



# Diversity gradients of Neotropical freshwater fish: evidence of multiple underlying factors in human-modified systems

Dayani Bailly<sup>1\*</sup>, Fernanda A. S. Cassemiro<sup>2</sup>, Kirk O. Winemiller<sup>3</sup>, José Alexandre F. Diniz-Filho<sup>4</sup> and Angelo A. Agostinho<sup>1,5</sup>

<sup>1</sup>Programa de Ecologia Aquática, Universidade Estadual de Maringá/NUPELIA, Avenida Colombo, 5790, Maringá PR 87020-900, Brazil, <sup>2</sup>Systema Naturae Consultoria Ambiental, Rua 58, 217, Jardim Goiás, Goiânia GO 74810-250, Brazil, <sup>3</sup>Department of Wildlife and Fisheries Sciences, Texas A&M University, College Station, TX 77843-2258, USA, <sup>4</sup>Departamento de Ecologia, Universidade Federal de Goiás, ICB, CP 131, Goiânia GO 74001-970, Brazil, <sup>5</sup>Departamento de Biologia, Universidade Estadual de Maringá, UEM/NUPELIA, Avenida Colombo, 5790, Maringá PR 87020-900, Brazil

## ABSTRACT

**Aim** Contemporary patterns of species diversity are the result of a hierarchy of natural processes and modern anthropogenic influences. However, studies of these patterns in human-modified systems from a macroecological perspective are lacking. Considering that fish assemblages in reservoirs reflect both long-term evolutionary responses of species and shorter term responses to anthropogenic stressors, we employed a multi-hypothesis approach using different magnitudes of predictors to analyse the processes that drive fish diversity in reservoirs at a broad spatial scale.

**Location** Brazil.

**Methods** We derived species richness from an extensive database of fish inhabiting Neotropical reservoirs, and using multiple regression analysis, we tested seven hypotheses that link species richness to continuous variables associated with regional, local and population components. We analysed the spatial structure using Moran's *I* autocorrelation coefficients and used spatial eigenvector mapping to explicitly account for the spatial component when testing the hypotheses by multiple regressions. Partial regressions were performed to map the relative contributions of the different components in explaining species richness.

**Results** Predictors related to six hypotheses were retained in the best-fit models, and our data supported the species–energy, metabolic, species–area, species–distance from the source and time of habitat alteration hypotheses. However, the predictions of the population abundance hypothesis (PAH) were not supported by the data. The shared effects of the different components explained the greatest proportion of the variation in species richness, indicating that distinct mechanisms related to these alternative hypotheses interact or are not spatially independent.

**Main conclusions** Our findings indicate that the latitudinal diversity gradient typically displayed by freshwater fish is maintained in human-modified habitats, such as reservoirs, and that multiple mechanisms drive fish diversity in reservoirs over large spatial scales. The lack of support for the PAH implies that mechanisms structuring diversity patterns can be influenced by anthropogenic stressors.

## Keywords

abundance, anthropogenic impacts, diversity hypotheses, latitudinal diversity gradient, metabolic theory of ecology, reservoir age, reservoirs, spatial autocorrelation, species richness

\*Correspondence: Dayani Bailly, Programa de Ecologia Aquática, Universidade Estadual de Maringá, Avenida Colombo, 5790, Maringá, PR, CEP: 87020-900, Brazil.  
E-mail: dayanibailly@gmail.com

## INTRODUCTION

Species richness is not distributed equally in space, and perhaps the most pervasive pattern is the global latitudinal gradient that is observed in numerous animal and plant taxa (Brown, 2014). However, when species richness is analysed at smaller spatial scales, divergent patterns often are observed among different ecoregions, habitats and taxa (see Olson *et al.*, 2001; Osborne & Wiley, 1992; Costa *et al.*, 2007). Since the 19th century, numerous hypotheses and models have been proposed to explain patterns of species diversity, and these explanations have recently been synthesized into a more focussed set of testable hypotheses. Most studies explicitly associate alternative hypotheses with measurable characteristics of ecosystems or evolutionary aspects of species and clades (Whittaker *et al.*, 2001; Willig *et al.*, 2003; Ricklefs, 2004; Brown, 2014). Although many different mechanisms have been proposed to explain diversity gradients, most ecologists share the view that the number of species coexisting in ecological communities is the result of a hierarchy of evolutionary and ecological processes operating at local to regional scales (Ricklefs, 2004; Rahbek, 2005). Additionally, it is increasingly apparent that contemporary patterns of species diversity are affected by human activities (Rathert *et al.*, 1999; Williams *et al.*, 2005), and consequently, the underlying mechanisms are difficult to unravel because anthropogenic stressors may have already altered species assemblages (Nogués-Bravo *et al.*, 2008).

Freshwater ecosystems worldwide are particularly vulnerable to anthropogenic impacts (Saunders *et al.*, 2002; Abell *et al.*, 2008). Humans have appropriated more than 50% of the globally available surface freshwater (Jackson *et al.*, 2001; Sabo *et al.*, 2010); pollution and deforestation impact watersheds and aquatic systems, and more than one million dams currently fragment rivers and regulate flows (Nilsson *et al.*, 2005; Poff *et al.*, 2007). By 2030, large reservoirs will affect c. 1.6 million km of currently unregulated rivers (Grill *et al.*, 2015), further altering patterns of freshwater biodiversity. Impoundments modify ecological patterns and processes within, above, and below reservoirs (Agostinho *et al.*, 2008); shifts in community composition result from proliferation of some populations and reduction, or even extirpation, of others (Agostinho *et al.*, 1999). Reservoir age is critical in this scenario, with older reservoirs generally having fewer lotic-adapted fish species than newly formed impoundments (Agostinho *et al.*, 1999, 2008).

Across all major landmasses, the species richness of freshwater fishes decreases with latitude (Oberdorff *et al.*, 1995, 2011) and increases along longitudinal fluvial gradients (Osborne & Lewis, 1992; Ibañez *et al.*, 2009) in response to regional factors. When rivers are impacted by impoundments, the reduction of fish species richness with reservoir ageing (Agostinho *et al.*, 1999, 2007) occurs in response to local factors regardless of latitude or the position of the reservoir along the fluvial gradient. In addition, species richness can be influenced by population factors such as body

size of individuals and population abundance (Isaac *et al.*, 2005). Thus, a comprehensive analysis of the mechanisms underlying species richness in habitats directly influenced by human activities, such as construction of reservoirs, that takes regional-, local- and population-level processes into account would be fundamental to understanding the forces that drive fish diversity gradients.

Fish assemblages in reservoirs reflect both the long-term evolutionary dynamics that create regional native faunas as well as the shorter term responses of local populations to anthropogenic stressors. Therefore, we used a multi-hypothesis approach with different magnitudes of predictors (or components) to analyse characteristics and processes that drive and support fish diversity in reservoirs at broad spatial scales. We used a correlative approach to test seven alternative hypotheses (see Table 1) that link species richness to continuous variables that reflect regional, local and population components. Owing to a positive autocorrelation in regression residuals, the spatial component was also analysed. We then assessed the relative contribution of each component in explaining the variation in fish species richness in reservoirs. The analysis of the population component is a new approach that refines identification of potential processes that drive richness patterns. Most current evidence supporting alternative hypotheses for diversity gradients has been biased towards terrestrial biota (Field *et al.*, 2009) in natural systems, which restricts application of macroecological concepts for conservation of the biodiversity. By examining aquatic biota within human-altered ecosystems, our study addresses this gap and expands our knowledge of species richness gradients.

## MATERIALS AND METHODS

### Biological data sets

Two data sets (see Appendices S1 and S2 in Supporting Information) were used to assess the relationship of fish species richness in Neotropical reservoirs with multiple predictor variables. The reservoirs spanned a broad region between 2° and 29° S and 38° and 55° W, with a cumulative reservoir surface area of c. 23,275 km<sup>2</sup> (Fig. 1). Data set I included 39 reservoirs, and species richness data were obtained from standardized samplings. Fish were captured using gill nets with mesh sizes ranging from 2.4 to 16.0 cm unstretched knot length; exposure time was standardized to 24 h; nets were examined in the morning, afternoon, and night; and nets were installed in the lacustrine region of the reservoirs (see Thornton, 1990). Given that inconsistent sampling effort is a potential cause of spurious results in analyses of species richness (Gotelli & Colwell, 2001), we used data set I to ensure that variation in species richness was not related to differences in the sampling effort.

Because the use of a single survey method at a single location can underestimate the species richness in studies comparing patterns across large spatial scales, we also evaluated

**Table 1** Summary of the hypotheses proposed to explain species richness gradients and variables used to test them in this study.

| Hypothesis   | Features of the explanation  | Representative variables   |
|--|--|--|
| Species–energy hypothesis (S-EH; Wright, 1983; Evans <i>et al.</i> , 2005)*  | Based on a modification of island biogeography theory, the S-EH replaces area by energy and argues that the richness of one trophic level should be determined by the amount of energy available from the lower levels. S-EH predicts a positive relationship between species richness and energy available within the ecosystem with lower latitude regions receiving more solar energy on an annual basis                                    | Terrestrial net primary productivity<br>Precipitation              |
| Metabolic hypothesis (MH; Allen <i>et al.</i> , 2002; Brown <i>et al.</i> , 2004; but see Hawkins <i>et al.</i> , 2007)* | The species richness of ectothermic organisms along latitudinal gradients results from the dependence of individual metabolic rates on temperature. MH takes metabolic activation energy into account to precisely relate the temperature with species richness and predicts that richness should vary linearly with the inverse of temperature with a slope ranging from $-0.6$ to $-0.7$ eV  | Reciprocal temperature   |
| Species–distance from source hypothesis (S-DSH; Osborne & Lewis, 1992)† <sup>a</sup>                                     | S-DSH predicts that new fish species are added faster than headwater species are lost as one moves downstream. Thus, within a watershed, the greater the distance from the headwater source, the greater the species richness  | Distance from the headwater source                                 |
| Species–area hypothesis (S-AH; MacArthur & Wilson, 1967)† <sup>b</sup>   | S-AH constitutes one part of island biogeography theory and predicts that the living space of greater areas should be preponderant to encompass greater number of species. Thus, the greater area, the greater the species richness  | Reservoir area   |
| Time of habitat alteration hypothesis (THAH)† <sup>c</sup>   | Successional changes in the environmental conditions of reservoirs with ageing result in diverse responses in the original fish populations. It is expected that more recent habitats support greater number of species. Thus, the greater the age reservoir, the lower the species richness   | Reservoir age  |
| Size–diversity hypothesis (S-DH, Marzluff & Dial, 1991; Brown, 1995)*  | Species richness is a decreasing function of body size because the speciation rates are assumed to be inversely related to body size. In an interaction with historical hypotheses, which predict that there are more species in the tropics due to greater climatic stability (Whittaker, 1977; Tedesco <i>et al.</i> , 2005), a greater number of small-bodied species would be expected in lower latitude regions due to greater speciation | Standard length of individuals                                     |
| Population abundance hypothesis (PAH) or more-individuals hypothesis (MIH; Srivastava & Lawton, 1998)*                   | This hypothesis is related to S-EH and predicts that more productive areas support larger populations. It is expected the increase in number of species with population abundance due to reduced extinction risk of larger populations, which, in turn, results in the greater accumulation of species over geologic time-scales   | Terrestrial net primary productivity<br>Precipitation<br>Abundance |

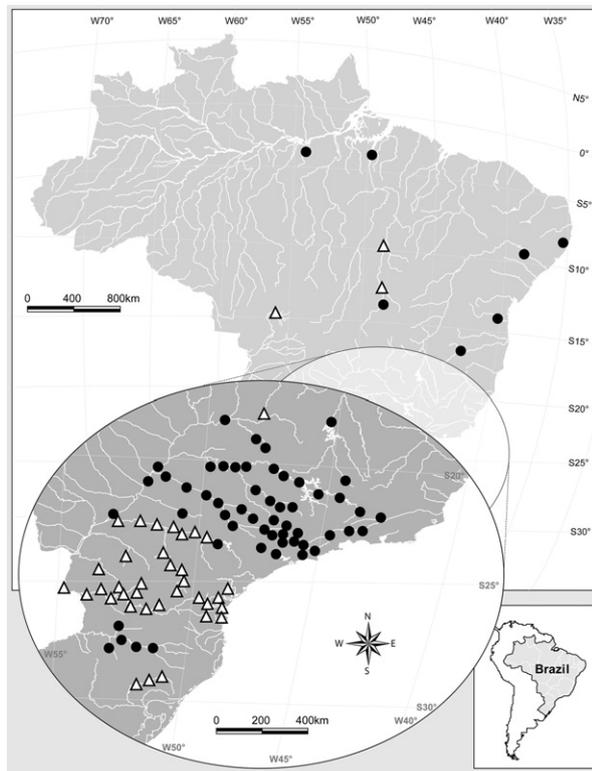
\*Hypotheses commonly used to explain latitudinal diversity gradients.

†Hypotheses that operate independently of latitudinal variation. <sup>a</sup>Hypothesis acting in an ecoregional context at the level of hydrographic basin.

<sup>b</sup>Although it is independent of latitudinal variation, this hypothesis can be associated with latitudinal diversity gradients due to the greater area of tropical regions. <sup>c</sup>Hypothesis acting in a local context, independently of ecoregional variation.

patterns of fish species richness for data set II, a comprehensive compilation of species richness data from published and unpublished studies by UEM/NUPELIA and collaborating institutions. Data set II encompassed richness species data from surveys of 100 reservoirs that involved multiple survey methods without standardization of effort and included information from both lacustrine and transitional zones of reservoirs (Thornton, 1990). Given that reservoirs of data set I are also included in data set II, we were able to use data set I to validate data set II with respect to effects of the sampling effort on species richness. We observed a positive and significant relationship between species richness of data sets I and II ( $y = -3.38 + 1.5x$ ;  $P = 0.00$ ;  $r^2 = 0.95$ ), indicating sampling effort did not affect species richness in data set II.

Reservoirs in the data sets were located within eight hydrographic basins: Amazon, east Atlantic, north-east Atlantic, south Atlantic, Paraná-Paraguay, São Francisco, Tocantins-Araguaia and Uruguay. Although non-native fish species are present in all of these river basins, in many cases occurrences in reservoirs represent recent colonization of a changing novel environment that may or may not lead to long-term population establishment. Reliable information about population status is lacking for most non-native species in most reservoirs in the data sets. Consequently, non-native species were counted along with the native species for estimates of species richness in both data sets, and this assumes that the relatively small numbers of non-natives also were components of regional species pools during the



**Figure 1** Map showing the locations of the reservoir fish assemblages analysed in this study. The large circle encompasses an area in southern and south-eastern of Brazil with high density of reservoirs. Triangles correspond to the reservoirs in data set I, and triangles and black circles correspond to the reservoirs in data set II.

sampling intervals (see Appendix S3 for information about native and introduced fish species considered in this study).

### Predictors of species richness

We analysed patterns of fish species richness in reservoirs at broad spatial scale using a modelling approach that differentiates the relative contributions of sets of predictors (or components) related to (1) four alternative hypotheses commonly used to explain latitudinal diversity gradients and (2) three hypotheses more directly related to diversity gradients in freshwater environments, which operate independently of latitudinal variation (see Table 1). The regional, local, population and spatial components, the variables that constitute each component, and the hypotheses related to each explanatory variable are described below.

#### Regional component

To examine the influence of the regional component on fish richness, we used terrestrial net primary productivity (TNPP:  $\text{kg C}^{-1} \text{m}^{-2} \text{year}^{-1}$ ), mean precipitation (PREC: mm), mean temperature (TEMP:  $\text{Kelvin}^{-1}$ ) and distance from the source (DS: m; length of the upstream flow from the central node), excluding latitude as predictor. The first four variables were

obtained from <http://www.sage.wisc.edu/atlas> (accessed in February 2014), and the last was obtained from <http://eros.usgs.gov> (accessed in February 2014).

We used the environmental variables TNPP, PREC and TEMP to evaluate the *species–energy hypothesis* (S-EH) (1). The literature that examines the relationship between energy availability and species richness encompasses three different definitions of ‘energy’: radiation energy (light), chemical energy (Gibbs free energy in reduced carbon compounds in tissues) and thermal energy (heat) (Clarke & Gaston, 2006). Here, we refer to chemical energy (productivity) as TNPP and PREC (see below) and thermal energy as TEMP.

Aquatic net primary productivity data were not available for the studied reservoirs, so we used TNPP and PREC as measures of productivity. The first variable has been used in studies of freshwater fish richness patterns because terrestrial and aquatic primary productivity co-vary closely (Livingstone *et al.*, 1982). The second variable was used as a proxy of net primary productivity in terms of the amount of chlorophyll-*a* in reservoirs. Greater precipitation increases runoff, stream discharge and the delivery of nutrients into the main body of a reservoir, which in turn stimulates phytoplankton productivity (see Ahn *et al.*, 2002).

We used temperature as a measure of environmental energy within the broader context of the metabolic theory of ecology (MTE; Brown *et al.*, 2004), with mean annual temperature used to test the *metabolic hypothesis* (MH) (2) (Allen *et al.*, 2002) in a multi-hypothesis approach. Based on the principles of thermodynamics and biochemical kinetics, this hypothesis posits that log-transformed species richness,  $S$ , should decrease linearly with the reciprocal of temperature ( $\text{TEMP}^{-1}$ ) according to the formula  $\ln(S) \propto 1/kT$ , where  $k$  is the Boltzmann constant ( $8.62 \times 10^{-5} \text{ eV K}^{-1}$ ) and  $T$  is the temperature in degrees Kelvin. This relationship should display a slope between  $-0.6$  and  $-0.7 \text{ eV}$  (Brown *et al.*, 2004). A recent study supported the MH prediction for both data set I and II (Bailly *et al.*, 2014), so to assess whether these predictions are maintained when other predictors are added to the model, we used richness transformed as the natural logarithm ( $\ln$ ) and the environmental temperature transformed as  $1/kT$ . Finally, the *species–distance from the source hypothesis* (S-DSH) (3) was evaluated by including DS in the analysis.

#### Local component

Two explanatory variables represented the local component: surface area (AREA:  $\text{m}^2$ ) and age (AGE: years) of the reservoirs. The former is related to the *species–area hypothesis* (S-AH) (4), and the latter is related to the *time of habitat alteration hypothesis* (THAH) (5). Both the AREA and AGE data were compiled from the published literature and reports from collaborating institutions. AGE was estimated by subtracting the year of dam closure from the year of the fish survey, and if a given reservoir had been surveyed multiple times, only the most recent survey was considered.

### Population component

Two explanatory variables represented the population component: species body size (BS; cm) and average abundance of the populations (ABUND: ind 1000 m<sup>-2</sup> net 24 h<sup>-1</sup>). BS is related to the *size–diversity hypothesis* (S-DH) (6) and was based on mean standard length (distance between the snout and last vertebra) of captured specimens. ABUND is related to the *population abundance hypothesis* (PAH or the *more-individuals hypothesis*, MIH; Srivastava & Lawton, 1998) (7). Because the PAH considers productivity along with population abundance to explain species richness patterns, two assumptions must be met for this hypothesis to be accepted: (1) both productivity and abundance should be retained in the best-fit model, and (2) the relationships of both productivity and abundance with species richness should be positive. The population component was only analysed for data set I due to limited availability of body size and abundance data. Similar to species richness, population abundance can be underestimated by use of a single survey method at a single location within each reservoir. Because fish abundance data were not available for multiple survey locations within all reservoirs in the data sets, our analysis only applies to the lentic region of reservoirs with respect PAH.

Response variable and the independent variables TNPP, PREC, S-DSH, AREA, AGE, BS and ABUND were log-transformed (ln). The hypotheses, their respective predictions, and related predictor variables are summarized in Table 1.

## DATA ANALYSIS

### Multiple regression and variable selection

We used multiple regression (ordinary least squares, OLS) (Sokal & Rohlf, 1995) to model the influence of regional, local and population variables on fish species richness. We generated models with multiple variables based on the Akaike information criterion (AIC) (Burnham & Anderson, 2004; Diniz-Filho *et al.*, 2008) for model selection. Specifically, we obtained the  $\Delta AIC_i$  value, which corresponds to the difference between the  $AIC_i$  of each model and the minimum AIC found for the set of models. For a given model, a  $\Delta AIC$  value  $> 7$  indicates a poor fit relative to the best model, and a value  $< 2$  indicates that the model is equivalent to the model with the minimum AIC (Burnham & Anderson, 2004).

### Autocorrelation analysis and the spatial component

Species richness data are frequently spatially autocorrelated, which leads to autocorrelated residuals in OLS regression models; consequently, Type I errors may be strongly inflated (Legendre *et al.*, 2002; Diniz-Filho *et al.*, 2003). We added eigenvector-based spatial filters to the OLS multiple

regression to account for these spatial patterns, a procedure called spatial eigenvector mapping (SEVM) (Diniz-Filho & Bini, 2005). To implement SEVM, we first analysed the spatial autocorrelation in species richness data and multiple regression residuals using spatial correlograms of Moran's *I* coefficients (see Diniz-Filho *et al.*, 2003) calculated for 15 distance classes. When positive autocorrelation was detected in the non-spatial OLS residuals, we used SEVM to delimit the spatial component and added it to the model. In SEVM, the geographical coordinates (latitude and longitude) of each cell (reservoir) are used to construct a pairwise matrix of the geographical distance between cells with a given truncation distance. This distance was set by the intercept of the spatial correlogram of species richness, that is, the geographical distance at which the autocorrelation is zero. The eigenvectors obtained by principal coordinates analysis of this distance matrix express the relationships between cells representing the reservoirs at various spatial scales. These eigenvectors (spatial filters), which describe the spatial structure of the richness data, were used as additional predictors in the OLS modelling. To represent the spatial component, we used eigenvectors with Moran's *I* coefficients  $> 0.1$  in the SEVM (Diniz-Filho & Bini, 2005).

### Relative importance of the components in explaining the richness pattern

Partial regressions (Legendre & Legendre, 2012) were used to quantify the relative contributions of the different components (regional, local, population/spatial) in explaining species richness by evaluating the shared effects of the variables, which are otherwise undetected in the interaction. Given that a positive autocorrelation was not observed in the regression residuals for data set I, the set of explanatory variables or components evaluated for this data set were regional (R), local (L) and population (P). In contrast, the analysis of the spatial structure of the data revealed a positive autocorrelation in the regression residuals for data set II. Therefore, considering that there were no population attribute data available for this data set, the third component of the partial regression corresponded to spatial structure (S), which was represented by spatial filters. For each data set, the total variation in species richness was partitioned into three components (R, L and P for data set I and R, L and S for data set II) according to Lobo *et al.* (2002). The deviated percentages of explanation were calculated by eight different subcomponents, which constitute the partial regression: the exclusive effects of the regional (a), local (b) and population/spatial variables (c); the variation due to the shared effect of the regional and local components (d); the regional and population/spatial components (e); the local and population/spatial components (f); the three components (g) and the variation not explained by the independent variables included in the analyses (h). All analyses were performed in SAM 4.0 (Rangel *et al.*, 2010).

## RESULTS

When analysed at broad spatial scale, fish species richness in reservoirs followed a latitudinal gradient with higher values at lower latitudes, except for those reservoirs located in the semiarid region of Brazil (Fig. 2a, b).

For data set I, AIC selected the variables PREC (regional),  $TEMP^{-1}$  (regional), AREA (local), AGE (local) and ABUND (population) for the best-fit model, which explained 91.71% of the variation in species richness ( $AICc = 5.56$ ,  $\Delta AICc = 0.0$ ,  $F = 73.36$ ,  $P < 0.001$ ). Because positive autocorrelation in the regression residuals was not observed at short distances (Moran's  $I = -0.16$ ), the SEVM method was not applied.

For data set II, the regional variables PREC,  $TEMP^{-1}$  and DS and the local variables AREA and AGE were retained in the best-fit OLS model, which explained 67.1% of the variation in species richness ( $AICc = 116.89$ ,  $\Delta AICc = 0.0$ ,  $F = 38.35$ ,  $P < 0.001$ ). For this data set, the Moran's  $I$  value for species richness in the first distance class of the spatial correlogram (0–0.81 km) was equal to 0.381 ( $P < 0.001$ ), confirming the strong spatial structure of species richness in this data set. The value of Moran's  $I$  for the residuals of the OLS multiple regression was still significant ( $I = 0.11$ ,  $P = 0.016$ ), so it was necessary to account for the effect of autocorrelation using the SEVM method. The inclusion of the spatial filters with Moran's  $I$  higher than 0.1 (eigenvectors 1–8) into the model (truncation distance of 335 km) increased the  $R^2$  value to 71.0 ( $F = 16.17$ ,  $P < 0.001$ ) and reduced the autocorrelation in the regression residuals in the first distance class ( $I = -0.01$ ;  $P = 0.96$ ).

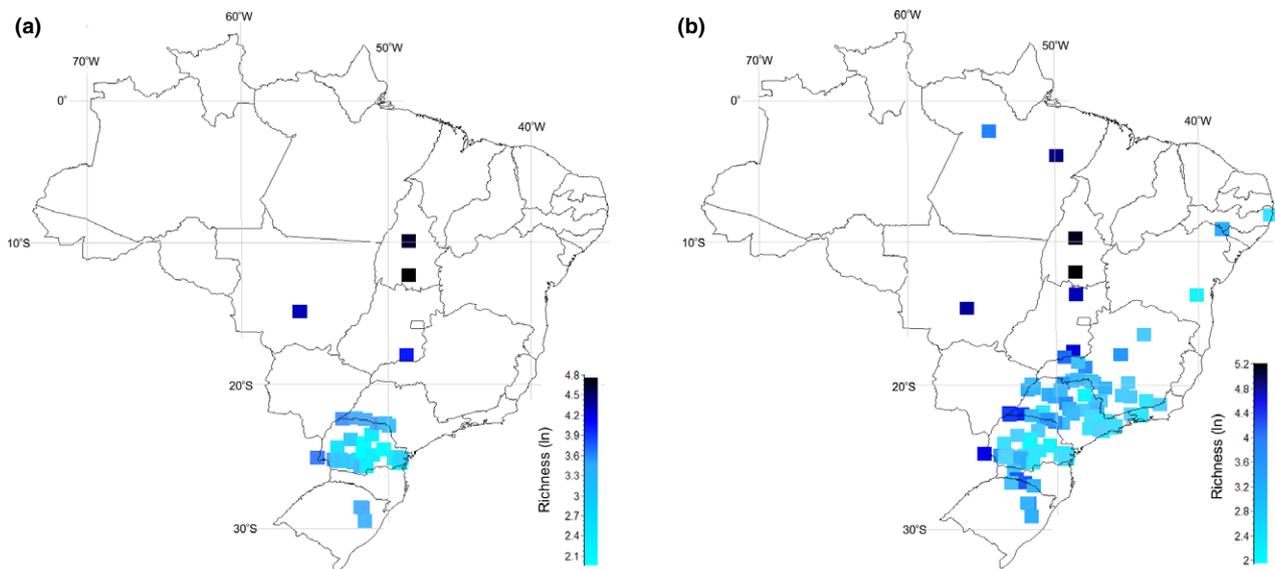
Effects of the predictor variables on fish species richness were indicated by  $b$  coefficient values, and the relative importance of individual predictors were indicated by the standardized slopes. For data set II, these were interpreted as the SEVM slopes, which are partial with respect to geograph-

ical structures defined by spatial filters (Table 2). In general, PREC, AREA and DS were positively correlated with richness, and  $TEMP^{-1}$ , AGE, and ABUND (this variable was only available for data set I) were negatively correlated with species richness. The value of  $b$  for the inverse of temperature was  $-0.80$  ( $CI_{95\%} = -1.17; -0.43$ ) for data set I and  $-0.77$  ( $CI_{95\%} = -1.36; -0.19$ ) for data set II. Thus, for both data sets, the quantitative predictions of the MTE were maintained when other descriptors (in addition to temperature) were taken into account because values of  $b \pm IC$  fell within the range of  $-0.6$  and  $-0.7$  eV predicted by MTE.

In general, the partial regressions revealed that the interaction among the three components evaluated in each data set was the most influential factor when modelling fish species richness in reservoirs. For both data sets, variation associated with the shared effect of the different components (g) was greater than the sum of the exclusive effects of each component (Fig. 3a, b). Among exclusive effects, the local component explained the greatest proportion of variance in species richness, especially for data set I. Finally, the unexplained variation in species richness (h) was higher for data set II than data set I.

## DISCUSSION

Reservoir construction results in drastic changes to the environment and fish species assemblages (Agostinho *et al.*, 2008), and yet large-scale latitudinal gradients in species richness persist. Our results show that this gradient was best modelled by the overlap of a set of factors, supporting the idea that none of the alternative hypotheses explaining biodiversity gradients is alone sufficient to explain the patterns of freshwater fish species richness across spatial scales. The regression analysis inferred support for S-EH (species-energy hypothesis), MH (metabolic hypothesis), S-DSH (species–distance from the source hypothesis), S-AH (species–area



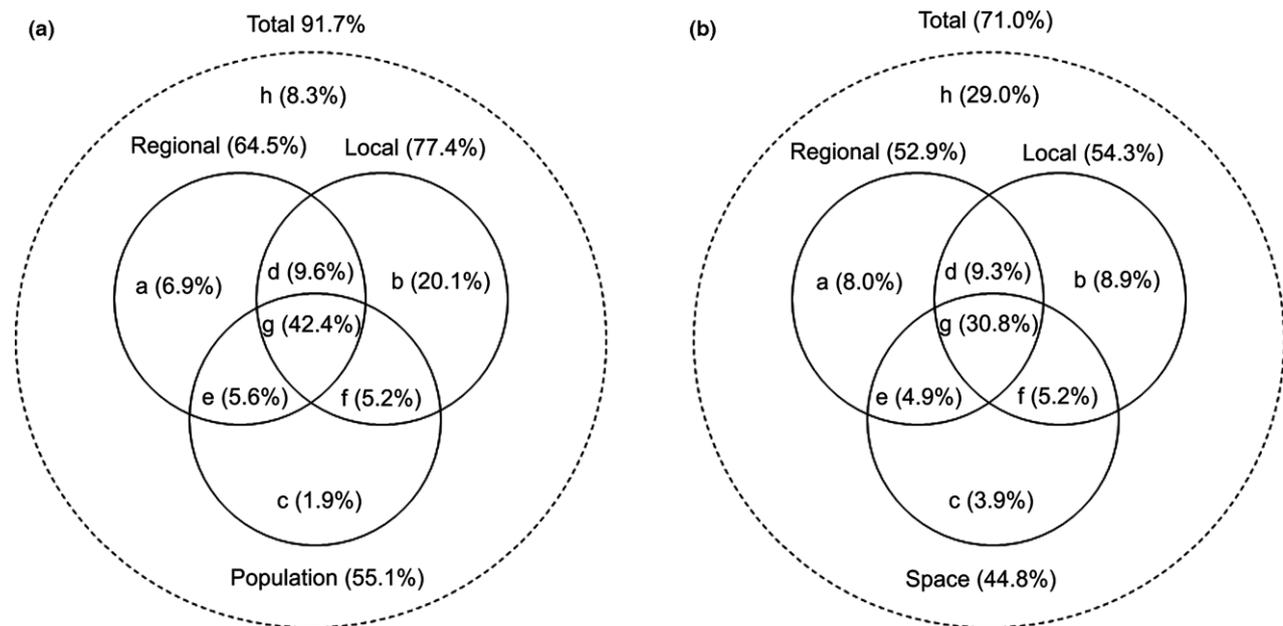
**Figure 2** Richness patterns of fish richness in Neotropical reservoirs: (a) data set I and (b) data set II.

**Table 2** Summary of the results of the multiple regression analysis for data sets I and II including the regression slopes ( $b$ ), standardized coefficients ( $\beta$ ) and probabilities ( $P$ ). SEVM, spatial eigenvector mapping; CI, confidence interval.

| Data set I (39 assemblages)                              | OLS*                          |                      |       |         |
|--|-------------------------------|----------------------|-------|---------|
|  | $b \pm CI$                    | $\beta \pm CI$       | $t$   | $P$     |
| Precipitation (mm)                                       | 0.62 (0.04; 1.20)             | 0.11 (0.01; 0.22)    | 2.16  | 0.038   |
| Temperature (Kelvin <sup>-1</sup> )                      | -0.80 (-1.17; -0.43)          | -0.33 (-0.48; -0.18) | -4.44 | < 0.001 |
| Area (km <sup>2</sup> )                                  | 0.09 (0.05; 0.14)             | 0.28 (0.14; 0.41)    | 4.105 | < 0.001 |
| Age (years)  | -0.22 (-0.28; -0.16)          | -0.41 (-0.52; -0.29) | -7.29 | < 0.001 |
| Abundance (ind 1000 m <sup>-2</sup> 24 h <sup>-1</sup> ) | -0.18 (-0.32; -0.05)          | -0.22 (-0.38; -0.05) | -2.73 | 0.01    |
| Data set II (100 assemblages)                            | OLS + spatial filters (SEVM)† |                      |       |         |
|  | $b \pm CI$                    | $\beta \pm CI$       | $t$   | $P$     |
| Precipitation (mm)                                       | 0.38 (0.10; 0.66)             | 0.17 (0.05; 0.30)    | 2.70  | 0.008   |
| Temperature <sup>-1</sup> (Kelvin <sup>-1</sup> )        | -0.78 (-1.36; -0.19)          | -0.33 (-0.58; -0.08) | -2.65 | 0.01    |
| Distance from source (m)                                 | 0.21 (0.07; 0.35)             | 0.27 (0.09; 0.45)    | 3.01  | 0.003   |
| Area (km <sup>2</sup> )                                  | 0.09 (0.03; 0.14)             | 0.26 (0.10; 0.42)    | 3.17  | 0.002   |
| Age (years)  | -0.17 (-0.26; -0.08)          | -0.27 (-0.41; -0.12) | -3.65 | < 0.001 |

\*The model was composed of two regional variables (temperature and precipitation), two local variables (area and age) and one population variable (abundance) ( $R^2 = 0.917$ ). For this data set, there was no autocorrelation in the regression residuals.

†The model was composed of two regional variables (temperature and precipitation), two local variables (area and age) and eight spatial variables (eigenvector filters) ( $R^2 = 0.71$ ).



**Figure 3** Results from partial regression showing the contributions of the different components to the model  $R^2$  for data set I (a) and data set II (b); a = pure effect of the regional component, b = pure effect of the local component, c = pure effect of the spatial component, d = variation due to the combined effect of the regional and local components, e = variation due to the combined effect of the regional and spatial components, f = variation due to the combined effect of the local and spatial components, g = variation due to the interactive effect of the three components and h = variation not explained by the predictor variables.

hypothesis) and THAH (time of habitat alteration hypothesis). In contrast, the predictions of PAH were not supported by our analysis.

Consistent with our results, studies of river fish assemblages at broad spatial scales have provided empirical support for a positive, linear species–energy relationship (Oberdorff *et al.*, 1995, 2011; Guégan *et al.*, 1998; Kang *et al.*, 2014; Pelayo-Villamil *et al.*, 2015). However, the

mechanisms linking energy availability to species richness are not well understood. The rationale for the PAH (or MIH, Srivastava & Lawton, 1998) has been discussed extensively in the ecological literature, that is, areas receiving high energy inputs should have greater amount of food resources and thus support larger populations, which buffer species from extinction (Abrams, 1995; Isaac *et al.*, 2005). Although the proxy variable used here for reservoir primary productivity

and population abundance were retained in the best-fit model, the latter was not positively related to species richness, rejecting the PAH. In the present study, higher mean population abundance was associated with lower species richness. This is a typical scenario of anthropogenically impacted systems, whereby a new environmental condition favours a subset of pre-adapted species. This pattern appears to be common in reservoirs, in which a relatively small number of fish species thrive within the lentic environment, but most are extirpated from the affected river reach (Agostinho *et al.*, 1999, 2007). Conditions within new reservoirs tend to favour fishes with opportunistic life history strategies. These species allocate relatively large proportions of their available energy and biomass to early and continuous reproduction, reducing generation time and increasing the intrinsic rate of population increase, which yields enhanced ability for rapid colonization of disturbed habitats (Winemiller, 1995; Wootton, 1998). It is important to emphasize that, in this case, the greater abundance of opportunistic fishes is not associated with increased ecosystem productivity *per se*. Rather, these species have life history traits that enable successful reproduction, feeding, and survival in unstable lentic habitats, such as reservoirs. During later stages of reservoir maturation, there often is an increase in population abundance of certain cichlids (e.g. *Cichla* and *Geophagus* species) and other fishes with equilibrium life history strategies that have well-developed parental care behaviour and apparently are well adapted to more stable environmental conditions.

Additional mechanisms make the link between energy availability and species richness (see Srivastava & Lawton, 1998; Evans *et al.*, 2005; McGlynn *et al.*, 2013). The *niche breadth hypothesis* (or *more specialization hypothesis*; De Angelis, 1994; Abrams, 1995) could apply to fishes in reservoirs. This hypothesis predicts that in more productive areas, resources are sufficiently abundant to support a greater number of species that are resource specialists, with resultant niche partitioning facilitating species coexistence (Abrams, 1995; Vázquez & Stevens, 2004; Evans *et al.*, 2005). In the Tucuruí Reservoir, one of the most species rich in the world, 67% of the fishes have been found to be trophic specialists consuming almost exclusively one food item (Mérona *et al.*, 2001).

Consistent with results from studies of other aquatic systems (Smith *et al.*, 2010; Knouft & Page, 2011; Griffiths *et al.*, 2014; Pelayo-Villamil *et al.*, 2015), temperature was significantly and positively associated with the gradient of fish species richness in Neotropical reservoirs. Similarly, a recent study found that fish species richness in Brazilian reservoirs was affected by thermal energy in accordance with the predictions of the MTE (Bailly *et al.*, 2014). In contrast to previous criticisms on the generality of this theory (Hawkins *et al.*, 2007; but see Cassemiro & Diniz-Filho, 2010), the present study, by supporting the MH while accounting for the influence of other factors in addition to temperature, provides further support for MTE predictions. Higher environmental temperatures elevate body temperatures and metabolic rates of ectothermic animals, such as freshwater fish. Under such conditions, most biological pro-

cesses would be accelerated, leading to shorter population generation times and faster mutation rates, which should increase speciation rates (Brown *et al.*, 2004; Allen *et al.*, 2006). In this manner, species diversity gradients would be related to evolutionary processes mediated by temperature (Brown *et al.*, 2004; Brown, 2014).

Predictions of the S-AH were also supported by our data. At least two mechanisms proposed to explain the increase in species richness with area (see Rosenzweig, 1995; Wootton, 1998; Storch *et al.*, 2003) are plausible for reservoirs. First, the greater richness observed in larger reservoirs could be due to a simple sampling effect; in larger reservoirs where greater survey effort is required, rare species have a better chance of being detected. Second, larger reservoirs encompass more diverse habitats, including former lotic habitats and marginal lagoons that are submerged during reservoir filling and contribute potential colonists. In freshwater systems, the S-AH probably interacts with the S-DSH because larger reservoirs are usually located far from the headwaters, in regions with greater habitat availability and more species than smaller tributaries. Hydrology and other abiotic variables tend to be more stochastic in upland tributary streams reducing species persistence, and, consequently, local extirpations may occur more frequently resulting in relatively low local species richness (Schlosser & Ebel, 1989; Oberdorff *et al.*, 2001). Conversely, larger stream reaches in lowland areas have more predictable environments (Schlosser & Ebel, 1989; Oberdorff *et al.*, 2001). Thus, reservoirs located in the lower portions of drainage networks tend to be more species rich, a pattern observed in our study for data set II. It is important to mention that DS was not a significant determinant of species richness in data set I because the positions of the vast majority of reservoirs in the watersheds in this data set are similar, controlling the effect of this variable (please see Fig. 1).

With regard to the THAH, we found lower species richness in older reservoirs. When new reservoirs are filled, they capture fish species from river reaches, floodplain habitats, and tributary streams; but as a lake matures, many of these species decline and disappear due to the lack of requisite physiological, behavioural and/or reproductive adaptations (Agostinho *et al.*, 1999, 2007, 2008). In particular, because their reproduction is strongly dependent on natural flow regimes, migratory species decline following reservoir formation (Agostinho *et al.*, 2007, 2008). In South American rivers, many apex predators are migratory fishes, and their decline in maturing reservoirs may also contribute to a greater abundance of prey species, particularly small opportunistic fishes, some of which may persist even during the later stages of maturation (Agostinho *et al.*, 1999).

Evaluation of competing hypotheses of the species richness pattern is enhanced by mapping the explanatory power of each component, or variable category, and their degree of redundancy (Rangel *et al.*, 2010). For both data sets, partial regressions revealed that the interaction among the three components explained most of the variation in species richness. This implies that mechanisms previously described for

individual hypotheses potentially interact to shape fish richness pattern in reservoirs. Substantial redundancy among groups of variables is commonly reported in studies of species richness gradients conducted over large spatial scales for which most variation cannot be entirely partitioned among the components, and the unique effect of each set of predictors is generally low (Diniz-Filho *et al.*, 2009). Regarding the exclusive effect of components, local factors were relevant to explain the richness pattern in reservoirs, especially for data set I, indicating that singly the described mechanisms for S-AH and THAH are the most effective to structure the species richness in reservoirs. Although predictions of five competing hypothesis are supported by our analysis, considerable unexplained variation remains, especially for data set II. This could be related to historical factors not addressed here, but that have been identified as influencing current distributions of freshwater fish species (see Tedesco *et al.*, 2005; Leprieur *et al.*, 2011).

Our study expands the theoretical framework for understanding gradients of freshwater fish diversity. Findings support the idea that multiple mechanisms account for patterns of fish diversity in reservoirs over large spatial scales, and also demonstrate that forces acting along latitudinal and fluvial gradients influence species richness in these human-modified ecosystems. At the same time, natural mechanisms producing diversity patterns probably are modified, at some level, by anthropogenic stressors, which might account for lack of support for the PAH from our analysis. In addition to summarizing data on fish assemblages in Neotropical reservoirs, this study should aid fisheries conservation by providing insight into regional, local and population factors influencing reservoir biodiversity.

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## SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

**Appendix S1** Baseline data of the fish assemblages in the studied reservoirs.

**Appendix S2** Presence-absence matrix of the fish species in each studied reservoir for data sets I and II.

**Appendix S3** List of species composing the fish assemblages of the analyzed reservoirs per hydrographic basin.

## BIOSKETCH

**Dayani Bailly** is interested in fish biogeography and ecology as well as patterns of diversity across a range of spatial scales and the structure and function of aquatic systems.

Author contributions: D.B., A.A.A. and J.A.F.D-F. conceived the idea; A.A.A. provided the sampled species richness data and institutional support; J.A.F.D-F. delineated the analytical protocol, and D.B. performed the statistical analyses; F.A.S.C. and K.O.W. contributed the theoretical perspectives. All of the co-authors contributed to the writing of the manuscript.

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