Received: 19 April 2017 | Revised: 20 December 2017 | Accepted: 15 February 2018
DOI: 10.1002/aqc.2910

RESEARCH ARTICLE

WILEY

Ecological influences of human population size and distance to urban centres on fish communities in tropical lakes

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Funding information
Conselho Nacional de Desenvolvimento Científico e Tecnológico, Grant/Award Number: 309014/2013-1; Coordenação de Aperfeiçoamento de Pessoal de Nível Superior, Grant/Award Number: 1286-15-135227/14-3883/2010; Eletrobras, Grant/Award Number: 4500057477; Fundação Amazônia Paraense de Amparo à Pesquisa, Grant/Award Number: 108/2008; Fundação de Amparo à Pesquisa do Estado de São Paulo, Grant/Award Number: 1998/16160-5; Instituto de Desenvolvimento Sustentável Mamirauá

Abstract

1. Human population growth is a major cause of species extinction worldwide, and tropical fresh waters are among the most imperilled ecosystems. The identification of major drivers of human impacts on fish can benefit conservation programmes and management plans.
2. The influences of the proximity to urban centres and human population size on six ecological indicators of fish communities (abundance, biomass, richness, diversity, average size, and size dominance pattern) were investigated in 48 floodplain lakes of five main rivers of the Brazilian Amazon (Tocantins, Tapajós, Negro, Solimões, and the Lower Amazon). These ecological indicators were also compared among the rivers studied and checked for any influence of the environmental variables of lakes (size, shape of natural shoreline, distance to the main river channel, depth, transparency, conductivity, and dissolved oxygen).
3. Lake distance to urban centre was positively related to average fish size and dominance of large fish, indicating direct human effects caused by fisheries or indirect effects by habitat alteration (e.g. deforestation). Unexpected positive relationships between human population size and the richness and diversity of fishes were found, and may be caused by ecological compensatory effects, the abundance of rare non-fished species, or the proximity of an urban centre to ecotone areas. The other ecological indicators were unrelated to anthropogenic variables. Environmental factors affected fish communities, but did not change the conclusions regarding the effect of the anthropogenic variables. River basin was strongly related to species richness, diversity, biomass, and abundance of fish. Distance to the river channel was positively related to fish biomass.
4. The disappearance of large fish threatens the food security of riverine communities, and may harm essential ecosystem services. Conservation measures, including local management initiatives, protected areas, fisheries monitoring, and the

enforcement of existing fishing rules need to be improved or established near urban centres in order to restore healthy fish communities in the Brazilian Amazon.

KEYWORDS

Amazon Basin, ecological indicators, environmental impact assessment, fish, fisheries management, fishing, floodplain, lake

1 | INTRODUCTION

Anthropogenic changes have affected ecological processes on a global scale, increasing the rate of biological extinctions (Steffen, Grinevald, Crutzen, & McNeill, 2011). The human population is growing at a faster pace in regions that are biodiversity hotspots or important biodiversity areas, such as in the Amazon Basin (Williams, 2013). Therefore, it is important to understand the spatial patterns of human impacts to inform conservation planning, especially in tropical developing countries. Proximity to large human settlements may be associated with higher environmental degradation, owing to the increased demand for natural resources, more waste and pollution, or the greater probability of the introduction of invasive species (Halpern, Selkoe, Micheli, & Kappel, 2007; Spear, Foxcroft, Bezuidenhout, & McGeoch, 2013; Stuart-Smith et al., 2015). Regions with high human densities have higher rates of deforestation (Laurance et al., 2002), reduced species richness of birds and mammals (McKinney, Kick, & Fulkerson, 2010), as well as reduced functional diversity, biomass, and average trophic level of fish (Brewer, Cinner, Green, Fisher, & Wilson, 2012; Brewer, Cinner, Green, & Pressey, 2013; Clausen & York, 2008; D'agata et al., 2014).

Sites closer to urban centres or more densely populated regions show greater environmental degradation or higher fishing pressure on fish communities in tropical coral reefs (Aswani & Sabetian, 2009; Brewer, Cinner, Green, & Pandolfi, 2009). Increasing urbanization and populations may increase the demand for fish and lead to the disruption of food security and to fishery conflicts (McClanahan, Allison, & Cinner, 2015). Most of the studies on the influences of urban centres on fish communities are from marine ecosystems, and little information exists for broader-scale biodiversity patterns in fresh waters (Brooks, Holland, Darwall, & Eigenbrod, 2016). Nevertheless, their proximity to human settlements and development enterprises makes fresh waters one of the most severely threatened ecosystems in the world (Abell, 2002), with extinction rates up to five times greater than expected for terrestrial fauna (Sala et al., 2000). Eutrophication, riparian deforestation, dams, introductions of non-native species, and overfishing are among the more relevant human impacts on freshwater ecosystems (Brönmark & Hansson, 2002; Lobón-Cerviá, Hess, Melack, & Araujo-Lima, 2015; Richter, Braun, Mendelson, & Master, 1997; Winemiller et al., 2016). In some of the world's most populated freshwater ecosystems, the 'fishing down' process has reduced the overall size of exploited fish communities through the selective removal of larger fish (Welcomme, 1999; Welcomme et al., 2010). These changes in fish communities induced by excessive fishing can be expressed by the relationship between the dominance of numerical abundance and the dominance in biomass of all species in a given community, which is expressed by the abundance biomass curve (ABC curve; Warwick & Clarke, 1994; Yemane, Field, & Leslie, 2005). Fish communities in stable environments with low fishing pressure are expected to have a relatively high proportion of species with large body size and slow growth (typical of K strategists), which would tend to position the biomass curve above the numerical curve. Conversely, environments with high fishing pressure are expected to have a relatively high proportion of fish species with smaller body sizes and shorter life cycles (typical of r strategists), and consequently the biomass curve would tend to lie below the numerical abundance curve (Yemane et al., 2005).

The Brazilian Amazon has one of the highest per capita fish consumptions in the world (Isaac et al., 2015), which is sustained by widespread small-scale fisheries (Hallwass & Silvano, 2016; Isaac, Silva, & Ruffino, 2008) that exploit aquatic habitats with high diversity and endemism of fish species (Junk, Soares, & Bayley, 2007). Current conservation policies have not properly addressed these biodiversity-rich freshwater ecosystems in the Brazilian Amazon, which have been threatened by development projects (especially dams), habitat degradation (urbanization and deforestation), and overfishing (Ferreira et al., 2014; Hallwass & Silvano, 2016; Nepstad et al., 2002; Winemiller et al., 2016). This combination of hotspots in fish biodiversity, impending environmental threats, importance for food security, and lack of conservation policies make the Brazilian Amazon an excellent case study to investigate potential human impacts on freshwater fish.

Excessive fishing pressure might be related to increasing urban settlements in the Brazilian Amazon (Hallwass & Silvano, 2016; Petrere, Barthem, Córdoba, & Gómez, 2004), and previous studies have indicated a decrease in the abundance and size of a valuable commercial fish species near a major Amazonian city (Petrere, 1986; Tregidgo, Barlow, Pompeu, Rocha, & Parry, 2017). To the best of our knowledge, however, no study has evaluated the influence of urban centres on the ecological characteristics of fish communities there, or in other tropical freshwater ecosystems. The aim of this study was to investigate the influences of the proximity to urban centres and human population size (indicators of human pressure) on six ecological indicators of fish communities in five rivers of the Brazilian Amazon. The indicators analysed were numerical abundance, biomass, species richness, Shannon–Wiener diversity, average size, and size dominance pattern, estimated by a combination of the ABC curve and the *W* statistic (Yemane et al., 2005). Previous studies on tropical coral reefs indicate that these indicators might be affected by intensive fishing (Aswani & Sabetian, 2009; Brewer et al., 2009; Brewer et al., 2013; Vallès & Oxenford, 2015). This study thus tested the hypotheses that all ecological indicators would be positively related to the distance to urban centres, and inversely related to human population size. The ecological indicators of fish communities were compared among the five rivers studied to check for possible regional variations. Relationships between the ecological characteristics of fish communities and the local environmental variables (lake size, shape of natural shoreline, distance to the main river channel, depth, transparency, conductivity, and dissolved oxygen) were also checked to identify potential confounding factors.

2 | METHODS

2.1 | Study site

The region studied includes stretches of five large rivers in the Brazilian Amazon: Tocantins, Negro, Solimões, Tapajós, and the Lower Amazon (Figure 1). These rivers have seasonally inundated floodplains, which connect the aquatic habitats (main river, channels, lakes, and flooded forests) during the high-water season (Junk et al., 2007), but differ in their physical–chemical composition and productivity (Table 1). The Lower Amazon and Solimões rivers have white waters, with high conductivity, reduced transparency, neutral pH, and high concentrations of nutrients, and are thus more productive (Junk et al., 2007). The Tapajós and Tocantins rivers have clear oligotrophic waters, with low conductivity and pH close to neutral. The Negro River has black waters, which have low nutrient levels and acidic pH values, owing to large quantities of dissolved organic matter, such as humic and fulvic compounds (Goulding, Carvalho, & Ferreira, 1988). More information on the environmental characteristics, fish, and fisheries of each river can be found in previous studies (Begossi, Silvano, & Ramos, 2005; Keppeler, Hallwass, & Silvano, 2017; Silva & Begossi, 2009; Silvano et al., 2014; Silvano, Ramires, & Zuanon, 2009).

2.2 | Fish sampling

Data were analysed from previous studies (Keppeler et al., 2017; Silvano et al., 2009; Silvano et al., 2014), together with original data of 11 158 fish sampled in 48 floodplain lakes, from 2000 to 2013 (Table 1). Lakes with fewer than 10 individual fish collected were excluded from the analyses. Two sets of seven monofilament gillnets with distinct mesh sizes (15, 25, 35, 50, 60, 70, and 80 mm between adjacent knots) were used for sampling in open water. Gillnets had a length and height varying between 10 and 30 m, and between 1.5 and 2.5 m, respectively. The two sets of gillnets (panels with different mesh sizes attached in a crescent order) were placed in distinct areas within each lake, considering the suitability of sites for gillnet fishing. One end of the gillnets (smaller mesh) was tied to the marginal vegetation (shoreline) and the other end (larger mesh) was stretched towards the deeper zones of the lake. The gillnets were set in the water for a period of 8 to 10 h during the daytime (between 06:00 and 18:00 h), and were checked for fish every 2–4 h. Only samples taken in the low-water season were analysed, when fish sampling is more efficient owing to an increased fish density in restricted water bodies, resulting in increased catches with gillnets (Silvano, Amaral, & Oyakawa, 2000). Furthermore, it is precisely during the periods of receding water and low water when fishing boats usually increase

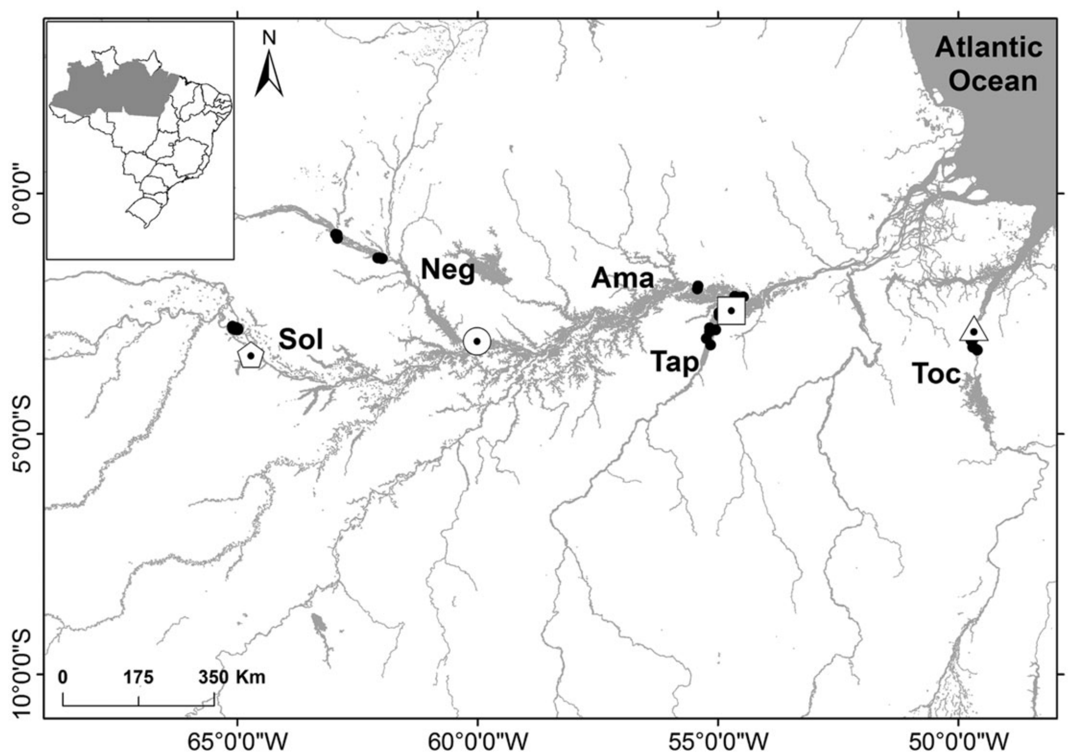

FIGURE 1 Location of the five rivers studied in the Brazilian Amazon Basin. Black circles indicate the sampled lakes. The rivers are indicated by abbreviations: Ama, Lower Amazon; Neg, Negro; Sol, Solimões; Tap, Tapajós; and Toc, Tocantins. Symbols with a small dot in the middle indicate urban centres: pentagon, Tefé; circle, Manaus; square, Santarém; triangle, Baião

TABLE 1 Location, number of floodplain lakes sampled, number of fish collected, sampling years, duration of the dry season (start and end months), water type, and source of data collected in five rivers in the Brazilian Amazon

River	No. lakes	No. fish	Year	Dry season[a]	Water	Urban centre	Distance (km) (min–max)	Cities (number of lakes)	Population of main cities (census year) [b]
Tocantins [c]	12	3321	2007	09–11	Clear	Baião	37.7 (18.7–58.4)	Baião (12)	36 882 (2010)
Negro	7	175	2000	12–03	Black	Manaus	353.2 (284.3–433.9)	Barcelos (7)	24 197 (2000)
Solimões [d]	14	1194	2003	10–12	White	Tefé	96 (85.5–103.3)	Uarini (14)	10 254 (2000)
Tapajós [e]	9	409	2013	10–12	Clear	Santarém	63.5 (10.0–113.8)	Santarém (7) Belterra (2)	294 580 (2010) 16 318 (2010)
Lower Amazon	6	6059	2006–2009	10–12	White	Santarém	64.2 (32.7–113.5)	Santarém (3) Óbidos (2) Monte Alegre (1)	294 580 (2010) 49 333 (2010) 55 462 (2010)

[a]The dry season period was established according to data gathered from the National Agency of Waters (ANA, http://hidroweb.ana.gov.br/). Numbers refer to months of the year.

[b]Census data of population sizes were gathered from the Brazilian Institute of Geography and Statistics (IBGE, http://www.censo2010.ibge.gov.br/sinopse/index.php? uf=13&dados=29).

[c]Silvano et al. (2014).

[d]Silvano et al. (2009).

[e]Keppeler et al. (2017).

the fishing effort in floodplain lakes (Keppeler et al., 2017). Gillnet sampling usually catches mostly open water or demersal fish, which include most or all fish regularly exploited by fisheries.

All fish collected were identified to species level, measured (standard length), and weighed; most of them were released alive or donated to local fishers afterwards. At least one individual of each species was anesthetized with clove oil, fixed in 10% formaldehyde, and identified in the laboratory. Voucher specimens were deposited in research institutions (Instituto Nacional de Pesquisas da Amazônia, Universidade Federal do Pará, and Universidade Federal do Oeste do Pará).

2.3 | Response variables: fish ecological indicators

Catch per unit effort (CPUE) of the biomass and number of sampled fish was calculated by dividing the total number or biomass sampled in each lake by the total duration (hours) of sampling, multiplied by the total area (m^2) of gillnets. The species richness of each lake was estimated through an individual-based rarefaction procedure (Gotelli & Colwell, 2011). The diversity index of Shannon–Wiener was also calculated (Pielou, 1966).

The average length of all fish individuals collected in each lake was calculated. In addition, the size dominance pattern (as measured by the ABC curve and the *W* statistic) for all fish species in each lake was assessed. The ABC is a graphical method to compare the dominance of numerical abundance with the dominance in biomass of all species in a given community (Warwick & Clarke, 1994). After plotting the ABC graphs, the area between the biomass and numerical abundance curves was calculated, resulting in the *W* statistic. This metric yields values that range between −1, when the fish community is dominated by small fish species (and the biomass curve lies below the numerical abundance curve), and + 1, when the fish community is dominated by large fish (and the biomass curve lies above the numerical abundance curve) (Warwick & Clarke, 1994; Yemane et al., 2005). This variable (*W* statistic) is hereafter named the 'size dominance pattern' of fish communities. The size dominance, measured by the *W* statistic, is a complementary variable to average fish size. Fish size considers the relative abundance of fish species with distinct sizes (e.g. if a large species is abundant, this would increase the values for fish size), whereas the *W* statistic considers all species irrespective of their abundances (e.g. abundant and rare large species have the same weighting in the analyses; Warwick & Clarke, 1994). However, the *W* statistic could be also partly affected by the condition factor of fish (Blanchard, LeLoc'h, Hily, & Boucher, 2004; Yemane et al., 2005).

2.4 | Explanatory variables: population size, distance from urban centres, and environmental variables

Amazonian rivers usually have relatively few cities, and most of them are small. Therefore, the analyses considered major cities that have larger fishing fleets and larger boats, which can exploit rivers and lakes over long distances (Table 1). These cities usually encompass the lakes under study within their municipality, so the lakes and fishers who exploit them are in the same range of any municipal management decisions. There may be other cities along the rivers studied, but these are usually a greater distance away (more than 50 km) or lack fishing fleets. Data were also obtained on the number of people living in the nearest city to each river (Table 1). Data from the Brazilian Institute of Geography and Statistics (IBGE - Instituto Brasileiro de Geografia e Estatística, 2015) for the closest year to when the fish in each lake were sampled were used for this purpose (Table 1). The population data were organized in three categories of population size: small (<30 000 inhabitants), moderate (30 000–60 000 inhabitants), and large (>60 000 inhabitants). Population size was not used as a continuous variable because the territory of each city usually included more than one lake (Table 1). Therefore, some lakes have identical values of population size (Table 1), compromising the homogeneity of the distribution of values. The software GOOGLE EARTH PROFESSIONAL was used to calculate the total river distance between each lake and the corresponding city or urban centres (Table 1). Human population size and distance to urban centres should indicate distinct categories of human influence on fish communities. Human population size of nearby cities might be considered a proxy of fish demand, related to local or regional fishing pressure to supply smaller urban markets, or for subsistence (Brewer et al., 2009; Brewer et al., 2012; Brewer et al., 2013; Hallwass, Lopes, Juras, & Silvano, 2011; McClanahan et al., 2015). On the other hand, the distance to urban centres is related to the access to larger markets and fishing costs, as market proximity facilitates fish commercialization and reduces fishing costs (for example, fuel and ice). Therefore, distance to urban centres could indicate fishing pressure to supply larger markets, including fishing by large commercial fishing boats (Brewer et al., 2009; Brewer et al., 2012; Brewer et al., 2013; Hallwass, Lopes, Juras, & Silvano, 2013; Isaac et al., 2008).

GOOGLE EARTH PROFESSIONAL was used to estimate the area and shape of the natural shoreline of the lakes studied, as well as their distance to the main river channel. These three environmental variables might influence fish communities (Keppeler et al., 2017; Silvano et al., 2014). As the area of a lake varies, and depends on the hydrological period, Landsat images were used from the low-water season of each river – the same season when fish sampling data were gathered. The shape of the natural shoreline was calculated using the following equation:

$$\text{Shape of natural shoreline} = \frac{L}{2\sqrt{\pi S}},$$

where L is the shoreline length (m) and S is the surface area (m^2) of the lake. Natural shoreline values increase as the lakes become more elongated; circular lakes have index values near 1. Lakes with high values of natural shoreline shapes may have higher environmental heterogeneity (possible refuges, and habitats for feeding and breeding, among others) and a higher concentration of nutrients derived from the surrounding terrestrial areas (Cole, 1975). The distance to the main river channel was measured as the shortest distance (m) between the floodplain lake and the main river through secondary channels during the low-water season. This variable is expected to reflect lake isolation (Granado-Lorencio et al., 2012; Tockner et al., 1999), which reduces the accessibility for fishermen (Silvano et al., 2014) and for some species of fish, which may then decrease fish richness and diversity (Uchida & Inoue, 2010).

Dissolved oxygen (DO), conductivity, transparency, and depth were measured during fish sampling. These physical–chemical parameters may vary according to the period of the day and with the position in the water column, so 12 measurements of each of these variables were made in each lake: six between 09.00 and 10.00 h, and six between 15.00 and 16.00 h, all at the water surface. The means of these measurements for each lake were included in the analyses. Unfortunately, owing to practical problems, it was not possible to measure all parameters for all lakes. Depth was measured for all lakes, except for those in the Solimões River (n = 34); transparency was measured (using a Secchi disc) in lakes of the Tapajós, Tocantins, and Lower Amazon rivers (n = 27); conductivity was measured in lakes of the Tocantins and Tapajós rivers (n = 21); and DO was measured in lakes of the Tocantins, Solimões, and Lower Amazon rivers (n = 30). More details of these measurements are given in previous studies (Keppeler et al., 2017; Silvano et al., 2009; Silvano et al., 2014).

2.5 | Data analysis

Model averaging (Burnham & Anderson, 2002) of multiple linear regression models was used to obtain estimates of the relative importance value (I) of six explanatory variables (distance from the urban centre, human population size, river, distance to the main river channel, lake size, and shape of natural shoreline) for each one of the six response variables (biomass, abundance, average size, size dominance pattern, species richness, and diversity of fishes). Model-averaging analysis was preferred instead of a classic model selection because the differences between the best model and the other model candidates were usually small. Model averaging was carried out according to the following steps: (i) multiple linear models with all possible combinations of fixed variables, and with a maximum of five explanatory variables per model, were fitted to the data; (ii) corrected Akaike information criterion (AICc) was used to measure the plausibility of each candidate model; (iii) the Akaike weight (wi) was calculated for each model and normalized across the set of candidate models, to sum to 1; (iv) the Akaike weights with cumulative weight lower than 0.95 were used to obtain averaged estimates for each parameter (Burnham & Anderson, 2002); and (v) the relative importance of each predictor variable was calculated by summing all Akaike weights over all models that include each predictor. The relative importance ranges from 0 to 1; the larger the value of the relative importance of a predictor, the more important it is compared with the others (Burnham & Anderson, 2002). The average estimates and confidence intervals (CIs) of each variable were calculated based on the entire list of candidate models with cumulative weight lower than 0.95. A variable was considered as a consistent predictor if the CI did not pass through zero, which indicates that the predictor has a clear negative or positive relationship with the response variable (Burnham & Anderson, 2002). Interaction terms were not included in the analyses because the distance of lakes to the urban centres could not be standardized, as data sampled in distinct research projects were used. Lakes at all human population levels could not be included for the same reason.

Previous exploratory analyses indicated that sampling year was unrelated to the six ecological indicators for fish, so this variable was not included in the analyses. Multicollinearity was verified in the data before conducting model-averaging analyses using the variance inflation factor (VIF; Nakazawa, 2014), which indicated low correlation among the predictors (VIF < 4). The CPUE of numerical abundance biomass was log transformed to achieve normal distribution, and the distance to the urban centre was log transformed to reduce the influence of extreme values.

Physical–chemical parameters of the water (DO, transparency, conductivity, and depth) were not included in the model-averaging analyses because these variables could not be measured for some lakes (see above). To check the potential influence of physical–chemical parameters on the ecological indicators for fish, and their potential correlation with the variables of interest (human population size and distance to urban centre), multiple analyses were conducted using subsets of the data set for which physical–chemical parameters were available. Three main exploratory analyses were conducted. First, linear regression models were carried out for each one of the six ecological indicators for fish using the local physical–chemical parameters as factors (response variables). As not all physical–chemical parameters were measured in all lakes, each physical–chemical parameter was evaluated individually. River, shape of natural shoreline, and lake size were included as covariates in these analyses, to check to what extent the physical–chemical parameters of water could be useful predictors of unexplained variability in fish data. The relative importance of individual physical–chemical parameters was evaluated comparing the AICc values of the models with and without each physical–chemical variable. If the model with a given physical–chemical variable had a ΔAICc value lower than 2, that variable was considered an important predictor. Second, the Spearman's rank correlation and association (measured as a coefficient of correlation in a linear regression) with distance to urban centre and human population size were checked. Third, if a high correlation (or association) had occurred, a stepwise regression (backwards with AICc) was carried out with both the physical–chemical parameter and the main variables of interest (human population size or distance to urban centre). This last analysis was conducted to verify whether these main variables remain important predictors after accounting for the influence of potential confounding factors (physical–chemical variables).

The stats package in R (R Development Core Team, 2015) was used to make the multiple linear regressions, and the MUMIN package (Barton, 2015) was used to calculate the AICc and to conduct the model averaging. The FMSB package of R (Nakazawa, 2014) was used to calculate the VIF.

3 | RESULTS

The distance from the urban centre and human population size were important variables to explain four out of six fish ecological indicators (Table 2). The first hypothesis was partly supported by the data: distance from the urban centre was a consistent predictor (Tables 2 and 3) that was positively correlated with average length (although this relationship was weak, R^2 = 0.143; Figure 2a) and size dominance pattern (with larger values of W in more distant lakes; R^2 = 0.326; Figure 2b). In spite of appearing in some of the best models (Table S1), the distance to the urban centre alone did not influence fish richness, Shannon diversity, numerical abundance, or biomass consistently (Tables 2 and 3).

Human population size was a consistent predictor of fish richness (R^2 = 0.17) and Shannon index (R^2 = 0.24; Tables 2 and 3); however, contrary to the second hypothesis, lakes in areas with low human population had lower richness and diversity than lakes in areas with moderate or large human populations (Figure 3). Also contrary to the second hypothesis, human population size was unrelated to the other ecological indicators of fish communities (numerical abundance, average length, size dominance pattern, and biomass; Tables 2 and 3).

Fish richness, Shannon diversity, biomass, and abundance (Table 2) all differed among rivers (Table 3). The Negro River had the highest values of size dominance pattern (W statistics higher than 0) among all rivers (Figure 4a). The Amazon River showed higher species richness and Shannon diversity (Figure 4b, c), whereas the Solimões River had lower species richness (Figure 4b). The average size of fishes was similar among rivers, being slightly lower in the Tapajós River (Figure 4d). The Solimões and Lower Amazon rivers had higher fish biomass (Figure 4e) and abundance (Figure 4f).

The shape of natural shoreline predictor showed relatively high averaged importance values associated with fish abundance, biomass, average body size, and size dominance pattern (Table 2). However, the CIs for shape of natural shoreline encompassed zero for all fish ecological indicators, which suggests a lack of consistency in the observed relationships, and hence this was not consistent among all models. The distance to the main river channel was present in the best models for fish biomass, abundance, and average body size; therefore, the distance to the main river channel had high averaged importance values for these variables (Table 2). Nevertheless, the distance to the river was a consistent predictor (with CIs that did not encompass the value 0) for biomass alone, showing a strong positive relationship (R^2 = 0.48; Figure 5; Table 3;). Lake size was unrelated to all six ecological indicators for fish (low averaged importance and CIs that encompass 0; Tables 2, 3).

Local physical–chemical parameters were associated with fish ecological indicators in a subset of the lakes (Table S2). The strongest relationships were a positive relationship between depth and size dominance pattern, and negative relationships between dissolved oxygen and fish abundance and biomass (Table S2). Dissolved oxygen was neither associated with human population size (R^2 = 0.322, F = 1.515, P = 0.238) nor correlated with distance to urban centre (ρ = −0.229, S = 4989, P = 0.232; Table S3). On the other hand, depth was positively correlated with both human population size (R^2 = 0.603, $F_{(2,31)}$ = 8.907, P = 0.001) and distance to the urban centre (ρ = 0.391, S = 3981, P = 0.021; Table S3). A correlation

TABLE 2 Model-averaged importance of predictors for the fish ecological indicators: size dominance pattern (W statistic), richness, Shannon diversity, average body size, biomass. and abundance in 48 floodplain lakes in five rivers of the Brazilian Amazon

Response variables	Predictor variables					
Fish ecological indicators	**Distance to urban centre**	**Human population**	**Shoreline**	**Lake size**	**Distance to main river channel**	**River[a]**
Size dominance pattern	**0.71**	0.03	**0.50**	0.38	0.20	0.38
Richness	0.40	**0.54**	0.17	0.21	0.21	**0.96**
Shannon diversity	**0.44**	0.42	0.18	0.16	0.15	**1**
Average body size	**0.81**	0.10	0.59	0.26	**0.65**	0.28
Biomass	0.18	0.02	0.41	0.18	**0.91**	**1**
Abundance	0.25	0.01		0.19	**0.69**	**1**

The two predictors showing the highest importance for each ecological indicator are marked in bold.

[a]River basin where lakes are located (Table 1).

TABLE 3 The parameter estimates and confidence intervals (CIs, in parentheses), generated by model-averaging analyses, for all predictors used to explain the variability of fish ecological indicators (Indicators) in floodplain lakes in five large rivers of the Amazon basin

	Parameter estimates (95% CIs)									
	Urban	Human population size		River comparisons						
Indicators	distance	Low vs Mod	Low vs High	Ama vs Neg	Ama vs Sol	Ama vs Tap	Ama vs Toc	Lake size	Shoreline	River distance
Size dominance pattern	**0.080 (0.020, 0.139)**	−0.014 (−0.119, 0.090)	0.001 (−0.120, 0.121)	**0.257 (0.109, 0.405)**	0.109 (−0.026, 0.245)	0.035 (−0.090, 0.160)	0.053 (−0.080, 0.186)	−0.024 (−0.063, 0.016)	−0.022 (−0.053, 0.008)	−0.000 (−0.001, 0.001)
Richness	−0.717 (−1.770, 0.336)	**3.550 (0.339, 6.762)**	1.790 (−0.515, 4.096)	0.017 (−3.938, 3.974)	−1.824 (−5.383, 1.734)	−1.056 (−3.284, 1.172)	**−3.153 (−5.233, −1.073)**	−0.006 (−0.723, 0.711)	0.061 (−0.325, 0.447)	−0.005 (−0.024, 0.015)
Diversity	−0.255 (−0.605, 0.096)	**1.105 (0.064, 2.147)**	0.456 (−0.328, 1.240)	−0.613 (−1.863, 0.637)	−1.051 (−2.121, 0.017)	**−0.835 (−1.546, −0.123)**	**−1.256 (−1.943, −0.567)**	−0.003 (−0.204, 0.197)	0.036 (−0.092, 0.164)	−0.000 (−0.007, 0.006)
Body size	**0.109 (0.019, 0.199)**	0.102 (−0.094, 0.298)	0.119 (−0.141, 0.379)	0.056 (−0.228, 0.341)	−0.081 (−0.352, 0.189)	**−0.232 (−0.453, −0.010)**	−0.124 (−0.352, 0.104)	0.016 (−0.059,0.091)	−0.042 (−0.092, 0.007)	0.001 (−0.000, 0.003)

Definitions: Urban distance, distance to urban centre; Ama vs Neg, Amazon vs Negro; Ama vs Sol, Amazon vs Solimões; Ama vs Tap, Amazon vs Tapajós; Ama vs Toc, Amazon vs Tocantins; Shore, shape of natural shoreline; River distance, Distance to the main river channel; Diversity, Shannon diversity; Body size, Average body size. The predictors that showed values of CI not encompassing 0 are marked in **bold**, which indicates greater confidence for this predictor explaining the variability of the corresponding ecological indicator.

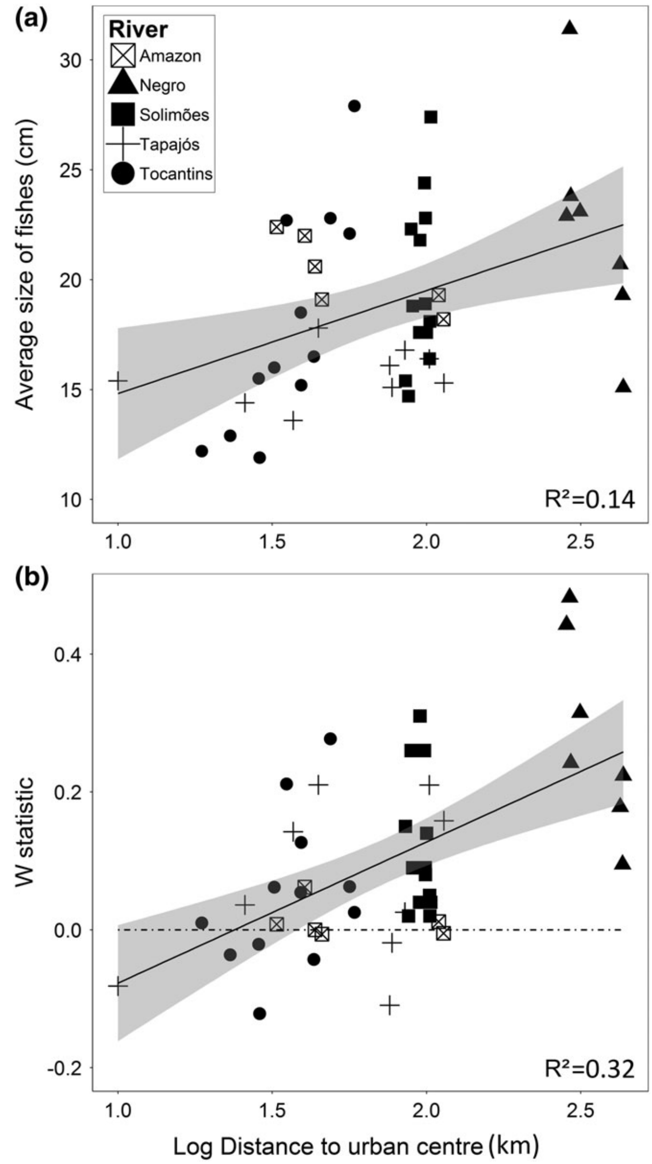

FIGURE 2 Relationship of the explanatory variable distance from the urban centre with the two ecological indicators (response variables) of the fish communities in five rivers (48 lakes) in the Brazilian Amazon: (a) average size; (b) size dominance pattern (W statistic). Tendency lines were fitted through a simple linear regression. The grey shaded area around the tendency lines represent 95% of the confidence interval of the regression

between conductivity and human population size was also observed ($R^2 = 0.840$, $F_{(2,18)} = 21.76$, $P < 0.001$; Table S3). Stepwise regressions including distance to urban centre and depth selected models with distance to urban centre alone to explain fish size (response variable). On the other hand, the stepwise method selected models with both depth and distance to an urban centre to explain the size dominance pattern (W statistic; Table S4). These analyses thus indicated that distance to the urban centre still had a strong relationship with fish size and size dominance pattern, even after accounting for the effect of depth for a subset of the lakes (n = 34). Similarly, human population size was still an important variable for explaining fish diversity and richness when conductivity was included in the models (Table S4). On the other hand, the stepwise regressions

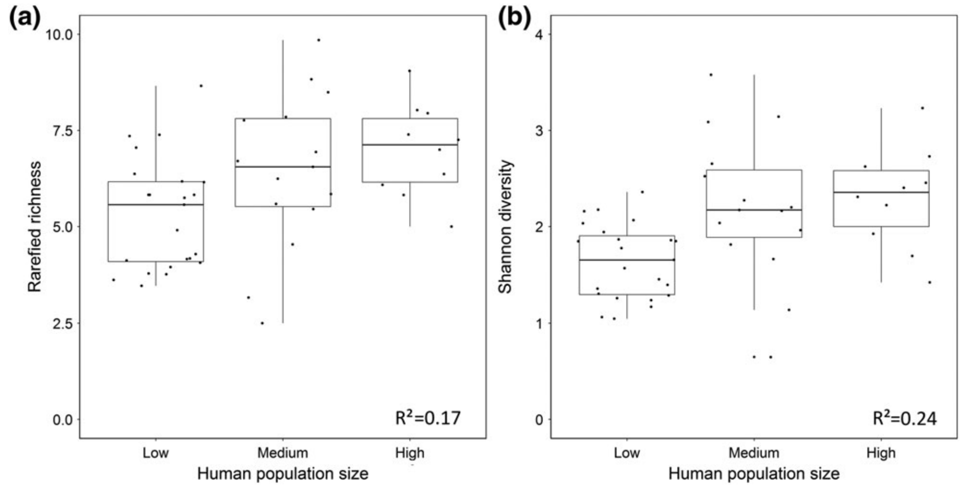

FIGURE 3 Relationship of (a) fish richness and (b) Shannon diversity with population size in five rivers (48 lakes) in the Brazilian Amazon: Low, less than 30 000 inhabitants; Medium, 30 000–60 000 inhabitants; and High, more than 60 000 inhabitants. Points are for the sampled lakes. Central horizontal lines within the boxes are the median values; upper and lower hinges are the third and first quartiles, respectively; and whiskers indicate the maximum and minimum values

including both depth and human population size as predictors of fish richness and diversity were not selected as the best model; the null model without predictors was selected (Table S4). Models with depth and human population size alone as predictors had similar values of AICc, which indicated that both variables had similar contributions in explaining fish richness and diversity of fish in this subset of lakes (n = 34).

4 | DISCUSSION

4.1 | Human influences: population size and distance to cities

Few studies have compared the abundance and the diversity of freshwater fish among fishing pressures or management regimes (Lorenzen, Garaway, Chamsingh, & Warren, 1998; Silvano et al., 2009, 2014). Moreover, no study has evaluated potential human pressures on fish communities in the Amazon Basin at a broad scale of five rivers. Distance to urban centres and human population size were related to some of the ecological indicators of fish communities, thus indicating potential ecological effects of these pressures on floodplain lakes in the Brazilian Amazon. The distance to urban centres was positively related to the average fish size and to the size dominance pattern of the lakes, which indicated that distant lakes have larger fish than lakes closer to urban centres. Such a decrease in fish size and size dominance pattern near urban centres conforms to previous studies that indicated the gradual depletion of large commercial fish through selective fisheries near large Amazonian cities (Castello et al., 2013; Castello, Arantes, Mcgrath, Stewart, & Sousa, 2015; Garcia, Tello, Vargas, & Duponchelle, 2009; Petrere, 1986; Petrere et al., 2004). These impacts on fish communities may be related to increased fishing pressure linked to an increased demand for fish, as well as to improvements in fishing techniques, such as larger motorized boats and synthetic gillnets (Hallwass & Silvano, 2016; Isaac et al., 2008). If fishing intensifies, the preferred commercial fish species could disappear and fishing will progressively reduce the size of individuals of other fish species, as predicted by the processes of ‘fishing down’ in tropical rivers (Welcomme, 1999; Welcomme et al., 2010). An adverse influence of proximity to urban centres and human population density on fish biomass and diversity has been observed in marine ecosystems, such as coral reefs (Aswani & Sabetian, 2009; Brewer et al., 2012; Brewer et al., 2013; Cinner, Graham, Huchery, & Macneil, 2012), where these human influences can reduce the fish phylogenetic and functional diversity of fish populations (D'agata et al., 2014).

Although a decrease in fish diversity related to higher population densities has been observed in marine ecosystems (Brewer et al., 2012; Gelcich, Godoy, Prado, & Castilla, 2008; McClanahan, Marnane, Cinner, & Kiene, 2006), such a relationship has not been observed in this study. The relationship between human population size and fish diversity was the opposite of the expected: a lower fish diversity and richness were found in lakes near cities with lower population sizes. More detailed studies would be needed to check for the underlying causes of this pattern, but at least three explanations are possible. First, the removal of large fish, some of which may be top predators (Castello et al., 2015) or better competitors, could lead to an ecological compensatory effect, hence increasing the abundance and diversity of non-exploited fish. Second, there are many rare fish species in the Brazilian Amazon (Hercos, Sobansky, Queiroz, & Magurran, 2013; Silvano, Hallwass, Juras, & Lopes, 2016). Most of these rare species might not be affected by fishing, which is usually selective and directs most fishing effort on a few preferred fish species (Hallwass & Silvano, 2016; MacCord, Silvano, Ramires, Clauzet, & Begossi, 2007). Third, some lakes in the Lower Amazon river (Table 1), which showed higher richness and diversity (Figure 4b, c), are located near the more populated city of Santarém and near the confluence of the Amazon and Tapajós rivers (Figure 1). The confluence of these two rivers might form an ecotone and increase species diversity, as some Amazonian fish migrate between rivers with nutrient-rich and nutrient-poor waters (Benedito-Cecilio & Araujo-Lima, 2002).

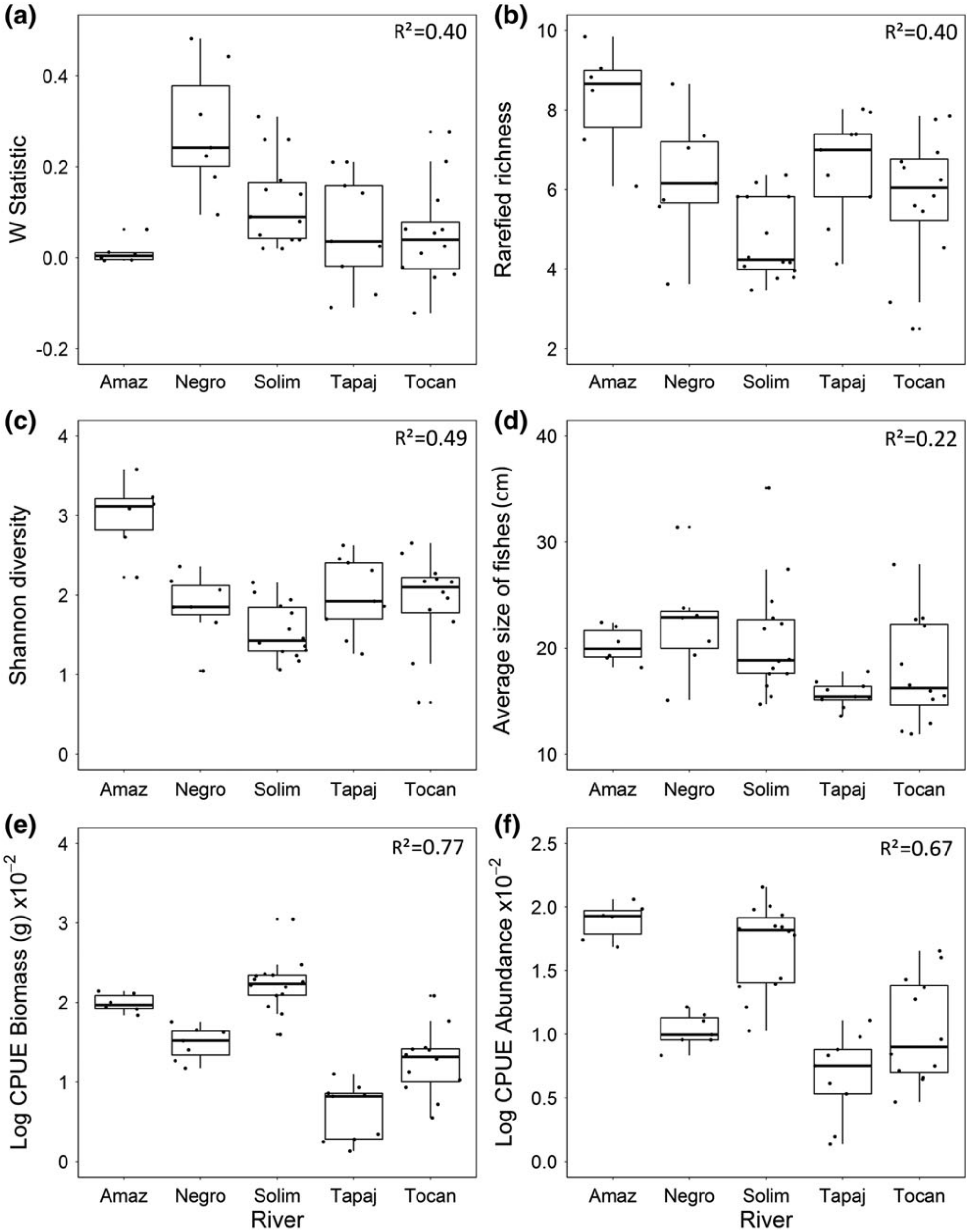

FIGURE 4 Comparison of the response variables (fish ecological indicators) among the five rivers studied in the Brazilian Amazon (n = 48 lakes): (a) size dominance pattern (W statistic); (b) rarefied richness; (c) Shannon diversity; (d) average size of fishes; (e) biomass; and (f) abundance. The numbers of lakes sampled in each river are shown in Table 1. Points are the sampled lakes. Central horizontal lines within the boxes are the median values; upper and lower hinges are the third and first quartiles, respectively; and whiskers indicate the maximum and minimum values

Fish diversity in these floodplain lakes of the Brazilian Amazon may take longer to change in response to fishing pressure, compared with the size structure of the fish community. This may be partly related to the influence of the flood pulse, which can add new species to fish communities during the high-water season, when flooding connects the lakes to other aquatic habitats (Hurd et al., 2016). However, responses of fish diversity to fishing pressure may differ in other tropical freshwater ecosystems subjected to a more intense fishing pressure. For example, in the Tonlé Sap, a large tropical floodplain lake in the Mekong River (Southeast Asia), indiscriminate multi-species fisheries have caused declines in fish diversity, while maintaining high fish biomass because of fast-growing fish species (McCann et al., 2016).

4.2 | Environmental influences on fish communities

Although the observed relationships between anthropogenic factors (distance from urban centre and population size) and fish communities were consistent in the lakes studied, the coefficients of determination were low (R^2 values lower than 0.33). This indicated a high variability in the data set and the potential influence of other variables. Nevertheless, it is almost impossible to control or even account for all variables that can affect fish in complex ecological systems, such as floodplain lakes in the Amazon Basin. These lakes have heterogeneous environmental characteristics, such as water depth, turbidity, dissolved oxygen, lake area, forest cover, presence of macrophytes and connectivity with other lakes and rivers, which could influence the structure of fish

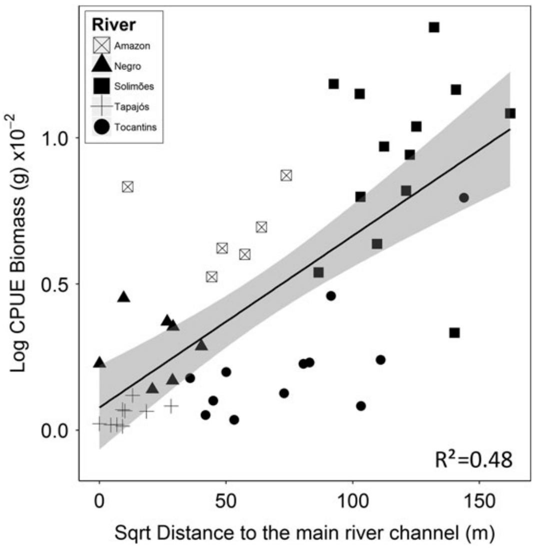

FIGURE 5 Positive relationship between distance to the main river channel and the catch per unit effort (CPUE) of fish biomass collected in floodplain lakes of the five main rivers in the Brazilian Amazon

assemblages (Freitas, Siqueira-Souza, Florentino, & Hurd, 2014; Keppeler et al., 2017; Petry, Bayley, & Markle, 2003; Tejerina-Garro, Fortin, & Rodríguez, 1998). Some environmental parameters, such as depth, dissolved oxygen, and conductivity, were related to some fish ecological indicators, such as fish abundance, size, size dominance pattern, and diversity. At least some of the fish species in the Amazon floodplain lakes have a structure of meta-populations or single populations occurring over large areas, being influenced not only by local conditions, but also by regional forces, such as the occurrence of droughts and the influence of the flood pulse (Hurd et al., 2016). The results presented here indicate that human pressures, such as distance to urban centres or major markets (population size), could be one of the regional forces that affect fish communities in the Brazilian Amazon.

In this study, the ecological indicators of fish communities differed among the river basins studied in the Brazilian Amazon. The two white water rivers (Lower Amazon and Solimões) showed a higher fish abundance in number and biomass, which may be partly because white water rivers are usually more productive than clear and black water rivers (Santos & Santos, 2005). Other factors that have contributed to the higher numbers of fish sampled in these two rivers could be the larger area of the Lower Amazon and a well-established co-management system at the studied site in the Solimões River, the Mamiraua Sustainable Development Reserve (Silvano et al., 2009). Notwithstanding the influences of river basin, shape of natural shoreline, and distance to the main river channel, one of the human pressures (distance to urban centre) still had a stronger influence on fish size and size dominance pattern (Table 2). Lakes in at least three of the rivers with distinct water types (Negro, Solimões, and Tocantins) showed higher values of average fish size and *W* statistic (size dominance pattern) when located further away from urban centres (Figure 2). These results indicated that the observed relationships between human pressures and fish ecological indicators were not biased by the local environmental conditions of the lakes studied.

4.3 | Conservation implications

Most of the lakes studied (and all those that are located further from urban centres) showed values of *W* statistics larger than 0, which indicated that the size dominance pattern of these communities is biased towards large fish (Warwick & Clarke, 1994; Yemane et al., 2005). These results suggest that the fish communities near urban centres in the Brazilian Amazon may be in an initial stage of the fishing-down process, compared with more heavily fished regions of Africa and Asia (Allan et al., 2005). The present results thus reinforce the argument that the Brazilian Amazon provides an invaluable and perhaps unique opportunity of managing and conserving a rich fish biodiversity and healthy fish stocks with large fish species (Junk et al., 2007).

Although this was not the focus of this study, the observed patterns indicated linkages between the conservation of forest and fish. The lakes located in the Negro and Solimões rivers usually had larger fish and a positive size dominance pattern (*W* statistics larger than 0; Figure 2a, b). These two rivers are located in the more remote and less deforested north-western Amazon, indicating positive feedbacks among remoteness, forest maintenance, and the ecological integrity of fish communities in floodplain lakes. Forest cover is positively related to fish abundance and diversity in Amazonian floodplain lakes, as flooded forests are important sources of food and shelter for fish (Arantes et al., 2017; Lobón-Cerviá et al., 2015). Therefore, the observed human influences on Amazonian fish communities could be partly attributed to increased deforestation near urban centres. Human population density, highways, the availability of infrastructure, and the severity of the dry season are among the main drivers of deforestation in the Amazon (Laurance et al., 2002; Laurance, Albernaz, Fearnside, Vasconcelos, & Ferreira, 2004); however, land-use patterns, economic growth, and the absence of deforestation detection systems can be more strongly related to deforestation than to human population size (Moran, 1993; Soares-Filho et al., 2010). Nevertheless, roads are linked to increased occupation and higher deforestation in the Brazilian Amazon (Brondizio & Moran, 2012; Laurance et al., 2004). Therefore, development projects that increase urbanization and access to markets in remote Amazonian regions might also bring unintended adverse consequences for fish conservation and fisheries sustainability.

Distance to the main river channel was positively related to fish biomass in the floodplain lakes studied, as observed on a smaller scale in the Tocantins River (Silvano et al., 2014). This indicated that more isolated lakes may be less fished than more accessible lakes. This pattern also showed that impacts from increased fishing pressure may offset the advantages to fish dispersal owing to the enhanced connectivity in lakes closer to the river. Distance to the main river channel did not consistently explain the variation in other ecological indicators of fish communities, including species diversity and richness, which suggests that fish species are able to disperse to more distant lakes. If this is the case, a combination of local management initiatives in more accessible lakes (near the main river channel) with natural fish spillover from isolated unmanaged lakes could increase the overall diversity and fisheries sustainability in the floodplain.

Although considered to be an important threat to Neotropical freshwater fishes (Pelicice et al., 2017), non-native fish species were not recorded in this study (Table S5), and do not yet seem to be a major conservation issue for Amazonian fish communities. Brazilian government policies of increasing aquaculture in the Amazon may add an impact from non-native fish species (Padial et al., 2017), however, and this impact may be higher near larger cities, which have a higher demand for fish and logistical incentives for aquaculture.

Ecosystem services regularly provided by fish in tropical fresh waters include seed dispersal (Correa et al., 2015), and nutrient cycling and transporting (Mcintyre, Jones, Flecker, & Vanni, 2007). Some fish species found in the lakes studied could provide these ecosystem services, including frugivorous species (*Colossoma macropomum*, *Piaractus brachypomus*, *Myleus* spp., *Myloplus* spp., *Mylossoma* spp.), and detritivorous species (*Prochilodus nigricans* and *Semaprochilodus* spp.) (Table S5). The provisioning of ecosystem services may be associated with fish size, as larger fish are more efficient in providing several services, such as seed dispersal, which can be compromised by the overfishing of larger individuals (Anderson, Nuttle, Saldanã Rojas, Pendergast, & Flecker, 2011; Correa et al., 2015; Costa-Pereira & Galetti, 2015). Besides maintaining ecological processes, some fish species found in this study also sustain provisioning ecosystem services in the form of food and income to local people. These species include large frugivores, the large migratory catfishes (*Brachyplatystoma filamentosum* and *Pseudoplatystoma* spp.) and the pirarucu (*Arapaima gigas*) (Table S5). These large fish have been heavily exploited by commercial fisheries in the Brazilian Amazon (Castello et al., 2015; Petrere et al., 2004), and the decline in their population and body size could have deleterious socio-economic impacts by threatening the food security and increasing the poverty of riverine people (Béné et al., 2016). Therefore, the observed decrease in fish size near urban centres may adversely affect ecosystem services, as the large fish that are the major providers of these services have been selectively targeted by fishers throughout the Amazon (Hallwass & Silvano, 2016). Payments for ecosystem services provided by fish, or even their associated habitats (e.g. reproductive or feeding areas, including flooded forests), could be a solution for restoring or at least maintaining some fish populations (Bladon, Short, Mohammed, & Milner-Gulland, 2016).

The results of this study indicate that conservation and fishery management measures are required to overcome the observed trend of reduced fish size in lakes close to major cities in the Brazilian Amazon. These measures should aim to restore the size structure of these fish communities, in order to secure the maintenance of fish populations and the ecosystem services that they provide, including ecological processes and food provision to local people. One option would be to establish protected areas near to urban centres and more accessible floodplain lakes, aiming to increase the abundance of larger fish. Another option would be to promote co-management systems, as co-management with fishing restrictions imposed by the fishers themselves has increased fish abundance in floodplain lakes (Almeida, Lorenzen, & McGrath, 2009; Silvano et al., 2009; Silvano et al., 2014). These co-management arrangements might be partly responsible for the observed lack of adverse effects of human population size on fish communities in the lakes studied; however, at least some of these managed lakes are located far from major urban centres (Silvano et al., 2014). A third option may be a dynamic combination of management tools, including quotas, closed seasons, gear restrictions, and spatial closures, which consider the economic needs of fishers on a regional basis (Hallwass et al., 2013). As well as fishing restrictions, mechanisms to improve monitoring, enforcement, and compliance would be needed in large Amazonian cities.

The results of this study also have implications for large-scale conservation planning. The lakes located far from urban centres or in less populated regions have a higher potential for fish conservation. Therefore, distant lakes should be carefully considered when assessing the impacts of large development projects, such as dams (Hoeinghaus et al., 2009; Winemiller et al., 2016), or when planning conservation areas for protecting fish diversity (Nogueira et al., 2010). This standardized and broad-scale study indicated that human influences on fish communities observed in tropical marine ecosystems might also occur near larger urban centres in tropical fresh waters. Government policies in South America (including Brazil) have not adequately addressed the conservation of freshwater ecosystems and the rich biodiversity of Neotropical freshwater fishes, including those in the biodiversity-rich Amazon Basin (Castello et al., 2013; Pelicice et al., 2017). In such a context, data provided here can support basin-wide conservation planning to protect fish stocks or properly assess environmental impacts in the Amazon and other rivers in biodiversity-rich regions (Winemiller et al., 2016), where human populations have increased at a faster rate (Williams, 2013).

ACKNOWLEDGEMENTS

We thank: J.A.S. Zuanon for fish identification; Evandro Augusto Veit for the English revision of the manuscript; the Instituto Chico Mendes para Conservação da Biodiversidade (ICMBio), for permits to sample fish; the Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (CAPES) for funding research in the Tapajós River (883/2010), for financial support to present this work at an international conference (5227/14-3), for a PhD scholarship to F.W.K. (1286-15-13), and for a postdoctoral scholarship to G.H.; the Fundação de Amparo a Pesquisa do Estado de São Paulo (FAPESP/SP) for funding the research in the Negro River (1998/16160-5); the Eletronorte/ANEEL (contract 4500057477) for funding the research in the Tocantins River and for research grants to R.A.M.S and G.H.; the Instituto de Desenvolvimento Sustentável Mamirauá (IDSM) for funding the research in the Solimões River; the Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq) (557121/2005-1) and Fundação Amazônia Paraense de Amparo à Pesquisa (FAPESPA) (108/2008), for funding research in the Amazon River; and the CNPq for a research grant to R.A.M.S.

FUNDING INFORMATION

We received funding from the following sources: the Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (CAPES), for research in the Tapajós River (883/2010), for financial support to present this work at an international conference (5227/14–3), for a PhD scholarship to F.W.K. (1286–15-13), and for a postdoctoral scholarship to G.H.; the Fundação de Amparo a Pesquisa do Estado de São Paulo (FAPESP/SP) for research in the Negro River (1998/16160–5); the Eletronorte/ANEEL (contract 4500057477) for research in the

Tocantins River and for research grants to R.A.M.S and G.H.; the Instituto de Desenvolvimento Sustentável Mamirauá (IDSM) for research in the Solimões River; the Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq) (557121/2005–1) and Fundação Amazônia Paraense de Amparo à Pesquisa (FAPESPA) (108/2008), for research in the Amazon River; and the CNPq for a research grant to R.A.M.S.

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How to cite this article: Keppeler FW, de Souza AC, Hallwass G, et al. Ecological influences of human population size and distance to urban centres on fish communities in tropical lakes. *Aquatic Conserv: Mar Freshw Ecosyst*. 2018;1–14. https://doi.org/10.1002/aqc.2910