FEOW model. The autocorrelation of each model was evaluated with a Moran 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 regression coefficient for each variable was spatialized. We performed the GWR using the Gaussian Spatial Weighting Function and calculated Moran's I and the Akaike information criterion for all models on the spatial analysis for macroecology software (SAM(Rangel et al., 2010)).

Results

Spatial autocorrelation

We defined 17 distance classes for the three matrices. In the first distance class, the W Global, the W Basin and the W FEOW matrices presented an autocorrelation of 0.459 (Moran's $I=0.459$, $p=0.005$; Table S5), 0.495 (Moran's $I=0.495$, $p=0.005$; Table S6) and 0.569 (Moran's $I=0.569$, $p=0.005$; Table S7), respectively. The Moran's I index of the W Global matrix had 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 S5, Figure S1).

GWR results

The GWR performed on the W Global matrix displayed R^2 values varying from 0.095 to 0.677 (Table S5, Figure S1a) and a maximum AIC equal to 5,981,448 (Table S5, Figure S1a). When we considered the relationship between the Moran's I index and the AIC (Table S5, Figure S1a), a fourth distance class was selected as the optimum radius to investigate the spatial heterogeneity of the relationships. The GWR performed on the W Basin matrix displayed R^2 values varying from 0.195 to 0.376 (Table S6, Figure S1a) and a maximum AIC of 4,651,543 (Table S6, Figure S1b). In this case, the fourth distance class was also selected as the optimum radius for the GWR, according to the relationship between the Moran's I index and the AIC (Table S6, Figure S1b). When we considered the GWR performed on the W FEOW matrix (Table S7, Figure S1c), the Moran's I index exhibited 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 S7, Figure S1c). The distance classes had R^2 values varying from 0.180 to 0.250 (Table S7, Figure S1c) and a maximum AIC equal to 4,668.212 (Table S7, Figure S1c), the sixth distance class was selected after observing the existing relationship between the Moran's I index and the AIC (Table S7, Figure S1c). The three GWR models selected as the optimum model in each of the connectivity matrices did not exhibit spatial autocorrelation in the selected distance classes (Figure S2).

Best GWR (and connectivity matrix) model used to understand stationarity

The comparison between the three best GWR models (according to the relationship of the AIC and the Moran's I index; Table 1) had a W Global matrix associated to a radius

of 664.053 km as the best way to assess the spatial heterogeneity present in the relationships (Table 1). The GWR of the W Global matrix showed absence of spatial autocorrelation, Moran's index of residuals (dotted line) equal to or close to zero, in all distance classes (Figure S3) as well as presented a prediction power of 40% ($r^2 = 0.400$; $p < 0.001$) for observed richness (Figure S4a). When we considered each of the hydrographic units separately, most basins showed a correlation greater than the global one (Amazonian basin, 45.6%, $r^2 = 0.456$, $p < 0.001$, Figure S4b; Tocantins, 59.4%, $r^2 = 0.594$, $p < 0.001$, Figure S4d; São Francisco, 72.9%, $r^2 = 0.729$, $p < 0.001$, Figure S4e; east transect of the Atlantic basin, 59.6%, $r^2 = 0.596$, $p < 0.001$, Figure S4f; Paraná, 56.8%, $r^2 = 0.568$, $p < 0.001$, Figure S4g; Southeast transect of the Atlantic basin, 87.3%, ($r^2 = 0.873$, $p < 0.001$, Figure S4h), except for the North/Northeast transect of the Atlantic basin, which exhibited a prediction power of 21.2% ($r^2 = 0.212$; $p = 0.005$; Figure S4c).

Stationarity in richness distributions

The model (W Global matrix associated to a radius of 664.053 km) revealed an absence of stationarity in the relationships between the ichthyofauna and the tested hypotheses (water-energy, terrestrial primary productivity, and climatic temporal heterogeneity; Fig. 2). The GWR showed that stream ichthyofauna richness was mainly related to the annual temperature oscillation (Fig. 2a), evapotranspiration in June (Fig. 2b), and terrestrial primary productivity (Fig. 2c). The average precipitation (Fig. 2d), precipitation variation (Fig. 2e), and evapotranspiration in January (Fig. 2f) showed weak correlations with richness.

Gradients and patterns of non-stationarity

The relationship between temperature oscillation and fish richness exhibited two gradients: (i) from east (positive values) to west (negative values); and (ii) from northwest (negative) to southeast (positive; Fig. 2a). The evapotranspiration in June also exhibited a northwest-southeast (positive) gradient, with no significant correlation in the coastal area,

in the Amazonian-Tocantins transition, and in the northwestern extreme of the Amazonian region (Fig. 2b). The terrestrial primary production exhibited an inverse gradient of evapotranspiration in June, with positive values in both the Amazon basin and the north/northeastern transect from the Atlantic to the Tocantins region, with no significant correlation values in the Paraná hydrographic basin, São Francisco, and Southeast transect of the Atlantic region. It also exhibited negative values in the east and southeast transect of the Atlantic basin, resulting in a north-to-south gradient, where the northern portion (closer to the equator) is more associated with average annual precipitation (Fig. 2c). The oscillation in precipitation (Fig. 2e) exhibited positive values in the Amazon basin and the extreme west of the north/northeast transect of the Atlantic basin. The evapotranspiration in January (Fig. 2f) exhibited some positive values in the south of the Amazon basin and the north of the north/northeast transect of the Atlantic basin.

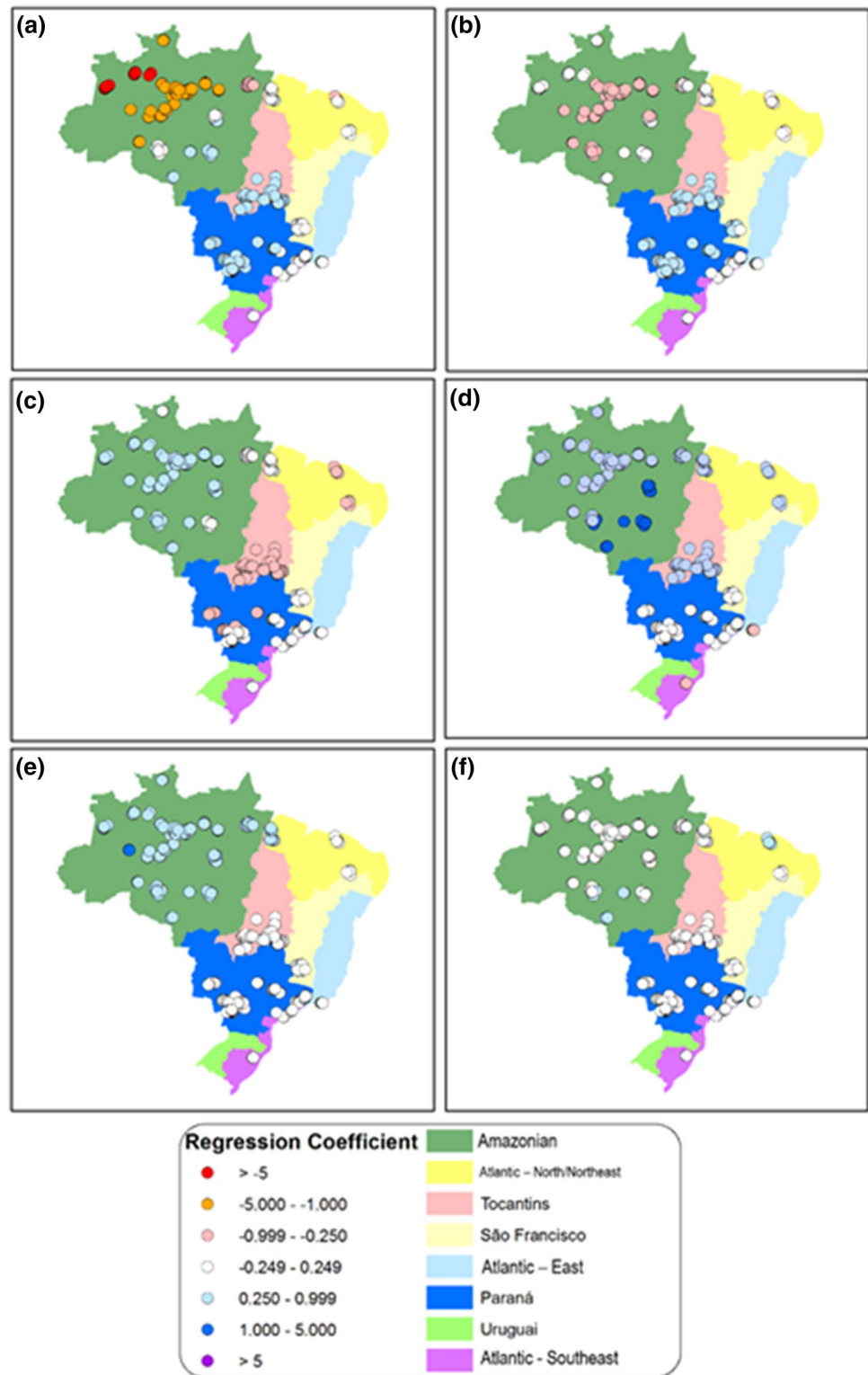
Three regions with distinct characteristics were identified by the analysis: (i) the Amazonian region, composed of sites located in the central and the extreme western border of the Amazon basin; (ii) the transition region, composed of the sites situated in the eastern border of the Amazon basin; and (iii) the central region, composed of sites from the Tocantins, São Francisco, and Paraná River basin (Fig. 2). All regions were organized in a gradient with the transition region exhibiting no relationship between fish richness and environmental variables (Fig. 2). The Amazonian region presented a negative relationship of temperature oscillation (Fig. 2a) and evapotranspiration in June with fish richness (Fig. 2b), and a positive one of terrestrial primary productivity (Fig. 2c), average precipitation (Fig. 2d), and precipitation variation (Fig. 2e) also with fish richness. The Brazilian central region exhibited an inverse relationship when compared with the Amazonian one, that is, a positive relationship of fish richness with temperature oscillation (Fig. 2a) and evapotranspiration in June (Fig. 2b). It also exhibited a negative relationship between terrestrial primary productivity (Fig. 2c) and fish richness. The average precipitation (Fig. 2d) was positively correlated with fish richness in the Tocantins basin

Table 1 Results of the spatial autocorrelation analysis and the GWR between the three connectivity models used

W Model	Spatial structure				GWR								
	Classes	Count	Centroid		Moran's I	p	I (max)	I/I(max)	AIC	Δ AIC	r ²	F (r ²)	p (r ²)
Degrees	km												
Global	4	25,042	5.976	664.053	-0.017	0.011	1.050	-0.016	4199.044	0.000	0.677	17.888	0.000
Basin	4	10,778	3.628	403.143	0.128	0.005	1.073	0.119	4532.436	333.392	0.376	35.314	0.000
FEOW	6	2512	4.380	486.706	0.024	0.357	2.083	0.012	4609.100	410.056	0.250	31.404	<0.001

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

Fig. 2 Spatialization of the Geographically Weighted Regression (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) Variation in Annual Precipitation, and f) Evapotranspiration in January



but not in the São Francisco and Paraná basins. The variation in precipitation (Fig. 2e) did not exhibit any relationship with fish richness in the Brazilian central region. The higher fish richness in streams of the Amazonian region is associated with areas that have constant temperature and

energy input, with rain abundant and homogeneously distributed throughout the year in areas with denser vegetation (greater terrestrial primary productivity). In contrast, for the Brazilian central region, the greatest fish richness occurred in areas where temperature and water input are

heterogeneous, with abundant rain and sparse vegetation (lower terrestrial primary production).

Discussion

Non-stationarity in fish richness distribution

The absence of stationarity relationships that we found can be a consequence of environmental heterogeneity, usually associated with altitude variations that cause climatic anomalies and changes in the local conditions (Kerr & Packer, 1997; O'Brien et al., 2000; Rahbek & Graves, 2001). Depending on the location and altitude variation, the landscape heterogeneity can increase or decrease diversity. The presence of mountain ranges, like the Serra do Mar (southwest) in this study, results in an increased humidity in its windward side and the formation of drier and warmer areas on its leeward side due to the blockage of wind and humidity by the windward side. The local variation in temperature, precipitation, and wind influence microclimate, which consequently change habitat availability and quality. As a result, sites favored by the windward effect can have greater species richness whereas those under the leeward influence may have lower richness, as predicted by all of our 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 & Tejerina-Garro, 2015). Additionally, geographic heterogeneity increases geographic area (O'Brien et al., 2000) and allows events of allopatric speciation to occur by interrupting gene flow among populations due to physical discontinuities in the riverbed (waterfalls and dams), or physiochemical changes (pH, temperature (Rahbek & Graves, 2001). An increase in available areas favors the occurrence of more individuals and species in a region. Lower temperatures are common in regions with high elevation, such as the Serra do Mar (2366 m) and Serra do Espinhaço (2072 m), whereas areas of lower elevations (near the ocean) tend to have higher temperatures. This thermal difference can make species diversity lower than what would be predicted for the region due to the local extinction of species that are less tolerant to colder weather conditions (Girard et al., 2015; Mas-Martí et al., 2014). This mechanism can occur in regions that have high altitudes, such as what we observed in the Brazilian central region in this study. On the other hand, geographic heterogeneity (quantified by the topography) can create more complex habitats allowing for the coexistence of more species than regions with not as high altitudes (Bickford & Laffan, 2006).

Patterns and probable processes explaining non-stationarity

Regarding the macroecological variables, the climate was found to be the most important factor influencing the distribution of stream fish richness. Sixty percent of the diversity gradients examined in a previous study had their observed patterns explained by climatic factors, some of them with R-squared values 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. (2003), who found that temperature is more important in high latitudes (colder places) than in low ones (tropical regions). In this study, the temperature variation was observed as the factor that had the greatest influence on fish richness, exhibiting positive relationships in the Brazilian central region and negative ones in the Amazonian region. 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 fish. Fish populations found in the Brazilian central region are embedded in a savannah landscape characterized by a tropical climate with a well-defined dry season and rainfall concentrated in only one portion of the year (Marengo & 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 40 °C (Santos et al., 2011a). Fishes from the Amazonian region are located in areas with an equatorial climate, where annual precipitation is of 2,000 mm distributed equally throughout the months of the year, with an average soil temperature of 27 °C varying less than 3 °C (Santos et al., 2011b). Therefore, fish populations that are present in areas of savannah, which are predominant in sampled sites of the Brazilian central region, are exposed to a greater range of temperature variation, thus limiting 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 and species that are and are not tolerant to temperature variation may coexist on this region (Fialho et al., 2008; Joy & Death, 2004; McDermot & Rose, 2000; Murray & Innes, 2009; Pouilly et al., 2006; Yan et al., 2011). Consequently, the variation in the temperature may lead to a negative correlation 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-driven diversification

(as well as precipitation) in recent taxonomic groups favoring diversity gradients has ample acceptance in the recent literature (Hawkins & Porter, 2003b; Hawkins et al., 2003; Rodríguez et al., 2005). Two mechanisms are proposed to explain the influence of temperature on the richness gradient: 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) (Hawkins et al., 2003).

The results presented here suggest that the richness is explained by the trophic cascade and the metabolic requirements mechanisms. The actual estimate of evapotranspiration (AET) in June, which represents the measurement of energy input in the system, is the variable with the second greatest importance in explaining the observed richness patterns. In fact, elevated rate of energy input (sun light) leads to high stream temperatures, such that small streams (1st to 3rd order) tend to be less thermally stable and more susceptible to temperature variation than larger streams. This variable was negatively related to stream fish in the Amazonian region and positively related to it in the Brazilian Central region, therefore supporting the idea of physiological restriction. This result strengthens the idea that Amazonian fish have a low tolerance to thermal variation and the inverse occurs in 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 & Rosemond, 2004). Forested riparian zones provide large inputs of leaves and terrestrial insects into the instream environment (Meyer et al., 2007), as is the case of the sampled streams (1st and 3rd order). Terrestrial resources enter streams in two ways; (i) vertically—when leaves, fruits, seeds, and plant parts directly fall into the streams; and (ii) horizontally—when rainfall or inundation carries plant matter from adjacent areas into streams (Junk W., Bayley E.P., 1989; Junk & Wantzen, 2004). Thus, there is increased resource availability for primary consumers due to the entry of allochthonous resources, which supports a richer and more abundant food web.

A particularity of the 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 one. Organisms in regions that terrestrial primary production had negative effect on richness, including aquatic ones, are exposed to a greater thermal amplitude (Marengo & Valverde, 2007), which, together with increased terrestrial primary productivity, limits species richness. This effect possibly occurs due to the increased surface shading of the streams' main

channel caused by dense riparian vegetation, since greater primary productivity is related to areas with denser vegetation (England & Rosemond, 2004). The dense vegetation stabilizes the local microclimate (Monadjem & Reside, 2008; Vieira et al., 2015) reducing climatic heterogeneity (cold water) and consequently species richness, possibly due to the local extinction of fishes that have a higher optimum temperature.

Macroecological hypotheses and their relationship with non-stationarity

The Water-Energy hypothesis is the main predictor of species richness considering the physiological mechanism (Hawkins et al., 2003). This hypothesis predicts a positive relationship between species richness and water quantity in lower latitudes and energy in higher ones (Hawkins et al., 2003). This relationship was observed in the study for fish richness in Brazilian streams, where streams located close to the equator (lower latitudes and in the Amazonian region) had a positive relationship with water availability (average annual precipitation) and a negative one with energy input (AET in June). Streams with higher latitudes (Brazilian Central region) had a positive relationship between energy input and fish richness, whereas water availability was not related to it. The tradeoff between water, energy, and diversity seems to be more dependent on water scarcity than energy restriction. Hawkins et al. (2003) 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 this region is in an area of high latitude. In another study, Kessler (2001) found that pteridophyte richness was a function of precipitation. This relationship was observed in Andean regions, where energy (temperature, AET) would be expected to act as the limiting factor (Hawkins et al., 2003). 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 they are non-mutually exclusive (Hawkins et al., 2003). In conclusion, the diversity patterns of fishes in streams are a function of climatic variables and terrestrial primary production, where both the water-energy dynamic and the metabolic restriction mechanism play important roles. The metabolic restriction mechanism separates Brazil into two regions: (i) The Amazonian one, with a more stable climate and populations with low tolerance to thermal variation; and (ii) the Central one, with greater temperature amplitude and populations that are more resistant to thermal variation.

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Declarations

Conflict of interest The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.


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