

Seasonal dynamics of the fish assemblage in a floodplain lake at the confluence of the Negro and Amazon Rivers

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The temporal effect of discharge and limnology on fish composition and species diversity in a floodplain lake at the confluence of the Amazon and Negro Rivers was evaluated. Species richness, abundance and assemblage composition were strongly influenced by seasonal discharge of the Amazon and Negro Rivers, which affects lateral connectivity, water conductivity and temperature. As a consequence, temporal β -diversity was high in the lake and the assemblage was dominated by seasonally transient species. Relatively large species known to feed on resources within the floodplain were captured almost exclusively during the flood period. During the dry season, the assemblage was dominated by fishes adapted to harsh conditions of high temperature and low dissolved oxygen concentrations. An open system with high spatial and temporal heterogeneity created by the meeting of two large rivers with different water chemistry, Lago Catalão has a dynamic fish assemblage. Given its high temporal β -diversity and abundance of fishes, many of great importance in local fisheries, Lago Catalão and other floodplain lakes in this region merit special attention for conservation.

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INTRODUCTION

Spatial heterogeneity and dynamic hydrology of rivers and floodplains support high biodiversity and affect functional processes (Junk *et al.*, 1989; Ward *et al.*, 1999; Tockener & Stanford, 2002). Flood pulses cause lateral connectivity that influences water quality (Thomaz *et al.*, 2007), nutrient dynamics (Melack & Forsberg, 2001) and life cycles of many organisms within floodplain aquatic habitats (Junk, 1985; Junk & Piedade, 1997; Arrington *et al.*, 2006; Neves dos Santos *et al.*, 2008). In tropical floodplain rivers, periodic flood pulses also have a strong influence on patterns of fish distribution and abundance (Junk *et al.*, 1989; Arrington & Winemiller, 2004). During high-water periods, many fishes migrate from the river channel into lakes, forests and savannahs to exploit food resources, to spawn or brood fry (Lowe-McConnell, 1987; Goulding *et al.*, 1988). Abundance of juveniles of large and medium-sized species also increases within floodplain habitats, especially those containing dense

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stands of aquatic macrophytes that harbour invertebrate prey and provide cover for predator avoidance (Gomes & Agostinho, 1997; Sánchez-Botero & Araújo-Lima, 2001; Scarabotti *et al.*, 2011). During the low-water periods, most floodplain lakes are isolated from the active river channel, and abiotic and biotic features are strongly influenced by local dynamics (including predator-mediated processes), which leads to lower similarity among lakes (Rodríguez & Lewis, 1997; Tejerina-Garro *et al.*, 1998; Saint-Paul *et al.*, 2000). In response to shifting influences of lateral exchange of water and organisms *v.* internal ecosystem and community processes, community structure of floodplain lakes often undergoes large seasonal changes. In addition, seasonal flood pulses could cause high temporal β -diversity in a local community, as have been shown for spatial β -diversity (Bozelli *et al.*, 2015).

Floodplain habitats associated with large rivers in the Amazon encompass an area of *c.* 800 000 km² (Melack & Hess, 2010) and harbour *c.* 50% of the Amazonian fish diversity, including almost all commercially important species (Junk *et al.*, 2007). Despite their importance, Amazon floodplain landscapes are being altered at alarming rates as human activities expand into these areas (Junk, 2007, 2013; Renó *et al.*, 2011; Castello *et al.*, 2013). In addition to losses from direct anthropogenic actions, climate change appears to be affecting regional hydrology (Gloor *et al.*, 2013; Satyamurty *et al.*, 2013), which increases the urgency for increasing knowledge of the ecology of Amazonian floodplains (Barletta *et al.*, 2010; Junk, 2013).

In the central Amazon, the confluence of white waters (muddy water) of the Amazon River (locally named Rio Solimões) and black acidic waters of the Negro River creates one of the world's most conspicuous ecotones. Each of these rivers supports not only numerous fishes adapted to its own physicochemical and related ecological conditions, but also fishes that apparently can live within a broad spectrum of environmental conditions (Saint-Paul *et al.*, 2000). Nonetheless, there has not been any research that examines fish assemblage structure in the region of the confluence of these rivers in the central Amazon. Heterogeneous and dynamic floodplain landscapes in this region may partially account for high species diversity (Ardura *et al.*, 2013). At their confluence, the two rivers share a common floodplain that contains several floodplain lakes and temporary channels that seasonally connect them to the rivers. The largest lake in this floodplain is Lago Catalão. Limnological studies have revealed that each river influences the lake's water quality during particular phases of the annual flood pulse (Brito *et al.*, 2014; Caraballo *et al.*, 2014), which changes the water level *c.* 10 m on average (Bittencourt & Amadio, 2007).

Floodplains adjacent to the meeting of the waters support high diversity of aquatic plants (Bleich *et al.*, 2014) and also contain important habitats for reproduction by several migratory fishes of importance to commercial and subsistence fisheries (Carvalho de Lima & Araujo-Lima, 2004; Leite *et al.*, 2006). This area, therefore, has been proposed as priority area for conservation (Ardura *et al.*, 2013). Population genetics research on two commercially important fishes, *Colossoma macropomum* (Cuvier 1816) and *Prochilodus nigricans* Spix & Agassiz 1829, revealed that genetic diversity is lower in this area compared with other regions in the Amazon Basin (Ardura *et al.*, 2013). This finding is surprising given the proximity of two large rivers with very different water conditions and opportunities for dispersal, especially during the annual flood pulse when lateral connectivity is high. Indeed, other species showed greater genetic diversity in this region as a consequence of ecological diversifying selection according to water type (Cooke *et al.*, 2012, 2014). This study analysed fish

assemblage composition within Lago Catalão with respect to seasonal hydrology. It was hypothesized that temporal β -diversity would be high because occurrences of many species would be influenced by changes in water physico chemistry and accessibility of food resources in the floodplain.

MATERIALS AND METHODS

STUDY AREA

This study was carried out in Lago Catalão, an Amazonian floodplain lake located near Manaus at the confluence of the Amazon and Negro Rivers ($3^{\circ} 08' - 3^{\circ} 14' S$; $59^{\circ} 53' - 59^{\circ} 58' W$) (Fig. 1). The rainfall regime in the west, north-west and south-west portions of the Amazon Basin causes a cyclic water-level fluctuation that can be grouped into four phases: rising season, typically between January and April; flood season, typically between May and July; receding season, typically between August and September; dry season, typically between October and December (Bittencourt & Amadio, 2007; Espinoza-Villar *et al.*, 2009). This seasonal water-level fluctuation (flood pulse) influences the connectivity of the lake with both rivers. Lago Catalão is completely connected with both rivers during the flood season and may be totally isolated during the dry season (Brito *et al.*, 2014). Limnological studies in this region show that lake water characteristics are mainly controlled by the flood pulse regime of the two rivers (Almeida & Melo, 2009; Brito *et al.*, 2014; Caraballo *et al.*, 2014). Although the lake receives a large input of water from both rivers, the Negro appears to have greatest influence on water quality during the early rising-water period, resulting in lower values of conductivity and pH, and the Amazon has dominant influence during most other periods (Brito *et al.*, 2014; Caraballo *et al.*, 2014). The seasonality of connectivity with both rivers and isolation during the dry season and correlated changes in water level also influence dissolved inorganic nutrient concentrations (Aprile & Darwich, 2013) and local phytoplankton productivity (Almeida & Melo, 2011).

SAMPLING AND DATA ANALYSIS

Sampling was performed monthly from June 2010 to July 2011 and from April 2013 to October 2014 (33 months), which encompassed two and a half hydrological cycles and each of the four hydrological phases (rising, flood, receding and dry). Fishes were collected using 10 gillnets with different mesh sizes (30, 40, 50, 60, 70, 80, 90, 100, 120–140 mm between opposite knots), each measuring 10 m in length and from 1.5 to 3.5 m in height. Total monthly fishing effort was $257.26 \text{ m}^2 \times 24 \text{ h}$. Gillnets were set in the same area in a direction running from near shore towards deeper water offshore. During the flood season, gillnets were deployed along the flooded forest border, where the probability of fish capture is generally higher due to higher fish densities near the forest compared with open waters (pers. obs.). Nets were deployed for 24 h, with fishes removed every 6 h. Captured fishes were euthanized in an ice bath and transported in boxes of ice to the laboratory where they were identified, measured for standard length (L_S , mm) and weighed (g). Fish surveys were authorized by IBAMA through licence #101932, and procedures followed the INPA's ethics committee rules (protocol number 33/2012).

During each survey, dissolved oxygen (mg l^{-1}), conductivity ($\mu\text{S cm}^{-1}$) and water temperature ($^{\circ}\text{C}$) were recorded using a multi-variable meter. Although pH could be an important proxy for the relative influence of Negro v. Amazon waters on Lago Catalão, this information was only obtained during portions of the study period and therefore was not included in the analyses. Caraballo *et al.* (2014), however, showed that in years with strong Negro influence during rising-water season, conductivity within the lake declines markedly to values as low as $20\text{--}50 \mu\text{S cm}^{-1}$. Therefore, conductivity was used as a proxy for the influence of Negro River on Lago Catalão. Water-column transparency was not measured; a previous study, however, recorded highest values (*c.* 1 m) during the rising-water season, and during other periods transparency was *c.* 0.6 m (Brito *et al.*, 2014). Depth, aquatic macrophyte abundance and the amount of surrounding forest can also influence fish assemblage structure in floodplain lakes

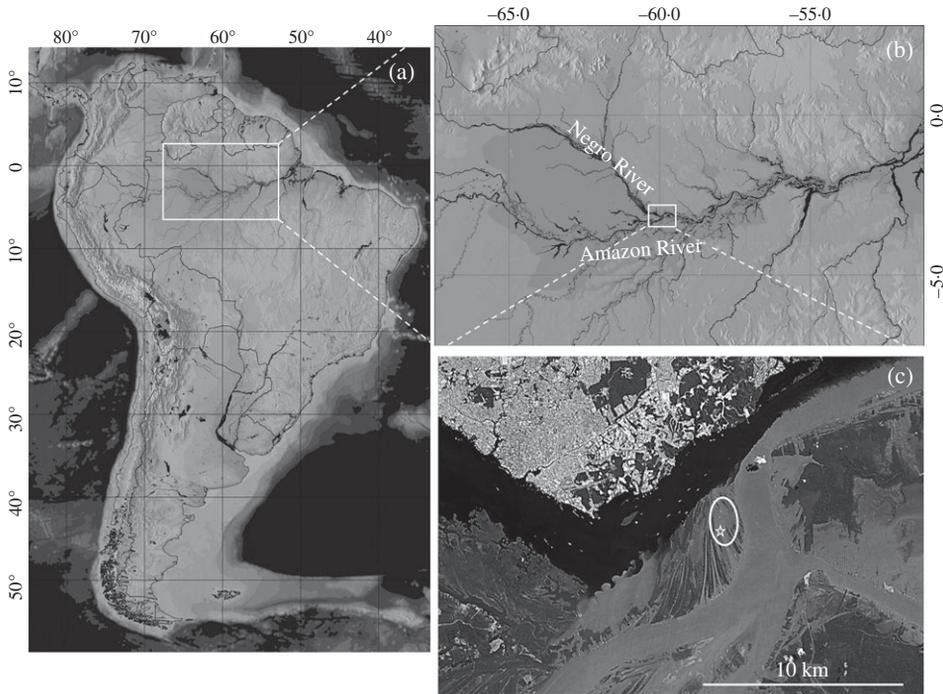


FIG. 1. Location of Lago Catalão; \square highlight location of the study area in relation to (a) South America and the Amazon Basin and (b) Central Amazon. (c) The \bigcirc indicates the perennial portion of Lago Catalão, and the \star indicates the sampling site selected to span a gradient between flooded forest and pelagic area within the lake.

(Pouilly & Rodríguez, 2004; Correa *et al.*, 2008; Scarabotti *et al.*, 2011). At the survey site, aquatic and terrestrial vegetation within littoral habitats vary seasonally more than spatially, and therefore temporal samples are assumed to be fairly representative for the lake as a whole. Measures of water discharge ($\text{m}^3 \text{s}^{-1}$) were obtained from the Brazilian National Water Agency's (Agência Nacional de Águas, ANA) measurements, which were taken at the narrowest portion of the Amazon River *c.* 2.5 km downstream from its confluence with the Negro River. Hydrological phases were classified according to Bittencourt & Amadio (2007), which are based on centennial data of water level recorded at Manaus harbour (*c.* 5 km from the study area). Phase thresholds were: flood season, water level >26 m; receding season, water level between 26 and 20 m; dry season, water level <20 m; rising season, water level between 26 and 20 m.

Relationships between abiotic variables and fish abundance (monthly total number of individuals collected) and species richness (monthly total number of species collected) were analysed using forward stepwise multiple linear regression (one for each dependent variable). All values were transformed as the natural logarithm. The F criterion for independent variables to enter was set at 1.00, and the F value to remove variables was set at 0.99, with tolerance set at 0.0001. Environmental variables were dissolved oxygen, conductivity, water temperature and discharge; water level was not included due to its high correlation with discharge ($r = 0.95$).

To assess how much of the variation in assemblage composition can be statistically explained by temporal changes in abiotic factors, canonical correspondence analysis (CCA) was performed using the same environmental and species abundance data (ln transformed). Statistical significance of correlations between biotic and abiotic components extracted from CCA was determined by a Monte-Carlo test based on 999 permutations. For this analysis, rare species with low frequencies in monthly samples (frequency of occurrence <10) and low abundance (<16 specimens) were omitted because they can skew results (Gauch, 1982); these criteria resulted in

a total of 54 species included in the data matrix and a total of 85 species excluded from the data matrix.

Temporal β -diversity, which implies gain and loss of species due to environmental filtering or biotic interactions (Legendre, 2014), was estimated using Jaccard's similarity index based on presence and absence of species in monthly surveys. Similarity values were tested against a null model using a simulation that assumed the probability of species occurrence is proportional to species frequency in a set of samples (method r1 in oecosimu R). Temporal β -diversity was calculated according to between-hydrological season and between-year differences. Over the study period, two dry-season samples, three rising season samples and four samples each for flood and receding season were obtained, and therefore the possible number within-season, between-year comparisons differed among seasons. A *t*-test was used to compare the mean value for similarity between seasons within a year (data set also included comparisons between consecutive seasons during consecutive years) with the mean value of similarity between different years (comparisons between the same season in different years).

Species occurrence over time was analysed with a modification of the method of Collins (2000) and Ferreira (2007). Core species were defined as those that occurred in >70% of the monthly surveys; occasional species were defined as those that occurred in >20 and <70% of surveys; satellite species occurred in <20% of the surveys. To test whether frequently occurring species had higher average abundance than infrequently occurring species, linear regression was performed on ln-transformed frequency and abundance data. For this analysis, all species captured during the study were included. All analyses were performed with R software (R Development Core Team; www.r-project.org). Multiple regressions were run using the function lm in the default stats library (Oksanen *et al.*, 2014); CCA was run using the function cca in the vegan library; the null model and permutation test between observed and simulated Jaccard's similarity values were performed using oecosimu in the vegan library.

RESULTS

SEASONAL VARIATION IN ASSEMBLAGE STRUCTURE AND RELATIONSHIPS WITH ABIOTIC FACTORS

Surveys produced 6410 fish specimens representing 139 species. Abiotic environmental variables showed pronounced temporal variation associated with seasonal connections between the lake and the Amazon and Negro Rivers (Fig. 2). Conductivity and temperature were higher during the dry season. Conductivity dropped from 140 to *c.* 20 $\mu\text{S cm}^{-1}$ during the rising-water season when Negro River water entered the lake. Dissolved oxygen had a seasonal pattern during 2010–2011, and was the least predictable variable during 2013–2014. Fish abundance from monthly surveys varied from 31 to 741 specimens, and species richness ranged from 15 to 49. Abundance was negatively correlated with discharge [$P < 0.001$; Fig. 3(a)], and positively correlated with conductivity [$P < 0.05$; Fig. 3(b)]; dissolved oxygen and temperature did not contribute significantly to the model and were excluded from the final model (Table I). Species richness was significantly and negatively correlated only with discharge [$P < 0.001$; Fig. 3(a)]. Dissolved oxygen and temperature contributed significantly to the model, but did not have statistically significant correlations with species richness (Table I).

The first two CCA axes modelled nearly 75% of the variance in the relationship between the Lago Catalão fish assemblage (based on 54 non-rare species and 5994 specimens) and abiotic variables. Correlations between assemblage axis scores and physical and chemical variables were high and significant for the complete model (Table II). The gradient defined by the first canonical axis was strongly associated with

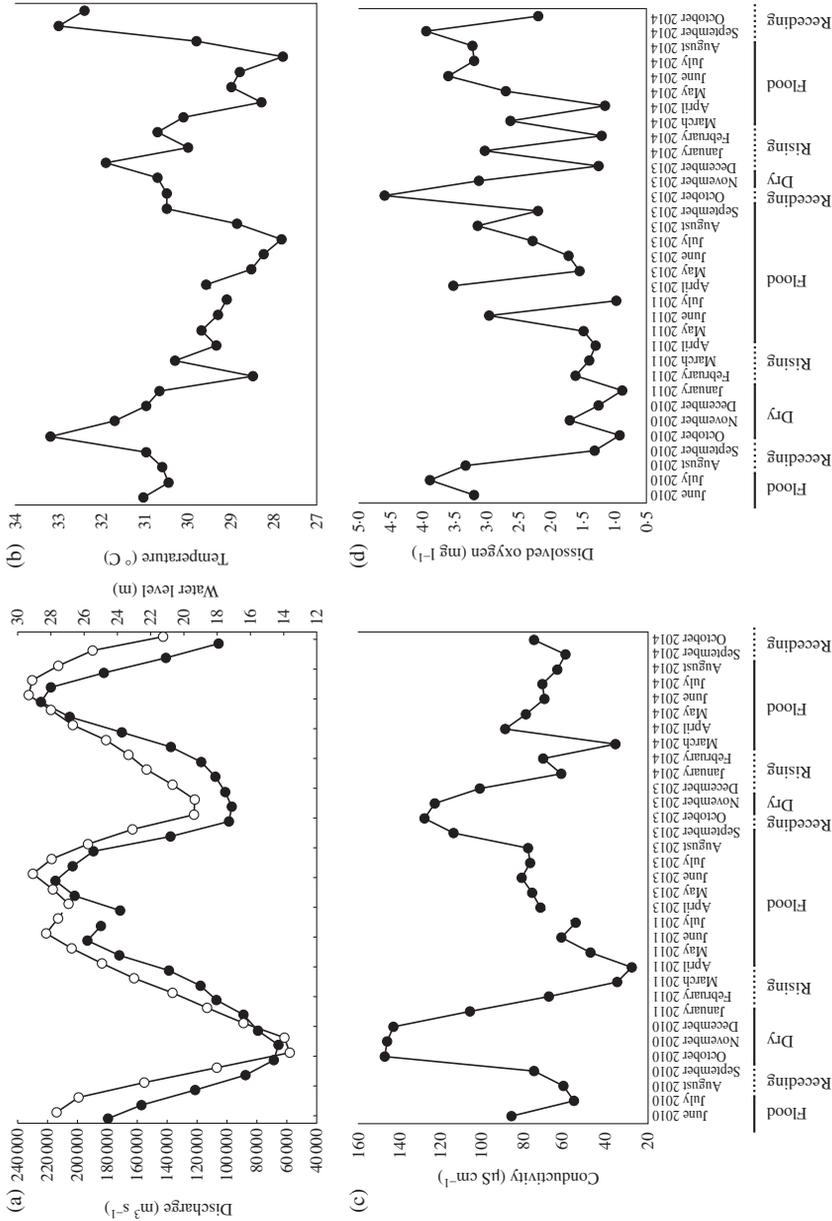


FIG. 2. Temporal variation of (a) discharge (●) and water level (○), (b) temperature, (c) conductivity and (d) dissolved oxygen in Lago Catalão from June 2010 to July 2011 and from April 2013 to October 2014.

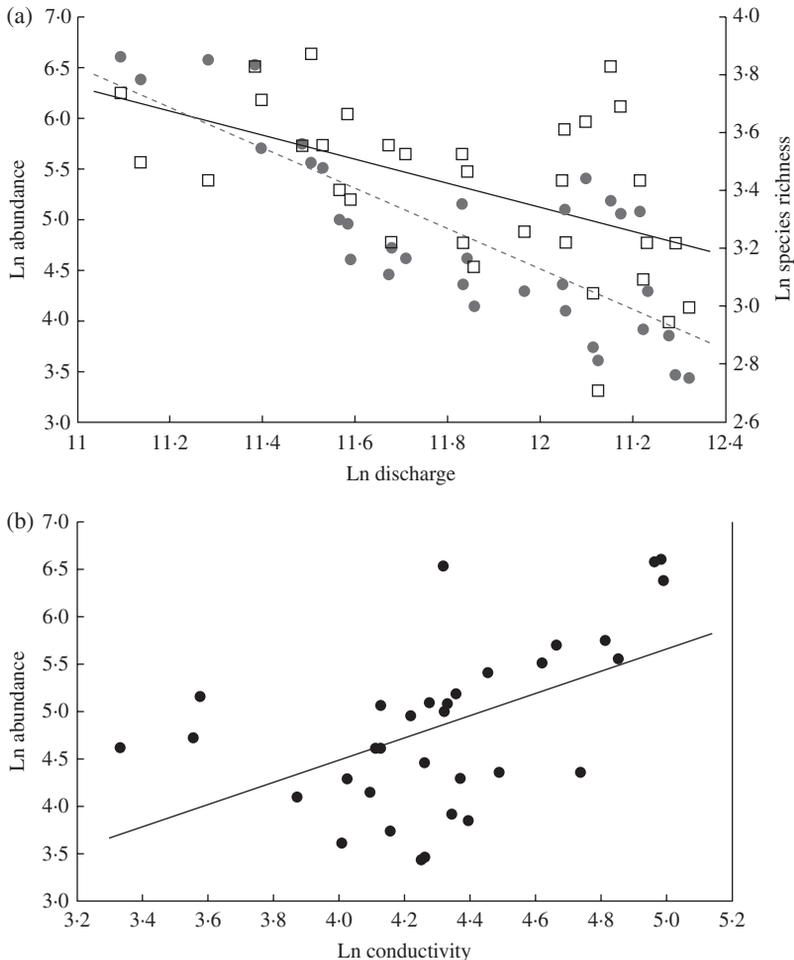


FIG. 3. Relationships of (a) fish abundance (\bullet ; $y = 28.4120 - 1.9919x$; $P < 0.001$) and species richness (\square ; $y = 8.3143 - 0.4144x$; $P < 0.01$) with discharge of the Amazonas River and (b) the relationship of abundance with conductivity ($y = -0.2171 + 1.1758x$; $P < 0.05$) on ln scales.

seasons. Dry-season samples had negative scores, and flood-season samples had positive scores; rising and receding seasons had intermediate scores and high overlap. This gradient was strongly influenced by Amazon River discharge (connecting and disconnecting the lake to the river seasonally) and conductivity increased in the receding and dry months (Fig. 4).

Species positioned at the extremes of the gradient defined by the first CCA axis (Table II) had relatively low abundance and were collected only during either the flood or dry season. Species with the most negative scores on CCA1 (dry season occurrence) were *Auchenipterus britskii* Ferraris & Vari 1999, *Hydrolycus scomberoides* (Cuvier 1819), *Auchenipterichthys coracoideus* (Eigenmann & Allen 1942), *Curimata knerii* Steindachner 1876, *Curimatella meyeri* (Steindachner 1882) and *Psectrogaster amazonica* Eigenmann & Eigenmann 1889 (Table II). Species with largest positive

TABLE I. Results of multiple regressions with reduced model with species abundance and richness *v.* abiotic environmental variables. Data were ln transformed to reduce distribution skew and kurtosis

		Model						
Dependent	Independent	<i>n</i>	β	<i>t</i>	<i>P</i>	<i>R</i> ² adjusted	<i>F</i>	<i>P</i>
Abundance	Intercept	33	3.78	2.94	<0.01	0.62	27.07	<0.001
	Discharge		-0.65	-5.60	<0.01			
	Conductivity		0.29	2.50	<0.05			
Richness	Intercept	33	10.72	2.24	<0.05	0.30	5.70	<0.01
	Discharge		-0.87	-3.63	<0.01			
	Dissolved oxygen		0.28	1.72	>0.05			
	Temperature		-0.33	-1.44	>0.05			

scores on CCA1 (flood season occurrence) were *Brycon amazonicus* (Spix & Agassiz 1829), *Semaprochilodus taeniurus* (Valenciennes 1821), *Ageneiosus dentatus* Kner 1858, *Ageneiosus ucayalensis* Castelnau 1855, *Plagioscion squamosissimus* (Heckel 1840), *Mesonauta festivus* (Heckel 1840), *Rhaphiodon vulpinus* Spix & Agassiz 1829, *Dekeyseria amazonica* Rapp Py-Daniel 1985, *Pellona castelnaeana* Valenciennes 1847, *Hypophthalmus marginatus* Valenciennes 1840 and *C. macropomum* (Table II). Samples from rising and receding-water periods contained not only many cichlids (*e.g.* *Cichla monoculus* Spix & Agassiz 1831 and *Heros spurius* Heckel 1840), but

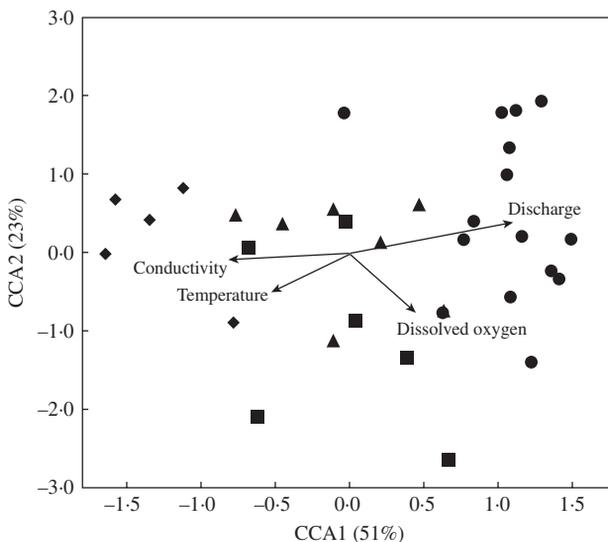


FIG. 4. Ordination plot of Lago Catalão surveys (conducted from June 2010 to July 2011 and April 2013 to October 2014) for the first two gradients (axes) derived from canonical correspondence analysis (CCA); vectors represent correlations of environmental variables with the two gradients; scores on the first two axes for species with highest scores appear in Table II. Symbols designate hydrological season: flood (●); receding (■); dry (◆); rising (▲).

TABLE II. Canonical correspondence analysis (CCA) results for Lago Catalão fish species and abiotic variables

	CCA1	CCA2	CCA3	CCA4
Correlations of environmental variables with axes				
Dissolved oxygen	-0.41	0.633	-0.207	0.293
Conductivity	0.672	0.003	-0.527	0.088
Temperature	0.482	0.328	-0.166	-0.583
Discharge	-0.81	-0.245	-0.137	0.188
Eigenvalues	0.169	0.076	0.046	0.039
Species variance data				
% of explained variance	0.51	0.231	0.138	0.118
% cumulative	0.51	0.742	0.881	1
Monte-Carlo permutation test for eigenvalues				
Pearson correlation for species – environmental variables	0.892	0.818	0.812	0.827
<i>P</i> (permutation test full model)	0.001			
Correlation values for species with strongest positive scores in axis 1				
<i>Brycon amazonicus</i>	1.166	0.816		
<i>Semaprochilodus taeniurus</i>	0.890	0.237		
<i>Ageneiosus ucayalensis</i>	0.750	-0.107		
<i>Ageneiosus dentatus</i>	0.746	0.803		
<i>Plagioscion squamosissimus</i>	0.702	-0.337		
<i>Mesonauta festivus</i>	0.694	0.101		
<i>Rhaphiodon vulpinus</i>	0.653	-0.245		
<i>Dekeyseria amazonica</i>	0.633	-0.076		
<i>Pellona castelnaeana</i>	0.605	0.082		
<i>Colossoma macropomum</i>	0.596	0.093		
<i>Hypophthalmus marginatus</i>	0.559	0.023		
<i>Semaprochilodus insignis</i>	0.525	0.090		
Correlation values for the species with strongest negative scores in axis 1				
<i>Auchenipterus britskii</i>	-0.963	0.212		
<i>Hydrolycus scomberoides</i>	-0.787	-0.338		
<i>Auchenipterichthys coracoideus</i>	-0.769	0.228		
<i>Curimata knerii</i>	-0.720	-0.203		
<i>Curimatella meyeri</i>	-0.673	0.210		
<i>Psectrogaster amazonica</i>	-0.660	0.281		
<i>Anodus</i> sp.	-0.460	0.334		
<i>Potamorhina altamazonica</i>	-0.451	-0.059		
<i>Hoplias malabaricus</i>	-0.441	0.033		
<i>Plagioscion montei</i>	-0.392	-0.459		
<i>Auchenipterus nuchalis</i>	-0.391	0.313		
<i>Serrasalmus</i> sp.n.	-0.339	-0.089		

also a mix of sedentary and short and medium-distance migratory species [*Triporthus albus* Cope 1872, *Hypoptopoma gulare* Cope 1878, *Serrasalmus elongatus* Kner 1858, *Mylossoma aureum* (Spix & Agassiz 1829), *Pellona flavipinnis* (Valenciennes 1837), *Schizodon fasciatus* Spix & Agassiz 1829 and *Hemiodus immaculatus* Kner 1858] (Table SI, Supporting Information).

TABLE III. Jaccard similarity index for pair-wise comparisons of fish assemblage samples among hydrological seasons and years. Comparisons between seasons in the same year and consecutive seasons are underlined. Comparisons between same season in different years are in parentheses

	Flood 2010	Receding 2010	Dry 2010	Rising 2011	Flood 2011	Receding 2011	Rising 2013	Flood 2013	Receding 2013	Dry 2013	Rising 2014	Flood 2014
Receding 2010	0.53											
Dry 2010	<u>0.35</u>	0.50										
Rising 2011	0.42	<u>0.41</u>	0.44									
Flood 2011	(0.51)	0.35	<u>0.37</u>	0.37								
Receding 2011	0.47	(0.41)	0.42	<u>0.48</u>	0.43							
Rising 2013	0.42	0.43	0.43	<u>0.53</u>	<u>0.38</u>	0.40						
Flood 2013	(0.50)	0.49	0.40	0.51	(0.52)	0.52	0.49					
Receding 2013	0.37	(0.45)	0.43	0.41	0.38	(0.48)	<u>0.43</u>	<u>0.39</u>				
Dry 2013	0.34	0.47	(0.53)	0.40	0.39	0.43	<u>0.45</u>	<u>0.42</u>	<u>0.42</u>	0.40		
Rising 2014	0.51	0.47	0.41	(0.48)	0.35	0.41	(0.48)	0.45	0.43	<u>0.39</u>	0.49	
Flood 2014	(0.49)	0.42	0.36	0.40	(0.43)	0.43	0.39	(0.49)	0.47	<u>0.39</u>	<u>0.37</u>	
Receding 2014	0.39	(0.39)	0.31	0.38	0.37	(0.44)	0.40	0.38	(0.41)	0.39	<u>0.37</u>	0.36

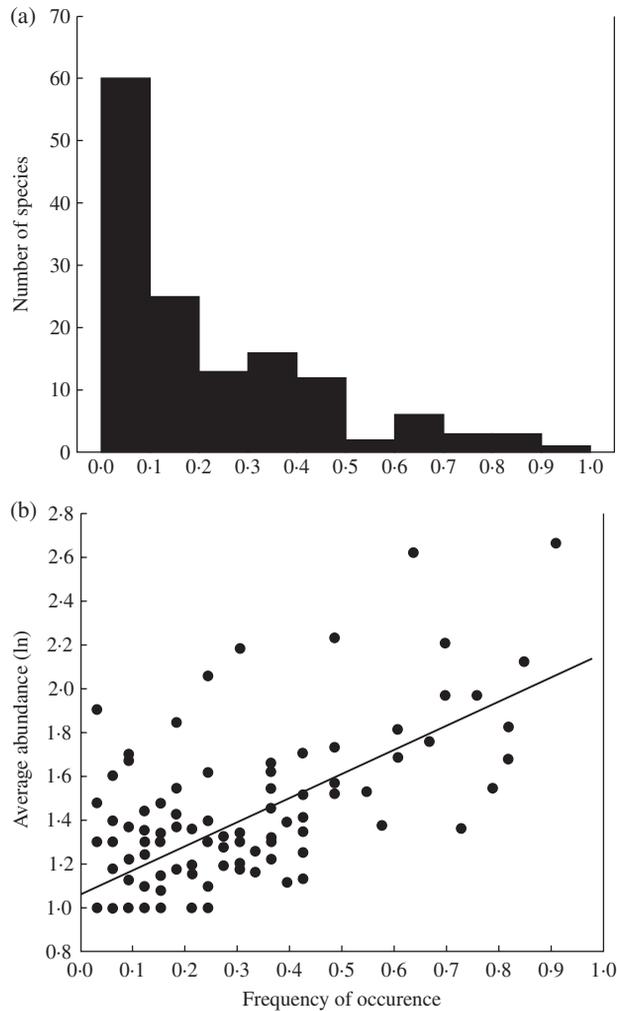


FIG. 5. (a) Histogram with number of species with various frequencies of occurrence over time and (b) linear regression of \ln species average abundance and frequency of occurrence over time ($y = 0.1396 + 0.9653x$; $P < 0.001$).

Temporal β -diversity

Jaccard similarity between different seasons of the same year (mean = 0.43) was lower than the Jaccard similarity of the same season between years (mean = 0.47) (t -test = 2.22, d.f. = 30, $P < 0.05$; Table III). The mean Jaccard similarity index for all pair-wise seasonal comparisons was 0.41, indicating high temporal β -diversity, and this value was higher than expected by a null model (mean = 0.36; permutation test, $P < 0.001$). Eighty-two species were classified as satellite species, 50 were occasional species and only seven [*Acestrorhynchus falcirostris* (Cuvier 1819), *Hoplosternum littorale* (Hancock 1828), *Pygocentrus nattereri* Kner 1858, *Rhytidodus microlepis* Kner 1858, *S. fasciatus*, *T. albus* and *Triportheus angulatus* (Spix & Agassiz 1829)] were core species that occurred in >70% of monthly samples [Fig. 5(a) and

Table SI (Supporting Information)]. More frequent species had higher average abundance ($r = 0.69$, $P < 0.001$) [Fig. 5(b)]. Proportional contributions of core and occasional species to the total assemblage were highest during the dry season (core: rising = 7%, flood = 6%, receding = 8%, dry = 10%; occasional: rising = 49%, flood = 46%, receding = 50%, dry = 53%); proportional contribution of satellite species was highest during the flood season (rising = 43%, flood = 46%, receding = 41%, dry = 35%).

DISCUSSION

The fish assemblage of Lago Catalão undergoes major compositional changes during water-level fluctuations associated with the annual flood pulse of the central Amazon region; consequently, temporal β -diversity was high. Seasonal changes in water level result in changes in lateral connectivity and aspects of the lake's abiotic environment, including water quality, degree of floodplain forest inundation and aquatic macrophyte cover (Junk & Piedade, 1997). Core species (those occurring in >70% of monthly samples) tended to be more abundant throughout the entire study period; however, the fish assemblage was dominated by occasional (occurrence >20 and <70%) and satellite (occurrence <20%) species, and the proportional contribution of these groups to the assemblage varied seasonally. Similar seasonal variation in fish assemblage structure in floodplain lakes has been documented for river basins in many tropical (Rodríguez & Lewis, 1997; Tejerina-Garro *et al.*, 1998; Galacatos *et al.*, 2004; Jackson *et al.*, 2013; Silva *et al.*, 2013) and temperate (Winemiller *et al.*, 2000; Zeug *et al.*, 2005; Bleesey *et al.*, 2012) regions. Although several studies have examined seasonal change in fish assemblages of floodplain lakes, studies reporting values for temporal β -diversity are scarce. Freitas *et al.* (2010) found 47–60% assemblage turnover between flood and dry seasons in island lakes of the Amazon River in the central Amazon. The mean Jaccard similarity for between-season comparisons is equivalent to *c.* 60% species turnover. High seasonal turnover in fish assemblages observed in this study and by Freitas *et al.* (2010) suggest a general phenomenon in floodplain lakes of the central Amazon. Comparison of observed Jaccard similarity values with values simulated by a null model indicated that seasonal species turnover was greater than expected by chance. It should be noted that data sets involving large species pools tend to produce null models with relatively low expected values (Chase *et al.*, 2011). A question that arises from these results is whether high diversity and turnover rates found in this study are uniquely derived from the influence of two of the world's largest rivers. Previous research showed that segments of the Amazon River just downstream from confluences with major tributaries have higher species diversity of gymnotiformes than stretches located above confluences (Fernandes *et al.*, 2004). Gascon & Smith (2004) suggested that when large rivers join, distinctive biotas of each river may persist over considerable distances downstream. They further proposed that species coexistence might be enhanced by greater food availability and habitat stability in these confluence zones. Opposing this hypothesis is the fact that no species were captured in Lago Catalão that are exclusively Negro River inhabitants and considered exclusively adapted to black waters. What is clear is that the lake's proximity to two rivers and long periods of lateral connectivity result in a local community dominated by temporary residents.

Lateral migration during the flood pulse allows fishes to exploit habitats and resources (Lowe-McConnell, 1987; Winemiller & Jepsen, 1998; Petry *et al.*, 2003a).

Fish abundance and species richness in Lago Catalão were highest during the dry season, a finding consistent with those from studies of floodplain lakes in the Orinoco River and other parts of the Amazon (Rodríguez & Lewis, 1994; Fernandes, 1997; Saint-Paul *et al.*, 2000; Galacatos *et al.*, 2004; Lin & Charamaschi, 2005; Silva *et al.*, 2013). During the flood season, fish abundance and species richness in survey samples are generally lower due to expansion of aquatic habitat that reduces per-unit-area densities of fishes (Saint-Paul *et al.*, 2000). The large number of fishes captured from Lago Catalão during the dry season of 2010 probably was a consequence of a drought that was considered one of the strongest of the century (Marengo *et al.*, 2011). Petry *et al.* (2003b) also found higher fish diversity in disconnected floodplain lakes of the Paraná River during dry years. These authors suggested that, despite having harsh environmental conditions during drought, disconnected lakes promote species coexistence because they are more productive than connected lakes. Extreme drought conditions sometimes result in massive fish mortality in central Amazon floodplain lakes (pers. obs.), which should contribute to reduce local species richness.

Lateral connectivity during high-water periods apparently facilitated entry of migratory fishes into Lago Catalão; these species included *B. amazonicus*, *S. taeniurus*, *P. squamosissimus*, *R. vulpinus*, *P. castelnaeana*, *C. macropomum*, *A. dentatus* and *A. ucayalensis*. Granado-Lourencio *et al.* (2005) found that floodplain lakes closer to the active river channel had greater abundance of migratory fishes during the annual flood pulse compared with lakes located further from the river and that were less connected. In Mamoré River, flowing from Bolivia to Brazil, the type of lateral connection (seasonal *v.* permanent) strongly influences fish assemblage composition in floodplain lakes (Pouilly & Rodríguez, 2004). Some of the species found in Lago Catalão only during the food season, or captured in much greater numbers during the flood season, were detritivores and periphyton grazers (*S. taeniurus*) and frugivores (*e.g.* *B. amazonicus* and *C. macropomum*), two trophic guilds with strong dependence on flooded forests (Goulding *et al.*, 1988; Claro-Junior *et al.*, 2004; Oliveira *et al.*, 2006; Correa & Winemiller, 2014). Some studies suggest that availability of food resources in floodplains is directly proportional to the flooded area (Claro-Junior *et al.*, 2004), which in turn is influenced by the magnitude of the flood pulse (Melack & Hess, 2010). In this study, flood periods were sampled during years with flood pulses of relatively large magnitude and long duration, especially during 2013 and 2014. This could have contributed to greater frequencies of occurrence of migratory fishes in the lake, although most of the specimens were immature [average L_S : *B. amazonicus* 178.5 mm, *S. taeniurus* 109 mm and *C. macropomum* 144 mm; Table SI (Supporting Information)]. In the Paraná River, years with intense floods were found to be associated with greater juvenile survival and recruitment of the migratory detritivore *Prochilodus lineatus* (Valenciennes 1837) (Gomes & Agostinho, 1997). Other fish species captured from Lago Catalão only during the flood season included carnivores and piscivores (*e.g.* *P. squamosissimus*, *R. vulpinus*, *P. castelnaeana*, *A. dentatus* and *A. ucayalensis*). This suggests that prey availability is greater in floodplain lakes compared with the river channel during flooding periods. When flooding recedes (August to September) and water drains from the lake into the main channel, these piscivores and many of their prey move with it (Fernandes, 1997). Migratory piscivores, frugivores and detritivores were extremely absent or rare within present dry-season surveys.

During the dry season, lateral connectivity declines until migration between the lake and river channel is no longer possible. The area of the lake also declines during this period, and assemblage structure should be strongly influenced by local processes, such as aquatic primary production, predation and competition. Under these circumstances, changes in species relative abundance may be a function of differential mortality from predation and stressful abiotic (*e.g.* hypoxia) and biotic (*e.g.* parasitism) conditions (Rodríguez & Lewis, 1994). These factors can also influence distributional patterns of species among floodplain habitats (Rodríguez & Lewis, 1997; Tejerina-Garro *et al.*, 1998; Layman & Winemiller, 2005). Water temperature and conductivity in Lago Catalão were high, and dissolved oxygen concentrations were often low during dry seasons. The fish assemblage during this time was dominated by *A. britskii*, *A. coracoideus*, *C. knerii*, *C. meyeri*, *P. amazonica*, *Psectrogaster rutiloides* (Kner 1858), *T. albus* and *T. angulatus*, which are mostly small species that are either non-migratory or migrants over short distances among local habitats. Some of the most abundant species captured during the dry season (five species of Curimatidae and two species of *Triportheus*) were fishes with special adaptations for coping with hypoxia (Winemiller, 1989; Jucá-Chagas, 2004; Soares *et al.*, 2006). Fernandes (1997) suggested that conditions of Amazonian floodplain lakes during the dry season could be a strong filter, selecting for a sub-set of resident species able to cope with stressful abiotic conditions, and another sub-set of migratory species that exit the lakes before conditions become severely degraded. Interannual consistency of a distinct species composition dominated by core species during the dry season in Lago Catalão supports this hypothesis. Core species experienced a greater degree of environmental variation, (*e.g.* enduring harsh dry-season conditions), and most of these species are widely distributed in the Amazon [*e.g.* *A. falcistrostris*, *R. microlepis*, *T. albus*, *T. angulatus*, *H. littorale* and *P. nattereri*; Reis *et al.* (2003)], a pattern that suggests tolerance to the range of environmental conditions that occur in floodplain aquatic habitats seasonally.

The confluence of the Amazon and Negro Rivers just downstream from Lago Catalão is a unique geographic feature with circumstances that may contribute to high fish diversity and abundance. Although influenced by two large rivers with divergent water chemistry, Lago Catalão had a fish assemblage dominated by species restricted to white waters (Amazon River) and those commonly encountered in both black (Negro River) and white waters, but none of the captured species would be considered black-water specialists [Saint-Paul *et al.*, 2000; Table SI (Supporting Information)]. Henderson & Crampton (1997) compared fish assemblages in floodplain lakes in central Amazon that had white *v.* black waters and found high similarity. They suggested that black-water fish assemblages might comprise a subset of white-water assemblage. They further proposed that dissolved oxygen concentration and biotic interactions are more important than differences in chemistry of black *v.* white water in determining species distributions, and findings from Lago Catalão appear consistent with this interpretation.

Natural flood regimes in tropical floodplains sustain biodiversity and productivity of important fisheries (Lowe-McConnell, 1987; Ward *et al.*, 1999; Winemiller, 2004). The central Amazon supports abundant migratory fishes with high market value, including *C. macropomum* and *P. nigricans*. Recent population genetics research (Ardura *et al.*, 2013) estimated that the central Amazon region receives fewer immigrant *C. macropomum* and *P. nigricans* than the number of fish emigrating to other regions of

the basin. Consistent with recommendations derived from recent assessments of Amazonian fisheries (Batista & Petrere, 2007; Arantes *et al.*, 2013; Freitas *et al.*, 2014), this study emphasizes the need for protected areas with extensive floodplains and lateral connectivity to maintain fish diversity and productivity in the central Amazon.

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Supporting Information

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

Table SI Seasonal abundance, frequency of occurrence over time (FOT) and range in standard length (L_S) of the species in Lago Catalão (confluence of the Amazonas and Negro Rivers, central Amazon, Brazil) during the period of June 2010 to July 2011 and April 2013 to October 2014. Monthly data were grouped in hydrological seasons. Trophic category was inferred by stomach content analysis and published literature

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