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Relationships between forest cover and fish diversity in the Amazon River floodplain

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Abstract

1. Habitat degradation leads to biodiversity loss and concomitant changes in ecosystem processes. Tropical river floodplains are highly threatened by land cover changes and support high biodiversity and important ecosystem services, but the extent to which changes in floodplain land cover affect fish biodiversity remains unknown.

2. We combined fish and environmental data collected in situ and satellite-mapped landscape features to evaluate how fish species with different ecological strategies and assemblage structures respond to deforestation in floodplains of the Amazon River. We surveyed 462 floodplain habitats distributed along a gradient of land cover, from largely forested to severely deforested. Rather than analyse only taxonomic metrics, we employed an integrative approach that simultaneously considers different aspects of fish biodiversity (i.e. β diversity and taxonomic and functional assemblage structure) to facilitate mechanistic interpretations of the influence of land cover.

3. Spatial patterns of fish biodiversity in the Amazon River floodplain were strongly associated with forest cover as well as local environmental conditions linked to landscape gradients. Several species and functional groups defined by life-history, feeding, swimming/microhabitat-use strategies were positively associated with forest cover. Other species, including some that would usually be considered habitat generalists and species directly dependent on autochthonous resources (e.g. planktivores), were most common in areas dominated by herbaceous vegetation or open water habitats associated with the opposite extreme of the forest cover gradient. β diversity and the degree of uniqueness of species combinations within habitats were also positively associated with forest cover.

4. *Synthesis and applications*. Our results demonstrating that spatial patterns of fish biodiversity are associated with forest cover, indicate that deforestation of floodplains of the Amazon River results in spatial homogenization of fish assemblages and reduced functional diversity at both local and regional scales. Floodplains world-wide have undergone major land cover changes, with forest loss projected to increase during the next decades. Conserving fish diversity in these ecosystems requires protecting mosaics of both aquatic habitats and floodplain vegetation, with sufficient forest cover being critically important.

1 | INTRODUCTION

Habitat degradation generally causes biodiversity loss and changes in ecosystem processes (Estes et al., 2011; Gibson et al., 2011; Haddad et al., 2015). Human-driven land cover changes are a primary driver of endangerment for ~80% of vertebrate taxa globally (Pereira, Navarro, & Martins, 2012), particularly in the tropics where land cover changes are causing disproportionate impacts on global biodiversity (Laurance, Sayer, & Cassman, 2014). Most studies documenting the effects of land cover changes on tropical biodiversity have focused on terrestrial ecosystems (e.g. Gibson et al., 2011; Stuart et al., 2004), but there have been few studies of tropical freshwater ecosystems, which are being rapidly modified (Dudgeon et al., 2006; Sala et al., 2000). Tropical freshwater ecosystems support high biodiversity and important ecosystem services (Davidson, 2014; Tockner & Stanford, 2002). Tropical fishes in particular are highly vulnerable to habitat degradation, with this group comprising over 31% of freshwater species listed as at risk of extinction by the IUCN (Arthington, Dulvy, Gladstone, & Winfield, 2016; Darwall & Freyhof, 2016). A few studies have documented effects of land cover change on the taxonomic structure of fish communities in tropical streams (e.g. Bojsen & Barriga, 2002; Cetra, Petrere, & Barrella, 2017; Teresa & Casatti, 2012; Appendix S4); however, the effects of land cover changes on fish diversity and assemblage structure in tropical rivers and floodplains remains poorly documented. Loss of riparian vegetation can impact aquatic organisms by reducing energy and nutrient subsidies and altering water quality and habitat (Arthington, Godfrey, Pearson, Karim, & Wallace, 2015; Pusey & Arthington 2003, and see Appendix S4). In the Amazon and most other major tropical regions, large forest areas are being cleared for the development of agriculture, hydropower and human settlements.

Previous studies have shown that many floodplain fishes of the Amazon Basin have evolved strategies that enable exploitation of habitats and food resources in flooded forests and shrublands during seasonal pulses. In some cases, a major proportion of fish biomass is derived from carbon and energy sources in floodplain forests (Anderson, Nuttle, Rojas, Pendergast, & Flecker, 2011; Forsberg, Araujo-Lima, Martinelli, Victoria, & Bonassi, 1993; Goulding, 1980). The abundance and biomass of commercially important fishes in the Amazon was found to be directly related to the amount of floodplain forest (Lobón-Cerviá, Hess, Melack, & Araujo-Lima, 2015). The diversity and assemblage structure of Amazonian fishes thus should be affected by deforestation (Castello & Macedo, 2016; Renó, Novo, Suemitsu, Rennó, & Silva, 2011), and better understanding of this issue is essential for both fisheries management and biodiversity conservation.

Here, we evaluated how fish species with different ecological strategies and assemblage structure respond to forest cover in floodplains of the Amazon Basin. We used an integrative approach that simultaneously considers different aspects of fish biodiversity in order to facilitate mechanistic interpretations of potential effects of land cover changes on ecological communities (e.g. Villéger, Miranda, Hernández, & Mouillot, 2010). Land cover and associated environmental variables can differentially affect species depending on their functional traits. In fishes, patterns of trait covariation are consistently associated with environmental gradients; therefore, a functional diversity perspective has good potential to reveal mechanisms structuring communities (Gutiérrez-Cánovas, Sánchez-Fernández, Velasco, Millán, & Bonada, 2015; Mouillot, Graham, Villéger, Mason, & Bellwood, 2013). Functional traits and performance measures can be combined to explore niche dimensions associated with ecological strategies (Winemiller, Fitzgerald, Bower, & Pianka, 2015). For example, traits and performance measures associated with maximization of reproductive success, acquisition and assimilation of resources and fulfilling metabolic demands can be combined to classify organisms according to life-history, trophic and habitat dimensions respectively (e.g. Ockinger et al., 2010; Ribeiro, Teresa, & Casatti, 2016). The between-habitat aspect of diversity, or β diversity, provides a conceptual means to interpret the organization of communities under environmental change and is increasingly used to understand factors affecting community structure (Socolar, Gilroy, Kunin, & Edwards, 2016; Whittaker, 1972). Research based on empirical measures of β diversity has shown that habitat degradation can increase community similarity and decrease turnover of species across spaces through reductions in structural complexity and diversity of habitats, leading to biotic homogenization (e.g. see Hewitt, Thrush, Halliday, and Duffy 2005 for benthic infauna and epifauna), with responses depending on taxonomic group, scale and region (Socolar et al., 2016).

We tested three hypotheses. The first was that several fish species and functional groups are positively associated with forest cover and associated environmental variables. The second hypothesis was that variation in β diversity among habitats is due to compensatory changes in species abundance (i.e. turnover) or fluctuations in total fish abundance in local assemblages, both of which should be associated with gradients of forest cover. The third hypothesis was that the degree of uniqueness in species composition is associated with gradients of forest cover. We expect that fishes that directly exploit food resources that originate from forests are abundant at locations having dense forest cover. For example, fish species directly dependent on allochthonous resources (e.g. fruits, seeds and vegetative detritus) as well as species with traits that facilitate precision of movement for foraging or predator escape within structurally complex habitats should be positively associated with forest cover. Other fishes may be less dependent on forest cover, consequently, their spatial patterns of abundance may be equally strong but less predictable a priori or even associated with other land cover gradients (e.g. with open water or herbaceous

vegetation cover). For example, trophic guilds supported by autochthonous resources such as algae might be less dependent on forest cover because they benefit from greater primary production of habitats dominated by low herbaceous vegetation. Species having traits that enhance efficiency of sustained swimming in open water should also dominate local assemblages in unstructured habitats. If such spatial patterns are observed, we then expect that a decomposition of β diversity (following Legendre, 2014) will reveal strong patterns of species turnover and unique combinations of species across forest gradients.

We tested these hypotheses by analysing how fish ecological strategies and assemblage structure in floodplain habitats vary as a function of floodplain forest cover around the same habitats. The floodplain habitats were distributed along a gradient of land cover conditions, from largely forested to highly deforested. We used the resulting possible relationships to infer the likely impacts on fish biodiversity of forest loss and replacement by non-forest habitats.

2 | MATERIALS AND METHODS
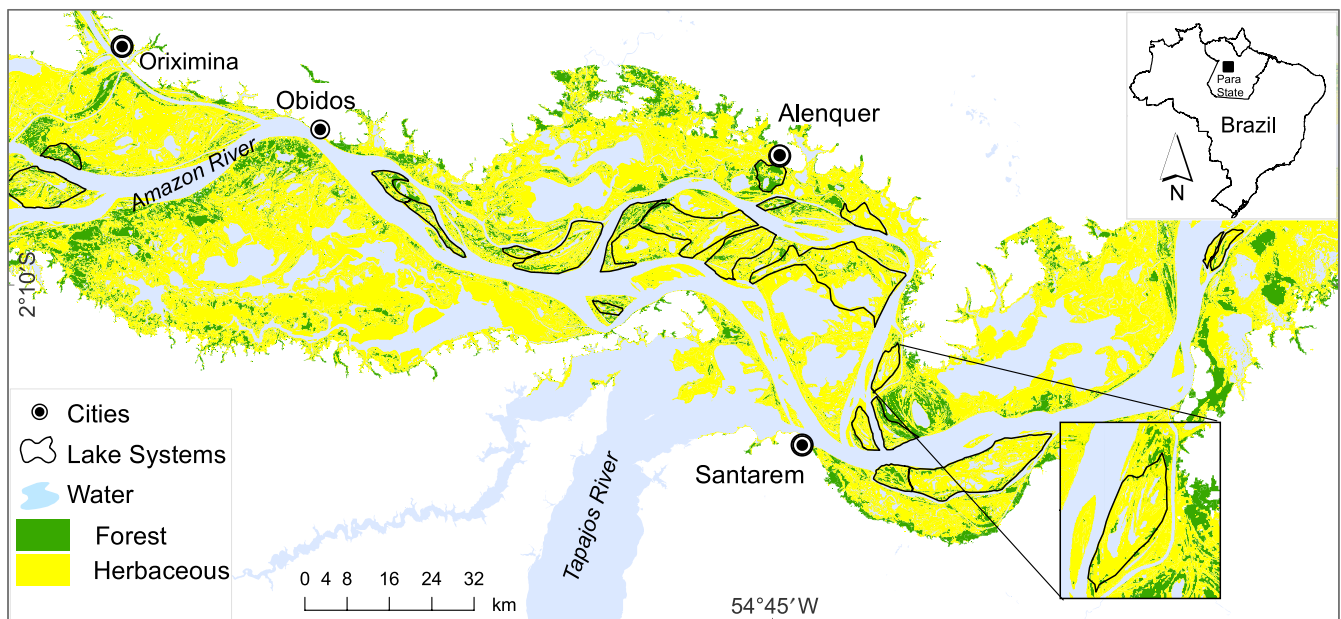
2.1 | Study area

The study was conducted on the floodplain of the lower Amazon River (referred to locally as *várzea*) in an area of 17,674 km² in Pará State, Brazil (Figure 1). The study area contains a mosaic of lakes and secondary channels surrounded by riparian vegetation ranging from forests to pastures (Junk, 1997). The annual river flood pulse is monomodal and varies in average 5.7 m creating marked differences in floodplain conditions between high-water periods, when most areas are flooded, and low-water periods when only lakes and connecting channels retain water. Historically, large areas of várzea were deforested for agriculture and cattle ranching, which led to a loss of 56% of floodplain forest cover by 2008 in the Lower Amazon (Renó et al., 2011) and to fragmentation of the remaining forest (Renó, Novo, & Escada, 2016). Over the past 30 years, 79% of the deforested area was replaced with herbaceous vegetation, 5% is bare soil where ground cover has not yet regenerated and 16% is open water in channels widened through bank erosion (Renó et al., 2011).

2.2 | Data collection

2.2.1 | Satellite imagery

Floodplain land cover (open water, herbaceous vegetation, forest; Table 1, and see Appendix S1) at low-water stage was mapped by L. Hess (unpubl. data, Appendix S1) at 30-m resolution using two contiguous Landsat Thematic Mapper images acquired on 30 November 2008 and 23 October 2009. Aquatic macrophyte coverage (Table 1, Appendix S1) was mapped using seven ALOS PALSAR swaths acquired during the early rising-water period in each of 5 years from 2006 to 2010. Land cover data and macrophyte cover metrics obtained from remotely sensed imagery were assembled according to spatial units defined as local catchments (or "lake systems"). Each local catchment contains lakes, interconnecting channels, forest and areas with herbaceous vegetation and aquatic macrophytes that are hydrologically connected for about 6–9 months per year (see inset in Figure 1). Local catchments are separated from each other by major secondary channels (areas of low elevation) and/or natural levees (areas of high elevation). We mapped 20 local catchments (Figure 1, median area: 23.4 km²) that encompassed a gradient of forest cover, ranging from 3% to 70%.

FIGURE 1 Study area in the lower Amazon showing low-water land cover and 20 local catchments that were studied. Land cover types are forest, herbaceous vegetation and open water (lakes and secondary channels). In the lower Amazon, the vegetation consists primarily of herbaceous vegetation with only 13% forest cover (Renó et al., 2011)

TABLE 1 Summary of estimates (medians, lower quartiles—LQ, upper quartiles—UQ) of floodplain land cover and environmental variables in the lower Amazon floodplain based on 462 habitats surveyed during five expeditions covering four different stages of the annual hydrological cycle

Variable	Description or method	Median	LQ	UQ
Land cover category				
Forest (%)	Per cent of closed-canopy tree cover and short trees, shrub or semi-shrub (including the aroid *Montrichardia arborescens*) in the local catchment	21.0	10.5	47.6
Open water (%)	Per cent of open water in lakes and channels during low waters in the local catchment (excluding the mainstem Amazon channel)	9.6	3.0	12.9
Herbaceous vegetation (%)	Per cent of soil, fresh sediments, grasses or forbs during low waters in the local catchment	66.9	42.6	74.5
Local environmental variables				
Aquatic macrophyte indices				
Macrophyte—geo-processing: Macro (geop)	Indices indicating the per cent of the local catchment with macrophytes present (during late December to January) in three or more of 5 years analysed (2006/2007 to 2010/2011). "Macro (geop)" provides large-scale estimates of coverage	17.1	13.0	22.5
Macrophyte—visual observation (%): Macro (obs)	Per cent of macrophytes estimated through visual inspection of the habitat. "Macro (obs)" characterizes an important feature of fish habitat at a local-scale matching that of our fish assemblage surveys	10.0	3.0	40.0
Physico-chemical water parameters				
Depth (m)	Averages based on measurements in various locations within each habitat	2.1	1.5	3.1
Dissolved oxygen (mg/L)		2.2	1.6	3.4
Transparency (cm)		44.5	30.0	60.0
Temperature (°C)		30.1	29.3	30.8

2.2.2 | Field surveys

Field surveys were conducted during five expeditions covering four different stages of the annual hydrological cycle at 462 habitat areas (open water, herbaceous vegetation and forest) within the 20 local catchments (Figure 1). For each habitat type within each local catchment, and during two dry periods and one rising-, high- and falling-water period, we collected fish using a standard set of nets with different mesh sizes (11 gillnets measuring 25 × 2 m, with mesh sizes 20, 30, 40, 50, 60, 70, 80, 90, 100, 120 and 130 mm, and one gillnet measuring 100 × 3 m, with a 180-mm mesh). For each season and all habitats sampled within each local catchment, average gillnet sampling effort was approximately 25 hr (*SD* ~ 4 hr). For the same seasons and habitats within each local catchment where we collected fish, we measured local environmental variables (see Table 1 for details).

2.3 | Statistical analyses

2.3.1 | Fish assemblage structure and functional traits classification

Biomass data were standardized as catch-per-unit of effort (CPUE = biomass of fishes caught divided by hours of net in water). Species occurring in <5% of the habitats surveyed and sampled habitats where no fishes were captured by the gear (12 of 462 habitats) were removed from the dataset. These steps resulted in a 450 × 60 site-by-species matrix for statistical analysis.

We classified species into functional groups based on life-history, feeding and swimming/microhabitat-use strategies (Appendix S2 and Table S1). We classified species according to five life-history strategies based on maximum body size, size at maturation, batch fecundity and parental investment per individual offspring (following Röpke et al., 2017; Winemiller & Rose, 1992): *equilibrium strategists with maturation at small size* (3 species) and *with maturation at large size* (5 species), *periodic strategists with maturation at small size* (22 species) and *with maturation at large size* (19 species) and *intermediate strategists* (11 species). We classified species according to six feeding strategies based on dietary information from published reports: *herbivores* (7 species), *omnivores* (9 species), *detritivores* (11 species), *invertivores* (6 species), *planktivores* (3 species) and *piscivores* (24 species). Finally, we classified species according to five strategies of swimming/microhabitat use based on morphological traits (Appendix S2, Table S2 and Figure S1): *nektonic maneuverable* fishes (21 species), *nektonic burst swimmers* (10 species), *surface dwellers* (2 species), *epibenthic maneuverable* fishes (15 species) and *benthic* fishes (13 species).

2.3.2 | Analysis of land cover and environmental data

The following data were $\log_{10}$ (x + 1) transformed: forest cover, open water area, aquatic macrophyte index, water depth and water transparency. Scatterplots and simple Pearson correlation tests (Zar, 1999) were used to evaluate collinearity among explanatory variables (Table 1). Correlations among variables were <0.4 except for forest and herbaceous cover, which were strongly and negatively correlated (−0.96) indicating

that one land cover category is found in the extreme of the gradient of the other category (i.e. where forest cover is low, herbaceous cover is high and vice versa). We excluded herbaceous cover from the analyses and assumed that response variables (e.g. species, functional groups) positively associated with forest cover were inversely associated with herbaceous cover, and vice versa. In subsequent analyses, we also assessed variance inflation factors (VIF), which generally were <3.0, indicating there was no multicollinearity among the remaining variables (Myers, 1990).

To account for spatial structure, we used principal coordinates of neighbour matrices (PCNM) to transform (spatial) distances to rectangular data suitable for constrained ordination or regression (Borcard & Legendre, 2002), and used the first two PCNM axes, which explained 54% of the spatial distance variability and were associated with large-scale spatial structure, as covariables in remaining analyses. We used this approach to minimize spatial autocorrelation that might inflate type I error (false positive result; see Legendre et al., 2002). This approach also enhanced parsimony by reducing the number of parameters (i.e. other PCNM axes) in remaining analyses. Moran's I analysis did not reveal significant spatial autocorrelation among local-scale environmental variables (Figure S2). These results do not, however, discount the possibility that spatial patterns could be detected by collecting and analysing data for different variables at different spatial and temporal scales. To account for seasonality, we used season as a covariable, as described below for each analysis.

2.3.3 | Taxonomic and functional assemblage structure

We investigated the potential influence of land cover and environmental variables (Table 1) on the taxonomic and functional structure of local fish assemblages using Partial Redundancy Analysis (pRDA) (Ter Braak & Verdonschot, 1995). The CPUE value of each taxon and functional group was Hellinger-transformed prior to pRDA. pRDA was performed using season and the first two axes of the PCNM as covariables to reduce influences of seasonality and spatial structure respectively. We tested for significance using a Monte Carlo permutation test with 999 random permutations under the null model of no effect.

2.3.4 | β diversity decomposition

We used an approach proposed by Legendre (2014) to explain variation in β diversity and its components along environmental gradients. First, we measured dissimilarity among all pairs of observations (sampling habitats) using the percentage difference (β_{Total}, Odum, 1950; known as the Bray–Curtis index). Second, we used the additive partitioning framework proposed by Podani, Ricotta, and Schmera (2013) and Legendre (2014) to decompose two components underlying the total amount of β diversity (β_{Total}) for all pairs of sites: spatial turnover ($\beta_{replacement}$) and abundance difference ($\beta_{abundance\ difference}$) (see Appendix S3). Third, we assessed associations between components of β_{Total} and the land cover and environmental variables (Table 1) using Partial Constrained Analysis of Principal Coordinates (CAP, function *capscale* from *vegan* package in R).

We also evaluated whether distinct land cover and environmental variables affected the relative contribution of the local habitats to β diversity (LCBD), which are comparative indicators of the ecological uniqueness of the sampled habitats for their contribution to β diversity (Legendre, 2014; Legendre & Cáceres, 2013). We built a linear mixed model (LMM) with a random-effects model, where LCBD was the response variable, standardized land cover variables, environmental variables and spatial structure were the fixed effects, and intercepts were allowed to vary according to season (random factor) (Zuur, Ieno, Walker, Saveliev, & Smith, 2009). The model was assessed with respect to normally distributed errors (visual inspection of residual plots and Shapiro–Wilk test) and multicollinearity (VIF).

Analyses were performed in R v. 3.2.0. pRDA and CAP were computed with the *vegan* package (Oksanen et al., 2013). β_{Total}, $\beta_{replacement}$, $\beta_{abundance\ difference}$ and LCBD were computed with functions *beta.dive()* and *beta.div.comp()* from Legendre (2014), and LMM was performed using the package *lmne* (Pinheiro, Bates, DebRoy, & Sarkar, 2014).
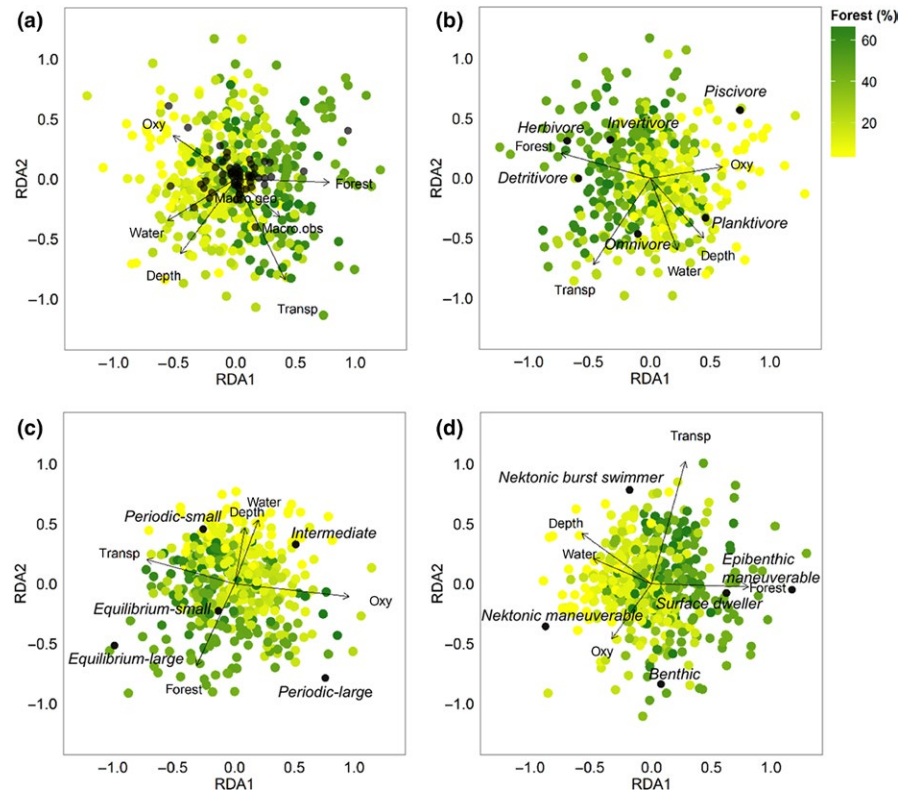
3 | RESULTS

3.1 | Taxonomic and functional assemblage structure

A forest cover gradient was strongly associated with axis 1 for fish assemblage structure based on taxonomy, feeding strategies and habitat-use strategies (average score for forest in axis 1 = 0.58), and with axis 2 for assemblage structure based on life-history strategies (Figure 2a–d). Taxonomic assemblage structure was strongly associated with this gradient of forest cover (permutation test pseudo-F = 3.105; p < .001; Figure 2a; Table 2). Several species that feed on terrestrial food resources (e.g. *Osteoglossum bicirrhosum*, *Colossoma macropomum*) and taxonomic groups that tend to be associated with structurally complex habitats (e.g. cichlids) were positively associated with forest cover (axis 1). Species generally considered to be habitat generalists (e.g. *Pygocentrus nattereri*) and nektonic fishes (e.g. *Pellona* spp., *Hypophthalmus marginatus*) tended to be associated with the opposite extreme of the forest gradient (i.e. less forest cover and more herbaceous vegetation).

Assemblage functional structures also were strongly associated with forest cover (p < .001; Figure 2b–d; Table 2). Herbivores, detritivores, invertivores and omnivores were positively associated with forest cover, and piscivores and planktivores were negatively associated with forest cover (Figure 2b). Equilibrium and periodic strategists tended to be more abundant when forest cover was greater, and species with maturation at large size had stronger relationships with forest than those with maturation at small size (Figure 2c). Intermediate strategists were inversely correlated with forest cover gradient. Epibenthic maneuverable species (e.g. cichlids) had the strongest association with forest cover, followed by surface dwellers (e.g. *O. bicirrhosum*) and benthic fishes (e.g. *Pterygoplichthys pardalis*) (Figure 2d). Nektonic maneuverable fishes (e.g. *Pellona* spp.) and nektonic burst swimmers (e.g. *Anodus elongatus*, *Hemiodus* spp.) were inversely associated with the gradient of forest cover.

Taxonomic structure was significantly associated with a gradient of greater water depth, transparency, dissolved oxygen, area of open water and macrophyte cover that was modelled by RDA axis 2

FIGURE 2 Redundancy Analyses (RDA) biplots showing associations of assemblage structures in terms of taxonomic composition (a) and functional groups of feeding (b), life-history (c) and microhabitat-use (d) strategies and statistically significant land cover and environmental variables (arrows). Biplots show RDA scores for the sampled habitats (450 points) in a gradient of forest cover that ranges from yellow, representing bare soil or meadows of herbaceous vegetation, to green, representing forested local catchments. Black points represent scores for species and functional groups. Arrow length and direction correspond to the variance that can be explained by each land cover and environmental variable. The tip of each arrow indicates the loading of each variable on axis 1 and 2. Species name abbreviations in plot (a) were removed to improve legibility; but see Table S1 for species names and loadings on the RDA axes

TABLE 2 Results of redundancy analyses (RDA) for fish taxonomic and functional assemblage structures and land cover and local environmental variables in the lower Amazon floodplain

Variable	Taxonomic composition			Feeding			Life history			Microhabitat use		
	Variance	F	Pr(>F)	Variance	F	Pr(>F)	Variance	F	Pr(>F)	Variance	F	Pr(>F)
Forest (%)	0.005	3.10	0.001	0.003	4.07	0.002	0.003	4.36	0.003	0.004	5.82	0.002
Water (%)	0.008	3.87	0.001	0.002	3.08	0.015	0.002	2.71	0.036	0.002	3.63	0.009
Macrophyte (geop)	0.003	2.27	0.002	0.001	2.03	0.091	0.001	2.08	0.092	0.000	0.71	0.597
Macrophyte (obs)	0.003	1.91	0.004	0.001	1.38	0.242	0.001	1.43	0.207	0.000	0.39	0.806
Depth (cm)	0.007	4.90	0.001	0.004	5.67	0.001	0.002	3.44	0.010	0.006	8.70	0.001
Dissolved oxygen (mg/L)	0.004	2.69	0.001	0.003	4.45	0.001	0.005	8.77	0.001	0.002	2.64	0.035
Transparency (cm)	0.005	3.36	0.001	0.003	4.51	0.001	0.003	5.01	0.002	0.005	7.97	0.001
Temperature (°C)	0.001	0.99	0.470	0.000	0.43	0.919	0.000	0.68	0.561	0.001	1.50	0.167
Residual	0.65			0.30			0.26			0.28		

(Figure 2a, Table 2). Temperature had negligible association with major environmental and assemblage structure gradients. Assemblage functional structures were associated with gradients defined by the same set of environmental variables, with the exception that aquatic macrophyte cover had weak associations, and temperature again having virtually no influence on ordinations (Figure 2b–d, Table 2).

3.2 | β diversity

Total β diversity and its replacement component were significantly associated with the gradient of forest cover, indicating that areas with

more forest cover tended to have greater spatial variation in species composition than those dominated by herbaceous vegetation or open water (p = .001, Table 3, Figure S3). β diversity also was associated with other land cover and environmental variables, except for temperature (Table 3, Figure S3); however, the $\beta_{\text{abundance difference}}$ component was only associated with water depth and transparency (Table 3, Figure S3).

Forest cover was positively associated with local contributions to β diversity (LCBD) (95% confidence interval >0; Figure 3), indicating that habitats with greater forest cover tended to have unique combinations of species. Transparency, depth and the large-scale estimate of aquatic

TABLE 3 Results of constrained analysis of principal coordinates (CAP) for β diversity components (β$_{replacement}$, β$_{abundance difference}$ and β$_{Total}$, Legendre, 2014; Podani et al., 2013) of local catchments in the lower Amazon floodplain (also see Figure S3)

	β$_{replacement}$			β$_{abundance difference}$			β$_{Total}$		
Variable	Sum of squares	F	Pr(>F)	Sum of squares	F	Pr(>F)	Sum of squares	F	Pr(>F)
Forest (%)	0.84	2.84	0.001	0.11	1.44	0.201	2.19	1.63	0.001
Water (%)	0.95	3.24	0.001	0.07	0.99	0.372	2.33	1.73	0.001
Macrophyte (geop)	0.66	2.23	0.001	0.02	0.19	0.991	1.78	1.32	0.001
Macrophyte (obs)	0.57	1.95	0.004	0.06	0.81	0.477	1.74	1.29	0.005
Depth (cm)	0.63	2.14	0.001	0.84	11.17	0.001	2.97	2.21	0.001
Dissolved oxygen (mg/L)	0.77	2.61	0.001	0.09	1.15	0.294	2.78	1.66	0.002
Transparency (cm)	0.48	1.63	0.016	0.54	7.11	0.001	2.30	1.71	0.001
Temperature (°C)	0.32	1.08	0.36	0.08	1.11	0.326	1.37	1.02	0.35
Residual	128.04			32.81			585.81		
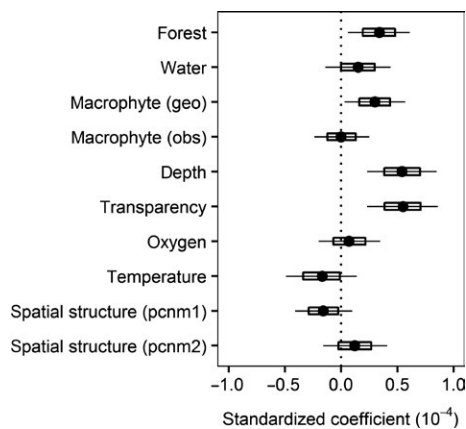
FIGURE 3 Standardized coefficients, standardized errors (box-and-whiskers) and 95% confidence intervals (bars) of the predictors for local contribution to β diversity indices (LCBD) in the lower Amazon floodplain. Variables were considered to have a significant effect on LCBD when 95% confidence interval (CI) of coefficients did not overlap zero

macrophyte cover based on remotely sensed images also were directly correlated with LCBD (Figure 3). The linear mixed-effects model explained 30% of the total variation in LCBD (R^2 = .30), with 15% of this variation being explained by the variables directly correlated with LCBD. Inspection of residual plots, Q–Q plots and Shapiro–Wilk normality test (W = 0.994, p > .09) demonstrated that errors were normally distributed (Figure S4), indicating that model assumptions were met.

4 | DISCUSSION

Our findings suggest that deforestation of Amazonian floodplain leads to spatial homogenization of fish assemblages and reduced functional diversity at both local and regional scales. As hypothesized, several species and functional groups based on life-history, feeding and swimming/microhabitat-use strategies were associated with forested areas in the floodplain. Several species, including some that would be considered habitat generalists and species directly dependent on autochthonous resources (e.g. planktivores), were most common in

areas dominated by herbaceous vegetation or open water that were associated with the opposite extreme of the forest cover gradient. β diversity and the degree of uniqueness in species combinations within habitats (LCBD) also were positively associated with forest cover. Spatial patterns of fish taxonomic and functional diversity appear to be influenced by the extent of forest cover as well the spatial configuration of land cover types and associated environmental variables. Forest loss, therefore, reduces spatial patterns of species turnover and likely increases the relative abundance and richness of species with good dispersal abilities and species classified as ecological generalists. Our findings thus support the view that land cover changes tend to cause the replacement of species having unique combinations of functional traits with species that are ecological generalists having traits shared with other species, resulting in greater functional redundancy within and between local assemblages (Casatti et al., 2015; Flynn et al., 2009; Gibson et al., 2011; Villéger et al., 2010).

These inferred effects of forest loss on fish biodiversity are in line with the view that environmental conditions associated with land cover act like a filter during local community assembly, as observed in studies involving other organisms and ecosystems (e.g. Casatti et al., 2015; Keck et al., 2014; Ockinger et al., 2010). In our study, several species were strongly associated with forest cover, because they directly exploit resources that originate from forest vegetation. In Amazonian floodplains, many herbivorous, detritivorous and invertivorous fishes enter flooded forests to consume allochthonous food resources (Correa et al., 2015; de Mérona & Mérona, 2004; Goulding, 1980). For example, herbivorous serrasalmids (e.g. *C. macropomum*, *Piaractus brachypomus*, *Myloplus* spp.) consume fruits and seeds that fall into the water, and detritivorous fishes feed on fine particulate organic matter of both autochthonous and allochthonous origin (Benedito-Cecilio & Araujo-Lima, 2002; Goulding, 1993), and on biofilms containing fungi and other micro-organisms (Lujan, German, & Winemiller, 2011). Epibenthic maneuverable fishes (e.g. cichlids) and benthic fishes (e.g. catfishes) are well adapted to forage within the structurally complex micro-habitats of flooded forests (Ribeiro et al., 2016). Fishes with equilibrium life-history strategies, such as the

mouth-brooding aruana (*Osteoglossum bichirosum*) and cichlids with bi-parental brood guarding, may have enhanced offspring survival and recruitment within structurally complex habitats of flooded forests that provide cover from predators. Conversely, herbaceous vegetation and areas of open water may provide fitness advantages for fishes that feed on abundant zooplankton supported by phytoplankton production stimulated by light exposure in areas lacking dense forest canopy cover (e.g. *Anchoviella guianensis*, *A. elongatus*, *Hypopthalmus marginatus*). These fishes, together with small characid fishes not captured in our gillnets, are major food resources for piscivorous fishes that pursue prey in open waters (e.g. *P. nattereri*, *Serrassalmus* spp., *Pellona* spp., *Acestrorhychus* spp.).

Our β diversity results indicated species turnover along the forest cover gradient, but no significant differences in overall fish abundance, which raises the question of whether there is community density compensation associated with species replacement along the gradient. Although our study provides some support for this density compensation hypothesis, it remains an open question. Contrary to our results, other studies (e.g. Lobón-Cerviá et al., 2015) found the standing biomass of commercially important species to be positively associated with forest cover. Given that functional structure of fish assemblages is strongly associated with land cover gradients, future studies of fish biomass in response to deforestation should focus on particular groups of species among the full functional diversity of fish assemblages.

Taxonomic and functional assemblage structures also were associated with gradients defined by local environmental variables, a finding consistent with other studies showing that a hierarchical network of interacting factors and processes, rather than just a single mechanism, influences fish assemblages in floodplain ecosystems (Freitas, Siqueira-Souza, Florentino, & Hurd, 2014; Kouamé et al., 2008; Tejerina-Garro, Fortin, & Rodriguez, 1998). Water transparency, depth and dissolved oxygen have been shown to be significant determinants of fish assemblage structure in other Neotropical river floodplains (Arantes, Castello, Cetra, & Schilling, 2013; Petry, Bayley, & Markle, 2003; Rodriguez & Lewis, 1997; Tejerina-Garro et al., 1998). Deeper aquatic habitats in the floodplain may support greater fish abundance because they are more stable during periods of extreme low water (Arantes et al., 2013). Several groups of diurnal fishes that rely strongly on vision (e.g. cichlids, clupeiforms) tend to occur in habitats with low turbidity (Rodriguez & Lewis, 1997; Tejerina-Garro et al., 1998). Nocturnal fishes that rely heavily on other sensory modalities that are effective under low light conditions (e.g. siluriforms and gymnotiforms that rely on olfaction and electroreception) tend to be abundant in turbid water bodies (Rodriguez & Lewis, 1997; Tejerina-Garro et al., 1998). In our study, dissolved oxygen was associated with assemblage structure and turnover of species probably because species respond differentially to hypoxic environments depending on their degree of tolerance (Junk, Soares, & Carvalho, 1983; Petry et al., 2003). We note that although we found significant associations of land cover and local-scale environmental variables with fish assemblage structure, a large amount of variation in assemblage structure was unexplained by these sets of variables. Although we factored out the direct influences of

hydrological seasonality from our analyses, part of this unexplained variation in the assemblage structure may be associated with its indirect influences (e.g. changes in habitat connectivity), which were not measured or controlled here, and can influence local community assembly in floodplains (Junk, 1997; Winemiller & Jepsen, 1998). Ecological processes in floodplains of tropical lowland rivers are driven by multiple deterministic and stochastic mechanisms that operate across a broad range of temporal and spatial scales (Hurd et al., 2016; Winemiller, 1996). Consequently, there is an urgent need to further develop approaches to reveal the mechanisms driving spatial patterns of biodiversity in these heterogeneous and dynamic systems. Our study suggests that such approaches must be based on complementary components of biological diversity (e.g. species functional traits), rather than approaches based solely on taxonomy.

4.1 | Conservation and management implications

Our results demonstrating relationships among spatial patterns of fish diversity and gradients of land cover and local environmental variables strongly imply that conservation of Amazonian fish diversity requires maintenance of substantial forest cover within the floodplain landscape mosaic. Floodplains throughout the world are being deforested for the development of agriculture, municipalities, hydropower and mining (Tockner & Stanford, 2002). Unfortunately, mitigations and conservation strategies in these ecosystems often suffer from deficiencies of design and implementation, or fail to protect landscapes at the scale of river catchments (Castello & Macedo, 2016). In the Brazilian Amazon, the existing protected area network was established based largely on the distributions of terrestrial taxa, with few protected areas specifically designated to protect aquatic ecosystems (Castello & Macedo, 2016). As a result, there are no protected areas encompassing floodplains within our study area. The Forest Code establishes protection of riparian vegetation, but only up to a maximum extent of 500 m from river banks, which is insufficient to protect the vast areas of floodplain in the lower Amazon. Based on our findings, the conservation of fish diversity requires protection of floodplain forests. For example, protecting the remaining 13% of forests in our study area would maintain about 60% of fish taxonomic diversity and 68% of functional diversity. Of course, in the long term, diverse terrestrial and aquatic habitats would need to be conserved over a much larger region. More research is needed to strengthen such estimates and to extrapolate to regional scales. Conserving aquatic biodiversity and ecosystem services not only requires protection of local landscape units but also must address impacts in upland areas of catchments, including construction of dams that alter river hydrology and sediment/nutrient dynamics.

CONFLICT OF INTEREST

The authors have no conflicts of interest.

AUTHORS' CONTRIBUTIONS

C.A., K.W., L.C. and M.P. designed research; C.A. and K.W. performed research; C.A., K.W. and L.L.H. analysed data and C.A., K.W., L.C., M.P., C.E.C.F. and L.L.H. wrote the paper.

DATA ACCESSIBILITY

Data are available from the Dryad Digital Repository https://doi.org/10.5061/dryad.d5s4g (Arantes et al., 2017).

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