

River dams and the stability of bird communities: A hierarchical Bayesian analysis in a tropical hydroelectric power plant

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Abstract

1. The effects of anthropogenic disturbance upon the stability of wildlife communities depend on the heterogeneity and connectivity of habitat remnants on multiple scales. The number of hydroelectric dams in biodiversity hotspots (Africa, South America and Asia) is growing rapidly. To establish their environmental impact, it is essential to understand the dynamics of wildlife communities before and following the establishment of dams.
2. We evaluated the impacts of the filling of the Serra do Facão hydroelectric reservoir in the São Marcos river, central Brazil, on the bird community. Using data from 1,145 surveys across 20 sampling sites over 8 years, 2 years before and 6 years after the filling of the reservoir, we assessed the resistance, i.e. maintenance close to an equilibrium state during the disturbance, and resilience, i.e. ability to return to the original state following the disturbance, of the bird community. We used spatiotemporal hierarchical Bayesian models to assess the effects of reservoir filling on five community parameters: abundance, richness, phylogenetic diversity, functional diversity and species composition.
3. In the period subsequent to reservoir filling, there was (a) a marked reduction in bird abundance, richness, phylogenetic diversity and functional diversity, and (b) a reduction in the proportion of forest species, coupled with an increase in the proportion of savanna species. Except for bird abundance, none of the other community attributes returned to their original levels, even after 6 years. Our findings indicate that Cerrado bird communities have both low resistance and low resilience to habitat loss associated with the establishment of hydroelectric reservoirs.
4. *Synthesis and applications.* The environmental costs of hydroelectric dams are still underestimated or neglected in Brazil. A new paradigm in the assessment of their environmental impacts is warranted, incorporating (a) models of spatiotemporal variations based on long-term monitoring with surveys initiated before disturbances and (b) measures of functional and phylogenetic diversity, such that society can understand the costs and benefits of the establishment of new hydroelectric dams and make informed decisions. Biodiversity loss could be minimized by ensuring the preservation and connectivity of alluvial habitats, capable of maintaining the supply of resources and the functional and phylogenetic attributes of bird communities associated with such habitats.

KEY WORDS

alluvial habitats, dams, disturbance, environmental assessment, functional diversity, hydroelectric, phylogenetic diversity, spatiotemporal Bayesian modelling

1 | INTRODUCTION

River basins are dynamic ecosystems that interconnect various types of habitats through complex exchanges of nutrients, resources and individuals, not just linearly along water courses, but also through the soil and air, across multiple spatial and temporal scales (Soranno et al., 2014). River engineering has impacted the connectivity of 60% of the major hydrographic basins world-wide (Nilsson, Reidy, Dynesius, & Revenga, 2005), mainly through hydroelectric dams to supply the energy demands of the growing human population (Manzano-Agugliaro, Alcayde, Montoya, Zapata-Sierra, & Gil, 2013; Panwar, Kaushik, & Kothari, 2011; Zarfl, Lumsdon, Berlekamp, Tydecks, & Tockner, 2015). The construction of 3,700 new, large and medium dams is expected during the forthcoming decades (Lehner et al., 2011; Poff & Schmidt, 2016; Wu et al., 2019), mostly in emerging countries of southeast Asia, South America, Africa, Balkans and Caucasus (Beifuss & Brown, 2010; Fearnside, 2015; Kareiva, 2012). The long-term socio-environmental consequences of these dams are still poorly known or even neglected (Bednarek, 2001; Richter et al., 2010; Ziv, Baran, Nam, Rodriguez-Iturbe, & Levin, 2012).

Large hydroelectric reservoirs can affect aquatic and terrestrial biodiversity through habitat loss and fragmentation, changes in the physical and chemical properties of the water and changes in seasonal flooding regimes (Finer & Jenkins, 2012; Liermann, Nilsson, Robertson, & Ng, 2012; Vörösmarty et al., 2010). The construction of large dams impacts feeding and reproductive sites, disturbing dispersal and migration processes of vertebrate populations across the landscape (Alho, 2011; Fearnside, 2001, 2006; Wu et al., 2019). These effects often promote a reduction of biodiversity, modifying competitive and predator-prey relationships and favouring generalist species (Amorim et al., 2017; Benchimol & Peres, 2015a; Cosson et al., 1999), ultimately affecting the stability of natural communities (Brandão & Araújo, 2008; Passamani & Cerboncini, 2013).

Even with their ability to fly, many bird species are sensitive to disturbances and bird communities show a decay in abundance and richness immediately after anthropogenic events and diverse responses in subsequent years (Bennett, Nimmo, Clarke, et al., 2014; Nilsson & Dynesius, 1994; Nimmo, Haslem, Radford, Hall, & Bennett, 2016). Even though reservoirs on small rivers can provide attractive habitats for waterbirds, they often submerge specific and seasonally flooded habitats, eliminating reproductive, feeding and resting sites for many bird species (Amorim et al., 2017; Books, 1985; Zeng et al., 2018). They also interrupt the natural dynamics of floods and droughts, important phenological triggers that signal food supplies and dispersion routes to birds, which forage and breed in riverine areas (Knutson & Klaas, 1997; Poff & Schmidt, 2016; Wu et al., 2019). Further, reservoirs fragment alluvial forests that are essential for maintaining bird diversity

and specific functional groups (Benchimol & Peres, 2015b; Bennett, Nimmo, & Radford, 2014; Lees & Peres, 2006). Finally, direct loss of birds can happen due to the mortality of eggs and nestlings, especially among species with reduced flight abilities (Décamps, Joachim, & Lauga, 1987; Frugé, 1992). In the Neotropical region, assessments of the impacts of dams on bird communities are scant (Benchimol & Peres, 2015c; Cosson et al., 1999; Fearnside, 2015).

Common approaches to draw inferences about the impacts of natural or human-induced perturbations on biological communities include the consideration of baseline data (e.g. BACI designs) and the assessment of spatial and/or temporal trends centred about the source of the perturbation (Eberhardt, 1976; Eberhardt & Thomas, 1991; Skalski, 1995; Smith, 2002). The use of Bayesian spatiotemporal modelling to generate representations of ecological processes over time can be an extraordinary tool in such situations (Cosandey-Godin, Krainski, Worm, & Flemming, 2015; Lindgren & Rue, 2015; Wang, 2018). Moreover, inference can be greatly improved when, in addition to taxonomic diversity (species richness), other components of biodiversity are also addressed. By focusing exclusively on species richness, environmental risk assessments can ignore impacts upon evolutionary and functional properties of biological communities (Chapman, Tobias, Edwards, & Davies, 2018; Corbelli et al., 2015; Devictor et al., 2010). Phylogenetic diversity measures the evolutionary time represented by different lineages in the community (Emerson & Gillespie, 2008; Tucker et al., 2017), whereas functional diversity measures the variation in morphological and physiological traits capable of affecting species contributions to ecosystem function and species responses to environmental change (Laureto, Cianciaruso, & Samia, 2015; Petley & Gaston, 2002). Phylogenetic and functional diversity are complementary and essential to understanding the structure, composition and dynamics of natural communities. Further, they can be more sensitive to detecting responses to environmental changes than traditional measurements of diversity (see even more general view by Devictor et al., 2010). Nevertheless, such approaches are still needed in tropical regions (Moreno et al., 2018; Vallejos, Padial, & Vitule, 2016).

Here, we use hierarchical Bayesian spatiotemporal models to evaluate the impacts caused by the formation of a hydroelectric reservoir in the São Marcos river, central Brazil, on the bird community. Hierarchical Bayesian models are a powerful tool to account for the several sources of uncertainty that characterize complex ecological problems, in our case the uncertainties due to spatiotemporal variability and measurement error (Cressie, Calder, Clark, Hoef, & Wikle, 2009; Kéry & Royle, 2015). By using survey data from before and after the filling of the reservoir, we were able to assess two different aspects of the stability of the bird community: its resistance, i.e. its maintenance close to an equilibrium state despite shifting environmental

conditions caused by the disturbance, and its resilience, i.e. its ability to return to the original state following the disturbance (Nimmo et al., 2016; Nimmo, Mac Nally, Cunningham, Haslem, & Bennett, 2015). We modelled the effects of time, flooded area, habitat type and climate seasonality on five community parameters: abundance, richness, phylogenetic diversity, functional diversity and species composition. We predicted that the impacts of the dam on bird communities would be more pronounced: (a) immediately after filling the reservoir; (b) closer to the reservoir and (c) in alluvial forests, because they are more prone to flooding than surrounding savanna habitats.

2 | MATERIALS AND METHODS

2.1 | Study area

We conducted the study around a 218.8 km² reservoir created by a dam in the São Marcos river ($18^{\circ}02'43.16''S$, $47^{\circ}40'32.29''W$), between Goiás and Minas Gerais states, central Brazil (Figure 1). The dam was built for the Serra do Facão hydroelectric power plant, with an installed capacity of 212.6 MW, to support the mining industry in the region (Reinaldo & de Mesquita, 2013). The São Marcos river belongs to the River Plate basin, the second largest watershed in South America, and is situated in the Cerrado biome, a global biodiversity hotspot (Myers, Mittermeier, Mittermeier, Fonseca, & Kent, 2000). Because of the steep relief and pronounced slope towards the São Marcos river, few islands were formed in the reservoir. The climate is tropical with dry winter (Aw) in Köppen's climate classification, characterized by an average annual temperature of 23.4°C, average annual precipitation of 1,500 mm and two well-defined seasons—a wet season from October to April, and a dry season from May to September (Alvares, Stape, Sentelhas, Goncalves, & Sparovek, 2013; Cardoso, Marcuzzo, & Barros, 2015). The vegetation consists of a mosaic of grasslands ('campo limpo'), shrubby grasslands ('campo sujo'), arboreal savannas ('cerrado sensu stricto') and rocky scrubs ('campos rupestres'), generally located in plateaus and slopes,

interspersed by gallery forests and dry forests ('mata seca'), which dominate in alluvial corridors (Amorim et al., 2017; Oliveira-Filho & Ratter, 2002; Ribeiro, Walter, Sano, & Almeida, 1998).

2.2 | Bird surveys

We selected 12 sampling sites in forest, and another 12 in open habitats, separated by at least 1 km to ensure spatial independence (Figure 1). The dam was completed in November 2009 and the reservoir became functional in October 2010 (Reinaldo & de Mesquita, 2013). Four forest sites were submerged with the filling of the reservoir (November 2009) and were surveyed only before that (F4, F5, F8 and F12; Table 1). We used the point count method, recording all birds seen or heard during 20 min, within a 50 m-radius circle (Bibby, Burgess, Hill, & Mustoe, 2000). We conducted surveys during peak bird activity times (06:00–10:00 and 16:00–19:00), from May 2008 to July 2015: 16 trimestrial field trips between May 2008 and February 2012, and six field trips between February 2013 and July 2015, at irregular intervals (4–10 months). During each field trip, we performed two to nine surveys at each site (one observer), totalling 1,145 surveys and 22 field trips. The variable number of surveys at each site resulted from our attempt to compensate for very cold or rainy days with increased sampling. At each sampling site, we spaced survey points by at least 200 m during the same field trip. On an average, we performed 52 surveys/field trip (37–88) and 47.8 surveys/site (9–88; Table S1).

2.3 | Community parameters

For each survey, we calculated five bird community parameters: abundance, richness, phylogenetic diversity, functional diversity and species composition. We estimated bird abundance and richness, respectively, as the total counts of individuals and species. To estimate phylogenetic diversity, we used Faith's index (Faith, 1992), corresponding to the sum of branch lengths in the phylogeny uniting

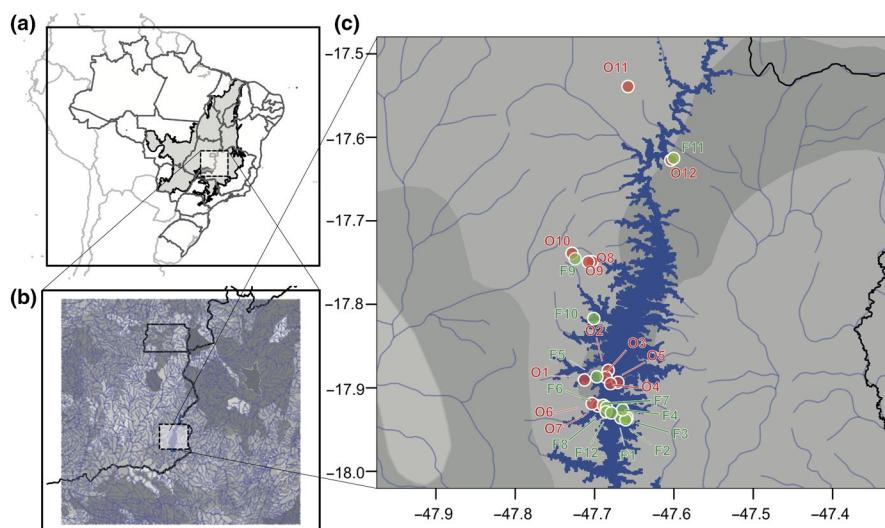


FIGURE 1 (a) Map of South America depicting the Cerrado biome (grey), with state borders of Brazil (black). (b) Hydrography of the São Marcos river, in central Brazil, with the Serra do Facão reservoir. (c) Distribution of the 24 sampling sites around the reservoir (blue), according to the two major habitat types: F – forest (green) and O – open areas (red)

TABLE 1 Posterior estimates ($M \pm SD$ and 95% credibility interval) of parameters from hierarchical Bayesian models relating bird community characteristics to environmental predictors around the Serra do Facão hydroelectric power plant, central Brazil. The full model for each community characteristic includes *Habitat*, *Humidity*, *NDVI* and *Time* as fixed effects, and *Elevation* as a random effect. Bold values indicate parameters significantly different from zero. See Supporting Information 2 – INLA Models for details

Community characteristic	Parameter	M	SD	$Q_{0.025}$	$Q_{0.975}$
Abundance (correlation structure 2)	Intercept	2.3390	0.1449	2.0466	2.6301
	Time	0.0039	0.0027	-0.0014	0.0093
	Humidity	-0.1701	0.0238	-0.2166	-0.1234
	Precipitation	0.1082	0.0254	0.0584	0.1582
Richness	Intercept	1.2834	18.2787	-34.6042	37.1407
	Habitat:Forest	0.7726	18.2608	-35.0795	36.5946
	Habitat:Open	0.5105	18.2600	-35.3401	36.3310
	Humidity	-0.0818	0.0237	-0.1283	-0.0352
	NDVI	-0.0355	0.0256	-0.0855	0.0150
	Time	0.0063	0.0043	-0.0010	0.0158
Phylogenetic diversity	Intercept	1.6477	18.2654	-34.2135	37.4790
	Time	0.0025	0.0014	0.0001	0.0054
	Humidity	-0.0312	0.0074	-0.0458	-0.0166
	NDVI	-0.0202	0.0079	-0.0358	-0.0046
	Distance	-0.0033	0.0093	-0.0215	0.0150
	Habitat:Forest	0.8520	18.2594	-34.9973	36.6714
	Habitat:Open	0.7955	18.2594	-35.0538	36.6149
Functional diversity	Intercept	0.0378	18.2574	-35.8076	35.8533
	Habitat:Forest	0.0137	18.2574	-35.8317	35.8292
	Habitat:Open	0.0241	18.2574	-35.8213	35.8396
	Humidity	-0.0058	0.0015	-0.0087	-0.0028
	Precipitation	0.0026	0.0014	-0.0002	0.0054
	Time	0.0001	0.0001	-0.0001	0.0003
Species composition	Intercept	0.1432	18.2576	-35.7027	35.9592
	Habitat:Forest	-0.6799	18.2576	-36.5257	35.1361
	Habitat:Open	0.8230	18.2576	-35.0228	36.6390
	Humidity	0.0909	0.0561	-0.0203	0.2020
	Precipitation	0.0030	0.0548	-0.1066	0.1113
	Time	-0.0029	0.0017	-0.0062	0.0005
	NDVI	-0.0209	0.0340	-0.0885	0.0452

all species in the survey and calculated with package *PICANTE* (Kembel et al., 2010). We produced a species tree uniting the 230 bird species in our study from 1,000 gene trees representing the global phylogeny of birds (Jetz, Thomas, Joy, Hartmann, & Mooers, 2012) and downloaded from BirdTree (www.birdtree.org). The species tree (Figure S1) was built from a single-linkage hierarchical clustering applied to a distance matrix representing the mean divergence time of each pair of tips for all gene trees (Maddison & Knowles, 2006), using package *APE* (Paradis, Claude, & Strimmer, 2004).

We used the following traits to estimate functional diversity: body mass, trophic guild, use of vegetation strata, preferred habitat, migratory lifestyle and riparian association. We obtained body mass values (g) from Dunning (2008) and assigned bird species to seven trophic guilds (carnivores, insectivores, frugivores, nectarivores, piscivores, granivores and omnivores, per Bagno & Marinho-Filho, 2001; Sick, 1997), six vegetation strata guilds (water, ground, understorey,

midstorey, canopy and above canopy) and three habitat guilds (forest, savanna, aquatic, per Bagno & Marinho-Filho, 2001; Silva, 1995, 1996). We regarded as migratory 25 species that perform cyclical, seasonal large-scale movements involving at least part of their populations, with high fidelity to their breeding grounds (Negret, 1988; Negret & Negret, 1981; Sick, 1983). We classified 22 species as riparian, because of their close association with riverine habitats and swamps (Alho, 2011; Brandão & Araújo, 2008). A list of species and their functional traits is in Appendix S1, the taxonomy following Remsen et al. (2015). With these traits, we built a distance matrix based on Gower's coefficient (Gower, 1971) and produced a functional dendrogram (Figure S2) with the unweighted pair-group method with arithmetic mean (UPGMA) using package *CLUSTER* (Maechler, Rousseeuw, Struyf, Hubert, & Hornik, 2018). We measured functional diversity as Rao's diversity coefficient or quadratic entropy (Botta-Dukat, 2005; Rao, 1982) using package *FD* (Laliberté & Legendre, 2010; Laliberté, Legendre, & Shipley, 2014).

To represent variation in species composition across surveys, we used the scores of the first axis of a detrended correspondence analysis (DCA) of bird survey data using package VEGAN (Oksanen et al., 2018). Scores along the first DCA axis (eigenvalue = 0.50) mainly represented a gradient of habitat association, separating forest (negative scores; e.g. *Penelope superciliaris*, *Amazona amazonica* and *Baryphthengus rufigularis*) and savanna species (positive scores; e.g. *Taoniscus nanus*, *Hirundinea ferruginea* and *Emberizoides herbicola*; Figure S3).

2.4 | Environmental predictors

To model the spatiotemporal changes in bird community parameters, we measured eight predictors, representing distinct environmental effects. To represent the shifting spatial gradient due to the effects of habitat flooding and proximity to the reservoir, we calculated, for each field trip and site, (1) the percentage of flooded areas within a 1-km radius around the centre of each site (% Flooded) and (2) the smallest between (a) the distance from the centre of each site to the reservoir and (b) the distance from the centre of each site to the nearest waterbody (Distance), from Landsat7 images (United States Geological Survey, <https://earthexplorer.usgs.gov/>), before and after the filling of the reservoir (November 2009 and June 2015). To represent the temporal environmental variation, we used (3) the number of months (Time) from the completion of the dam and onset of reservoir filling (November 2009 = 0) and (4) the survey periods (Period) grouped in three classes: before the onset of reservoir filling (2008–2009), the next 3 years after that (2010–2012, 'short-term') and the three subsequent years (2013–2015, 'medium-term'). To account for differences in vegetation cover among sites, we recorded (5) the vegetation physiognomy (Habitat) as forest (dry forest or gallery forest) or open (grasslands, shrubby grasslands, arboreal savannas or rocky scrublands) habitats, and measured (6) the Normalized Difference Vegetation Index (NDVI) from Landsat7 images within a 150-m radius from the centre of each site, at each field trip (Table S2). Finally, to account for climatic variation, we obtained monthly average (7) precipitation and (8) relative air humidity records from Catalão, Goiás state, 2.9 km from the dam (Instituto Nacional de Meteorologia, <http://www.inmet.gov.br/>). The variation in climate records was largely associated with the characteristic wet-dry seasonality of the Cerrado, with no meaningful trend attributable to the establishment of the reservoir (based on a time-series decomposition analysis, results not shown).

2.5 | Hierarchical Bayesian modelling

Before implementing hierarchical Bayesian models, we selected the best environmental predictors of each bird community parameter using a Guided Regularized Random Forest analysis, with package RRF (Deng, 2013; Deng & Runger, 2012, 2013) to minimize potential instances of collinearity and overdetermination (Dormann et al., 2013). Details about this step are provided in the Supporting Information. We used two powerful tools to model the spatiotemporal variation in

bird community parameters: Stochastic Partial Differential Equations (SPDE) combined with the Integrated Nested Laplace Approximations (INLA) algorithm. SPDE is an efficient approach to infer about a continuously indexed spatial process changing in time (e.g. a Gaussian random field with Matérn covariance structure) and to predict it at desired locations (Blangiardo & Cameletti, 2015; Cameletti, Lindgren, Simpson, & Rue, 2013; Lindgren, Rue, & Lindstrom, 2011). This is achieved by using a discretely indexed random process (i.e. a Gaussian Markov Random Field), represented as a neighbourhood mesh structure (Lindgren & Rue, 2015). The INLA approach is an efficient alternative to computationally intensive and time-intensive Markov Chain Monte Carlo methods normally used for Bayesian inference (Rue, Martino, & Chopin, 2009). Using the combined SPDE and INLA approaches, we modelled each bird community parameter across the study area for each year of study, accounting for the spatial dependency between sampling sites and for the effects of selected environmental predictors (see Appendix S1 for details). We calculated the mean values of bird abundance and richness at each site for each field trip and used the rounded (integer) values in statistical analyses, assuming they followed a Poisson distribution. We assumed the remaining parameters followed a Gaussian (normal) distribution, but \log_{10} -transformed the phylogenetic diversity values to improve their distribution and also scaled the values of NDVI, % Flooded, Distance, Precipitation and Humidity to zero mean and unit variance prior to analyses.

We implemented hierarchical Bayesian spatiotemporal models with the R-INLA package (Rue et al., 2009, 2017), using the default and recommended settings for priors (Held, Schrödle, & Rue, 2010) and the 'laplace' (most accurate) approximation to estimate the posterior marginal distributions of all model random effects and parameters (Martins, Simpson, Lindgren, & Rue, 2013). To select the best candidate models, we evaluated different combinations of spatiotemporal correlation structures and mesh designs, based on cross-validated predictive ordinate values (Ferkingstad, Held, & Rue, 2017). We created four mesh designs using the constrained refined Delaunay triangulation applied to sampling site locations, by varying the sizes of triangles within and outside the sampled area (Figure S4), attempting to minimize any boundary effects (Lindgren & Rue, 2015). We evaluated four spatiotemporal correlation structures by considering different temporal evolutions of the spatial random effect: (a) the spatial random effect is constant over time; (b) the spatial random effect is different each year of the study, constant within years; (c) the spatial random effect is correlated in consecutive years, constant within years and (d) the spatial random effect is different each month of the study.

3 | RESULTS

3.1 | Bird surveys, community parameters and environmental predictors

For 8 years, we recorded 14,505 individual birds, representing 230 species, 49 families and 22 orders (Table S3). Overall, the bird community around the Serra do Facão hydroelectric power plant

comprised mainly insectivorous species from midstorey strata of forest habitats (Figure S5). The five bird community parameters were significantly intercorrelated ($p < 0.001$), but there were high and positive correlations only between abundance, richness and phylogenetic diversity (Figure S6). Species composition was weakly and

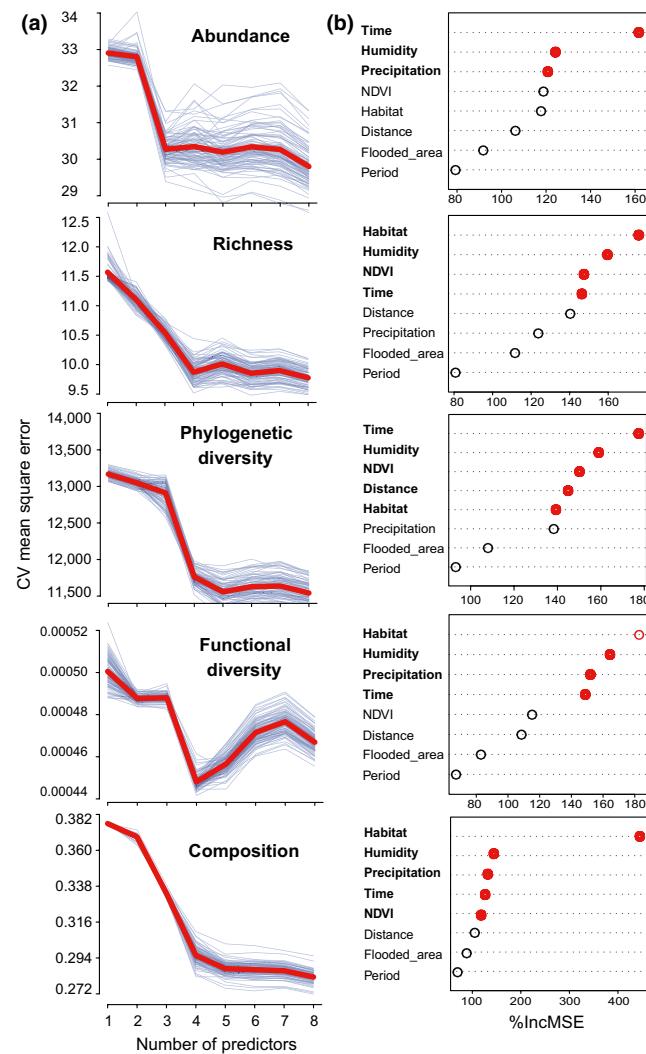


FIGURE 2 Importance of environmental predictors of bird community parameters around the Serra do Facão hydroelectric reservoir, in the São Marcos river, central Brazil. Importance is based on the per cent increase in mean square error (%IncMSE), obtained from 100 replicates of 10-fold cross-validation of a Guided and Regularized Random Forest analysis growing 10,000 trees.
(a) Matplot of the number of predictors selected, and (b) predictors ranked by %IncMSE, with selected ones highlighted in red

negatively correlated with abundance ($r = -0.19$), richness (-0.33) and phylogenetic diversity (-0.23), but positively correlated with functional diversity (-0.16); functional diversity was weakly correlated with abundance (0.21), richness (0.22) and phylogenetic diversity (0.40). The Guided and Regularized Random Forest analyses retained *Time* and *Humidity* as important predictors of all community parameters; *Habitat* as important of all but abundance; *Precipitation* of abundance, functional diversity of composition; *NDVI* of richness, phylogenetic diversity of composition; and *Distance* as important only of phylogenetic diversity (Figure 2).

3.2 | Spatiotemporal models, inference and prediction

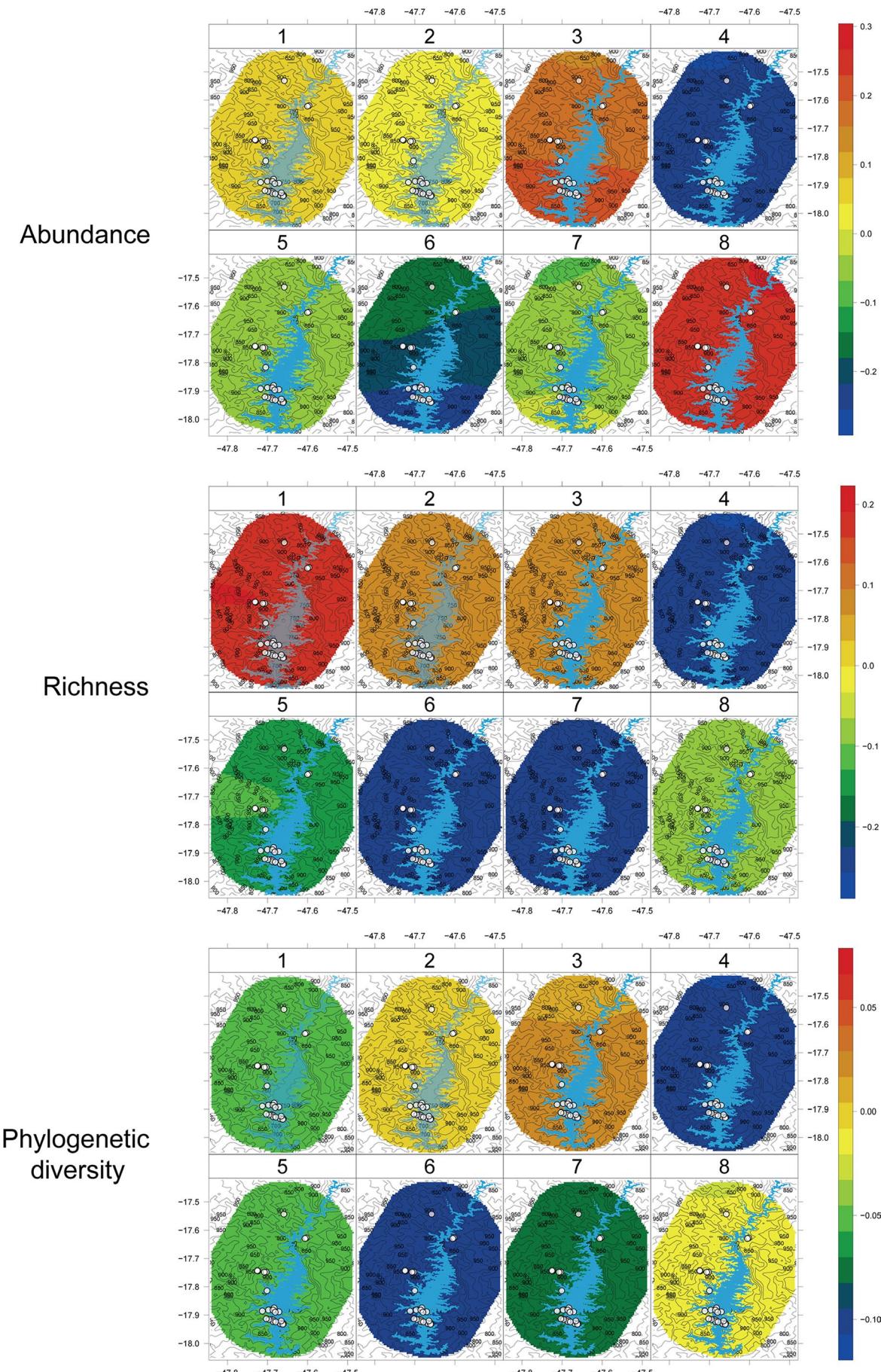
Cross-validated predictive ordinate values indicated that, overall, model performance was similar regardless of the spatiotemporal correlation structure or mesh design (Figure S7). Because correlation structure I ignores the temporal effects while correlation structure IV is unpractical, by regarding each month as an independent realization of the random field, we selected the best model between correlation structures II or III, with the corresponding best mesh design. As the final model for each community parameter was based on a different realization of the random field each year, the spatial effects differed from year to year (Figure 3). Overall, standard deviation patterns for the random fields reflected the amount of information, with reduced uncertainty in regions of greater concentration of sampling sites (Figure S8). Moreover, there was reduced uncertainty between 2009 and 2013 for all community parameters, except for phylogenetic diversity, whose standard deviation values were greater in 2010–2011 (Figure S8).

The final model for bird abundance was based on spatiotemporal correlation structure II and mesh design IV. Abundance was negatively correlated with *Humidity* and positively correlated with *Precipitation*, while the other predictors had no significant effect (Table 1). Immediately after the filling of the reservoir (2011), abundance declined sharply and recovered only in the last year of the study, reaching higher levels than in 2008 (Figure 3).

For bird richness, the final model was based on spatiotemporal correlation structure III and mesh design IV. Bird richness was negatively correlated with *Humidity*, while the other predictors had no significant effect (Table 1). Richness decreased steadily from 2009 on, never returning to original levels (Figure 3).

The final model for bird phylogenetic diversity was based on spatiotemporal correlation structure III and mesh design I. Phylogenetic

FIGURE 3 Bayesian spatiotemporal models depicting the variation in bird community parameters before (2008–2010) and after (2011–2015) the filling of a reservoir in the São Marcos river, central Brazil, associated with the building of the Serra do Facão hydroelectric power plant. The reservoir, which became functional in October 2010, is indicated in light blue. The sampling sites are indicated by white circles. Contour lines are elevation isolines, connecting points of equal elevation, indicated by numbers. The colours indicate levels of community parameters, according to the associated legend. Overall, bird abundance and diversity (richness, functional and phylogenetic diversity) declined markedly after reservoir filling and did not return to pre-filling levels, with the exception of abundance. Community composition changed from a predominance of forest species (cold colours), prior to reservoir filling, to a higher proportion of savanna species (warm colours), with the establishment of a distinct bird community after reservoir filling



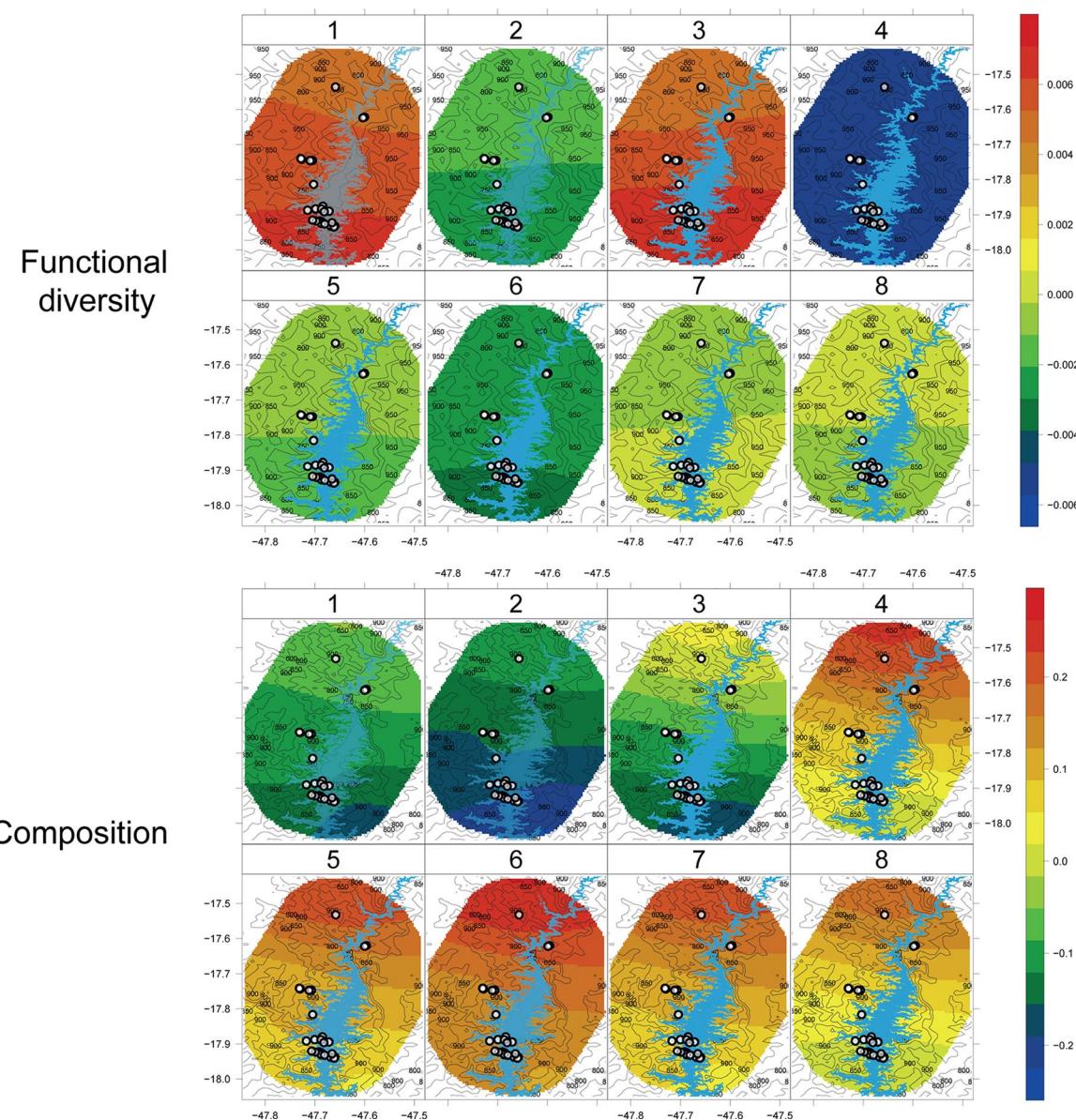


FIGURE 3 (Continued)

diversity was negatively correlated with *Humidity* and *NDVI*, but positively correlated with *Time*, while the other predictors had no significant effect (Table 1). Phylogenetic diversity reduced drastically in 2011, immediately after the filling of the reservoir, and only recovered in 2015 (Figure 3).

For bird functional diversity, the final model was based on spatiotemporal correlation structure II and mesh design III. Functional diversity was negatively correlated with *Humidity* and all other predictors had no significant effect (Table 1). The lowest values of functional diversity occurred in 2011, immediately after the filling of the reservoir, and recovered afterwards but never returned to original levels (Figure 3).

The final model for bird species composition was based on spatiotemporal correlation structure III and mesh design IV. None of the environmental predictors had a significant effect on species composition (Table 1). The smaller values of species composition indicate

a predominance of forest species in the first 3 years of the study; conversely, after 2011 there was increased dominance of savanna species (Figure 3).

In summary, bird abundance and diversity remained high in the first 3 years of the study (2008 and 2010) but declined markedly following the formation of the reservoir and, with the exception of abundance, did not return to original levels. In the first 3 years of the study, the bird community was dominated by forest species, but savanna species dominated following the formation of the reservoir, never returning to its original character (Figure 3).

4 | DISCUSSION

We used hierarchical Bayesian spatiotemporal models to assess the impacts of the flooding of the Serra do Facão hydroelectric power

plant reservoir on the bird community. We found that community parameters varied primarily with vegetation cover, the Cerrado's seasonal rhythms and time since reservoir filling. The retention of NDVI and *Habitat* as important predictors of community parameters highlights the effects of changes in vegetation cover upon Cerrado bird communities (Silva, 1995, 1996). Likewise, the selection of *Humidity* and *Precipitation* as important predictors of community parameters reflects the influence of climate seasonality on Cerrado birds, characterized by greater diversity (richness, phylogenetic diversity and functional diversity) at the end of the dry season, which coincides with the onset of the breeding season and arrival of most migratory species in central Brazil (Bagno & Marinho-Filho, 2001; Negret & Negret, 1981; Sick, 1983). Finally, our Bayesian spatiotemporal models evidenced a marked (a) reduction of diversity parameters and (b) increase in the proportion of savanna species following immediately after the reservoir filling, highlighting the low resistance of the bird community to the disturbance, and (c) the failure of community parameters to return to original levels, emphasizing the low resilience of the bird community.

In general, vertebrate communities are characterized by low resistance to floods (Knutson & Klaas, 1997; Munes, Dixon, Swanson, Merkord, & Benson, 2015, but see Mesquita et al., 2015). Dam floods impact resource availability and species interactions, affecting the reproductive success and survival of bird populations, even though populations of some species return to the mean value quite soon (Books, 1985). During the filling of reservoirs, many species are forced to flee, while opportunistic—usually predatory, piscivorous and insectivorous—species are attracted by the sudden supply of prey (Cosson et al., 1999; Passamani & Cerboncini, 2013). This thickening of opportunistic species in the remnants adjacent to reservoirs can promote the intensification of density-dependent processes (e.g. competition, predation, parasitism), with a subsequent restructuring of the communities (Alho, 2011; Brandão & Araújo, 2008). In the period of community restructuration following a disturbance, called relaxation time, some populations are locally extirpated, while other species colonize the newly formed environments (Metzger et al., 2009). This restructuring may result in loss of evolutionary lineages or relevant ecosystem functions, diminishing the ecological stability of communities (Chapman et al., 2018; Munes et al., 2015). In this study, there was a reduction of abundance, richness, phylogenetic diversity and functional diversity in the year following the filling of the reservoir, indicating the low resistance of the bird communities to the formation of the dam. For instance, some aquatic (herons, egrets, ducks, cormorants and ibises), migratory (doves, kites and swallows), predatory (hawks and owls) and large ground-dwelling birds (tinamous, guans and curassows) were no longer recorded after the fourth year of study. They represent ancient lineages or distinct functional groups that likely influenced community parameters after reservoir filling.

The reduction of richness, phylogenetic diversity and functional diversity was accompanied by a clear alteration of species composition, with an increased proportion of savanna species. The ecological stability of communities is related to environmental heterogeneity, since the formation of environmental gradients

allows populations to respond differently to extreme variations (the 'portfolio effect', Malpas, Smart, Dreditt, Sharps, & Garbutt, 2013; Schindler et al., 2010). Hence, the presence of alluvial habitats remnants is critical to maintaining ecological stability in riparian communities subjected to disturbance (Bennett, Nimmo, & Radford, 2014; Munes et al., 2015; Nimmo et al., 2016). The region around the Serra do Facão reservoir has been strongly altered by livestock, agriculture and mining in the last 300 years (Gomes, Rocha, Brandão, & Marinho, 2015). This is the second major dam built on the São Marcos river and there is no conservation unit greater than 10,000 ha within 250-km radius of the dam. Large and/or successive dams on the same river basin promote even more deleterious effects due to the synchronization of ecological processes (e.g. unavailability of reproductive sites; McCluney et al., 2014; Wang, 2018; Wu et al., 2019), and to the reduction of spatial heterogeneity; after all, the margins of a newly formed reservoir generally do not replicate the same alluvial habitats that previously existed (Alho, 2011; Brandão & Araújo, 2008; Cosson et al., 1999; Zeng et al., 2018). The reduced proportion of forest birds after the filling of the Serra do Facão reservoir corroborates the prediction that dam impacts are more pronounced on forest environments (Gomes et al., 2015).

The prediction of a spatial gradient in relation to the reservoir was not corroborated in our study. However, the clear reduction of diversity even in areas far from the reservoir demonstrates the high sensitivity of bird communities to the disturbance. In general, the ecological sensitivity of bird communities stems from the notorious flight capacity of most species, whose individuals can quickly cross large distances between the remnants of a riparian macrosystem (Bennett, Nimmo, & Radford, 2014; Kerr, Riley, Feldman, & Bohannan, 2002; Negret & Negret, 1981; Sick, 1983). However, this also allows anthropogenic disturbances to trigger changes in ecological processes at wider spatial scales, beyond the edges of riverine macrosystems (Nilsson & Dynesius, 1994; Poff & Schmidt, 2016; Wang, 2018). Analogous to spatial unfolding, anthropogenic impacts, even if intense and time-restricted, may have indirect effects on communities over much longer time-scales (Benchimol & Peres, 2015b; Emerson & Gillespie, 2008; Petley, Evans, Fishburn, & Gaston, 2007). The low resilience of bird communities to the creation of river reservoirs is demonstrated in our study, where richness, phylogenetic diversity and functional diversity remained at lower levels even 6 years after the formation of the reservoir. Relaxation time against disturbances can extend for up to 50 years in temperate zone or tropical communities (Cosson et al., 1999; Jones, Peres, Benchimol, Bunnefeld, & Dent, 2019; Metzger et al., 2009; Palmeirim, Peres, & Rosas, 2014).

4.1 | Implications for biodiversity conservation

Our results highlight the low resistance and low resilience of bird communities after the creation of a hydroelectric dam, with pronounced changes in species composition after the disturbance, and

the failure to recover levels of taxonomic, phylogenetic and functional diversity even after 6 years. Future studies should determine the patterns of heterogeneity, connectivity and ecological interactions that influence the resilience of animal communities to such disturbances. This is one of the few works to evaluate hydroelectric dam impacts on Neotropical communities over a period of more than 5 years, with pre-disturbance sampling (Amorim et al., 2017; Benchimol & Peres, 2015a; Bennett, Nimmo, Clarke, et al., 2014; Gomes et al., 2015), and also one of the first to consider other facets of diversity in impact assessments (Chapman et al., 2018; Devictor et al., 2010). Future research should focus on crucial periods of reservoir filling, when ecological processes are intensified, and also maintain long-term sampling efforts that allow for long periods of relaxation of biotic communities (Wu et al., 2019).

In general, the environmental costs of hydroelectric dams are still underestimated or neglected during feasibility analyses; and the decision of new investments in the energy matrix mainly serves economic interests that aim to export commodities by emerging countries (Benchimol & Peres, 2015b; Fearnside, 2014, 2015). Guidelines that would minimize environmental losses include: (a) avoiding barring major river basin courses, giving preference to smaller secondary courses; (b) considering the geographic location and landscape aspects in the choice of new dams, to maintain the connectivity of natural remnants; and (c) ensuring the preservation of areas near reservoirs, capable of maintaining the supply of resources and conserving the functional and phylogenetic attributes of regional communities (Benchimol & Peres, 2015a, 2015b; Brandão & Araújo, 2008; Fearnside, 2005; Jones et al., 2019; Wu et al., 2019; Ziv et al., 2012). The planning of new dams must weigh (trade-offs) economic and conservationist interests, rather than considering only one side, which in the future will result in the infeasibility of both, with negative consequences for wildlife communities and the human society.

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AUTHORS' CONTRIBUTIONS

T.L.S.A., L.P.G. and J.S.M.-F. conceived the ideas and designed the experiment; T.L.S.A., S.B.B. and I.P.d.F. executed the experiment and collected the data; T.L.S.A. and G.R.C. analysed the data and led the writing of the manuscript. All authors contributed critically to drafts and approved the final manuscript for publication.

DATA AVAILABILITY STATEMENT

Data are available via the Dryad Digital Repository <https://doi.org/10.5061/dryad.j6q573n9f> (Abreu et al., 2020).

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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