FISH DIVERSITY, BIOMASS AND TROPHIC DYNAMICS IN RELATION TO LANDSCAPE GRADIENTS IN THE FLOODPLAIN OF THE AMAZON RIVER

A Dissertation

by

CAROLINE CHAVES ARANTES

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Chair of Committee,	Kirk O. Winemiller
Committee Members,	Thomas E. Lacher
	Richard T. Woodward
	X. Ben Wu
Head of Department,	Michael Masser

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ABSTRACT

Floodplains are among the most biologically productive, but also threatened ecosystems in the world with global loss of natural systems exceeding 60%. Human development activities, including the construction of dams, mining and conversion of forests to croplands and pastures, are rapidly changing floodplains landscapes, likely impacting fish diversity, aquatic food webs, and fishery production. My dissertation investigates the possible effects of land-cover changes on fish diversity and biomass in the lower Amazon River floodplain, and evaluates how food webs vary across different scales in this changing landscape. Field expeditions were conducted during four phases of the annual hydrological cycle in several habitats across a gradient of landscape conditions, from highly deforested to mostly forested areas, along the Amazon River floodplain. The study surveyed fish assemblages and obtained data on local environmental variables and fisheries management practices as well as samples of fish muscle tissue and basal production sources for analysis of stable isotope ratios. In addition, landscape features were mapped based on satellite imagery.

Spatial patterns of fish biomass distribution and biodiversity 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. Beta-diversity and the degree of uniqueness of species combinations within habitats were also positively associated with forest cover. Basal production sources and fishes showed considerable variation in C and N stable isotope ratio values across the landscape. Analysis of stable isotope data using Bayesian mixing models indicated that aquatic macrophytes and suspended particulate organic material (POM) were the principal sources contributing to the biomass of most fish species at the regional scale; however, contributions of different production sources to fish biomass varied within a given local hydrological unity area. These results suggest that spatial variation in the isotopic ratios and proportional contributions of basal sources to fish biomass are probably influenced by multiple factors, including variation in the quality and quantity of basal sources associated with differences in watershed vegetation across the landscape. In addition, these results demonstrate that because estimated contributions of production sources to fish biomass varied according to the spatial scale of analysis, study designs should carefully consider not only replication and temporal scale, but also spatial scale. Finally, results showing that spatial patterns of fish diversity and biomass are associated with forest cover, indicate that forest loss in the Amazonian floodplain results in spatial homogenization of fish assemblages and reduced functional diversity and fishery production. Maintaining fish diversity and fisheries production in floodplain ecosystems of the Amazon River requires protecting mosaics of both aquatic habitats and floodplain vegetation, with sufficient forest cover being critically important.

To my family.

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CHAPTER I

GENERAL INTRODUCTION

Ecological patterns and processes (e.g., species distributions, flow of material and energy in food webs) are influenced by the landscape features, such as geomorphology and the composition and spatial configuration of vegetation cover (Turner 1989). Yet, natural landscapes structures in ecosystems worldwide have been increasingly modified by human land use, potentially affecting species diversity, abundance, movement and interactions (e.g., through food webs) as well as flow of nutrients across landscapes (Estes et al. 2011; Gibson et al. 2011; Newbold et al. 2015). Improved understanding of the effects of land cover changes on ecological patterns and processes across landscapes is required for maintaining biodiversity and ecosystem services. Accordingly, incorporating spatial relationships in land-using planning is necessary, particularly in decisions for determining priority habitats for conservation (Turner 1989; Margules & Pressey 2000).

Predicting the full range of effects caused by land-cover changes in diverse tropical ecosystems requires consideration of how spatial dynamics of different ecological patterns and processes respond to landscape gradients (e.g., Villéger et al. 2010). In biodiverse ecosystems, ecological responses of organisms to landscape gradients may vary markedly within and across taxonomic groups (Dirzo & Raven 2003; Newbold et al. 2015; Frishkoff et al. 2016). Although species richness and population abundance are usually expected to decline as land-use intensifies, certain species can thrive in modified landscapes as a result of trait mediated processes (e.g., combination of traits, such as body size, generation time, degree of specialization, food preferences that impact organisms performance and thus fitness) (Frishkoff et al. 2016; Villéger et al. 2017). For example, studies have found major changes in spatial patterns of species distribution in degraded tropical rainforests, with large increases in the abundance of generalist species (Gardner et al. 2009). Therefore, a functional diversity perspective, as opposed to a strictly taxonomic approach, can be useful to reveal processes structuring ecological communities along spatial gradients in biodiverse ecosystems (Mouillot et al. 2013; Gutiérrez-Cánovas et al. 2015; Liu et al. 2016). In addition, consideration of the spatial structure and dynamics of food webs is central to understanding relationships between species diversity and environmental heterogeneity as well as the dynamics of species interactions and energy flow in changing landscapes (Holt 2002; Hedlund et al. 2004).

The effects of human land development on spatial ecological patterns and processes can be seen clearly in Amazonian ecosystems. The Amazon possesses the most extensive tropical forest in the world and harbors a substantial proportion of global biodiversity, yet in recent decades, this region also has suffered the greatest extent of tropical deforestation (Fearnside 2005; Laurance, Sayer & Cassman 2014). Unfortunately, land-cover change scenarios in the Amazon are not expected to improve in the near future, with predictions showing that current trends in agricultural expansion will eliminate a total of 40% of Amazon forests by 2050 (Soares-Filho et al. 2006). Such impact includes losses of at least two-thirds of the forest cover of six major watersheds

(Soares-Filho et al. 2006). How such changes in Amazonian landscapes affect ecological processes is a core question for conserving its ecosystems and the biological diversity they support. In upland Amazonian forests, large-scale conversion of forests to agricultural landscapes has been reported to alter plant, animal and microbial diversity as well as biogeochemical cycles and nutrient dynamics (Lavelle & Pashanasi 1989; Dale et al. 1994; Bierregaard 2001; Herpin et al. 2002; Rodrigues et al. 2013). However, the effects of land cover changes on floodplains ecosystems, vital components of the Amazon basin, are still unknown.

Floodplain ecosystems in the Amazon sustain high biodiversity and provide a myriad of natural products and services to human populations (Junk, Soares & Bayley 2007; Castello et al. 2013). These floodplains can span hundreds of square kilometers (Hess et al. 2003) and are fertile and productive, especially in areas dominated by so-called whitewater rivers that carry high loads of suspended sediments (Melack et al. 2009). The fish fauna of the Amazon lowlands is extremely diverse, though not fully documented. The Amazon Basin contains 6000-8000 fish species, including described and undescribed species, with about half of this diversity thought to inhabit river floodplains (Schaefer 1998; Reis, Kullander & Ferraris 2003; Junk, Soares & Bayley 2007). Fishes are the most important food resource for Amazonian populations. The potential fishery yield of the Amazon lowlands has been estimated to be more than 425,000 tons/yr (Bayley 1998). Per capita fish consumption is estimated at 94 kg/yr and 40 kg/yr for rural floodplain communities and urban populations, respectively, and these values are, on average, about four times higher than the world average (Isaac & Almeida 2011).

In Amazon floodplains, seasonal inundations and flooded riparian vegetation play important roles in maintaining high fish diversity and fishery production (Goulding 1980; Junk et al. 1989). In these ecosystems, fish production is stimulated by seasonal inundations that allows fishes to spawn, avoid predation and exploit abundant food resources within vegetated flooded habitats (Goulding 1980; Junk et al. 1989). Many fishes inhabit lakes or river channels during the annual low-water period and migrate laterally into flooded forest habitats when the river water-level rises at the beginning of the flood pulse (Fernandes 1997; Castello 2008; Arantes et al. 2013). These lateral migrations into flooded forests are performed not only by resident floodplain species (e.g., cichlids), but also by species that migrate longitudinally along river channels (e.g., *Semaprochilodus* spp.; Ribeiro de Brito & Petrere 1990). Some large catfish species migrate along river channels from the estuary to the headwaters (e.g., *Brachyplatystoma* spp.), but young juveniles enter nursery habitats in floodplains and adults prey on floodplain-dependent species (Barthem et al. 2017). In flooded habitats, many fishes feed on abundant fruits, seeds, plant debris, algae, terrestrial invertebrates, phyto-and zooplankton, herbaceous plants and aquatic macrophytes (Mérona & Mérona 2004). Accordingly, flooded forests provide important sources of carbon and energy that support fish biomass (Araujo-Lima et al. 1986; Forsberg et al. 1993; Oliveira et al. 2006). Flooded forests facilitate reproduction and recruitment of various fish species (e.g., osteoglossids and many cichlids) and provide protection from predators (e.g., many characids that spawn in the channel have offspring that take refuge in floodplains) (Bayley & Petrere 1989). In addition, introduction of allochthonous materials from flooded riparian vegetation into aquatic habitats influences flow of material and energy through food webs across the landscape (Junk 1997).

Despite the importance of Amazonian floodplains for sustaining fish biodiversity and fish stocks that provide for livelihoods of rural communities, their landscapes have been increasingly altered by human activities. These changes in land cover have unpredictable consequences for the fish fauna and fishery production. Human development activities, including the construction of dams, mining and conversion of forests to croplands and rangelands, are rapidly degrading floodplains riparian forests. Over 50% of floodplain forest in the Lower Amazon were deforested by 2008 (Renó et al. 2011), compared to about 20% of upland forests in 2012 (Hansen et al. 2013). What are the possible effects of these landscape changes on fish diversity and biomass? Does the flow of energy and matter vary across these changing landscapes? My dissertation addresses these questions by developing comprehensive analyses of how different aspects of fish diversity, fish biomass and aquatic food webs vary across landscape gradients, from highly deforested to mostly forested areas, in the Lower Amazon River floodplain. My study is designed to overcome limitations in dealing with the complexities of this ecosystem, including its high spatio-temporal habitat heterogeneity and exceptionally high taxonomic and functional diversity of fishes (McConnell & Lowe-McConnell 1987; Junk 1997). My research applied extensive spatial and temporal sampling effort in order to understand the relationships between ecological factors: the flood pulse, landscape gradients and diverse ecological strategies of fishes. Field surveys were conducted during five boat-based expeditions that covered four phases of the annual hydrological cycle in several habitats across the gradient of landscape conditions in the lower Amazon River floodplain. I sampled fish assemblages and collected data on local environmental variables and presence of local management practices. I also collected samples of fish muscle tissues and major basal production sources supporting fish biomass for stable isotope analysis, and used satellite imagery to map landscape features.

This dissertation is organized according to three main research projects. In chapter II, I evaluate how fish ecological strategies and assemblage structure in floodplain habitats vary as a function of forest cover. In chapter III, I evaluate the relationship between fish biomass and forest cover gradients, and how the strength of this relationship may depend on species functional traits. Both chapters use functional perspective and complementary analyses to provide a more holistic understanding of the relationships between fish diversity, fish biomass, the landscape and associated environmental gradients. Findings in these chapters are used as the basis to infer possible impacts of land-cover change on fish biodiversity and fishery production. In chapter IV, I examine how resources supporting fish biomass differ among food webs of aquatic habitats in the floodplain. Based on stable isotope analysis, I estimate food web structure across different spatial scales, and results provide the basis for discussing potential causes for patterns of spatial variation. Together these chapters address the challenge of understanding and predicting ecological process and patterns in a changing tropical diverse ecosystem, and provide a foundation for further development of conservation plans for the Amazon.

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CHAPTER II

RELATIONSHIPS BETWEEN FOREST COVER AND FISH DIVERSITY IN THE AMAZON RIVER FLOODPLAIN*

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., Stuart et al. 2004; Gibson et al. 2011), but there have been few studies of tropical freshwater ecosystems, which are being rapidly modified (Sala et al. 2000; Dudgeon et al. 2006). Tropical freshwater ecosystems support high biodiversity and important ecosystem services (Tockner & Stanford 2002; Davidson 2014), with this group comprising over 31% of freshwater species listed as at risk of extinction by the IUCN (Darwall & Freyhof 2016, Arthington et al. 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; Teresa & Casatti 2012: Cetra et al. 2017 and supplementary references); however,

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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 (Pusey & Arthington 2003, Arthington et al. 2015). In the Amazon and most other major tropical regions, large forest areas are being cleared for 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 derives from carbon and energy sources in floodplain forests (Goulding 1980; Forsberg et al. 1993; Anderson et al. 2011). 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 et al. 2015). The diversity and assemblage structure of Amazonian fishes thus should be affected by deforestation (Renó et al. 2011; Castello et al. 2013), and better understanding of this issue is essential for both fisheries management and biodiversity conservation.

Here, I evaluated how fish species with different ecological strategies and assemblage structure respond to forest cover in floodplains of the Amazon Basin. I 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 et al. 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 (Mouillot et al. 2013; Gutiérrez-Cánovas et al. 2015). Functional traits and performance measures can be combined to explore niche dimensions associated with ecological strategies (Winemiller et al. 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 (Whittaker 1972; Socolar et al. 2016). Research based on empirical measures of beta diversity has shown that habitat degradation can increase community similarity and decrease turnover of species across space through reductions in structural complexity and diversity of habitats, leading to biotic homogenization (e.g., see Hewitt et al. (2005) for benthic infauna and epifauna), with responses depending on taxonomic group, scale, and region (Socolar et al. 2016).

I tested three hypotheses. The first was that several fish species and functional groups are positively associated with forest cover and associated environmental variables at the local scale. 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. I 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, I 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.

I tested these hypotheses by analyzing 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. I used the resulting possible relationships to infer the likely impacts on fish biodiversity of forest loss and replacement by non-forest habitats.

MATERIALS AND METHODS

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 (ANA 2014) 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 et al. 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).

Data collection

Satellite imagery

Floodplain land cover (open water, herbaceous vegetation, forest; Table 1, and see Appendix A.1) at low-water stage was mapped by L. Hess (unpublished data, Appendix A.1) 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 A.1) was mapped using seven ALOS PALSAR swaths acquired during the early rising-water period in each of five 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 hydrological unities (LHUs) (or *"lake systems"*). Each LHU contains lakes, interconnecting channels, forest, and areas with herbaceous vegetation and aquatic macrophytes that are hydrologically connected for about six to nine months per year (see inset in Figure 1). LHUs are separated from each other by major secondary channels (areas of low elevation) and/or natural levees (areas of high elevation). Twenty (20) LHUs were mapped (Figure 1, median area: 23.4 km^2) that encompassed a gradient of forest cover, ranging from 3 to 70%.

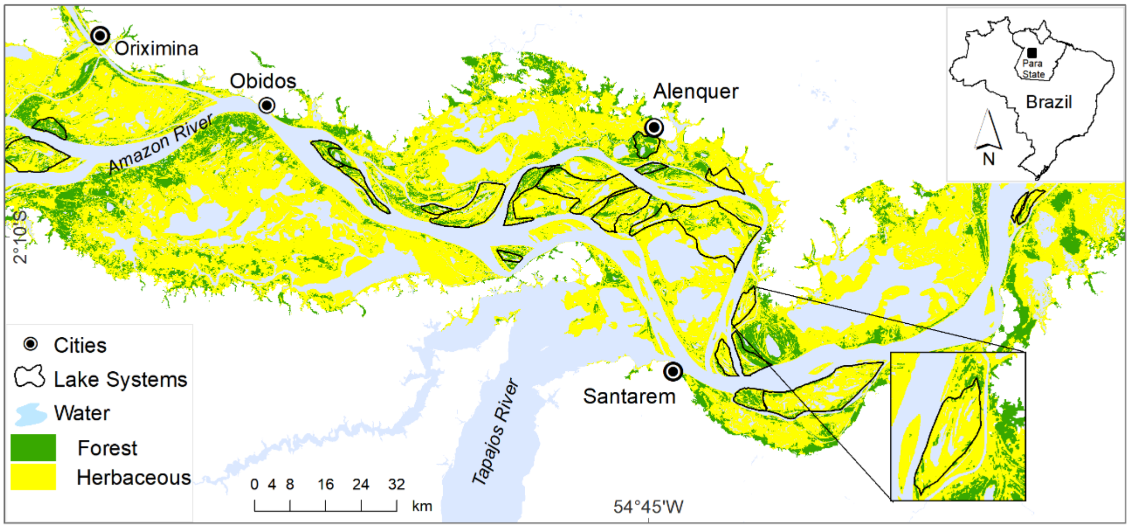

Figure 1: Study area in the lower Amazon showing low-water land cover and 20 local hydrological unities that were studied. Land cover types are forest, herbaceous vegetation, and open water (lakes and secondary channels). In the lower Amazon, the vegetation consists primarily of herbaceous vegetation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

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 LHUs (Figure 1). For each habitat type within each LHU, and during two dry periods and one rising-, high-, and falling-water period, fish were collected using a standard set of nets with different mesh sizes (11 gillnets measuring 25 x 2 meters, with mesh sizes 20, 30, 40, 50, 60, 70, 80, 90, 100, 120, and 130 mm, and one gillnet measuring 100 x 3 meters, with 180 mm mesh). For each season and all habitats sampled within each LHU, average gillnet sampling effort was approximately 25 hours (SD ~4 hours). For the same seasons and habitats within each

LHU where fish were collected, local environmental variables were measured (see Table 1 for details).

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 surveys during five seasonal surveys.

Variable	Description or method	Median	LQ	UQ
Land cover category				
Forest (%)	Percent of closed-canopy tree cover and short trees, shrub, or semi-shrub (including the aroid *Montrichardia arborescens)* in the local hydrological unitiy	21.0	10.5	47.6
Open water (%)	Percent of open water in lakes and channels during low waters in the local hydrological unitiy (excluding the mainstem Amazon channel)	9.6	3.0	12.9
Herbaceous vegetation (%)	Percent of soil, fresh sediments, grasses or forbs during low waters in the local hydrological unitiy	66.9	42.6	74.5
Local environmental variables				
Aquatic macrophyte indices				
Macrophyte - geoprocessing: Macro (geop)	Indices indicating the percent of the local hydrological unitiy with macrophytes present (during late December to January) in 3 or more of 5 years analyzed (2006/2007 to 2010/2011). “Macro (geop)” provides large-scale estimates of coverage.	17.1	13.0	22.5
Macrophyte - visual observation (%): Macro (obs)	Percent 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 (^{0}C)		30.1	29.3	30.8

Statistical analyses

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.

I classified species into functional groups based on life history, feeding and swimming/microhabitat-use strategies (Appendix A.2 and A.11). I 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 Winemiller & Rose (1992) and Röpke et al. (2017): *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), *intermediate strategists* (11 species). I 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, I classified species according to five strategies of swimming/microhabitat use based on morphological traits (Appendix A.2, A.3 and A.4): *nektonic maneuverable* fishes (21 species), *nektonic burst swimmers* (10 species), *surface dwellers* (2 species), e*pibenthic maneuverable* fishes (15 species), and *benthic* fishes (13 species).

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). I 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, I 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, I used Principal Coordinates of Neighbor 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. I 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 (Appendix A.5). These results do not, however, discount the possibility that spatial patterns could be detected by collecting and analyzing data for different variables at different spatial and temporal scales. To account for seasonality, I used season as a covariable, as described below for each analysis.

Taxonomic and functional assemblage structure

I investigated the potential importance 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. I tested for significance using a Monte-Carlo permutation test with 999 random permutations under the null model of no effect.

Beta diversity decomposition

I used an approach proposed by Legendre (2014) to explain variation in β diversity and its components along environmental gradients. First, I measured dissimilarity among all pairs of observations (sampling habitats) using the percentage difference (β_{Total}, Odum 1950, known as the Bray-Curtis index). Second, I used the additive partitioning framework proposed by Podani, Ricotta & 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 A.6). Third, I 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).

I 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 & Cáceres 2013; Legendre 2014). I built a linear mixed model (LMM) with a random-effect 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 et al. 2009). The model was assessed with respect to normally distributed errors (visual inspection of residual plots and Shapiro-Wilk test) and multicollinearity (Variance Inflation Factor).

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 et al. 2014).

RESULTS

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-$F = 3.105$; $p < 0.001$; 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 ($p < 0.001$; 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., *Osteoglossum 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 modeled by RDA axis 2 (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 that had weak associations, and temperature again having virtually no influence on ordinations (Figure 2b-d, Table 2).

Beta 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 ($p = 0.001$, Table 3, Appendix A.8). β diversity also was associated with other land cover and environmental variables, except for temperature (Table 3, Appendix A.8); however, the $\beta_{abundance\ difference}$ component was only associated with water depth and transparency (Table 3, Appendix A.8).

Forest cover was positively associated with local contributions to β diversity (LCBD) (95% confidence interval >0; Figure 3, Appendix A.9), indicating that habitats with greater forest cover tended to have unique combinations of species. Transparency, depth and the large-scale estimate of aquatic macrophyte cover based on remotely sensed images also were directly correlated with LCBD (Figure 3). The linear mixed-effect model explained 30% of the total variation in LCBD ($R^2 = 0.30$), 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 ($W = 0.994$, $p > 0.09$) demonstrated that errors were normally distributed (Appendix A.10), indicating that model assumptions were met.

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.

	Taxonomic composition			Feeding			Life history			Microhabitat use		
Variable	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 (^{0}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		

Table 3: Results of Constrained Analysis of Principal Coordinates (CAP) for β-diversity components ($\beta_{replacement}$, $\beta_{abundance\ difference}$ and β_{Total}, Legendre 2014, Podani *et al.* 2013) of local hydrological unities in the lower Amazon floodplain (also see Appendix A.6).

Variable	$\beta_{replacement}$			$\beta_{abundance\ difference}$			β_{Total}		
	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 (^{0}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		

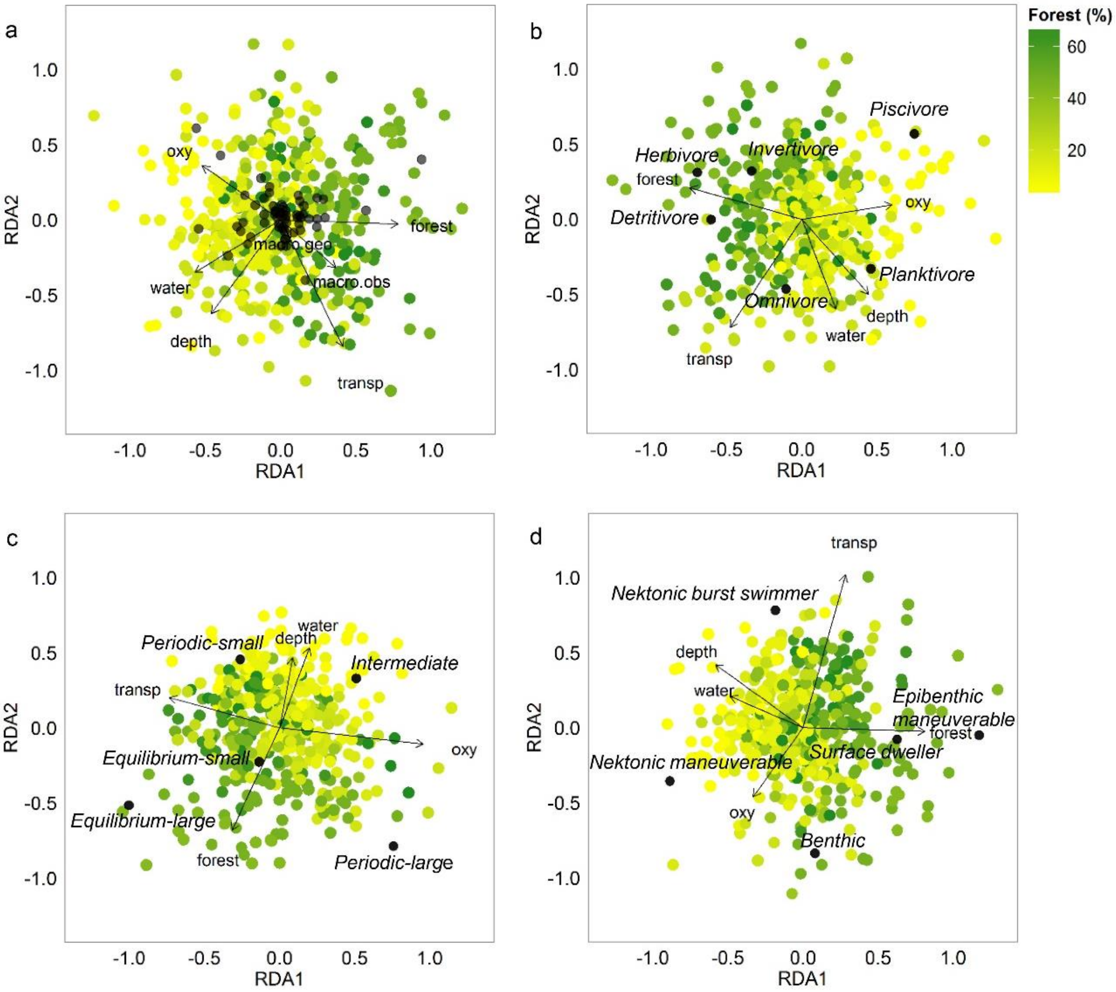

Figure 2: Redundancy Analyses (RDA) biplots showing associations of assemblage structures in terms of taxonomic composition (a) and functional groups of feeding (b), life history (c), and microhabitat use (d) strategies and statistically significant land cover and environmental variables (arrows). Biplots 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 hydrological unitiy. 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 Appendix A.11 for species names and loadings on the RDA axes.

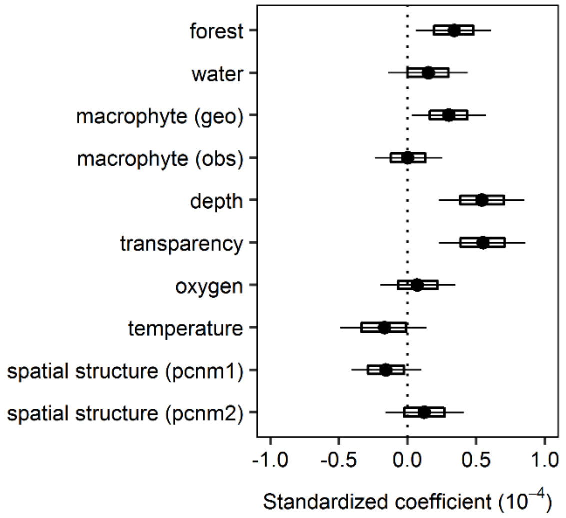

Figure 3: Standardized coefficients, standardized errors (box-and-whiskers), and 95% confidence intervals (bars) of the predictors for local contribution to β diversity indices (LCBD) in the lower Amazon floodplain. Variables were considered to have a significant effect on LCBD when 95% confidence interval (C.I.) of coefficients did not overlap zero.

DISCUSSION

This study’s finding 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. This study’s findings thus support the view that deforestation 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 functionally redundancy within and between local assemblages (Flynn et al. 2009; Gibson et al. 2011; Villéger et al. 2010; Casatti et al. 2015).

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., Ockinger et al. 2010; Keck et al. 2014; Casatti et al. 2015). In this study, several species were strongly associated with forest cover, because they directly exploit resources that originate from forest vegetation. In Amazonian floodplain, many herbivorous, detritivorous and invertivorous fishes enter flooded forests to consume allochthonous food resources (Goulding 1980; Mérona & Mérona 2004; Correa et al. 2015). For example, herbivorous serrassalmids (e.g., *Colossoma 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 (Goulding 1993; Benedito-Cecilio & Araujo-Lima 2002), and on biofilms containing fungi and other microorganisms (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, Teresa & Casatti 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, Anodus elongatus, Hypopthalmus marginatus*). These fishes, together with small characid fishes not captured in this study's gillnets, are major food resources for piscivorous fishes that pursue prey in open waters (e.g., *Pygocentrus nattereri*, *Serrassalmus* spp., *Pellona* spp., *Acestrorhychus* spp.).

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 this study provides some support for this density compensation hypothesis, it remains an open question. Contrary to this study's 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 (Tejerina-Garro, Fortin & Rodriguez 1998; Kouamé et al. 2008; Freitas et al. 2014). Water transparency, depth, and dissolved oxygen have been shown to be significant determinants of fish assemblage structure in other Neotropical river floodplains (Rodriguez & Lewis 1997; Tejerina-Garro, Fortin & Rodriguez 1998; Petry, Bayley &

Markle 2003; Arantes et al. 2013). 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, Fortin & Rodriguez 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, Fortin & Rodriguez 1998). In this 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, Bayley & Markle 2003). I note that although I 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 I factored out the direct influences of hydrological seasonality from the 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 (Winemiller & Jepsen1998; Junk 1997). 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 (Winemiller 1996; Hurd et al. 2016). 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. This 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.

Conservation and management implications

This study's results demonstrating relationships among spatial patterns of fish diversity and gradients of land cover and local environmental variables strongly implies 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 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 this 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 this study's findings, conservation of fish diversity requires protection of floodplain forests. For example, protecting the remaining 13% of forests in this 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.

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CHAPTER III

FISH BIOMASS AND FUNCTIONAL DIVERSITY ARE POSITIVELY ASSOCIATED WITH FOREST COVER IN THE AMAZON RIVER FLOODPLAIN

INTRODUCTION

Floodplains are among the most biologically productive, but also threatened ecosystems in the world, with global conversion and loss exceeding 60% (Davidson 2014; Reis et al. 2017). These ecosystems have been severely impacted by cumulative effects of global climate change, deforestation and hydroelectric dams, leading to losses of aquatic biodiversity and productivity (Tockner & Stanford 2002; Smokorowski & Pratt 2007; Tockner et al. 2008). Several influential riverine models of the structure and function of temperate and tropical floodplains have stressed that riparian zones provide significant production sources for aquatic food webs sustaining fish biomass (e.g., Junk et al. 1989; Thorp & Delong 1994). In rivers with large and relatively unaltered floodplains, major fish biomass is derived from allochthonous sources of organic matter produced within riparian zones, including seeds, fruits, fallen insects as well as decaying forest vegetation (Junk et al. 1989; Tockner, Malard & Ward 2000). Flood pulse frequency and duration and the extent of inundation of riparian zones influence fish movement and access to this organic matter. Inundation of riparian vegetation also brings nutrients from the floodplain to the river, supplementing local (i.e., autochthonous) production (Thorp et al. 1998). These riparian zones within floodplains provide not only major sources of carbon and energy, but also critical spawning and nursery habitat for many fishes (e.g, Copp & Penáz 1988; Goulding 1993; Ward, Tockner & Schiemer 1999; Górski et al. 2016). Fish biomass in floodplains is therefore likely affected by degradation of riparian zones.

Loss of riparian forests in floodplains of the Amazon is of particular concern. These forests support a diverse fauna of fishes, including several species that are important sources of protein and income sustaining millions of people (Bayley & Petrere 1989). Seasonal inundation prompts fish to migrate into flooded forests and shrublands where they find abundant food and protection from predators that enhance survival, growth, and fishery production (Junk et al. 1989; Forsberg et al. 1993; Goulding 1993; Oliveira et al. 2006). Amazon River production sustains per capita fish consumption that is four times greater than the global average (Isaac & Almeida 2011). The degree to which losses of floodplain forest impact fish biomass in the Amazon is unclear. By 2008, over 50% of the floodplain in the lower Amazon was deforested, primarily driven by expansion of cattle ranching and crop production (Renó et al. 2011; Hansen et al. 2013). Construction of large hydroelectric dams is clearing and submerging large areas of forest along major Amazon tributaries (Castello et al. 2013).

Previous studies have shown that forest loss in the Amazon floodplains can change the structure of fish assemblages, but estimates of the effects of deforestation on fish biomass have been contradictory. Fish species and their associated functional traits varied across gradients of forest cover, but without apparent differences in total fish biomass among habitats (Arantes et al. 2017). In the Central and Lower Amazon, biomass of commercially important fishes was found to be higher where forest cover was higher (Lobón-Cerviá et al. 2015). The relationship between fish biomass and forest cover may be affected by non-random, trait-based processes driving populations responses to environmental gradients, as found for other systems (e.g., Rolhauser & Pucheta (2016) for plants, Teresa & Casatti (2017) for stream fishes). For example, forest loss may favor generalists and fast-growing species, at the expense of specialists or species dependent upon structurally-complex habitats, which may result in no changes or even increases in total biomass in deforested areas (e.g.,Lorion & Kennedy 2009; Ribeiro, Teresa & Casatti 2016). Greater ability to predict the responses of fish biomass to deforestation could be gained by evaluating this issue from a functional perspective.

Here, I evaluated how fish biomass responds to forest cover gradients, and how the strength of response may depend on species functional traits. I conducted fisheries-independent surveys (thus avoiding sources of bias often associated with fisheries-based surveys) and used satellite-mapped landscape data for floodplains of the lower Amazon River. Data were collected during four phases of the river’s annual hydrological cycle and spanning a gradient of forest cover, from nearly pristine to highly deforested areas. I modeled relationships between forest cover and the total biomass of local fish communities as well as groups of species possessing different functional traits and degrees of importance for fisheries. I used the resulting estimates to infer the vulnerability of fish populations and fishery production on forest loss and replacement by non-forest habitats.

MATERIALS AND METHODS

The study was conducted in the floodplains of the lower Amazon River (referred to locally as *várzea*) in an area of 17,674 km² in Brazil (Figure 4). The study area contains a mosaic of forests and herbaceous vegetation, lakes, and secondary channels. The annual flood pulse is monomodal and water level varies 4 to 8 m annually (mean of 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. Over the past 40 years, large areas of várzea in the lower Amazon were deforested for agriculture (Sheikh, Merry & McGrath 2006; WinklerPrins 2006; Renó et al. 2011). Jute (*Corchorus capsularis*) plantations and cattle ranching were the dominant agricultural activities during the 20th century, leading to a loss of 56% of floodplain forest cover by 2008 (Renó et al., 2011). Over the past 30 years, 78% of the deforested area was replaced with herbaceous vegetation, 5% is bare soil where ground cover has not yet regenerated, and 16% contains open water (Renó et al., 2011).

Floodplain forest was mapped at 30-m resolution using Landsat Thematic Mapper images (see methods details in Arantes et al. 2017 and Table 4), and data obtained from this remotely sensed imagery were assembled according to spatial units defined as local hydrological unities (LHUs) (or *"lake systems"* sensu Arantes et al. 2017; Castello et al. 2017). I mapped 20 LHUs (Figure 4, median area: 23.4 km^2) that encompassed a gradient of forest cover ranging from 3 to 70%. Fish biomass data were obtained from standardized fish surveys conducted in 462 floodplain habitats within 20 LHUs distributed approximately 250 km along the lower Amazon River (Figure 4).

Biomass data were standardized as catch-per-unit of effort (CPUE = biomass of fishes caught divided by hours of net in water).

Data analyses examined the relationship between fish biomass and forest cover. Specifically, I used regression models to test whether greater forest cover is related to greater biomass of fishes, both collectively within local habitats and for groups of species possessing different functional traits and degrees of importance for local fisheries. Species were grouped according to their degree of importance in local fisheries and this classification was based on their relative contribution to total yields landed in the main cities in the lower Amazon following Isaac et al. (2016) and Castello et al. (2017) (Figure 5). Fish of *high-importance* (28 species) contributed $\geq$ 85% of the total landing. Fish of *medium-importance* (83 species) contributed 15% of the total landing. Seventy-four species were classified as having *low-importance* and were rarely landed (<15% of the total) for sale as food, although some of them are used as bait or sold as ornamental fish. The other categories comprised functional groups based on trophic, migratory, life history, and swimming behavior/microhabitat-use strategies. I classified species according to eight trophic strategies based on dietary information from published reports: *herbivores* (18 species), *omnivores* (47 species), *detritivores* (28 species), *invertivores* (23 species) *planktivores* (10 species), *piscivores* (45 species) and *piscivores-macroinvertivores* (14 species). I classified species according to four migratory strategies also based on information on dispersal behavior from published reports. Migratory strategies of Amazon fish often are related to reproduction and/or feeding ecology and influenced by seasonal hydrology and physical-chemical conditions of habitats in the riverscape. Migration categories were s*edentary* (55 species), *local* migrators (120), *regional* migrators (8 species) and *long-distance* migrators (3 species). I classified species according to six life history strategies based on maximum body size, size at maturation, batch fecundity, and parental investment per individual offspring following Winemiller & Rose (1992) and Röpke et al. (2017): *equilibrium strategists with maturation at small size* (16 species), *equilibrium strategists with maturation at large size* (16 species), *periodic strategists with maturation at small size* (73 species), *periodic strategists with maturation at large size* (43 species), *intermediate strategists* (32 species) and *opportunistic* (5 species). Finally, I classified species according to five strategies of swimming behavior/microhabitat use based on the classification of Arantes et al. (2017) that uses traits associated with swimming performance and vertical position within the water column during foraging, phenotypes that influence fitness along gradients of habitat structural complexity and other environmental features (Gatz 1979; Winemiller 1991): *nektonic maneuverable* fishes (41 species), *nektonic burst swimmers* (18 species), *surface dwellers* (2 species), *epibenthic maneuverable* fishes (57 species), *benthic-slow* (36 species), *benthic-fast* (23 species) and *gymnotiforms* (8 species). Due to their small sample sizes, the opportunistic life history strategy, long-distance migrators and habitat-use group classified as gymnotiforms were not included in the analyses. Detailed descriptions of species classifications and references can be found in the Appendices B.1 and B.3.

The analyses also accounted for seasonality, habitat type, presence/absence of local fisheries management, local environmental conditions (five variables were reduced to two in the form of scores on the first two axes from principal components analysis, PCA) and three additional land-cover variables (i.e., percent of open water, herbaceous vegetation and macrophyte cover within LHUs) that along with forest represent the principal land-cover types available for fishes within the floodplain (see Table 4 for descriptions and Figure 4 for images). These variables were selected because they have been reported to influence fish composition and fisheries yields in the Amazon floodplains (Petry, Bayley & Markle 2003; Isaac et al. 2016). I fitted generalized linear models assuming a Poisson-Gamma distribution of CPUE with a log-link function. This model was chosen because it performs well with the type of distribution that is typical of fish CPUE data, with many zeros and having continuous gamma distribution for positive values (Shono 2008; Peel et al. 2013). I excluded herbaceous vegetation cover from analyses because it was highly correlated with forest cover (-0.96), and assumed that response variables (e.g., multispecies CPUE, CPUE of groups) that were positively related to forest cover were inversely associated with herbaceous cover. Correlations among other independent variables were < 0.4, including correlation between forest cover and presence or absence of management (r=0.15). PCA was used to ordinate habitats according to the local environmental variables (Appendix B.3). PC1 described a gradient of water transparency and dissolved oxygen concentration, and PC2 modeled a gradient of macrophyte cover, water temperature and depth. Statistical significance was corrected for multiple comparisons (Bonferroni correction) (Figures 6 and 7). Model fit and assumptions were judged by visual inspection of randomized quantile residuals (Dunn & Smyth 1996). Moran's I statistic was used to evaluate whether there was significant spatial dependence in the data that was not accounted by models (Sokal & Oden 1978; Cressie 2015) (see also Appendix B.2).

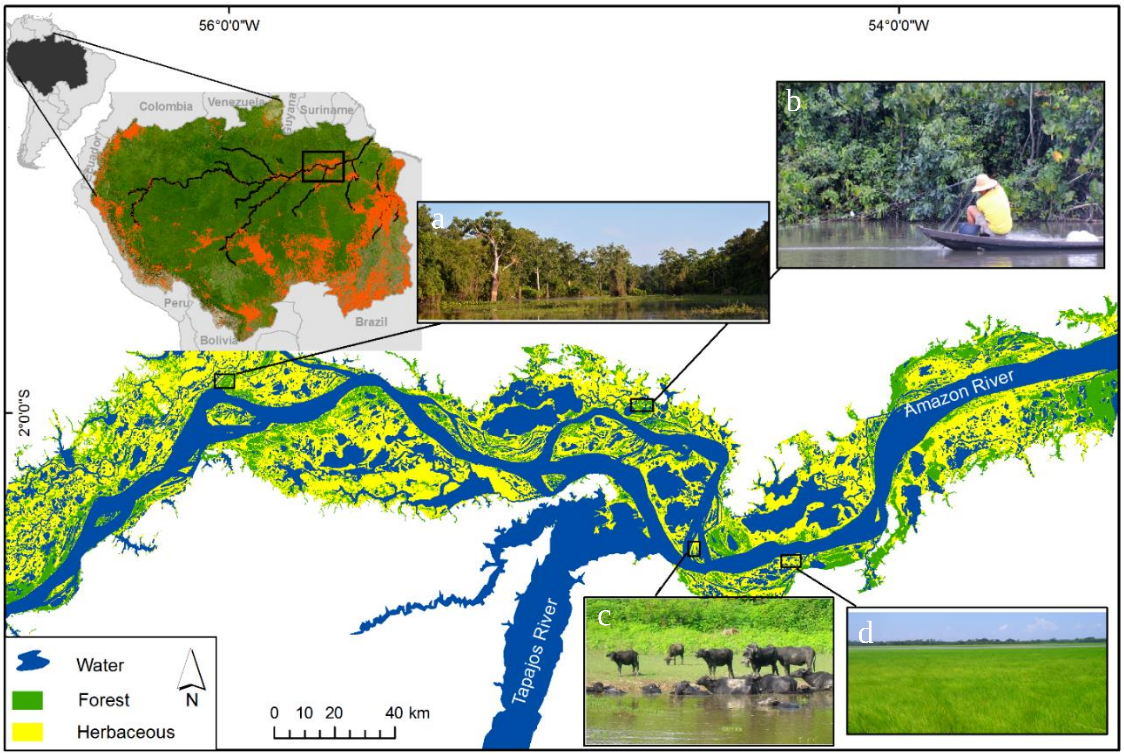

Figure 4: Study area in the lower Amazon showing land cover during the low-water period. Land-cover types are forest, herbaceous vegetation, and open water (lakes and secondary channels). In the lower Amazon, vegetation consists primarily of herbaceous vegetation with only 13% forest cover (Renó et al. 2011). Top left maps show the location of the Amazon Basin in South America (shaded black), deforested areas within the basin are shaded in red (Renó et al. 2011; Castello et al. 2013; Renó, Novo & Escada 2016) and the study reach is enclosed in the rectangle. Photos: (a) forest surrounding a floodplain lake, (b) gillnet being setup for fish samplings, (c) water buffalo raised by local farmers, (d) floodplain area covered by herbaceous vegetation.

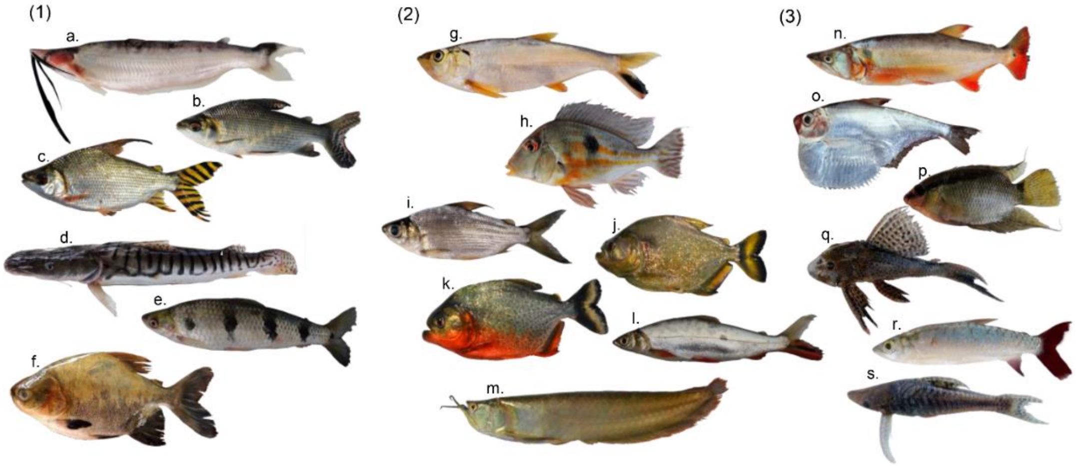

Figure 5: Examples of species possessing relatively high (1), medium (2) and low (3) importance for local fisheries (see Appendix B.10). (1) a. *Hypophthalmus fimbriatus*, b. *Prochilodus nigricans*, c. *Semaprochilodus insignis*, d. *Pseudoplatystoma tigrinum*, e. *Schizodon fasciatus*, f. *Colossoma macropomum* (2) g. *Pellona castelnaeana*, h. *Geophagus proximus*, i. *Curimata inornata*, j. *Serrasalmus maculatu*s, k. *Pygocentrus nattereri*, l. *Hemiodus microlepis*, m. *Osteoglossum bicirrhosum*, (3) n. *Acestrorhynchus abbreviatus;* o. *Pristigaster cayana;* p. *Mesonauta insignis*, q. *Hypostomus plecostomus*, r. *Chalceus macrolepidotus*, s. *Hypoptopoma gulare.*

Table 4: Summary of estimates (lower quartile-LQ, median, upper quartile-UQ) and descriptions or methods of floodplain land-cover and local environmental variables in the lower Amazon floodplain based on 462 habitats surveyed during periods encompassing four stages of the annual hydrological cycle. A principal components analysis (PCA) was used to ordinate habitats according to gradients defined by local environmental variables (see Appendix B.3).

Variable	Description or method	LQ	Median	UQ
Land-cover category				
Forest (%)	Percent of closed-canopy tree cover and short trees, shrub, or semi-shrub (including the aroid *Montrichardia arborescens*) in the local hydrological unity obtained from remotely sensed imagery.	10.5	21.0	47.6
Open water (%)	Percent of open water in lakes and channels during low waters in the local hydrological unity (excluding the mainstem Amazon channel) obtained from remotely sensed imagery.	3.0	9.6	12.9
Herbaceous vegetation (%)	Percent grasses or forbs and soil and fresh sediments, during low waters in the local hydrological unity obtained from remotely sensed imagery.	42.6	66.9	74.5
Macrophyte - geoprocessing: Macro (geop)	Indices indicating the percent of the local hydrological unity with macrophytes present (during late December to January) in three or more of 5 years analyzed (2006/2007 to 2010/2011) "Macro (geop)", a large-scale estimate of coverage, mapped using seven ALOS PALSAR (Appendix A.1).	13	17.1	22.5
Local environmental variables (PC1 and PC2)				
Macrophyte - visual observation (%): Macro (obs)	Percent coverage of water body by macrophytes as estimated through visual inspection of the habitat. "Macro (obs)" matches the scale of our local fish assemblage surveys.	3.0	10.0	40.0
Depth (m)	Averages based on measurements in various locations within each habitat.	1.5	2.1	3.1
Dissolved oxygen (mg/l)		1.6	2.2	3.4
Transparency (cm)		30.0	44.5	60.0
Temperature (^{0}C)		29.3	30.1	30.8

Table 4. Continued…

Variable	Description or method	LQ	Median	UQ
Season category				
Low water, rising water, high water and falling water	The river water level begins to rise during December and reaches its maximum during late May or early June. The water level starts to fall during August, reaching its minimum during November. Low water levels reduce aquatic habitats and their connectivity, and high-water levels greatly expand the flooded area and aquatic habitat.			
Floodplain habitat type category				
Lake (open water)	Floodplain depressions that normally hold water throughout the flood cycle			
Secondary channel (open water)	Channels transporting river waters across sections of floodplains.			
Flooded forest	Riparian forests are inundated for 6-9 mo/yr, depending on elevation of the terrain. Food is generally abundant, and many fishes feed on plants, detritus, or invertebrates in newly flooded areas.			
Flooded herbaceous (campo)	Grasses or forbs or sparse and short shrubs that are inundated for about six to nine months per year, depending on terrain elevation.			
Management	Classified as present or absent based on interviews with local fishers and community leaders. Management was considered to be present when there were restrictions on fishing gear, species, location or seasons.			

RESULTS

Fish biomass was positively related with forest cover, with the strength of this relationship dependent on the group analyzed. Habitats within LHUs with greater forest cover tended to have greater total fish biomass ($p=0.03$) and biomass of species that are important for commercial fisheries ($p=0.02$). Biomass of detritivores and equilibrium strategists that mature at large sizes also were positively and strongly associated with forest cover ($p<0.0001$, Figure 6). Piscivore-macroinvertivores, sedentary, regional migrators as well as surface dwellers also had greater biomass in LHUs with more forest cover ($p<0.001$, Figure 6). Biomass of benthic-slow and epibenthic-maneuverable species were moderately associated with forest cover ($p=0.008$ and $p=0.003$, respectively) (Figure 6). Among trophic groups, biomass of herbivores, invertivores and omnivores tended to be greater in LHUs with more forest cover, but this relationship was not statistically significant ($p=0.09$, $p=0.1$ and $p=0.1$, respectively). Among life history groups, equilibrium strategist with maturation at small size and periodic strategists with maturation at small and large sizes had positive but statically non-significant associations with forest cover ($p=0.09$, $p=0.1$ and $p=0.09$, respectively) (Figure 6). Biomass of species of low importance for fisheries also was slightly greater where forest cover was greater, but again this relationship was not significant ($p=0.1$) (Figure 6). Biomass of species of middle importance for fisheries was not associated with forest cover ($p=0.4$). Biomass of the following functional groups also was not significantly associated with forest cover: piscivores, planktivores, fishes having intermediate life history strategy, local migrators, and species classified as having benthic-fast, nektonic-burst or nektonic-maneuverable swimming behavior (Figures 6 and 7).

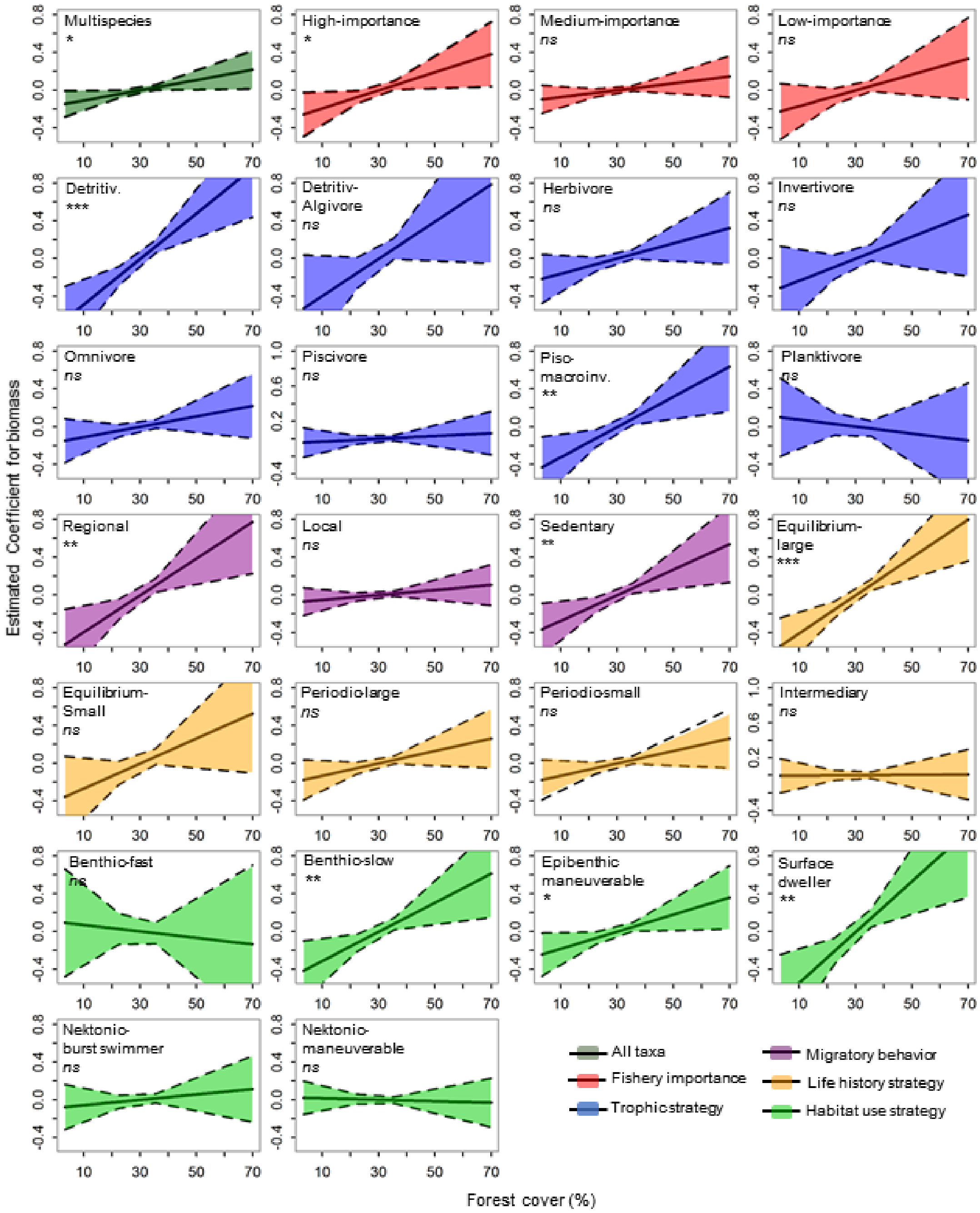

Figure 6: Estimated regression coefficient (partial effects) of forest cover on the relative biomass of fish (CPUE) for each fish group. Steepness of the slopes indicate the strengthen of the relationship with forest cover. Confidence intervals (95%) are shaded in color; ***P ≤ 0. 0001; **P ≤ 0.01; * P ≤0.03; ns P>0.03.

Most groups (58%) had significantly greater biomass where management was present (Figure 7, Appendix B.4). Fish biomass also was influenced by habitat type within LHUs areas; the biomass of most (80%) fish groups was greatest in flooded forest when compared to other habitats, when the effects of other variables were controlled statistically (Appendix B.5). Fish biomass also was influenced by hydrology (Figure 7). Again, after controlling for other variables, strongest relationships between fish biomass and forest cover were generally observed during the low- water season followed by the falling-water period (Appendix B.6). Few fish groups had significant relationships with other land-cover variables (open water 19% of groups and macrophytes 12%), and with local environmental conditions (PC1 19% of groups and PC2 15%).

Plots of randomized quantile residuals showed that the models had good fit. Residuals were generally normally distributed with no apparent trends (Appendix B.7). Values for Moran's I did not differ from random sampled Moran's I expectations, indicating no significant spatial dependence in the data (Appendix B.8).

Figure 7: Regression coefficients for CPUE of multispecies (all taxa), of groups of species possessing different degree of importance for fisheries (high-importance, mid-importance and non-important) and different functional traits (groups of trophic, migratory, life history, and swimming/microhabitat-use strategies) as function of forest cover (For), open water (War), the large-scale estimate of aquatic macrophyte cover (Mcf), local environmental variables (reduced in PCA1 (Env1), which describes a gradient of water transparency and dissolved oxygen and PCA2 (Env2), which describes a gradient of macrophyte cover, water temperature and depth), habitat type (Hab), season (Seas) and presence of management (Man). Circle sizes represents the relative contribution of predictors, shown by standardized coefficients. Lines below the coefficients indicate negative effects. Coefficients are presented only for significant relations analyzed in the models ($p<0.03$). Deviance explained (%) are presented for all regression models.

DISCUSSION

This study’s results imply that forest loss likely reduces fish biomass, functional diversity and fisheries production at local and regional scales in the Amazon. The results showed that fish biomass, including biomass of species that are of high importance for fisheries, is positively associated with forest cover in Amazonian floodplains. These results suggest that this positive relationship between forest cover and fish biomass is driven by the responses of a relatively few functional groups (38%), which appear to be strongly dependent on forests, and therefore, are most vulnerable to forest loss. These functional groups comprise species possessing a diverse range of ecological strategies, as detritivores and equilibrium strategists with maturation in large size, piscivore-macroinvertivores, surface dwellers, benthic-slow, sedentary, epibenthic-maneuverable species as well as species that perform regional migration. Biomass of other functional groups were less evident or not related with forest, including species possessing good dispersal capability and some that would be considered habitat generalists.

These results depicting distinct reponses of functional groups to forest cover support the view that trait-mediated environmental filtering drives populations responses to environmental gradients (Rolhauser & Pucheta 2016; Teresa & Casatti 2017). Those few functional groups associated with forest may enhance feeding opportunities, growth rates or/and reproductive success within forested areas. Detritivores may select forested areas to feed because forests contain abundant detritus and perhaps detritus of superior nutritional value (e.g., high levels of amino acids) (Goulding 1980, 1993; Bowen 1984). Several prochilodontid species and sedentary-benthic fishes, such as loricariids, feed on organic matter derived from forest (e.g., leaves and wood) after its decomposition by fungi and bacteria and on biofilms containing these decomposer microorganisms (Goulding 1993; Lujan, German & Winemiller 2011). Fishes with equilibrium life history strategies, such as the mouth-brooding aruana 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. Several fishes that migrate longitudinally along river channels (i.e, regional migrators) (e.g., *Prochilodus nigricans*, *Semaprochilodus* spp., *Brycon* spp., *Colossoma macropomum*) return to floodplains during high-water periods and likely select flooded forested areas where they can find refuge and feeding opportunities that may increase their survival and growth rates (Goulding 1980; Ribeiro de Brito & Petrere 1990; Isaac & Ruffino 1996; Araujo-Lima & Goulding 1997; Benedito-Cecilio & Araujo-Lima 2002; Carvalho, Zuanon & Sazima 2009). Surface dwellers consume fruits and seeds (e.g., *Piaractus brachypomus*) or insects (e.g., *Osteoglossum bicirrhosum*) that fall into the water. Epibenthic maneuverable fishes (e.g., cichlids) are well adapted to forage and evade predators within the structurally complex micro-habitats such as those in flooded forests (Teresa, Casatti & Cianciaruso 2015; Ribeiro, Teresa & Casatti 2016). Conversely, other functional groups, such nektonic piscivores and planktivores, were not significantly associated with forest possibly because these groups can more effectively exploit resources in other land-cover types (e.g., open water, herbaceous vegetation). Planktivore biomass was slightly negatively (but not statistically significant) correlated with forest cover, possibly because of low phytoplankton production owing to light limitation beneath forest canopy, which in turn would limit zooplankton abundance.

Certain functional groups (e.g., herbivores, invertivores, local migrators) could have lacked associations with forest cover due to sampling constraints or because functional groups were defined too broadly, thus obscuring key determinants of spatial abundance patterns. Although this study employed extensive spatial and temporal sampling, greater sampling effort within local habitats might reveal stronger patterns for biomass of herbivores, invertivores, equilibrium strategists with maturation at small size and periodic strategists, which in this study were positively but not significantly associated with forest cover. Similar to several other functional groups, these fishes may benefit from food resources and refuges within flooded forest (e.g., several serrassalmidae feed on fruits and seeds (Goulding 1980; Correa et al. 2015), and all of these species were positively associated with forest in the study area (Arantes et al. 2017). Biomass of other fish groups (e.g, local migrators, medium importance for fisheries) had no relation with forest, however, these contained many species spanning a broad range of ecological strategies. For example, the group “local migrators” comprised more than a hundred species, including piranhas that have broad diets and high abundance in diverse habitats (e.g, *Pygocentrus nattereri, Serrassalmus* spp.). If I exclude these ecological generalists from the analysis, the biomass of local migrators is significantly greater where there is more forest cover. Stronger patterns might be revealed not only by increasing sampling effort, but also by using approaches to reduce redundancy and multidimensionality in functional trait datasets (e.g., Winemiller et al. 2015).

Along with forest cover, seasonal hydrology, local habitat conditions, and fisheries management influenced fish biomass, which is consistent with previous studies showing influences of these variables on local fish stocks, fish community dynamics and fishery yields in tropical floodplain rivers (e.g., Welcomme 1979; Winemiller et al. 2014; Isaac et al. 2016). In this study, the biomass of all functional groups was strongly related with seasonal hydrology, a finding consistent with previous studies that concluded hydrology is the major driver of fisheries production and assemblage dynamics in the Amazon floodplains (e.g, Castello, Isaac & Thapa 2015; Isaac et al. 2016). Most Amazon fishes, at a minimum, can undergo local-scale movements during various phases of the annual flood pulse. Given this potential for dispersal and habitat selection, it might be expected that biomass of most functional groups should be associated with local habitat conditions. During the height of the flood pulse, many fishes inhabit submerged areas of the floodplain; during floodwater recession these fishes are forced to migrate into channels or lakes (Fernandes 1997; Castello 2008; Arantes et al. 2013). The great expansion of aquatic habitat during the flood pulse results in lower catch rates in gillnets, the collecting gear employed in this study. Despite the fact that sampling should be less efficient during the high-water phase, most functional groups had greater biomass in flooded forest habitats when compared with the other habitats, supporting the inference that many Amazonian fishes have evolved a strong dependence on conditions and resources provided by flooded forests (Goulding 1990, 1993). Biomass of several functional groups, including species important for fisheries, were greater where local fisheries management exists, which is consistent with previous studies showing that

Amazonian fishing communities that implemented and enforced fishing regulations had nearly 50% more stock abundance compared to those without management (Almeida, Lorenzen & McGrath 2009; Castello et al. 2011)

A few functional groups had significant relationships between biomass and land-cover variables other than forest cover and those associated with local environmental conditions, however, for most groups, these variables were less important than forest cover. Surface dwellers were positively correlated with macrophyte cover within the LHU. Invertivores were positively correlated with water transparency. Nektonic-maneuverable fishes and intermediate life-history strategists were positively correlated with open-water cover. These variables are known to influence floodplain fishes, and therefore explained portions of the variance in spatial patterns of fish biomass, yet considerable variance remained unexplained for most groups. Given the vastness, heterogeneity and dynamics nature of the Amazon varzea, it seems unlikely that spatial distribution of fish biomass and mechanisms driving such patterns could be modeled completely. Because fishes and many other aquatic organisms disperse in response to seasonal hydrology, varzea metacommunities are very dynamic (Hurd et al. 2016). In addition, varzea fishes have evolved ecological strategies that allow them to exploit changing environmental conditions in the floodplain mosaic (e.g., flexible feeding behavior and/or compensatory responses in growth or fecundity (e.g., Arantes et al. 2010). Further understating of mechanisms driving spatial patterns of fish biomass in floodplains could be achieved by including additional geospatial variables relevant for fishes, such as estimates of habitat connectivity during various phases of the annual hydrologic cycle.

Amazonian fishes have evolved for tens of millions of years in pulsing fluvial systems surrounded by forest (Lundberg et al. 2010) and many are adapted to exploit resources and conditions of flooded forests (Goulding 1980). This study supports the inference that floodplain degradation, including deforestation and disruptions in natural flow regimes, negatively impacts functional diversity and fishery yields, with some functional groups being particularly vulnerable to these threats. These groups include species that constitute major conduits of matter and energy in food webs (Winemiller & Jepsen 1998; Benedito-Cecilio & Araujo-Lima 2002), influence nutrient cycling (Flecker 1996; Winemiller et al. 2014), and sustain important fisheries (Bayley & Petrere 1989; Batista et al. 1998). Riparian forests and natural hydrological regimes must be protected in order to maintain high levels of fish production in Amazon floodplains. This study's findings also indicate that, in addition to protecting landscapes and hydrology, fishery management at the local scale enhances biomass of diverse species, including those with greatest economic importance.

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CHAPTER IV

SPATIAL VARIATION IN AQUATIC FOOD WEBS IN THE AMAZON RIVER FLOODPLAIN: INSIGHTS FROM STABLE ISOTOPE ANALYSES

INTRODUCTION

Food webs are spatially variable and temporally dynamic (Warren 1989; Polis, Anderson & Holt 1997), particularly, in the heterogeneous landscapes of lowland rivers and floodplains in the tropics (Winemiller 1996). In these ecosystems, aquatic food webs reveal large spatio-temporal variation in species richness, the number and intensity of predator-prey interactions, and other food web proprieties (e.g., trophic link density, food chain length) (Winemiller 1990). Food webs in these ecosystems are also influenced by several factors occurring across multiple spatial and temporal scales (e.g., environmental gradients and disturbances) that influence sources of primary production, productivity, population abundance, and species interactions (Winemiller 1990). However, despite some advances, most studies of food web structure and function in floodplain ecosystems have not distinguished between local and regional processes. Improved understanding of spatial variation of food webs in dynamic, heterogeneous and species rich landscapes, such as lowland river-floodplains, is obviously challenging, yet essential for managing anthropogenic impacts affecting biodiversity and ecosystem services (Winemiller 1996, 2004; Polis, Anderson & Holt 1997).

Differences in features of aquatic food webs have been documented for rivers with distinct geochemistry (e.g., Benedito-Cecilio & Araujo-Lima 2002; Jepsen & Winemiller 2002) and patterns of spatial and temporal variation (e.g., Hoeinghaus, Winemiller & Agostinho 2007; Winemiller et al. 2014; Ou & Winemiller 2016). These studies have shown, for example, that patterns of material flow (e.g., availability of basal production sources and their contributions to fish biomass) diverge among large-rivers under different levels of impact from hydroelectric dams (e.g., Hoeinghaus, Winemiller & Agostinho (2007) for the Paraná River Basin in Brazil, and Ou & Winemiller (2016) for the Mekong River Basin in Cambodia). Some aspects of food web ecology vary seasonally and inter-annually in South American rivers that support migratory detritivorous fishes of the family Prochilodontidae (Winemiller & Jepsen 2004; Taylor, Flecker & Hall 2006 and Winemiller et al. 2014 in the Orinoco Basin, and Benedito-Cecilio & Araujo-Lima 2002 in the Amazon Basin). Much of this spatial variation in river food webs may be derived, either directly or indirectly, from differences in biophysical conditions of habitats among different reaches and watersheds (e.g., topography, sediments, hydrology, vegetation cover, etc.) (Winemiller & Polis 1996; Thompson & Townsend 2005). Spatial variation in food webs also may be influenced by differences in productivity gradients, nutrient dynamics and population interactions as well as pathways importing energy and nutrients from one ecosystem to another (i.e., food web spatial subsidies) (Power 1992; Polis & Hurd 1996; DeAngelis 2012).

In large river-floodplain systems, hydrological variation influences spatial habitat heterogeneity affecting spatial variation among, and exchanges between local food webs. Food web structure may be fairly constant across aquatic habitats of a floodplain because the flood pulse facilitates dispersion and interaction of aquatic organisms within a large region and may provide aquatic consumers with access to similar food resource spectra

(Junk et al. 1989; Hurd et al. 2016). However, local food webs in a heterogeneous floodplain landscape should vary as a function of differences in the quality and quantity of food resources, assemblage composition, and species interactions (Hedges et al. 1986; Winemiller 1990; Polis, Anderson & Holt 1997; Mortillaro et al. 2012; Correa, Winemiller & Cárdenas 2016; Arantes et al. 2017). Theories of the structure and function of rivers predict how energy flow and distributions of functional groups in local communities are influenced by patterns of organic matter production, transport, utilization and storage that change along fluvial gradients (Vannote et al. 1980; Thorp, Thoms & Delong 2006).

Does flow of energy and matter differ among food webs of aquatic habitats within a tropical river floodplain? To address this question, this study surveyed 109 habitats in the floodplain of the lower Amazon River during the descending phase of the annual flood pulse, and used stable isotope analysis to estimate food web structure. Specifically, the study analyzed the isotopic composition of primary production sources and fishes as well as the relative contribution of these sources to fish biomass across different spatial scales. Stable isotope analysis has emerged as a useful means to examine food web ecology, facilitating inferences about trophic pathways (Peterson & Fry 1987), trophic niche breadth and overlap (Layman et al. 2007), and food chain length (Post 2002).

Although a few studies have used stable isotope analysis to evaluate seasonality of primary sources of carbon for some fish species in the Amazon River floodplain (i.e., Araujo-Lima et al. 1986; Forsberg et al. 1993; Benedito-Cecilio et al. 2000; Benedito-

Cecilio & Araujo-Lima 2002; Oliveira et al. 2006; Mortillaro et al. 2015), very little is known about how isotopic composition of sources and, particularly, of fishes vary spatially. The limited information available showed evidences of upstream-downstream trends in the isotopic composition of productions sources, including δ^{13}C of C3 plants and C4 grasses (Martinelli & Richey 1991), suspended particulate organic matter (Hedges et al. 1986; Mortillaro et al. 2012) and tissues of two fish species (*Prochilodus nigricans* and *Colossoma macropomum,* Benedito-Cecilio et al. 2000). Production source contributions to biomass of Amazonian fishes from different functional groups and habitats have not been investigated. This study estimates these issues at two spatial scales, local and regional, within aquatic habitats in floodplains of the Amazon River.

MATERIALS AND METHODS

Study area, data collection and laboratory methods

This study was conducted within a 17,674-km² area in the floodplains of the lower Amazon River (referred to locally as *várzea*) in Brazil (Figure 8). The study area contains a mosaic of forests, non-forested areas dominated by herbaceous vegetation, lakes, and secondary channels. The river's annual flood pulse causes water level to vary from 4 to 8 m (mean = 5.7 m), creating differences in aquatic habitat availability and conditions when most areas are flooded versus when only lakes and connecting channels retain water.

The sampling units were local hydrological unities (LHUs) (or *"lake systems"* sensu Arantes et al. 2017; Castello et al. 2017) that contain lakes, interconnecting channels, forests, and areas with herbaceous vegetation and aquatic macrophytes that are hydrologically connected for about six to nine months per year (Figure 8). LHUs are separated by major secondary channels (areas of low elevation) and/or natural levees (areas of high elevation).

To capture possible spatial variation of isotopic composition of aquatic consumers and sources of production supporting fish biomass, fish muscle tissue and common basal production sources were collected from 109 locations spanning a range of aquatic habitats (open water, flooded herbaceous vegetation, flooded forest) across 7 to 19 LHUs, depending on the fish sampled. These LHUs were distributed approximately 250 km along the lower Amazon River (Figure 8). Sampling was conducted during the beginning of the falling-water stage of the annual hydrological cycle (Figure 8). Because an animal tissue does not immediately reflect the isotopic composition of the organism's diet, but rather integrates over some period of time (i.e., isotopic turnover rates) (Vander Zanden et al. 2015), I assumed that carbon and nitrogen ratios of fishes' muscle tissue largely reflected assimilation of sources during the high-water season.

I collected fish using gillnets and sampled muscle tissue of 14 representative dominant species belonging to various trophic guilds (Table 6). Fish muscle tissue samples were collected from the flank near the base of the dorsal fin and attempts were made to collect these samples from 3-5 individuals per LHUs. I also collected tissues from the most common C3 woody plants (*Crataeva* spp., *Vitex* spp.) (mostly leaves and few fruits), C3 aquatic macrophytes (e.g., *Eichhornia crassipes*, *Salvinia minima*) and C4 grasses (*Paspalum repens*), benthic algae (hereafter, phytomicrobenthos), and suspended particulate organic material from the water column (POM). I collected phytomicrobenthos by gently scraping submerged tree branches. This sampling technique was unlikely to produce a pure sample of benthic algae, and thus phytomicrobenthos samples were likely composed of a combination of periphyton, fine particulate organic matter, and associated microorganisms. I collected samples of suspended POM by filtering water samples through pre-combusted Whatman GF/F filters (pore size 0.7 µm) using a vacuum system under low pressure. There is some uncertainty on the exact origins of suspended POM, but previous analysis of fatty acids composition of this material in the lower Amazon suggested it to be derived primarily from autochthonous material, including C3 aquatic plants and phytoplankton dominated by cyanobacteria (Mortillaro et al. 2011). Vascular plant debris and soil humic material were also found to contribute to the pool of suspended POM in the Amazon (Hedges et al. 1986). Finally, I collected a common primary consumer (i.e., snails) from floating aquatic vegetation using a seine net. All samples were preserved in salt for later processing in the laboratory. A total of 449 samples of basal production sources, 34 samples of primary consumers and 656 samples of fish muscle tissue were analyzed for stable isotope ratios of carbon and nitrogen (Tables 5 and 6). Nitrogen isotopic ratios ($^{15}N/^{14}N$ as expressed by $\delta^{15}N$) can be used to define an organism's trophic position because the proportion ^{15}N in tissues of organism increases incrementally from the base to the top of food chains (i.e., ^{15}N enrichment, Post 2002). Carbon isotopic ratios ($^{13}C/^{12}C$, or $\delta^{13}C$) can be used to trace primary production sources assimilated by consumers because once carbon is fixed by a primary source (e.g., plant) $\delta^{13}C$ changes relatively little as material passes from one trophic level to the next (Fry 2006).

Samples were soaked in distilled water for 4-5 h, rinsed, and dried in an oven at 60º for approximately 48 h, following the protocol of Arrington & Winemiller (2002). After drying, samples were ground into fine powder using mortar and pestle, and subsamples were weighed (POM to the nearest 15-20 mg, and fish muscle tissue and tissues from other sources to the nearest 1.5-3 mg) and loaded into UltraPure tin capsules. Samples were analyzed for carbon and nitrogen isotope ratios using mass spectrometry at the laboratory at the Analytical Chemistry Laboratory of the Institute of Ecology, University of Georgia, USA. Isotope ratios were reported in parts per thousand (‰) standardized in relation to reference material (Pee Dee Belemnite for C, atmospheric nitrogen for N) and reported as $\delta X = [(R_{sample}/R_{standard})-1)] \times 10^3$, where $R = {}^{13}C/{}^{12}C$ or ${}^{15}N/{}^{14}N$ (the ratio of heavy and light stable isotopes of carbon or nitrogen). Because carbon:nitrogen ratios of samples were relatively low (typically below 3.5), no lipid corrections were necessary (Post et al. 2007).

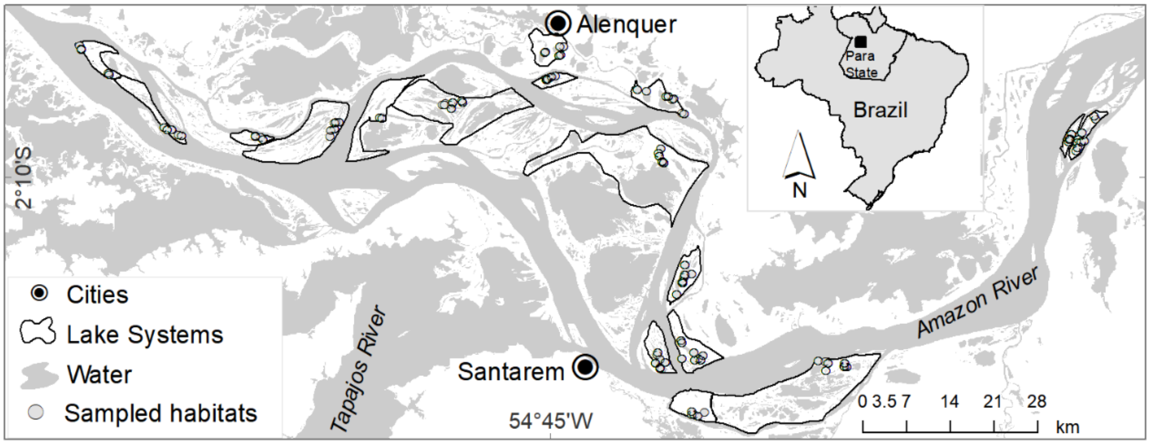

Figure 8: Study area, local hidrological unities (lake systems) and habitats sampled within local hidrological unities in the lower Amazon River floodplain.

Data analyses

Regional scale

I first analyzed general patterns of isotopic variation for fishes and primary producers and then estimated proportional contributions of each producer to fish biomass at a regional scale (i.e., combined data for all LHUs) using biplots of δ^{13}C and δ^{15}N and a Bayesian mixing model, respectively. Stable isotope mixing models use Bayesian statistical techniques that incorporate uncertainty and variation in input parameters in order to estimate proportional contributions of alternative sources to consumer biomass (Parnell et al. 2013). Data were evaluated to assure conformity with mixing model assumptions, including that consumer isotopic values fall within the polygon (isospace) defined by C and N isotopic values of sources when these are adjusted to account to trophic fractionation (TF) (Olive et al. 2003; Phillips et al. 2014). To adjust isotopic ratios of sources to create a polygon to test a given consumer, I multiplied averaged values for TF of C and N reported in the literature (e.g., Bastos et al. 2017) by the assumed trophic level of the consumer (Reid et al. 2008; Phillips et al. 2014). I estimated each consumer's trophic level using an equation that uses an assumed value for δ^{15}N enrichment and the trophic level of a baseline (e.g., in our case, this was a snail assumed to be a primary consumer) (R package tRophicPosition, Quezada-Romegialli, Jackson & Harrod 2017; Post 2002) (Table 6). Biplots of δ^{13}C and δ^{15}N of fish and TF-corrected values of basal production sources revealed that fish values fell outside the polygon defined by basal sources for five of 14 fish species, particularly two detritivores (*Curimata incompta*, *Potamorhina latior*), one planktivore (*Hypophthalmus marginatus*), one herbivore (*Rhytiodus microlepis*), and one omnivore (*Hemiodus microlepis*). Therefore, mixing models were not run for these species. Biplots also showed that five of the other species (the piscivores *Acestrorhynchus abbreviatus*, *Pygocentrus nattereri*, and *Plagioscion squamosissimus*, the herbivore *Schizodon fasciatus*, and the omnivore *Triportheus auritus*) had isotopic values falling mostly within the range of isotopic values for all sources, including the ^{13}C-enriched C4 grasses. For these species, all five alternative basal sources were included as inputs for the mixing model. Isotopic values for the final four species (*Pellona castelnaeana, Colossoma macropomum, Mylossoma aureum, Piaractus brachypomus*) fell within isotopic range of relatively ^{13}C-depleted production sources and out of the range of enriched sources such as C4 grasses. Therefore, I assumed these species had not assimilated carbon from C4 grasses, and I did not input this source for their mixing model analyses. Convergence diagnostics (Gelman diagnostics) were close to 1 (<1.1) indicating that the model performed well. Prior to all analyses, I also tested for differences in δ^{13}C and δ^{15}N of sources and consumers among habitats types within each

LHU using ANOVA. Isotope signatures were similar among habitats ($p>0.1$); therefore, I used the species mean and standard deviation for LHU as input for the mixing model.

Variations across the landscape

I evaluated possible differences in isotopic ratios ($\delta^{13}C$ and $\delta^{15}N$ as dependent variables) of each production source and fish species across LHUs (independent variables) using Multivariate Analysis of Variance (MANOVA). To assure that possible interspecific variation in $\delta^{13}C$ and $\delta^{15}N$ of sources (Correa, Winemiller & Cárdenas 2016) would not influence results, I ran separate tests for each woody plant and aquatic macrophyte taxon. Because a consumer's feeding habitat and assimilation dynamics may shift ontogenetically between-site differences in isotopic ratios of fish tissues could be influenced by differences in body size. Therefore, prior to these analyses, I also tested for possible differences in the length-frequency distributions of each fish species across LHU using Fisher's exact tests. Length frequency distributions did not differ significantly among LHU for any species ($p>0.05$), except for *P. latior* and *S. fasciatus*. For these two species, evaluations of differences on the isotopic composition across LHUs were performed using standard length (SL) as a covariate in MANCOVA. Phytomicrobenthos were not included in these analyses due to small sample sizes owing to the apparent scarcity of this material at most sites.

Whenever significant differences in isotopic composition were observed in the MANOVA or MANCOVA, univariate ANOVAs were performed to test for differences in either the $\delta^{13}C$ or $\delta^{15}N$ of each source and fish species. Assumptions for this analysis (e.g., residuals normality) were tested and met in all cases. Statistical significances of all tests were corrected for multiple comparisons (Bonferroni correction), with significance level (alpha) set at 0.01.

Finally, I assessed variation in the proportional contribution of each primary production source to the biomass of each fish species across LHUs. This assessment was based on results from the Bayesian mixing model for each species in each LHU (involving 7-19 LHU, depending on the species) and evaluation of coefficients of variation (CV) of proportional contributions across LHU. Procedures for mixing model analyses were the same as described above for the regional scale analysis.

RESULTS

Regional scale patterns

The five basal production sources (C3 woody plants, C3 aquatic macrophytes, C4 grasses, phytomicrobenthos, POM) and fishes showed considerable variation in δ^{13}C and δ^{15}N values across the region (Table 5 and 6, Figure 9). Isotopic values among all sources ranged from approximately -34‰ to -21‰ for carbon, and from -5‰ to 11‰ for nitrogen. The difference between minimum and maximum values of sources ranged from -7.3‰ (aquatic macrophytes) to -12‰ (phytomicrobenthos) for carbon and from 7‰ (grasses and phytomicrobenthos) to 11‰ (woody plants) for nitrogen.

Carbon isotopic values among fish species ranged from about -39‰ (*H. marginatus*) to -14‰ (*S. fasciatus*), and their variability within the same species ranged from -3‰ (*P. brachypomus*) to -16‰ (*R. microlepis*). The five fish species with isotopic values that fell outside the isospace of potential sources (*C. incompta*, *P. latior*, *H. marginatus, H. microlepis, R. microlepis*) had relatively ^{13}C-depleted values (Figure 9).

Twenty-nine percent of fishes had carbon isotopic signature values between those of C3 aquatic macrophytes and POM, while 38% had carbon isotopic signature values between those of the aquatic macrophytes and C4 grasses. Nitrogen isotopic values among fish species ranged from about 4‰ (*S. fasciatus*) to 15‰ (*P. castelnaeana*), and intraspecific variability ranged from ~2‰ (*A. abbreviatus*) to ~6‰ (*S. fasciatus*, *C. macropomum*).

The mixing model for the regional scale indicated that C3 aquatic macrophytes and POM were the principal sources contributing to the biomass of most fish species, with C4 grasses having an important contribution only to *S. fasciatus* (Table 7 and Appendix C.1). Except for *S. fasciatus*, grasses (when included in the model) and phytomicrobenthos likely were the least important basal production sources supporting fish biomass (Table 7 and Appendix C.1).

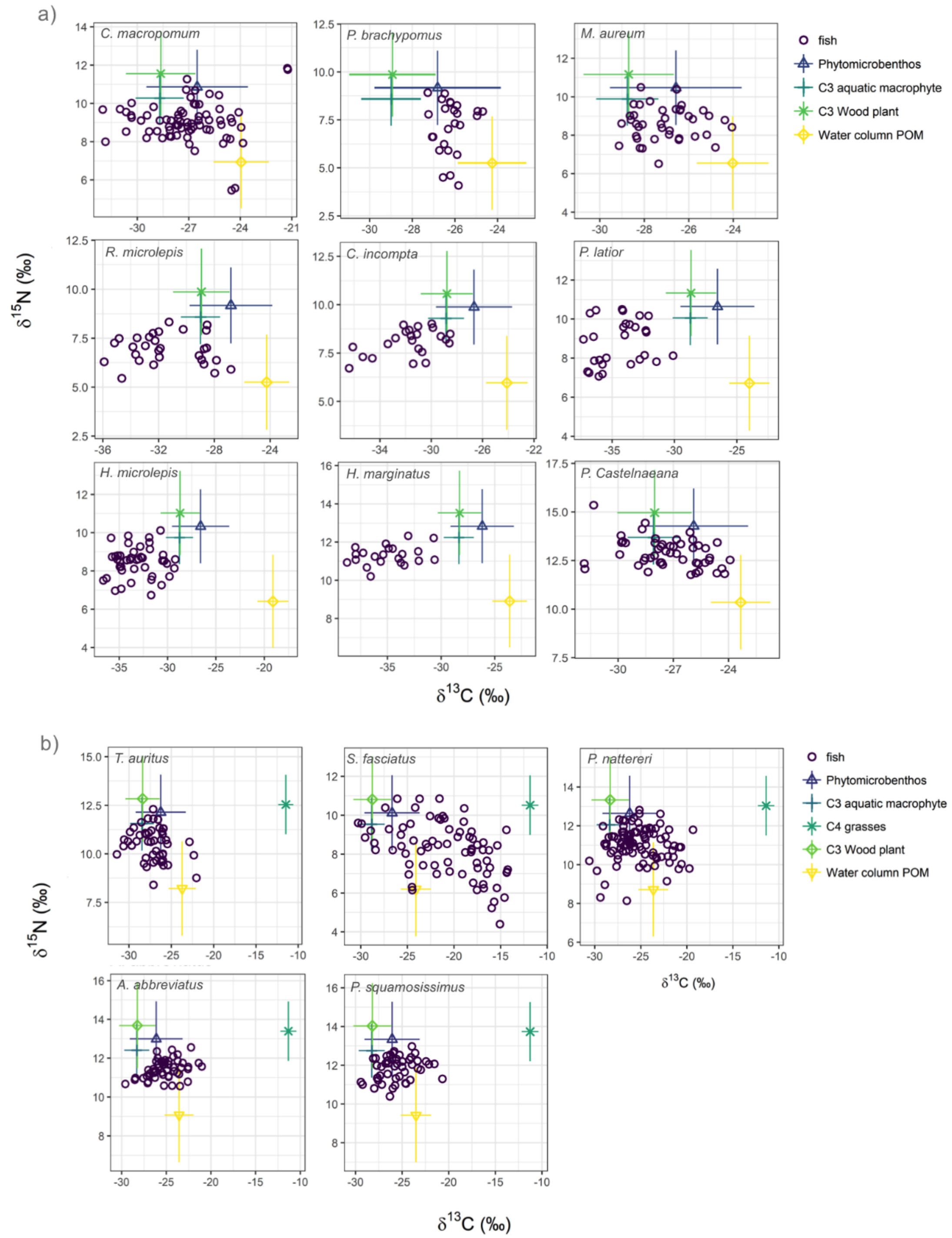

Figure 9: Biplots of δ^{13}C and δ^{15}N of primary producers, a) excluding and b) including C4 grasses, for fishes sampled at the regional scale in the lower Amazon River floodplain. δ^{13}C and δ^{15}N of sources for each fish plot are corrected for trophic fractionation (see methods).

Table 5: Means and standard deviations (St dev) of carbon and nitrogen stable isotope ratios ($\delta^{13}C$ and $\delta^{15}N$) for production sources in the lower Amazon region and results for MANOVA and ANOVA (*n* = number of samples). *Statistically significant result ($p \leq 0.01$).

Sources of production		*n*	Mean $\delta^{13}C$	St dev $\delta^{13}C$	Mean $\delta^{15}N$	St dev $\delta^{15}N$	MANOVA			ANOVA	
							df	F	Pr(>F)	$\delta^{13}C$ Pr(>F)	$\delta^{15}N$ Pr(>F)
Phytomicrobenthos		24	-27.68	2.91	4.32	1.88	-	-	-	-	-
C3 aquatic macrophytes	*Eichhornia crassipes*	79	-29.86	1.30	3.73	1.31	13	1.86	0.03	-	-
	Salvinia minima						11	2.78	0.00*	0.02	0.05
C4 grasses		161	-12.88	0.72	4.72	1.45	18	4.45	0.00*	<0.001*	<0.001*
Woody plants	*Crataeva* spp.	133	-29.80	1.95	5.02	2.15	12	3.14	0.00*	0.06	0.001*
	Vitex spp.						10	2.23	0.00*	0.17	0.001*
POM		52	-25.13	1.52	0.40	2.38	18	3.15	0.00*	0.001*	0.01*

Table 6: Means and standard deviations (St dev) of carbon and nitrogen stable isotope ratios (δ^{13}C and δ^{15}N) for fish species in the lower Amazon region and results from MANOVA and MANCOVA (the latter only for *S. fasciatus* and *P. latior*; SL= standard length) and ANOVA. Species trophic group, trophic level estimations (means; confidence intervals in parentheses) and sample number (*n*) are shown. *Statistically Significant (≤ 0.01).

Trophic strategy	Species/ Trophic level	*n*	Mean δ^{13}C	St dev δ^{13}C	Mean δ^{15}N	St dev δ^{15}N	MANOVA			ANOVA	
							df	F	Pr(>F)	δ^{13}C Pr(>F)	δ^{15}N Pr(>F)
Herbivores	*Colossoma macropomum* 3 (3.2-3.4)	71	-27.1	2.2	9.1	1.1	15	3.8	0.00*	<0.00*	<0.00*
	Piaractus brachypomus 2.6 (2.4-2.8)	25	-26.2	0.7	7.1	1.4	11	2.9	0.02	-	-
	Mylossoma aureum 3.03 (2.8-3.2)	40	-27.1	1.3	8.6	0.9	12	2.0	0.02	-	-
	Rhytiodus microlepis 2.6 (2.4-2.7)	29	-31.4	2.5	7.0	0.8	12	5.0	<0.00*	0.001*	<0.001*
	Schizodon fasciatus 3.8 (3.6-4.08)	75	-20.9	4.4	8.2	1.4	15	4.0	<0.00*	0.03	<0.001*
							1	0.2	0.80 (SL)		
Omnivores	*Hemiodus microlepis* 3.0 (2.8-3.2)	43	-33.1	2.0	8.5	0.8	11	2.9	<0.00*	0.001*	0.02
	Triportheus auritus 3.6 (3.4-3.8)	48	-27.1	1.9	10.5	0.8	14	2.6	<0.00*	0.03	<0.001*
Detritivores	*Curimata incompta* 2.9 (2.7-3.1)	23	-31.7	2.2	8.1	0.7	6	1.5	0.17	-	-
	Potamorhina latior 3.1 (2.9-3.2)	28	-34.4	2.0	8.8	1.2	8	4.3	<0.00*	0.08	0.001*
							1	5.4	0.02 (SL)		

Table 6 continued...

Trophic strategy	Species/ Trophic level	*n*	Mean $\delta^{13}C$	St dev $\delta^{13}C$	Mean $\delta^{15}N$	St dev $\delta^{15}N$	MANOVA			ANOVA	
							df	F	Pr(>F)	$\delta^{13}C$ Pr(>F)	$\delta^{15}N$ Pr(>F)
Planktivore	*Hypophthalmus marginatus* 3.6 (3.8-4.1)	22	-34.9	2.4	11.3	0.5	7	1.5	0.360	-	-
Piscivores	*Acestrorhynchus abbreviatus* 3.9 (3.6-4.1)	54	-25.19	1.8	11.4	0.5	14	5.3	<0.00*	0.001*	<0.001*
	Pellona castelnaeana 4.3 (4.1-4.54)	50	-27.3	1.9	12.9	0.7	12	2.1	0.01*	0.01*	0.05
	Pygocentrus nattereri 3.8 (3.6-4.0)	100	-25.3	2.4	11.1	0.9	18	1.8	0.01*	0.00*	0.37
	Plagioscion squamosissimus 4.0 (3.8-4.2)	48	-25.6	1.9	11.8	0.6	17	4.1	<0.00*	<0.001	<0.0001

Variation across the landscape

Isotopic compositions varied significantly across LHU for most production sources and fishes. The effects of LHU on δ^{13}C and δ^{15}N values was significant for all sources (C4 grasses, both woody plants taxa, and the aquatic macrophyte *S. minima*), but not for the aquatic macrophyte *E. crassipens* ($F_{11,28}$=1.86, p=0.03) (Table 5). δ^{13}C and δ^{15}N were significantly different between LHUs for most fish species, but not for *P. brachypomus, M. aureum, C. incompta* and *H. marginatus* (Table 6). Standard lengths were not related to variation in δ^{13}C or δ^{15}N across LHUs for the two species that had significant differences in length distributions among LHUs (*S. fasciatus* and *P. latior*) (Table 6).

Basal production sources showed statistically significant differences in both δ^{13}C and δ^{15}N for grasses and POM, significant differences only in δ^{15}N for the woody plants, and marginally non-significant differences in isotopic ratios of both elements for the aquatic macrophyte *S. minima* (ANOVA, p=0.02 for δ^{13}C and p=0.05 for δ^{15}N, Table 5). ANOVA also revealed three major patterns of δ^{13}C and δ^{15}N variation of fish tissues across LHUs (Table 6). Most species, including *C. macropomum, R. microlepis, A. abbreviatus* and *P. squamosissimus,* showed significant differences in both δ^{13}C and δ^{15}N across LHUs. *Hemiodus microlepis, P. castealneana* and *P. nattereri* showed differences only in δ^{13}C, whereas *S. fasciatus, P. latior* and *T. auritus* had significant spatial variation only in δ^{15}N. Except for non-significant variation in δ^{13}C for one woody plant taxon (*Vitex* spp., $F_{10,32}$=1.52, p=0.2) and in δ^{15}N for *P. nattereri* ($F_{18,81}$=1.1, p=0.4), variation associated with LHUs was marginally non-significant (p-values ranging from 0.03 to 0.08) for all tests (Table 6).

Mixing models results for LHUs indicated that, although C3 aquatic macrophytes and POM were the principal sources contributing to the biomass of most fish species and catchments, there was considerable variation (Table 7). Coefficients of variation (CV) showed that mean proportional contributions of production sources to fish biomass varied on average 37% across all sources and species, with some as high as 79% (C3 aquatic macrophytes for *P. brachypomus*) (Table 7). Species with largest variation in sources contributions across catchments were *P. brachypomus* (50% on average), *A. abbreviatus* (43%) and *P. nattereri* (42%). Smallest variation in source contributions across catchments was observed for *S. fasciatus* (26% on average) and *M. aureum* (24%). Relatively high CV values reflect high variation in the contributions of production sources to fish biomass within a given catchment area. For example, phytomicrobenthos and woody plants, the least important sources at the regional scale, turned out to be the most important sources (contributing >30%) for five species in five LHUs, and for four other species in seven LHUs. Conversely, C3 aquatic macrophytes and POM, the most important sources assimilated by fishes at the regional scale, turned out to be relatively unimportant (proportion contribution <7%) for five species in four catchments, and four other species in seven catchments.

Table 7: Means and 1–99th percentile ranges of estimated contributions of basal production sources to fish biomass in the floodplains of the lower Amazon. CV is the coefficient of variation of the proportional contribution of a given source across local hidrological unities. Phytomicrob = Phytomicrobenthos, C3 macroph = C3 aquatic macrophytes, Wood plant = wood plants, POM = particulate organic matter.

Species	Source	Mean	1st	99th	C.V. (%)
Colossoma macropomum	Phytomicrob.	0.09	0.02	0.21	39
	C3 macroph.	0.45	0.26	0.61	40
	Wood plant	0.10	0.02	0.23	32
	POM	0.36	0.30	0.43	41
Piaractus brachypomus	Phytomicrob.	0.13	0.03	0.26	52
	C3 macroph.	0.22	0.06	0.38	79
	Wood plant	0.15	0.03	0.31	32
	POM	0.50	0.42	0.59	37
Mylossoma aureum	Phytomicrob.	0.10	0.02	0.23	24
	C3 macroph.	0.45	0.27	0.61	26
	Wood plant	0.10	0.02	0.25	23
	POM	0.35	0.28	0.41	21
Schizodon fasciatus	Phytomicrob.	0.07	0.01	0.17	29
	C3 macroph.	0.07	0.01	0.16	23
	C4 grasses	0.30	0.24	0.37	27
	Wood plant	0.06	0.01	0.14	27
	POM	0.50	0.42	0.57	26
Pellona castelnaeana	Phytomicrob.	0.10	0.02	0.23	37
	C3 macroph.	0.55	0.37	0.71	44
	Wood plant	0.12	0.02	0.25	31
	POM	0.23	0.16	0.30	33
Pygocentrus nattereri	Phytomicrob.	0.14	0.03	0.28	42
	C3 macroph.	0.37	0.21	0.52	34
	C4 grasses	0.07	0.04	0.11	46
	Wood plant	0.09	0.02	0.20	47
	POM	0.34	0.28	0.39	41
Plagioscion squamosissimus	Phytomicrob.	0.14	0.03	0.30	26
	C3 macroph.	0.40	0.22	0.56	27
	C4 grasses	0.06	0.02	0.10	56
	Wood plant	0.10	0.02	0.22	23
	POM	0.30	0.23	0.37	30
Acestrorhynchus abbreviatus	Phytomicrob.	0.14	0.03	0.28	40
	C3 macroph.	0.38	0.22	0.52	33
	C4 grasses	0.08	0.05	0.12	48
	Wood plant	0.09	0.02	0.20	51
	POM	0.31	0.24	0.37	42
Triportheus auritus	Phytomicrob.	0.07	0.01	0.19	40
	C3 macroph.	0.55	0.35	0.69	36
	C4 grasses	0.02	0.00	0.04	34
	Wood plant	0.08	0.01	0.22	38
	POM	0.28	0.21	0.36	39

DISCUSSION

The results indicate that the isotopic ratios of production sources and fishes and the proportional contributions of sources to fish biomass vary across the Amazon floodplain landscape, even during a period of high connectivity. I also found that outcomes from stable isotope analyses are sensitive to spatial scale. Taken together, these results are consistent with the view that networks of local food webs interact within broader landscapes to produce a large trophic network at the regional scale (Holt 2002; Winemiller & Jepsen 2004), and that sampling protocols for stable isotope analyses must address spatial variability in isotopic composition (Correa, Winemiller & Cárdenas 2016). My findings also advance understanding of the flow of matter and energy in aquatic habitats of the Amazon floodplain.

Regional scale patterns

My results indicate that aquatic macrophytes and POM are important primary sources supporting fish biomass in the Amazonian floodplains, at least under high-water conditions of the annual flood pulse, which is consistent with previous findings for rivers that carry high loads of suspended fine sediments (Roach 2013; Ou & Winemiller 2016). The results also are consistent with studies that grouped together δ^{13}C values of tree parts, C3 aquatic macrophytes and, in some cases, even periphyton and phytoplankton, and found that C3 plants were the primary source of carbon for several Amazonian fish species (e.g., Araujo-Lima et al. 1986; Forsberg et al. 1993; Benedito-Cecilio et al. 2000; Oliveira et al. 2006). Leaves of C3 aquatic macrophytes tend to have relatively high mineral and protein content, and along with fruits and seeds, are probably among the most nutritious plants in the Amazon floodplain (Forsberg et al. 1993). Herbivorous fishes associated with aquatic macrophytes beds (i.e., floating meadows composed of C4 grasses, such as *Echinochloa polystachya* and *Paspalum repens*, and C3 macrophytes, such as *E. crassipes*, *Pistia stratiotes*, *Ceratopteris pteridoides,* and *S. minima*) were reported to avoid eating C4 grasses, while consuming and, in many cases, controlling C3 macrophyte growth (Junk 1979). The mixing model estimates indicate that most fishes had assimilated relatively little material from woody plants when compared to aquatic C3 macrophytes. This result, however, does not discount the importance of fruits and seeds that are consumed directly by several herbivorous fishes, especially those from the family Serrasalmidae (Goulding 1980; Correa et al. 2015). Most of the tissue samples collected here for frugivorous species, such as *Colossoma macropomum*, were from subadults, which tend to be less specialized frugivores and granivores than larger individuals (Forsberg et al. 1993; Araujo-Lima & Goulding 1997). Given overlapping ranges of δ^{13}C values of aquatic macrophytes and woody plants, it also is possible that the mixing model in the present study overestimated contributions from aquatic macrophytes versus woody plants. Nonetheless, my analysis of variation in proportional contributions of basal production sources to fish biomass across the landscape indicated that, depending on the LHU, woody plants tended to be an important basal source in food chains supporting several species (e.g., *P. nattereri*, *T. auritus*, *A. abbreviatus*, *P. castelnaeana*) and a moderately important source supporting several others (*C. macropomum*, *P. squamosissimus, M. aureum, P. brachypomus*).

POM had not been previously reported as an important production source supporting fish biomass in the Amazonian floodplains. Although previous studies (e.g., Forsberg et al. 1993) have used similar methods for sampling suspended POM, they reported ^{13}C-depleted values that suggested a stronger contribution from phytoplankton. Conversely, δ^{13}C values for POM in this study are intermediate between those of C3 plants and C4 macrophytes. Since it is unlikely that this suspended material was derived from ^{13}C-depleted production sources, such as phytoplankton, POM in this study could have been a mixture of detritus derived from aquatic and riparian plants with humic material from soil (Hedges et al. 1986).

The insignificant contribution of C4 grasses to the biomass of most fishes has been consistently shown by isotope studies in the Amazonian and other floodplain Rivers (Araujo-Lima et al. 1986; Forsberg et al. 1993; Thorp et al. 1998; Benedito-Cecilio et al. 2000; Benedito-Cecilio & Araujo-Lima 2002; Oliveira et al. 2006; Zeug & Winemiller 2008; Roach et al. 2009; Mortillaro et al. 2015; Ou & Winemiller 2016). Despite the fact that C4 grasses are responsible for a large amount of primary production in floodplain systems (e.g., Melack & Forsberg 2001), grasses seem to have low importance as a basal source in food chains supporting aquatic consumers. Apparently owing to relatively low digestibility, grasses are not consumed by many fish species (Minson 1971; Mortillaro et al. 2015). When based on analysis at the regional level, even *S. fasciatus*, a species known to feed on grasses, appears to have assimilated material originating from POM. However, analysis of variation in proportional contributions of grasses across the landscape indicated that, in many cases, some fish species (i.e., *S. fasciatus, P. natteri, A. abbreviatus* and *P. squamosissimus*) had assimilated substantial amounts of material originating from C4 grasses.

Biplots and ranges of $\delta^{13}C$ and $\delta^{15}N$ of fishes indicated that biomass of five of the fish species analyzed probably was supported, in part, by one or more relatively ^{13}C-depleted production source that were missing from this study. One candidate is phytoplankton. The range of $\delta^{13}C$ values for these fishes (-38.7‰ to -24.6‰) falls within the range of reported values for phytoplankton in the Amazon (from about -39‰ to -23‰, Araujo-Lima et al. 1986; Forsberg et al. 1993; Martinelli et al. 1994). Phytoplankton has been inferred to be one of the main sources of carbon supporting biomass of several fish species in the Amazon floodplain, such as detritivorous fishes (Araujo-Lima et al. 1986; Benedito-Cecilio et al. 2000), including *C. incompta* and *P. latior*, and the planktivorous catfish *H. marginatus*. Alternatively, the missing source in my analysis could be chemolithotrophic bacteria that are known to have $\delta^{13}C$ values significantly lower than phytoplankton (Peterson et al. 1980; Fry & Sherr 1988) and which could support higher consumers via detritus–microbial pathways. Improved knowledge of aquatic food webs in the Amazonian River and floodplains could be achieved by focusing research on the potential roles of phytoplankton and microbial loop in supporting fish biomass as well as developing alternative study designs and approaches to disentangle the influence of temporal and spatial variation at different scales.

Isotopic variation across the landscape

My results demonstrating that δ^{13}C and δ^{15}N signatures of sources and fishes and the proportional contributions of production sources to fish biomass varied across the landscape are consistent with earlier claims about the variable nature of food web structure (Warren 1989; Winemiller 1990, 1996). Nitrogen and carbon isotopic signatures of all production sources, except for δ^{13}C of woody plants, varied spatially, a finding consistent with previous studies showing variation in the isotopic signatures of C3 and C4 plants and POM along the Amazon River (Hedges et al. 1986; Martinelli & Richey 1991; Mortillaro et al. 2012). Similar to these studies, my investigation produced evidence of a longitudinal gradient; for example, a downriver decline in δ^{13}C among aquatic macrophytes and phytomicrobenthos (Appendix C.2). Such patterns may be caused by increases in the flux of more ^{13}C-depleted dissolved CO_2 from the river into the atmosphere in more downstream reaches, resulting in lower δ^{13}C of algae and aquatic macrophytes that assimilate this dissolved CO_2 (Martinelli & Richey 1991; Benedito-Cecilio et al. 2000). Spatial variation in δ^{13}C of POM as well as variation in δ^{15}N for some sources (Appendix C.2) may be explained by variation in geomorphology and in the extent of forest cover that may cause differences in the quality of decomposing organic materials and soils (Renó et al. 2011; Mortillaro et al. 2012). Based on results from the present investigation, I can only speculate on possible causes of δ^{13}C and δ^{15}N spatial variation; however, my findings provide a foundation for research focused on testing more specific hypotheses. Multiple factors have either been shown or suggested to influence isotopic composition of basal production sources (e.g., variation in biogenic

CO_2, differential diffusion rates of ^{13}C and ^{12}C during photosynthesis caused by changes in environmental conditions (e.g., river discharge, water velocity, canopy cover), other local abiotic factors, chlorophyll a density, availability of dissolved inorganic carbon from various pools, plant physiological processes, and genotype, etc., Depetris & Kempre 1993; Forsberg et al. 1993; Finlay, Power & Cabana 1999; Evans 2001; Finlay 2001; Dawson et al. 2002; Amundson et al. 2003; Ishikawa, Doi & Finlay 2012).

Spatial variation in $\delta^{13}C$ for certain fish species (e.g., *C. macropomum, R. microlepis, A. abbreviatus* and *P. squamosissimus, H. microlepis, P. castealneana* and *P. nattereri*), as well as variation for estimates of relative contribution of production to the biomass of fishes in general, may reflect differences in trophic pathways at various locations within the landscape. It is possible that local food chains may vary according to the abundance and quality of alternative production sources and food resources as well as local environmental conditions. This hypothesis is supported by previous studies showing that tropical fishes have evolved plasticity in feeding strategies that allows specialization when certain resources are more available or when alternatives are less available (Winemiller 1990; Dabrowski & Portella 2005; Correa & Winemiller 2014).

The spatial variation in $\delta^{15}N$ that was observed in several fish species (e.g., *C. macropomum, R. microlepis, A. abbreviates, P. squamosissimus, S. fasciatus, P. latior and T. auritus*) could be influenced by variations in $\delta^{15}N$ among sources or may reflect intraspecific differences in trophic position across the landscape. My results showing that length-frequency distributions of most fish species were similar among catchments suggest that there were no ontogenetic shifts in trophic positions in relation to location.

However, the trophic level of an organism or average trophic level of a population should be dynamic rather than constant (Polis & Strong 1996), and many factors could affect spatial variation in trophic ecology (e.g., life history traits, availability of alternative production sources supporting food chains, or availability of food resources). Conversely, spatial variation in $\delta^{15}N$ of production sources sometimes was accompanied by similar variation in fish $\delta^{15}N$. For example, $\delta^{15}N$ of grasses and *S. fasciatus* tissues tended to covary in space. It is therefore feasible that shifts in tropic levels and isotopic signatures of basal sources together explain spatial variation in $\delta^{15}N$ of fish tissues.

Some limitations of stable isotope analysis in ecology

The normal range of fish movement in floodplains is within LHUs, but some fishes migrate across catchments during high-water conditions. Some Neotropical fishes are highly migratory and undergo seasonal movements up to several hundred kilometers (Ribeiro de Brito & Petrere 1990; Barthem et al. 2017). Therefore, it is possible that $\delta^{13}C$ and $\delta^{15}N$ signatures in tissues of some fishes may actually reflect isotopic composition of production sources assimilated in another LHU. If this were the case, it could bias mixing-model estimates of proportional contributions of local basal sources to fish biomass. Replication of this study across hydrological stages of the Amazon, particularly during the end of the dry season when LHUs have been isolated from each other for about two months, might reveal even stronger patterns of spatial variation in food web structure.

Estimation of diets and production sources in food chains supporting consumers based on stable isotope analysis has some practical limitations (e.g., uncertainties with regards to isotopic tissue turnover time and trophic fractionation, lack of isotopic distinction among sources (end-members) in mixing models, possible missed sources, and isotopic variability in sources and consumers (and see Layman et al. 2012; Phillips et al. 2014). Nevertheless, results reported herein were based on large samples obtained over a large region. Mixing models bias were minimized because I assure conformity with mixing model assumptions (e.g., consumer isotopic values fell within the isospace and trophic fractionation were corrected based on the trophic structure composition). Furthermore, although these potential sources of bias could influence estimates of major production sources supporting fish biomass, they are unlikely to change results showing variation of proportional contributions of alternative sources within and across species according to LHUs. In addition, none of these practical limitations would interfere our results showing variation in the isotopic composition of sources and fishes across the lanscape. Therefore, my results produced evidence of how food webs vary along habitat gradients within the floodplain of the world’s largest river.

Conclusions

The isotopic composition of components of aquatic food webs in the Amazonian River floodplain vary spatially. The estimates of proportional contributions of production sources revealed the importance of C3 aquatic macrophytes and POM to biomass of most fish species and of POM and grasses to *Schizodon fasciatus* at the regional scale and, in many cases, in the LHUs scale. However, relative contributions of production sources to fish biomass varied within and across species according to LHUs. Accordingly, the most important sources assimilated by fishes at the regional scale, sometimes were relatively unimportant for certain species and catchments. Conversely, the least important sources to most species at the regional scale (e.g., phytomicrobenthos, wood plants) sometimes were very important at the local scale. Aquatic food webs vary spatially likely owing to multiple factors, including variation in the quality and quantity of basal sources associated with gradients of watershed vegetation, heterogeneity of abiotic environmental conditions over multiple spatial scales, and differences in structures of local populations and species assemblages. Although difficult, it would be interesting to further explore how these potential mechanisms mediate spatial variation in the contributions of various production sources to fish biomass as well as linkages between isotopic variation of sources and consumers across the landscape. Because estimated contributions of production sources to fish biomass varied according to the spatial scale of analysis, research efforts in general, must be cautious when assigning averages $\delta^{13}C$ and $\delta^{15}N$ based on only a few samples. Depending on the specific hypothesis being tested, study designs should carefully consider not only replication and temporal scale, but also spatial scale.

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CHAPTER V

GENERAL CONCLUSIONS

Understanding the influences of human-driven impacts on ecological systems is a fundamental goal of conservation science. Human pressures on natural resources are dramatically changing ecosystem structures and processes worldwide. However, ecological assessments of these impacts are generally lacking, with many important aspects poorly understood, especially for complex ecosystems such as lowland rivers and tropical forests. Floodplains are one of the most valuable ecosystems for supporting biodiversity and providing goods and services to society, however they are also one of the most threatened ecosystems on the planet (Davidson 2014; Reis et al. 2017). Agricultural practices, such as livestock grazing, timber harvest and cultivation of crops, and flood control infrastructure (e.g., levees and dams) have altered natural flow regimes, habitats, and the longitudinal and lateral connectivity of rivers and floodplains (Tockner & Stanford 2002). These changes have large effects on aquatic and terrestrial organisms and ecosystem services. To guide conservation efforts and natural resource management, there is an urgent need to quantify and predict effects of altered land cover and hydrology on biodiversity patterns within floodplains. My dissertation addresses this issue by improving understanding on the dynamics of the Amazonian floodplains, including how changes in the natural landscape affect ecological communities and fishery production in this ecosystem. The information produced here can be used to aid management and conservation of this vulnerable ecosystem and its associated fishery upon which local people depend for their livelihoods.

In chapters II and III, I combined fish and environmental data collected *in situ* and satellite-mapped landscape features to evaluate how fish assemblages with different structures and species with ecological strategies respond to deforestation in floodplains of the Amazon River. Rather than analyze only taxonomic metrics, I employed an integrative approach that simultaneously considers different aspects of fish biodiversity (i.e., alpha versus beta diversity, and taxonomic versus functional assemblage structure) and fishery production (i.e., total fish biomass plus subsets of species possessing different functional traits and relative importance in the fishery) to facilitate mechanistic interpretations of the influence of land cover. The results demonstrated that spatial patterns of fish biomass distribution and biodiversity are strongly associated with forest cover as well as local environmental conditions linked to landscape gradients in the Amazon River floodplain. Chapter III also demonstrated that in addition to forest cover the presence of management, type of habitat and hydrology influence fish biomass. In chapter IV, I investigated how flows of energy and matter in food webs vary among aquatic habitats of the lower Amazon River floodplain. Based on analyses of carbon and nitrogen stable isotope ratios, I demonstrated that trophic pathways vary across the landscape, likely owing to multiple factors (e.g., variation in quality and quantity of basal sources related to changes in watershed vegetation, heterogeneity of habitats and small-scale environmental gradients). My results on spatial patterns of fish diversity also suggest that forest loss in the Amazon results in spatial homogenization of fish assemblages and reduced functional diversity. In addition, results on spatial patterns of fish biomass distribution suggest that deforestation in the Amazon floodplain reduces fishery production and alters the biomass distribution of functional groups.

These findings complement previous studies showing combined effects of human activities, including global-climate change and disruption in natural flow regimes, in the ecosystems of the Amazon floodplains (Marengo et al. 2008; Gloor et al. 2013; Marengo & Espinoza 2016; Forsberg et al. 2017; Röpke et al. 2017). Climate change has altered natural patterns of precipitation, including the frequency of extreme events such as droughts and floods (Duffy et al. 2015; Marengo & Espinoza 2016) that affect floodplain hydrology (Sorribas et al. 2016) in the Amazon Basin. In turn, these climate-driven hydrological shifts directly or indirectly affect aquatic organisms. Structure of fish assemblages in the central Amazon have changed, with no indication of subsequent recovery, as a result of an extreme drought event and subsequent anomalous climatic events (Freitas et al 2013; Ropke 2017). Hydroelectric dams have been shown to reduce hydrological variability, block fish migration, disrupt sediment transport and alter physical-chemical characteristics of rives in the Amazon Basin (Araújo et al. 2013; Fearnside 2014; Castello & Macedo 2016; Winemiller et al. 2016). For example, a recent study showed that dams that are planned for construction in the western Amazon Basin will reduce the supply of sediments and nutrients (e.g., phosphorus and nitrogen) to the central and eastern regions of the basin (Forsberg et al. 2017). These reductions in sediments and nutrients will lead to major impacts on channel geomorphology and aquatic productivity, particularly, near the dams and in floodplains located far downstream (Forsberg et al. 2017). Studies also have inferred that dams in the tributaries of the Amazon River obstruct upstream migrations of long-distance migratory catfishes and downstream movements of their eggs and young juveniles (Barthem, de Brito Ribeiro & Petrere 1991; Duponchelle et al. 2016). Hydrological alterations after dam constructions in the Tocantins River, a large Amazon tributary, have changed species richness, population spatial distributions, and abundance patterns of nonmigratory fishes along the river (Araújo et al. 2013) and reduced fisheries production (Ribeiro, Petrere & Juras 1995). Besides suffering impacts from these major threats, Amazonian ecosystems and the fish populations they support are also vulnerable to pollution in the form of toxic wastes, including crude oil, that have resulted from expansion in oil exploration (Jochnick, Normand & Zaidi 1994; Finer et al. 2008) and mining activities that alter river morphology, increase suspended sediments loads and pollute water via the release of mercury (De Miguel et al. 2014).

The magnitude of current and future environmental impacts in the lower Amazon River are difficult to assess, because many of them interact synergistically. For example, construction of large hydroelectric dams also causes clearing and submerging large areas of forest along major Amazon tributaries (Castello et al. 2013). Large-scale deforestation is affecting atmospheric dynamics, leading to changes in patterns of precipitation and likely contributing to more extreme climatic events (Coe, Costa & Soares-Filho 2009; Borma, Nobre & Borma 2013). The resulting hydrological alterations from dam operations are perhaps the major extrinsic driver of impacts to fish populations and fisheries yields, with potential to damage regional income and food security.

So what measures are needed to improve development planning and to mitigate human impacts to biodiversity and ecosystem services in the Amazon? Obviously, much more research is needed, not only to understand the full range of potential human-driven impacts, but also to provide understanding of the dynamics of ecological process and patterns under natural conditions. What are the potential singular as well as synergistic effects of these impacts, and can we identify thresholds for ecological processes and patterns across variable spatial and temporal scales? How do ecological interactions and ecosystems processes (e.g., flows of matter and energy, nutrient cycling) respond to these various sources of floodplain degradation, and how do these responses affect biodiversity and ecosystem services? To what extent can scientific knowledge obtained for one location, be applicable to another location within and among floodplain systems? Some of these questions and others can be addressed by using current and emerging technologies, such as satellite-based monitoring, in conjunction with long-term monitoring of climate, hydrology, and ecology over vast areas. This will be essential to understand floodplain ecosystem dynamics and potential ecological resilience, as well as to inform natural resource managers and policy makers.

As I mentioned in chapter II, conservation strategies in the Amazon generally have focused on terrestrial biodiversity and ecosystems, and have failed to address aquatic components, including fish populations that support major fisheries (Castello & Macedo 2016). Conservation strategies in the Amazon need to move toward an integrated, basin-wide framework that deals with both scientific information and societal needs. Although considerable knowledge gaps remain, available information, including findings from this dissertation, provides a foundation for developing such a framework. For example, my findings indicate that conservation of fish diversity and fishery production requires protection of not only floodplain forests, but also a mosaic of land cover types within floodplains. My findings also suggest that, in addition to maintaining a land-cover portfolio that includes forests, shrublands and grasslands, maintaining hydrologic connectivity and improving fishery management at the local scale will enhance fish biomass and species diversity, including species having greatest economic importance. Better knowledge of ecological patterns and dynamics at local to regional spatial scales will be essential for conservation planning for the Amazon, and it is my hope that this dissertation advances us a few steps forward.

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APPENDIX A

CHAPTER II APPENDICES

Appendix A.1. Satellite imagery: Land cover data and macrophyte cover metrics

Landsat imagery was obtained from the USGS Earth Explorer site (http://earthexplorer.usgs.gov/) and ALOS PALSAR imagery was obtained from the Alaska Satellite Facility's Vertex Data Portal (https://vertex.daac.asf.alaska.edu/). The two contiguous Landsat Thematic Mapper images used to map floodplain land cover (acquired on 30 November 2008 and 23 October 2009) correspond to river stages of 2.14 m and 1.75 m at the Óbidos gauge (ANA 2014). Seven ALOS PALSAR swaths (fine-beam, HH-polarized, L-band synthetic aperture radar; resampled from 12.5 to 30 m) acquired during 2006 to 2011 were used to map aquatic macrophyte coverage (Table 1).

Floodplain land cover types mapped were: open water, herbaceous vegetation, and forest. Lakes and secondary channels (open water) are the principal aquatic habitats that are present during low-water periods, when other floodplain areas dry out (Junk 1997). During the annual flood pulse, areas covered by forest or herbaceous vegetation provide important food resources for many fishes, as well as spawning and nursery habitat. Herbaceous vegetation communities dominate the margins of lakes and channels; this land cover category was defined to include areas with grass, forbs, or bare soil during low-water periods. The forest category includes tall forest remnants (with emergent canopy heights to 40 m), regenerating forests (locally termed *capoeiras*) and pioneer forests, the latter two categories having lower and more variable canopy heights (Renó et al. 2011). The shrubby aroid *Montrichardia arborescens*, 1 to 4 m in height, often dominates pioneer forests in areas of low elevation and was included within the forest category.

Aquatic macrophyte cover within open-water and herbaceous areas comprised emergent or floating grasses (primarily, *Hymenachne amplexicaulis*, *Paspalum repens, P. fasciculatum, Oryza perennis*, and *Echinochloa polystachya*) or broad-leaved herbaceous plants (including *Eichhornia* spp., *Pistia* spp. *Salvinia* spp., and *Victoria* spp.). These floating meadows are highly variable seasonally and interannually, and attain their peak extent during the early rising-water period (December to mid-January; Silva et al. 2010). The macrophyte metric used here was the percent of the catchment having macrophyte cover during the early-rising water period during three or more of the five years imaged (Table 1).

Appendix A.2. Functional traits classification

I classified species into functional groups based on life history, feeding and habitat-use strategies. I classified species according to five life history strategies based on maximum body size, size at maturation, batch fecundity, and parental investment per individual offspring (Appendix A.11) following Winemiller & Rose (1992) and Röpke et al. (2017). Life history strategies identify suites of intercorrelated functional traits and their associations with patterns of environmental variation involving abiotic factors, disturbance regimes, resource availability and quality, population density, risk of predation or parasitism, and challenges for dispersal (Winemiller & Rose 1992, Winemiller 2005). Three species were classified as *equilibrium strategists with maturation at small size* (<120 mm standard length, SL), having low batch fecundity

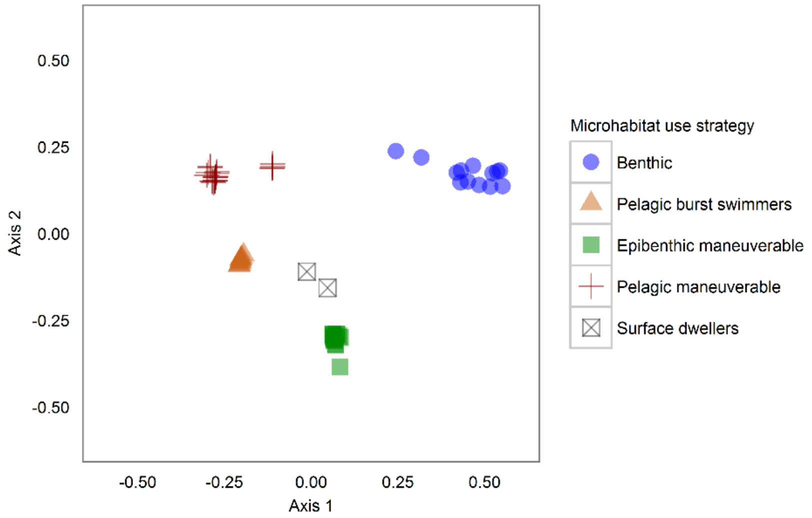
(<3,000), large oocytes (diameter 1.5 – 12 mm), well-developed parental care, and maximum body size between 97 - 269 mm SL. Five species were *equilibrium strategists with maturation at large size* (>170 mm SL), with low batch fecundity (<3,000), large oocytes (diameter 1.5 – 12 mm), well-developed parental care and maximum size >400 mm SL. Twenty-two species were *periodic strategists with maturation at small size* (between 63 – 148 mm SL), having batch fecundity between 6,762 and 74,227, small oocytes (diameter 0.5 – 1.3 mm), maximum size between 137 – 410 mm SL and no parental care. Nineteen species were *periodic strategists with maturation at large size* (>164 mm SL), with batch fecundity between 1,000 and 202,960, small oocytes (diameter 0.7 – 1.6 mm), no parental care and maximum size > 253 mm SL. Eleven species classified as *intermediate strategists* had batch fecundity between 1,000 and 9,000, relatively large oocytes (diameter 1.4–2 mm), and intermediate development of parental care (Röpke et al. 2017).

I classified species according to six feeding strategies based on dietary information from published reports (Appendix A.11). *Herbivores* (7 species) feed predominantly on C3 or C4 plant material (seeds, fruits or leaves) and on filamentous algae. *Omnivores* (9 species) ingest combinations of plant material, detritus, and invertebrates. *Detritivores* (11 species) predominantly ingest fine particulate organic matter and also algae and non-living macrophyte tissues. *Invertivores* (6 species) ingest variable fractions of aquatic and terrestrial insects, microcrustaceans from the benthos or water column, spiders, shrimps, and mollusks. *Planktivores* (3 species) ingest phytoplankton, zooplankton, and occasionally small amounts of plant material and detritus. *Piscivores* (24 species) ingest adult, juvenile, or larval fish, either whole or in pieces, including scales and fins.

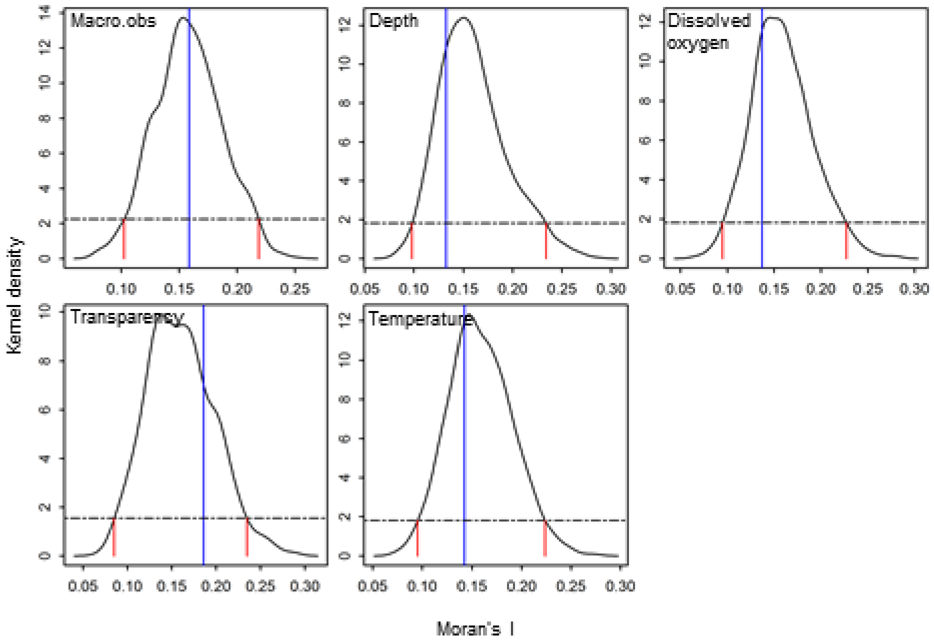
Finally, I classified species according to five strategies of swimming/microhabitat use based on morphological traits. I used traits associated with swimming performance and position in the water column during foraging, phenotypes that influence fitness along gradients of habitat structural complexity and other environmental features (Gatz 1979, Winemiller 1991). I quantified or classified species according to the following morphological traits: relative body depth, body depth below midline, degree of lateral body compression, and eye and mouth positions. Relative body depth, body depth below the midline, and eye position were measured using morphometric software (Thin-plate Spline program; Rohlf 2015). Degree of lateral body compression and mouth position classifications are described in the Appendix A.3. To visualize the relative position of fish species within trait space, a Principal Coordinates Analysis (PCoA) was carried out on the Gower's distance matrix (Appendix A.3 and Appendix A.4). *Nektonic maneuverable* fishes (21 species) had laterally compressed bodies and superior mouth position, whereas *nektonic burst swimmers* (10 species) had fusiform bodies and terminal mouth position. Both groups had morphological traits associated with efficient swimming performance based on a hydrodynamic body and feeding within the water column. *Surface dwellers* (2 species) had intermediate lateral body compression, superior mouths and either deep or fusiform bodies. *Epibenthic maneuverable* fishes (15 species) were a diverse group having relatively deep bodies that are less hydrodynamic than nektonic maneuverable fishes but efficient in making lateral and vertical turns. The two last groups also had more dorsally than laterally positioned eyes. *Benthic* fishes (13 species) had relatively wide bodies, dorsally located eyes, and inferior mouths, which are characteristic of bottom dwellers and relatively slow swimmers.

Appendix A.3. Functional traits related to microhabitat use and trophic ecology. Measurements were taken according to Gatz (1979) and Winemiller (1991).

Traits	Method
Relative body depth	Body height divided by SL
Depth below midline	Mid-line height divided by body height
Relative eye position	Distance from the eye to the base of the head divided by the head height
Degree of compression	Classified in three types: 1 for strongly laterally compressed bodies; 2 for slightly compressed bodies; and 3 for wider bodies
Mouth position	Classified in five types: 1 for bottom or totally inferior; 2 for sub-inferior or slight down-turned; 3 for terminal; 4 for supra-terminal, or slight up-turned; and 5 for superior



Appendix A.4. Principal Coordinates Analyses (PCoA) biplots showing the 5 functional groups of microhabitat use.



Appendix A.5. Comparisons of observed values of Moran's I and bootstrapped Moran's I. Plots show observed values of Moran's I (blue line) and kernel density estimate (essentially a smoothed histogram) of bootstrapped Moran's I generated by randomly assigning the latitude and longitude values to the local environmental variables values. The red vertical lines show the limits of the 95% confidence interval for the bootstrapped Moran's I. Observed Moran's I values were generally within confidence intervals indicating a lack of spatial dependence in the local environmental data.

Appendix A.6. Beta diversity decomposition

I used an approach proposed by Legendre (2014) to explain variation in β diversity and its components along environmental gradients. First, I measured dissimilarity among all pairs of observations (sampling habitats) using the percentage difference (β_{Total}, Odum 1950, known as the Bray-Curtis index). The percentage difference index between observation S_j and S_k is defined as:

$\beta_{Total} = (B + C) / (2A + B + C)$,

where A is the abundance of each species that exists both in S_j and S_k, B is the abundance of each species unique to S_j and C the abundance of each species unique to S_k. This dissimilarity index is not Euclidean, but the matrix of square-rooted dissimilarities is Euclidian.

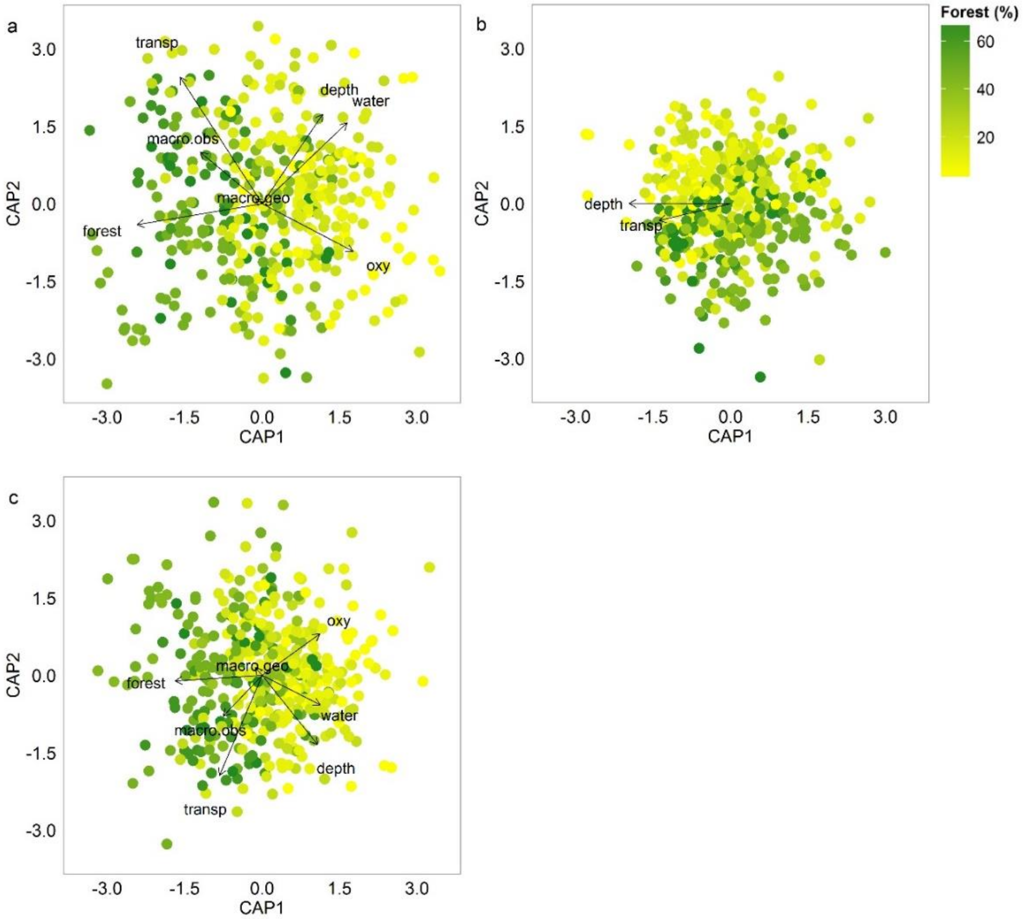
Second, I used the additive partitioning framework proposed by Podani et al. (2013) and Legendre (2014) to decompose two components underlying the total amount of β diversity (β_{Total}) for all pairs of sites: spatial turnover and abundance difference (Podani & Schmera 2011, Podani et al. 2013, Legendre 2014). Species turnover, herein $\beta_{replacement}$, refers to the replacement of species along an ecological gradient. $\beta_{replacement}$ implies the gain and loss of species due to environmental filtering, competition, or historical events (Leprieur et al. 2011). Abundance difference ($\beta_{abundance\ difference}$) refers to the fact that one community may include a larger abundance of species than another. Abundance difference may reflect the diversity of niches available at different locations:

$\beta_{replacement} = 2 \text{ x } \min(B,C) / (2A + B + C)$, and

$\beta_{abundance\ difference} = |B - C| / (2A + B + C)$

Third, I assessed associations between components of $\beta_{replacement}$, $\beta_{abundance\ difference}$, β_{Total}, and the eight land-cover and environmental variables (Table 1) using Partial Constrained Analysis of Principal Coordinates (CAP, function *capscale* from *vegan* package in R). CAP ordination uses the dissimilarity matrixes ($\beta_{replacement}$, $\beta_{abundance\ difference}$ and β_{Total}) and RDA in the same procedure described above for analysis of taxonomic and functional assemblage structures.

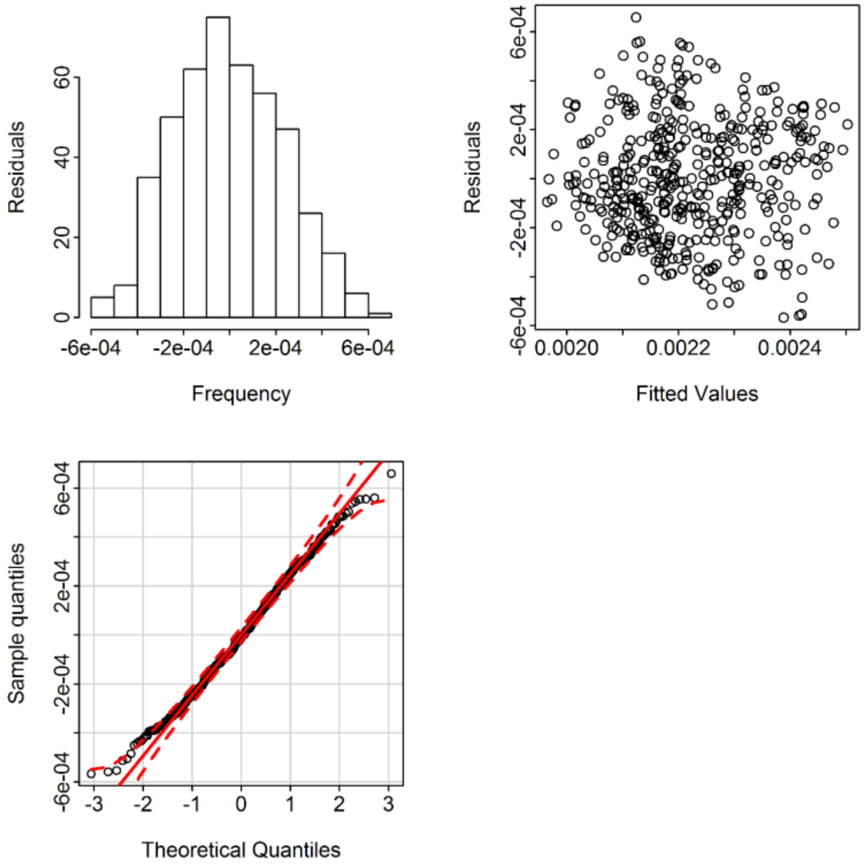
I also evaluated whether distinct land cover and environmental variables affect the relative contribution of the local habitats to β diversity. First, I computed local habitat contributions to β-diversity indices, herein LCBD, which are comparative indicators of the ecological uniqueness of the sampled habitats for their contribution to β-diversity (Legendre and Cáceres 2013, Legendre 2014). In the principal coordinates ordination (PCoA) diagram of the β_{Total} matrix, LCBD indices represent the squared distance of a habitat to the multivariate centroid (Legendre and Cáceres 2013). Large LCBD values indicate habitats that have strongly different species composition compared with a mean habitat, which can indicate that habitats have high conservation value or are potential candidates for ecological restoration (Legendre and Cáceres 2013). Second, I used a linear mixed model (LMM) to quantify the degree to which distinct floodplain land cover and environmental variables affected LCBD. I built a random-effects model, where LCBD was the response variable, and standardized land cover, environmental variables, and spatial structure were the fixed effects, whereas intercepts were allowed to vary according to season (random factor) (Zuur et al. 2009). The model was assessed with respect to normally distributed errors (visual inspection of residual plots and Shapiro-Wilk test), and multicollinearity (Variance Inflation Factor).



Appendix A.8. Constrained Analysis of Principal Coordinates (CAP) biplots showing associations of β-diversity components: (a) βreplacement, (b) βabundance difference and (c) βTotal and significant land cover and environmental variables (arrows). The biplots show CAP scores for the sampled habitats (450 points) in a gradient of forest cover that ranges from yellow, representing meadows of herbaceous vegetation, to green, representing forested local hidrological unities. The eigenvalues of the first (x) and second (y) canonical axes are 2.45 and 1.05; 1.53 and 1.67; and 4.77 and 2.71 for $\beta_{replacement}$, $\beta_{abundance\ difference}$ and β_{Total}, respectively. 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.

Appendix A.9. Summary of the linear mixed model showing standardized coefficients (10^{-4}), standardized errors (SE), and *t* and *p*-values of the predictors for LCBD indices in the lower Amazon floodplain.

Fixed effects	Estimate	SE	*t*-value	*p*-value
(Intercept)	22.57	0.53	42.57	0.00
Forest (%)	0.34	0.14	2.34	0.02
Water (%)	0.15	0.15	1.00	0.32
Macrophyte (geop)	0.30	0.14	2.17	0.03
Macrophyte (obs)	0.00	0.13	0.02	0.98
Depth (cm)	0.54	0.16	3.42	0.00
Dissolved oxygen (mg/l)	0.07	0.14	0.52	0.60
Transparency (cm)	0.55	0.16	3.40	0.00
Temperature (^{0}C)	-0.17	0.16	-1.07	0.29
Spatial structure (pcnm1)	-0.16	0.13	-1.20	0.23
Spatial structure (pcnm2)	0.12	0.15	0.83	0.41



Appendix A.10. Residual plots of the model presented in Figure 3 and Appendix A.9.

Appendix A.11. Taxonomic composition and life history, feeding, and microhabitat use strategies. Loadings on the RDA axes for the taxonomic composition analysis (Figure 2a) are shown. Feeding strategies classification was based on Barbarino & Winemiller (2003), Mérona and Rankin-de-Mérona (2004), Santos et al. (2008), Shibuya & Zuanon (2013), Röpke et al (2014), Correia & Winemiller (2014), Lopes et al. (2015) and Röpke et al. (2017). Life history classification was based on Röpke et al. (2017), and microhabitat use classification is described in Appendix A.2. Equilibrium with maturation at large size = Equilibrium-large; Equilibrium with maturation at small size = Equilibrium-small; Periodic with maturation in large size = Periodic-large; Periodic with maturation at small size=Periodic-small.

Family Species	Axis 1 scores	Axis 2 scores	Feeding	Life History	Habitat use
Acestrorhynchidae					
Acestrorhynchus abbreviatus	0.243	0.145	Piscivore	Periodic-small	Nektonic burst swimmers
Acestrorhynchus falcatus	0.129	0.123	Piscivore	Periodic-small	Nektonic burst swimmers
Acestrorhynchus nasutus	0.028	-0.077	Piscivore	Periodic-small	Nektonic burst swimmers
Anostomidae					
Leporinus trifasciatus	0.121	-0.028	Omnivore	Periodic-small	Epibenthic maneuverable
Rhytiodus argenteofuscus	-0.008	-0.049	Herbivore	Periodic-large	Nektonic burst swimmers
Rhytiodus microlepis	0.165	-0.401	Herbivore	Periodic-large	Nektonic burst swimmers
Schizodon fasciatus	0.118	0.162	Herbivore	Periodic-small	Epibenthic maneuverable
Auchenipteridae					
Ageneiosus dentatus	-0.167	0.098	Piscivore	Intermediate	Benthic
Ageneiosus inermis	-0.399	0.429	Piscivore	Periodic-large	Benthic
Parauchenipterus porosus	-0.048	0.091	Invertivore	Intermediate	Benthic
Callichthyidae					
Hoplosternum littorale	0.157	0.092	Invertivore	Intermediate	Benthic
Characiade					
Brycon melanopterus	0.150	0.035	Omnivore	Periodic-large	Epibenthic maneuverable

Appendix A.11. Continued.

Family Species	Axis 1 scores	Axis 2 scores	Feeding	Life History	Habitat use
Cichlidae					
Astronotus crassipinnis	0.135	0.014	Piscivore	Equilibrium-large	Epibenthic maneuverable
Cichla monoculus	0.241	-0.048	Piscivore	Equilibrium-large	Epibenthic maneuverable
Geophagus proximus	-0.012	-0.026	Invertivore	Equilibrium-small	Epibenthic maneuverable
Mesonauta insignis	0.040	-0.020	Omnivore	Equilibrium-small	Epibenthic maneuverable
Curimatidae					
Curimata incompta	0.087	-0.085	Detritivore	Periodic-small	Epibenthic maneuverable
Curimata vittata	0.133	-0.069	Detritivore	Periodic-small	Epibenthic maneuverable
Curimatella alburna	0.110	0.015	Detritivore	Periodic-small	Epibenthic maneuverable
Potamorhina altamazonica	0.031	-0.132	Detritivore	Periodic-small	Nektonic maneuverable
Potamorhina latior	0.037	-0.175	Detritivore	Periodic-small	Nektonic maneuverable
Psectrogaster rutiloides	0.024	-0.061	Detritivore	Periodic-small	Nektonic burst swimmers
Cynodontidae					
Cynodon gibbus	0.019	0.084	Piscivore	Periodic-large	Nektonic maneuverable
Hydrolycus scomberoides	0.020	0.037	Piscivore	Periodic-large	Nektonic maneuverable
Rhaphiodon vulpinus	-0.110	0.143	Piscivore	Periodic-large	Nektonic maneuverable
Doradidae					
Oxydoras niger	0.034	0.061	Invertivore	Periodic-large	Benthic
Engraulidae					
Anchoviella guianensis	-0.108	-0.019	Planktivore	Periodic-small	Nektonic maneuverable
Lycengraulis batesii	-0.249	-0.018	Invertivore	Periodic-small	Nektonic maneuverable
Erythrinidae					
Hoplias malabaricus	0.192	0.006	Piscivore	Intermediate	Benthic
Hemiodontidae					
Anodus elongatus	-0.218	-0.159	Planktivore	Periodic-small	Nektonic burst swimmers

Appendix A.11. Continued.

Family Species	Axis 1 scores	Axis 2 scores	Feeding	Life History	Habitat use
Hemiodus argenteus	0.031	-0.127	Omnivore	Periodic-small	Nektonic burst swimmers
Hemiodus microlepis	0.003	-0.175	Omnivore	Periodic-small	Nektonic burst swimmers
Loricariidae					
Hypoptopoma gulare	-0.037	0.058	Detritivore	Intermediate	Benthic
Loricariichthys sp.	0.008	0.100	Detritivore	Equilibrium-large	Benthic
Pterygoplichthys pardalis	0.297	0.016	Detritivore	Equilibrium-large	Benthic
Osteoglossidae					
Osteoglossum bicirrhosum	0.568	0.062	Invertivore	Equilibrium-large	Surface dweller
Pimelodidae					
Calophysus macropterus	-0.238	0.164	Piscivore	Periodic-large	Benthic
Hypophthalmus marginatus	-0.290	-0.046	Planctivore	Periodic-large	Epibenthic maneuverable
Pimelodus blochii	-0.040	0.038	Omnivore	Periodic-small	Benthic
Pseudoplatystoma tigrinum	0.108	0.032	Piscivore	Periodic-large	Benthic
Sorubim lima	0.001	0.038	Piscivore	Periodic-large	Benthic
Pristigasteridae					
Pellona castelnaeana	-0.544	-0.060	Piscivore	Periodic-large	Nektonic maneuverable
Pellona flavipinnis	-0.197	-0.115	Piscivore	Periodic-large	Nektonic maneuverable
Prochilodontidae					
Prochilodus nigricans	0.244	0.006	Detritivore	Periodic-large	Epibenthic maneuverable
Semaprochilodus insignis	0.010	-0.057	Detritivore	Periodic-large	Epibenthic maneuverable
Sciaenidae					
Plagioscion squamosissimus	-0.131	0.276	Piscivore	Periodic-large	Epibenthic maneuverable
Serrasalmidae					

Appendix A.11. Continued.

Family Species	Axis 1 scores	Axis 2 scores	Feeding	Life History	Habitat use
Colossoma macropomum	0.939	0.402	Herbivore	Periodic-large	Epibenthic maneuverable
Mylossoma aureum	-0.110	0.036	Herbivore	Periodic-small	Nektonic maneuverable
Mylossoma duriventre	-0.072	0.220	Herbivore	Periodic-small	Nektonic maneuverable
Piaractus brachypomus	0.036	0.030	Herbivore	Periodic-large	Surface dweller
Pristobrycon sp.	-0.022	0.015	Piscivore	Intermediate	Nektonic maneuverable
Pristobrycon striolatus	-0.032	0.054	Piscivore	Intermediate	Nektonic maneuverable
Pygocentrus nattereri	-0.561	0.609	Piscivore	Intermediate	Nektonic maneuverable
Serrasalmus eigenmanni	0.000	0.053	Piscivore	Intermediate	Nektonic maneuverable
Serrasalmus elongatus	0.033	0.006	Piscivore	Intermediate	Nektonic maneuverable
Serrasalmus maculatus	0.127	0.028	Piscivore	Intermediate	Nektonic maneuverable
Serrasalmus rhombeus	-0.074	0.180	Piscivore	Intermediate	Nektonic maneuverable
Triporthidae					
Triportheus albus	-0.266	-0.075	Omnivore	Periodic-small	Nektonic maneuverable
Triportheus angulatus	0.286	0.139	Omnivore	Periodic-small	Nektonic maneuverable
Triportheus auritus	-0.348	-0.239	Omnivore	Periodic-small	Nektonic burst swimmers

APPENDIX B

CHAPTER III APPENDICES

Appendix B.1. Species classification

We tested relations between forest coverage and fish biomass (CPUE) based on 25 fish groups distributed within 6 categories (Appendix B.10). Measures of total fish biomass in local habitats involved subsets of the 186 species that were surveyed in the region. Species were grouped according to their degree of importance in local fisheries and this classification was based on their relative contribution to total yields landed in the main cities in the lower Amazon following Isaac et al. (2016) and Castello et al. (2017). Fish of *high-importance* (28 species, 11 common names) contributed ≥ 85% of the total landing. Fish of *medium-importance* (83 species, 31 common names) contributed with 15% of the total landing. Both groups (high-importance and medium-importance) contain important species for subsistence fisheries in the Amazon (e.g., *Colossoma macropomum, Cichla monoculus, Prochilodus nigricans, Mylossoma* spp. *Myleu*s spp.) (Batista et al. 2008). Seventy-four species (39 common names) were classified as having *low-importance* and were rarely landed for sale as food, although some of them are used as bait or sold as ornamental fish.

The other categories comprised functional groups based on trophic, migratory, life history, and swimming/microhabitat-use strategies following Arantes et al. (2017). We classified species according to eight trophic strategies based on dietary information from published reports (Appendix B.10). *Herbivores* (18 species) feed predominantly on C3 or C4 plant material (seeds, fruits or leaves) and on filamentous algae. *Omnivores*

(47 species) ingest combinations of plant material, detritus, and invertebrates. *Detritivores* (28 species) predominantly ingest fine particulate organic matter and non-living macrophyte tissues, but also on filamentous algae. *Invertivores* (23 species) ingest variable fractions of aquatic and terrestrial insects, microcrustaceans from the benthos or water column, spiders, shrimps, and mollusks. *Planktivores* (10 species) ingest phytoplankton, zooplankton, and occasionally small amounts of plant material and detritus. *Piscivores* (45 species) ingest adult, juvenile, or larval fish, either whole or in pieces, including scales and fins. *Piscivores-macroinvertivores* (14 species) feed on the same sources as piscivores but also ingest significant fractions of diverse terrestrial or aquatic macroinvertebrates (e.g., Ephemeroptera, Chironomidae, Coleoptera, Crustacea, etc.).

We classified species according to four migratory strategies based on information on dispersal behavior from published reports. Migratory strategies of Amazon fish often are related to reproduction and/or feeding ecology and influenced by seasonal hydrology and physical-chemical conditions of habitats in the riverscape. *Sedentary* (55 species) were resident species that spend their entire life-cycles within floodplain habitats eventually performing short-distances movements. Sedentary species were small-bodied species, or had territorial behavior, or are known to be strongly associated with substrates or complex structured habitat (e.g., tree branches and aquatic vegetation). Species performing *local migration* (120) comprised a diverse group of fishes that migrate laterally from floodplain lakes or river channels onto flooded floodplain habitats following closely the dynamic ‘pulsing’ of water levels (Junk et al. 1989; Fernandes

1997; Carolsfeld 2003; Castello 2008). Species performing *regional migration* (8 species) migrate onto flooded floodplains habitats during high waters, but also conduct longitudinal migrations (often hundreds of kilometers) along river channels to spawn, particularly during falling waters (Goulding 1980; Ribeiro de Brito and Petrere 1990; Benedito-Cecilio and Araujo-Lima 2002; Barthem and Fabré 2004). *Long-distance* migrators (3 species) were species that migrate thousands of kilometers along river channels, though their juveniles often inhabit floodplain lakes (Barthem et al. 1991, 2017).

We classified species according to six life history strategies based on maximum body size, size at maturation, batch fecundity, and parental investment per individual offspring (Appendix B.10) following Winemiller & Rose (1992) and Röpke et al. (2017). Life history strategies identify suites of intercorrelated functional traits and their associations with patterns of environmental variation involving abiotic factors, disturbance regimes, resource availability and quality, population density, risk of predation or parasitism, and challenges for dispersal (Winemiller & Rose 1992, Winemiller 2005). Sixteen species were classified as *equilibrium strategists with maturation at small size* (<120 mm standard length, SL), having low batch fecundity, large oocytes, well-developed parental care, and maximum body size between 97 - 269 mm SL. Sixteen species were *equilibrium strategists with maturation at large size* (>170 mm SL), with low batch fecundity, large oocytes, well-developed parental care and maximum size >400 mm SL. Seventy-three species were *periodic strategists with maturation at small size* (between 63 – 148 mm SL), having varied batch fecundity size (average ~ 4,000), small oocytes, maximum size between 137 – 410 mm SL and no parental care. Forty-three species were *periodic strategists with maturation at large size* (>164 mm SL), with batch fecundity highly variable, small oocytes, no parental care and maximum size > 253 mm SL. Thirty-two species classified as *intermediate strategists* had batch fecundity between 1,000 and 9,000, relatively large oocytes, and intermediate development of parental care. Five species classified as *opportunistic* had small size (between 26–113 mm SL), early maturation (<60 mm SL), high and sustained reproductive effort but low batch fecundity and no parental care (Röpke et al. 2017).

Finally, we classified species according to five strategies of swimming/microhabitat use based on morphological traits. We based our classification on the classification of Arantes et al. (2017) that uses traits associated with swimming performance and vertical position within the water column during foraging, phenotypes that influence fitness along gradients of habitat structural complexity and other environmental features (Gatz 1979, Winemiller 1991). *Nektonic maneuverable* fishes (41 species) had laterally compressed bodies and superior mouth position, whereas *nektonic burst swimmers* (18 species) had fusiform bodies and terminal mouth position. Both groups had morphological traits associated with efficient swimming performance based on a hydrodynamic body and feeding within the water column. *Surface dwellers* (2 species) had intermediate lateral body compression, superior mouths and either deep or fusiform bodies. *Epibenthic maneuverable* fishes (57 species) were a diverse group having relatively deep bodies that are less hydrodynamic than nektonic maneuverable fishes but efficient in making lateral and vertical turns. The two last groups also had more dorsally than laterally positioned eyes. Most *Benthic-slow* (36 species) and *Benthic-fast* (23 species) had relatively wide bodies, dorsally located eyes, and inferior mouths, which are characteristic of bottom dwellers. Benthic-fast fishes had higher muscle mass and larger pectoral and caudal fins ratio areas than benthic-slow fishes; morphological traits associated with increasing swimming performance. A few benthic-fast (1 species) and benthic-slow (3 species—e.g., *Hoplias malabaricus*) fishes had terminal or superior mouths. *Gymnotiformes* (8 species) comprised a diverse group of electric fishes, either substrate or aquatic vegetation dwellers, that are inactive during daylight but actively forage during the night using weak electric organ to locate their prey (Fernandes et al. 2004; Carvalho et al. 2009). As mentioned herein, we did not include gymnotiforms, long-distance migrators and opportunistic strategists in the analyses due to their small sample size and complete absence at some levels of the categorical variables (i.e., seasons and habitat types).

Appendix B.2. Statistical Analyses

Modelling associations of fish biomass and forest

Fish biomass (CPUE) for each fish group was modeled as a function of linear predictors within a generalized linear model (GLM) framework using a Poisson-Gamma distribution:

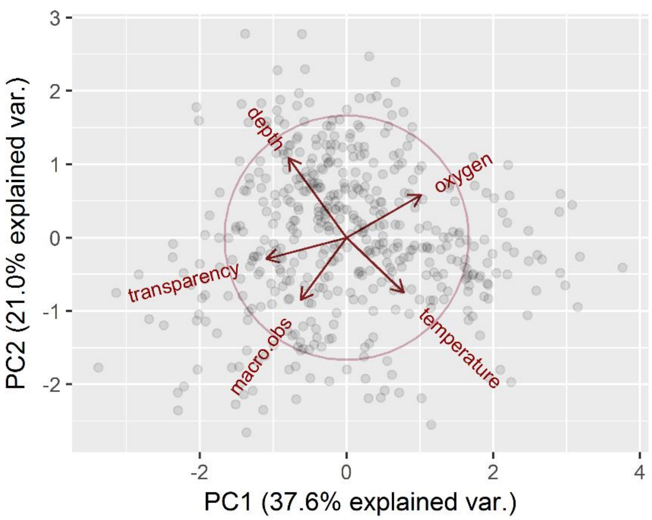
$$g(y_i) = \alpha + \boldsymbol{l_i}\boldsymbol{\varphi} + \boldsymbol{e_i}\boldsymbol{\beta} + \delta s_i + \theta h_i + \gamma m_i + \boldsymbol{\varepsilon_i}$$

where, g() is the log link function, *i* represents the data sampling habitat, y is fish biomass standardized by sampling effort (CPUE), ***l*** is a row vector of three measures of land cover (forest, open water, large-scale estimate of aquatic macrophyte cover), ***e*** is a row vector of two first PCA axis representing environmental covariates (PC1 represent gradients of transparency and dissolved oxygen and PC2 macrophyte cover, temperature and depth, Fig S1), *s* is a season factor variable, *h* is the habitat type factor, *m* is an indicator for the presence of management, and ε is the error term. Frequent zero catches, such as observed for our CPUE data, is a common issue in fishery modeling that have been addressed in a straightforward manner within the GLM framework by using a Poisson-Gamma distribution from the family Tweedie, the set of exponential distributions indexed by a power parameter (Jorgensen 1987; Peel et al. 2013). This distribution handles zero values uniformly with positive and continuous values and it was found to outperform other models used for CPUE data containing a point mass at zeros (e.g., delta models, generalized linear models with an additive constant) (Shono 2008; Carvalho et al. 2010; Li et al. 2011). For a random variable Y that is distributed Tweedie, $E(Y) = \mu$ and $Var(Y) = \varphi\mu^p$ where μ is the mean of the distribution, φ is the dispersion parameter, and *p* is an extra parameter (power parameter) that controls the variance of the distribution. The Tweedy family of distribution include the Normal (when p=0), Poisson (p=1) and Gamma (p=2) distributions. When, $p \in (1,2)$, such as in our study, the Tweedie distribution assumes the form of a compound Poisson-Gamma distribution, which allows modelling a variable that has both discrete and continuous components.

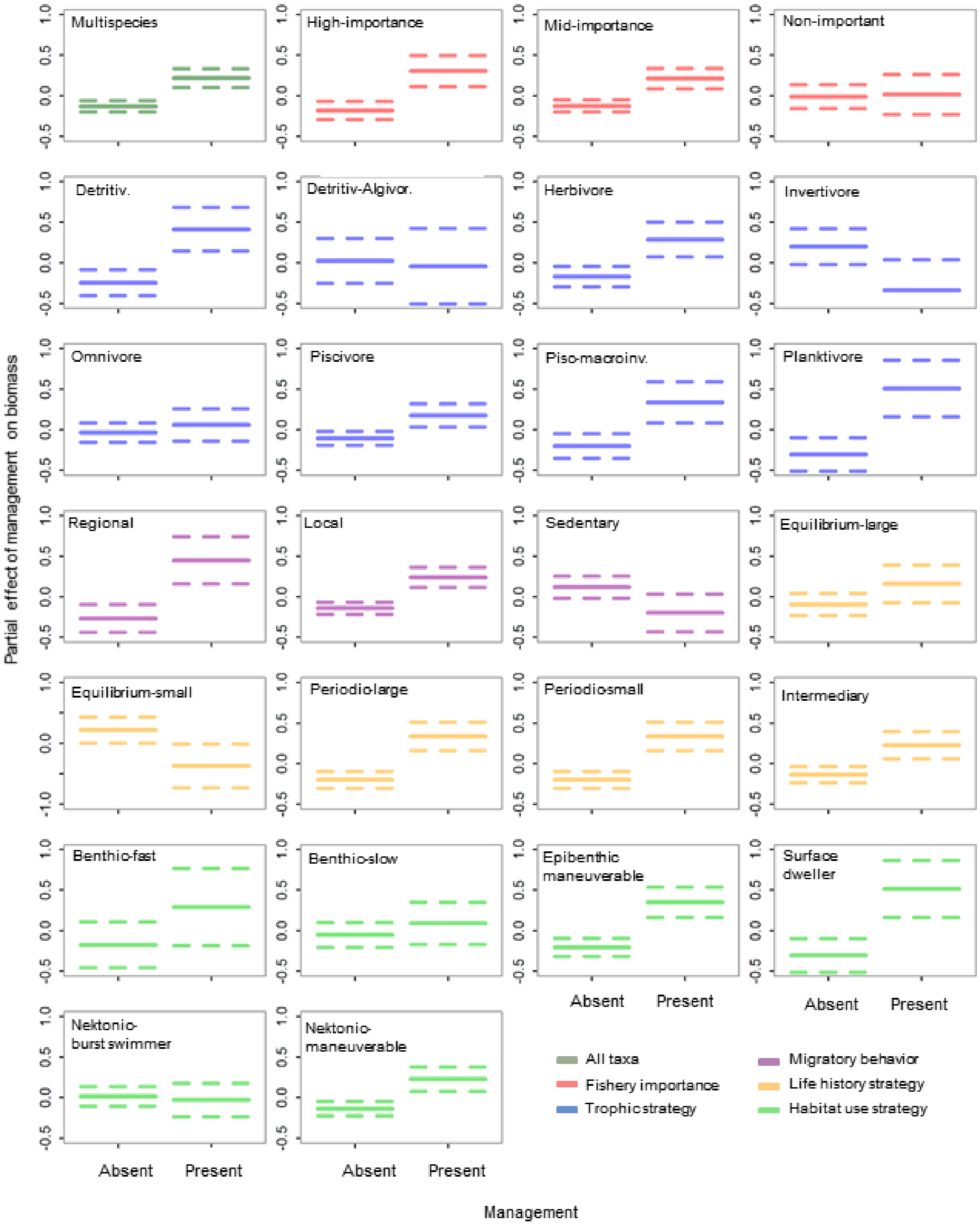
We assessed the quality of models fit via visual inspection of plots of model residuals. We used randomized quantile residuals as recommended by Dunn and Smyth (1996) and Dunn (2009) for model fits using the Tweedie family, and as used in several cases of fishery modeling studies (e.g., Tascheri et al. 2010; Peel et al. 2013). The randomized quantile residuals were examined for heteroscedasticity and approximate normality. Because the data have a non-Normal nature, Pearson and deviance residuals are intrinsically non-Normal, and difficult to interpret due to a large proportion of exact zeros (Peel et al. 2013). Instead, quantile residuals have an exact Normal distribution provided if correct response distribution is used and indications of non-Normality are interpretable as deficiencies in the model (Dunn 2009).

Spatial dependence is a common feature of ecological studies because data collected at sites that are located closer to each other tend to be more similar than data collected from sites that are farther apart (Legendre and Fortin 1989). Therefore, we also tested for spatial autocorrelation of the models' residuals using Moran's I statistics. Moran's I is a correlation coefficient that measures the overall spatial autocorrelation of the data (I=-1 indicates a perfect dispersion, I=0 indicates a perfect randomness, and I=1 a perfect clustering) (Sokal and Oden 1978). We tested whether Moran's statistics values differ from random by comparing the observed Moran's I from each model residuals with bootstrapped generated Moran's I. The Moran's I statistic was bootstrapped by randomly assigning longitude and latitude values to the residuals values and Kernel density estimates of the Moran's I statistics were used to calculate a 95% highest density region (i.e., confidence interval). Moran's I results indicated that data is not strongly dependent upon space across distances (see Figures S2); therefore, incorporating spatial autocorrelation was not a concern for our models.

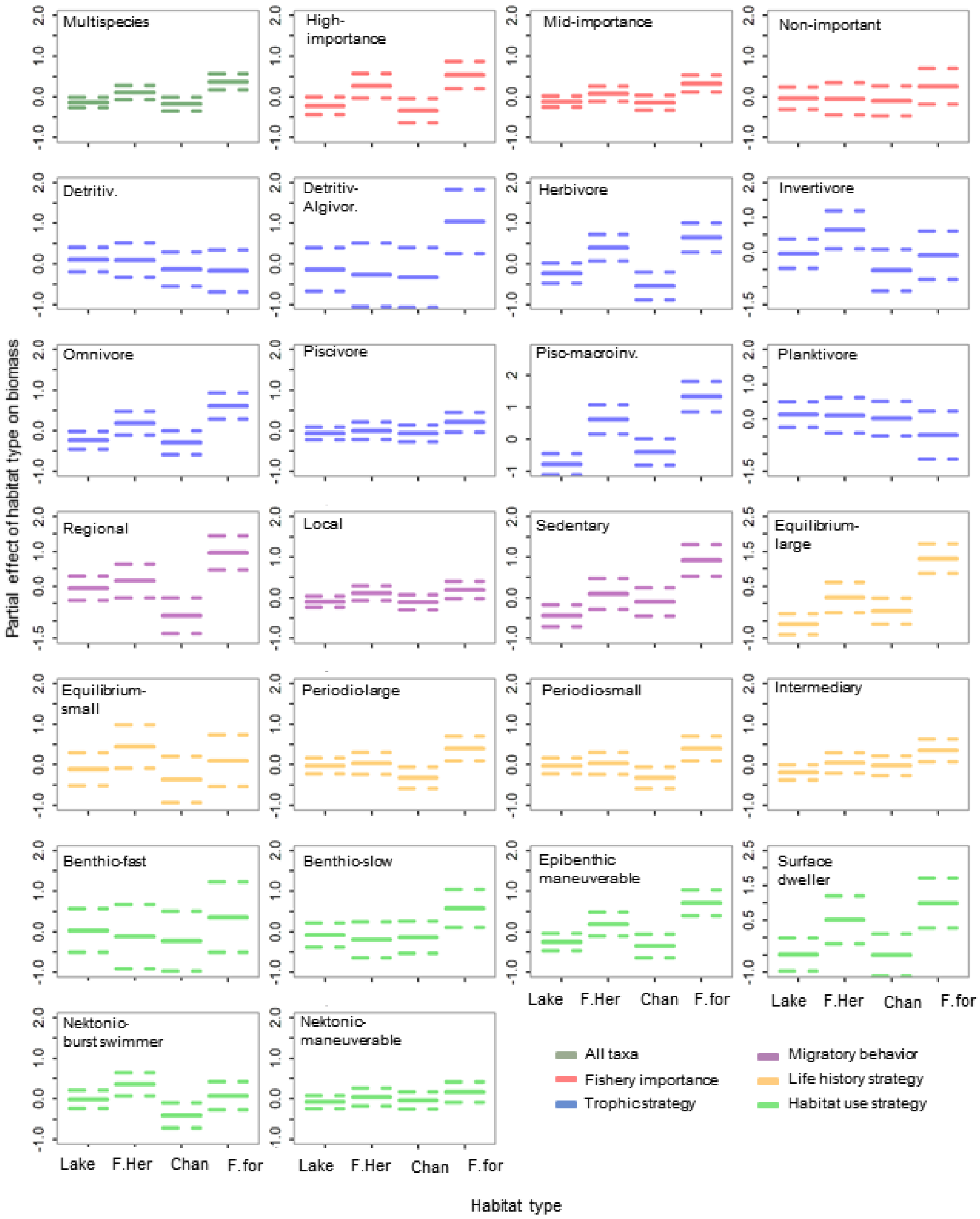
Analyses were performed in R v. 3.3.3. Models were fitted using the *statmod* (Giner and Smyth 2016) and *Tweedie* (Dunn and Smyth 2005) packages and Moran's I were calculated using the *ape* (Paradis et al. 2004), *geoR* (Ribeiro Jr et al. 2001) and *fields* (Nychka et al. 2005) packages.



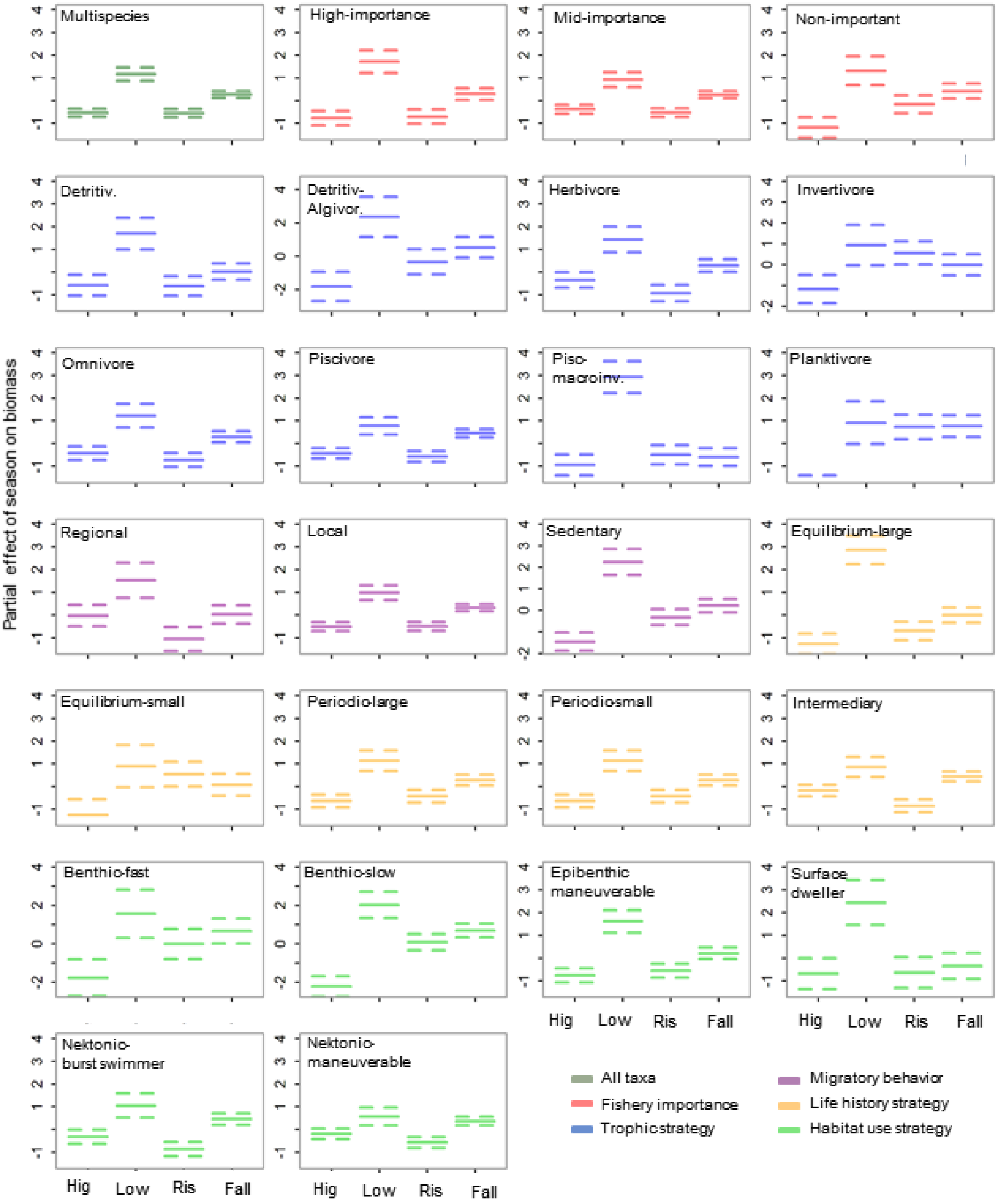
Appendix B.3. Principal components analysis with habitats ordination according to the local environmental variables: depth, dissolved oxygen, transparency, temperature and the local-scale estimate of aquatic macrophyte cover (macro.obs) (Table 1). PC1 is associated with a gradient of transparency (score -2.4) --dissolved oxygen (score 2.2) and PC2 with a gradient of macrophyte (score -1.6) and temperature (score -1.4) --depth (score 2.0). Data were standardized and PCA was performed using stats library and prcomp function in R software (R Core team 2017).



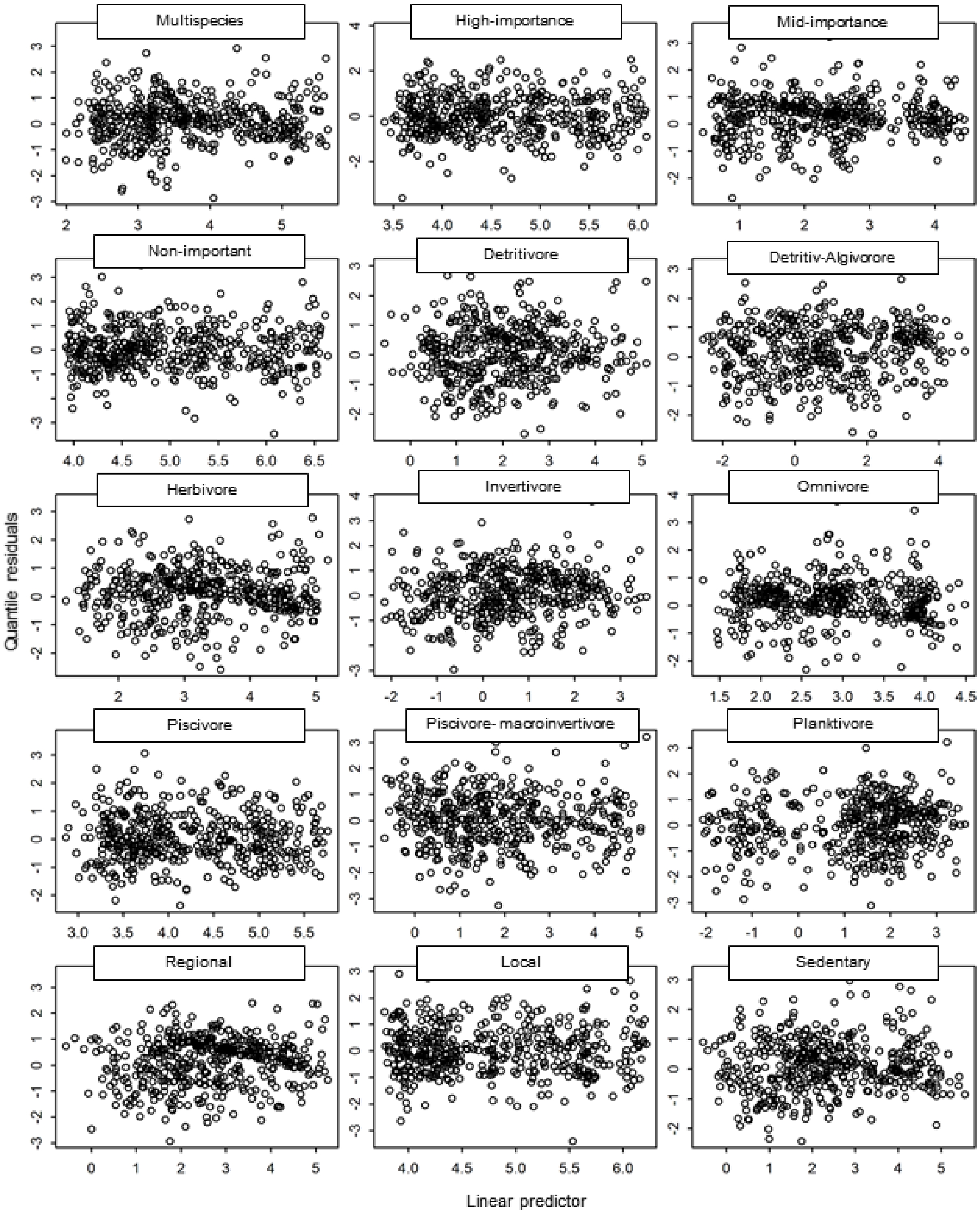
Appendix B.4. Partial effects of management on relative biomass (CPUE) for each fish group. The reference level is absence of management (coefficient = 0), meaning that the coefficient size for presence of management reflect its size being compared to that of absence of management while controlling for the effects of other variables.



Appendix B.5. Partial effects of habitat type on relative biomass (CPUE) for each fish group. Habitat type are: Lake, Flooded herbaceous (F.her), Channel (Chan), and Flooded forest (F.for) (See Table 4). The reference level is lake habitat type (coefficient = 0), meaning that the coefficient size for the other habitat types reflect their size being compared to that of lake while controlling for the effects of other variables.



Appendix B.6. Partial effects of season on relative biomass (CPUE) for each fish group. Seasons are: High water (Hig), Low water (Low), Rising water (Ris), and Falling water (Fall) (See Table 4). The reference level is high water (coefficient = 0), meaning that the coefficient size for the effect other seasons reflect their size being compared to that of high water season while controlling for the effects of other variables.


Multispecies
High-importance
Mid-importance
Non-important
Detritivore
Detritiv-Algivorore
Herbivore
Invertivore
Omnivore
Piscivore
Piscivore- macroinvertivore
Planktivore
Regional
Local
Sedentary
Quantile residuals
Linear predictor
2
3
4
5
3.5
4.0
4.5
5.0
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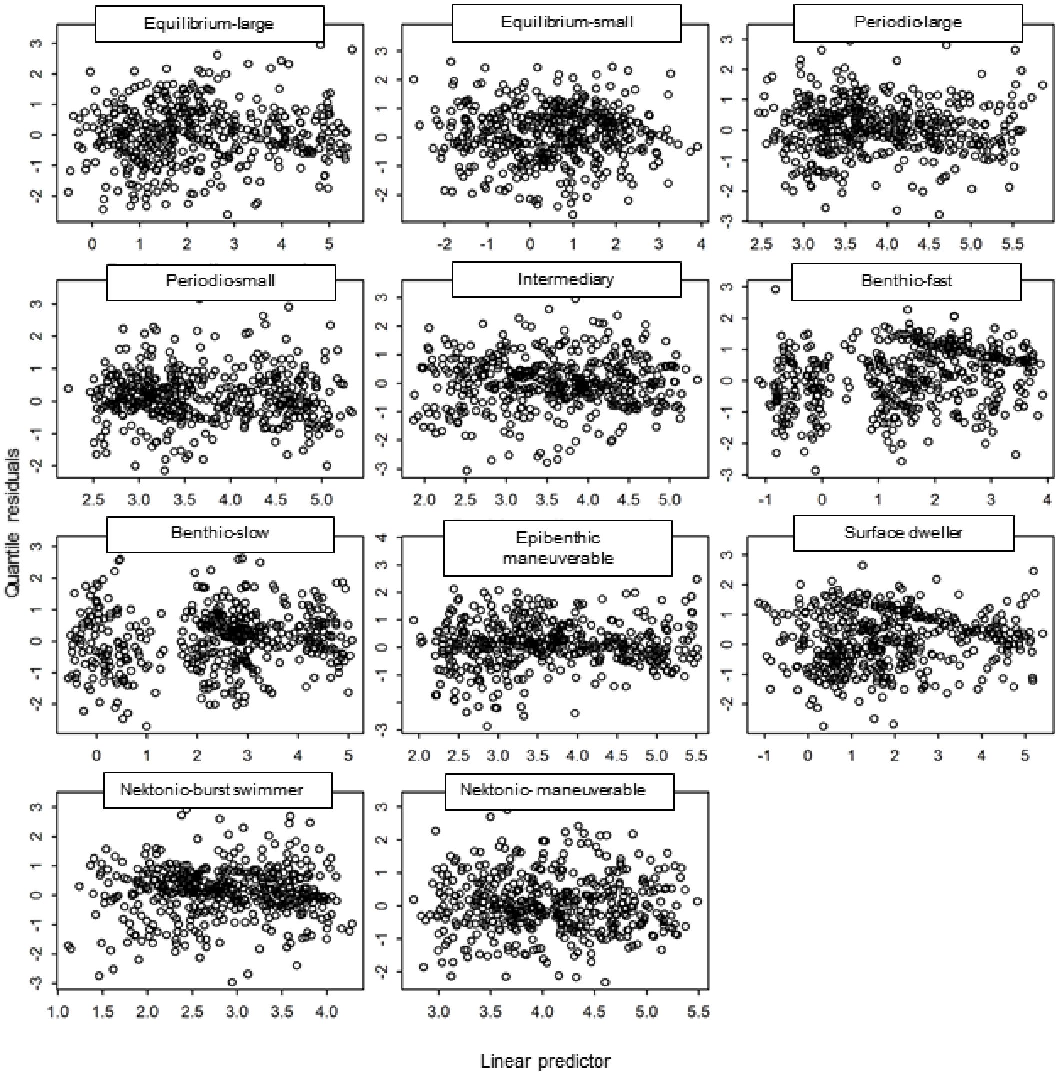
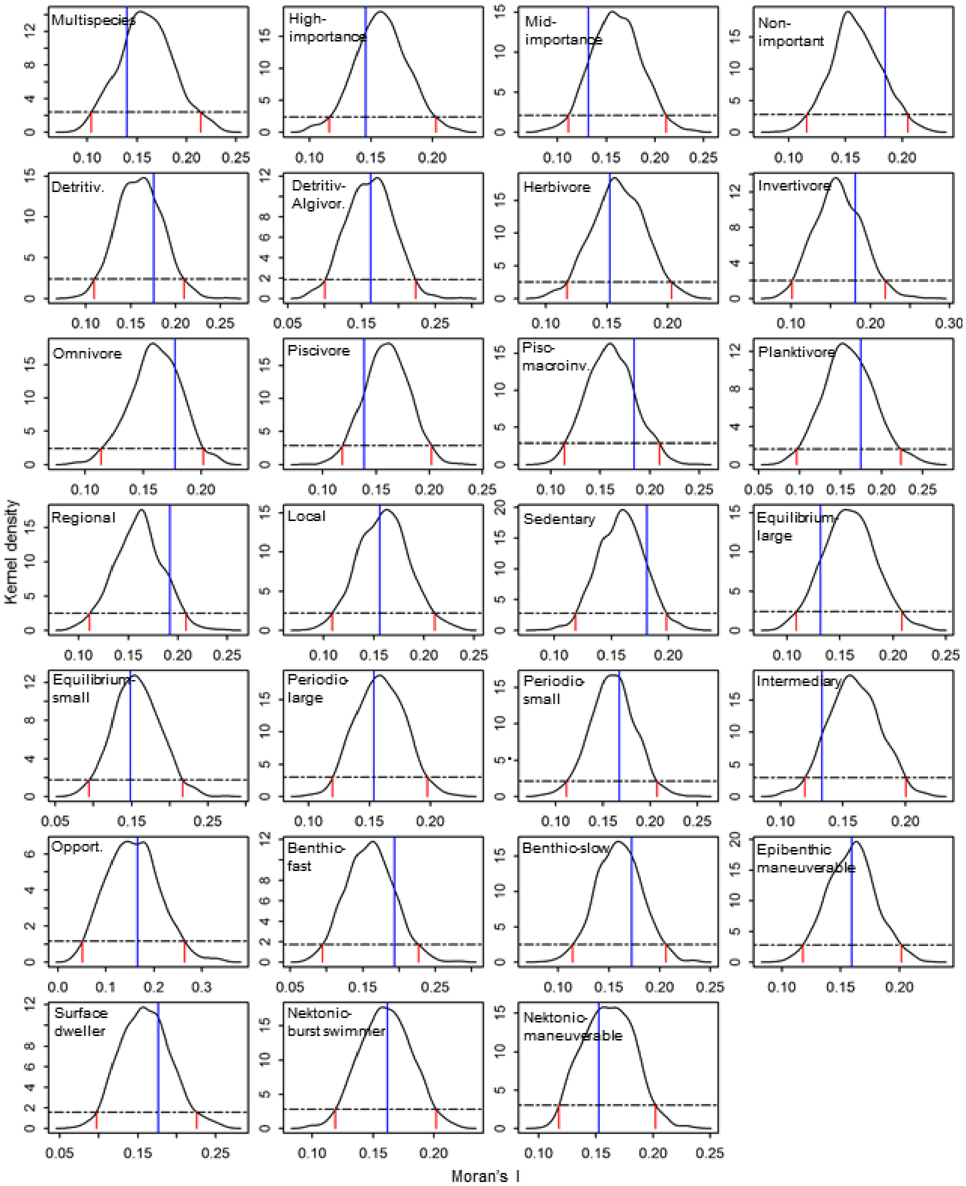


Appendix B.7. Randomized quantile residuals versus linear predictor for all models. Fish category is indicated on the top of the graphs (see Appendix B.10).



Appendix B.8. Observed values of Moran' I (blue line) and kernel density estimate (essentially a smoothed histogram) of bootstrapped Moran's I generated by randomly assigning the latitude and longitude values to residuals values. The red vertical lines show the limits of the 95% confidence interval for the bootstrapped Moran's I. Observed Moran's I values were generally within confidence intervals indicating a lack of spatial dependence.

Appendix B.10. Fish species (common and scientific names and families) and their degree of importance for regional fisheries, and trophic, migratory, life history and microhabitat use strategies. Trophic strategies classification was based on Barbarino and Winemiller (2003) Mérona and Mérona (2004), Santos et al. (2008), Shibuya and Zuanon (2013), Röpke et al. (2014), Correa and Winemiller (2014), Lopes et al. (2009) and Röpke et al. (2017). Migratory behavior classification was based on Goulding (1980), Junk et al. (1989), Ribeiro de Brito and Petrere (1990), Barthem et al. (1991), Fernandes (1997), Benedito-Cecilio and Araujo-Lima (2002), Carolsfeld (2003), Barthem and Fabré (2004), Castello (2008), Arantes et al. (2013) and Barthem et al. (2017). Life history classification was based on Röpke et al. (2017), and microhabitat use classification was based on Arantes et al. 2017. Piscivore/Macroinvertivore = Pisc./MacInv; Equilibrium with maturation at large size = Equilibrium-large; Equilibrium with maturation at small size = Equilibrium-small; Periodic with maturation in large size = Periodic-large; Periodic with maturation at small size=Periodic-small; Epibenthic maneuverable =Epib. maneuv.; Nektonic maneuverable=Nekt maneuv; Nektonic burst swimmers=Nekt swim.

Common name	Family Species	Fishery importance	Trophic	Migratory	Life history	Habitat use
	Anostomidae					
Aracu	*Laemolyta cf. proxima*	High	Herbivore	Local	Periodic-small	Nekt swim
	Laemolyta taeniata	High	Herbivore	Local	Periodic-small	Nekt swim
	Leporinus bimaculatus	High	Omnivore	Local	Periodic-small	Epib maneuv
	Leporinus fasciatus	High	Omnivore	Local	Periodic-large	Epib maneuv
	Leporinus friderici	High	Omnivore	Local	Periodic-large	Epib maneuv
	Leporinus trifasciatus	High	Omnivore	Local	Periodic-large	Epib maneuv
	Leporinus wolfei	High	Omnivore	Local	Periodic-large	Epib maneuv
	Pseudanos gracilis	High	Omnivore	Local	Periodic-small	Epib maneuv
	Rhytiodus argenteofuscus	High	Herbivore	Local	Periodic-small	Nekt swim
	Rhytiodus microlepis	High	Herbivore	Local	Periodic-small	Nekt swim
	Schizodon fasciatus	High	Herbivore	Local	Periodic-small	Epib maneuv
	Schizodon vittatus	High	Herbivore	Local	Periodic-small	Epib maneuv

Common name	Family Species	Fishery importance	Trophic	Migratory	Life history	Habitat use
	Loricariidae					
Acari/bodo	*Pterygoplichthys gibbiceps*	High	Detritivore	Sedentary	Equilibrium-large	Benthic-slow
	Pterygoplichthys pardalis	High	Detritivore	Sedentary	Equilibrium-large	Benthic-slow
	Pimelodidae					
Piracatinga	*Calophysus macropterus*	High	Piscivore	Local	Periodic-large	Benthic-fast
Mapara	*Hypophthalmus edentatus*	High	Planktivore	Local	Periodic-large	Epib maneuv
	Hypophthalmus fimbriatus	High	Planktivore	Local	Periodic-large	Epib maneuv
	Hypophthalmus marginatus	High	Planktivore	Local	Periodic-large	Epib maneuv
Fura calça	*Pimelodina flavipinnis*	High	Piscivore	Local	Periodic-large	Benthic-fast
Surubim	*Pseudoplatystoma fasciatum*	High	Piscivore	Local	Periodic-large	Benthic-fast
Caparari/ Surubim	*Pseudoplatystoma fm*	High	Piscivore	Local	Periodic-large	Benthic-fast
	Prochilodontidae					
Curimata	*Prochilodus nigricans*	High	Detritivore	Regional	Periodic-large	Epib maneuv
Jaraqui	*Semaprochilodus insignis*	High	Detritivore	Regional	Periodic-large	Epib maneuv
	Semaprochilodus taeniurus	High	Detritivore	Regional	Periodic-large	Epib maneuv

Common name	Family Species	Fishery importance	Trophic	Migratory	Life history	Habitat use
	Sciaenidae					
Pescada	*Plagioscion auratus*	High	Piscivore	Local	Periodic-large	Epib maneuv
	Plagioscion cf. surinamensis	High	Piscivore	Local	Periodic-large	Epib maneuv
	Plagioscion squamosissimus	High	Piscivore	Local	Periodic-large	Epib maneuv
	Pachypops trifilis	High	Pisc./MacInv	Local	Periodic-large	Epib maneuv
	Serrasalmidae					
Tambaqui	*Colossoma macropomum*	High	Herbivore	Regional	Periodic-large	Epib maneuv
	Arapamidae					
Pirarucu	*Arapaima sp.*	Mid	Piscivore	Local	Equilibrium-large	Benthic-fast
	Auchenipteridae					
Mandubé	*Ageneiosus inermis*	Mid	Piscivore	Local	Periodic-large	Benthic-slow
	Auchenipterus ambyiacus	Mid	Invertivore	Sedentary	Intermediate	Epib maneuv
	Auchenipterus nuchalis	Mid	Invertivore	Sedentary	Intermediate	Epib maneuv
	Callichthyidae					
Tamoata	*Hoplosternum littorale*	Mid	Invertivore	Sedentary	Intermediate	Benthic-slow
	Characidae					
Matrinchã	*Brycon cephalus*	Mid	Omnivore	Regional	Periodic-large	Epib maneuv
	Brycon falcatus	Mid	Omnivore	Regional	Periodic-large	Epib maneuv
	Brycon melanopterus	Mid	Omnivore	Regional	Periodic-large	Epib maneuv
Sardinha	*Triportheus albus*	Mid	Omnivore	Local	Periodic-small	Nekt maneuv
	Triportheus angulatus	Mid	Omnivore	Local	Periodic-small	Nekt maneuv
	Triportheus auritus	Mid	Omnivore	Local	Periodic-small	Nekt swim

Common name	Family Species	Fishery importance	Trophic	Migratory	Life history	Habitat use
	Cichlidae					
Acará	*Astronotus crassipinnis*	Mid	Pisc./MacInv	Sedentary	Equilibrium-large	Epib maneuv
	Astronotus ocellatus	Mid	Pisc./MacInv	Sedentary	Equilibrium-large	Epib maneuv
	Chaetobranchopsis orbicularis	Mid	Planktivore	Sedentary	Equilibrium-small	Epib maneuv
	Chaetobranchus flavescens	Mid	Planktivore	Sedentary	Equilibrium-small	Epib maneuv
	Geophagus proximus	Mid	Invertivore	Sedentary	Equilibrium-small	Epib maneuv
	Heros efasciatus	Mid	Omnivore	Sedentary	Equilibrium-small	Epib maneuv
	Mesonauta festivus	Mid	Omnivore	Sedentary	Equilibrium-small	Epib maneuv
	Mesonauta insignis	Mid	Omnivore	Sedentary	Equilibrium-small	Epib maneuv
	Satanoperca jurupari	Mid	Invertivore	Sedentary	Equilibrium-small	Epib maneuv
Tucunare	*Cichla monoculus*	Mid	Piscivore	Sedentary	Equilibrium-large	Epib maneuv
Jacunda	*Crenicichla johanna*	Mid	Pisc./MacInv	Sedentary	Equilibrium-small	Epib maneuv
	Crenicichla reticulata	Mid	Pisc./MacInv	Sedentary	Equilibrium-large	Epib maneuv
	Curimatidae					

Common name	Family Species	Fishery importance	Trophic	Migratory	Life history	Habitat use
Branquinha	*Curimata incompta*	Mid	Detritivore	Local	Periodic-small	Epib maneuv
	Curimata inornata	Mid	Detritivore	Local	Periodic-small	Epib maneuv
	Curimata vittata	Mid	Detritivore	Local	Periodic-small	Epib maneuv
	Curimatella alburna	Mid	Detritivore	Local	Periodic-small	Epib maneuv
	Curimatella meyeri	Mid	Detritivore	Local	Periodic-small	Epib maneuv
	Potamorhina altamazonica	Mid	Detritivore	Local	Periodic-small	Nekt maneuv
	Potamorhina latior	Mid	Detritivore	Local	Periodic-small	Nekt maneuv
	Potamorhina pristigaster	Mid	Detritivore	Local	Periodic-small	Nekt maneuv
	Psectrogaster amazonica	Mid	Detritivore	Local	Periodic-small	Nekt maneuv
	Psectrogaster essequibensis	Mid	Detritivore	Local	Periodic-small	Nekt maneuv
	Psectrogaster hy	Mid	Detritivore	Local	Periodic-small	Nekt maneuv
	Psectrogaster rutiloides	Mid	Detritivore	Local	Periodic-small	Nekt maneuv
	Cynodontidae					
Peixe-cachorro	*Cynodon gibbus*	Mid	Piscivore	Local	Periodic-large	Nekt maneuv
	Hydrolycus scomberoides	Mid	Piscivore	Local	Periodic-large	Nekt maneuv
	Rhaphiodon vulpinus	Mid	Piscivore	Local	Periodic-large	Nekt maneuv
	Doradidae					
Bacu-pedra	*Lithodoras dorsalis*	Mid	Herbivore	Long-dist	Periodic-large	Benthic-fast
Rebeca	*Megalodoras uranoscopus*	Mid	Herbivore	Long-dist	Periodic-large	Benthic-fast

Common name	Family Species	Fishery importance	Trophic	Migratory	Life history	Habitat use
Cujuba	*Oxydoras niger*	Mid	Omnivore	Local	Periodic-large	Benthic-fast
Bacu	*Pterodoras granulosus*	Mid	Herbivore	Local	Periodic-large	Benthic-fast
	Erythrinidae					
Jeju	*Hoplerythrinus unitaeniatus*	Mid	Piscivore	Sedentary	Intermediate	Benthic-slow
Traira	*Hoplias malabaricus*	Mid	Piscivore	Sedentary	Intermediate	Benthic-slow
	Hemiodontidae					
Charuto/ Cubiu/Erana	*Anodus elongatus*	Mid	Planktivore	Local	Periodic-small	Nekt swim
Charuto	*Hemiodus argenteus*	Mid	Omnivore	Local	Periodic-small	Nekt swim
	Hemiodus goeldii	Mid	Omnivore	Local	Periodic-small	Nekt swim
	Hemiodus immaculatus	Mid	Omnivore	Local	Periodic-small	Nekt swim
	Hemiodus microlepis	Mid	Omnivore	Local	Periodic-small	Nekt swim
	Hemiodus unimaculatus	Mid	Omnivore	Local	Periodic-small	Nekt swim
	Heptapteridae					
Mandi	*Pimelodella cristata*	Mid	Omnivore	Local	Periodic-small	Benthic-fast
	Pimelodella geryi	Mid	Omnivore	Local	Periodic-small	Benthic-fast
	Osteoglossidae					
Aruana	*Osteoglossum bicirrhosum*	Mid	Pisc./MacInv	Local	Equilibrium-large	Surf dweller
	Pimelodidae					
Filhote	*Brachyplatystoma filamentosum*	Mid	Piscivore	Long-dist	Periodic-large	Benthic-fast
Pirarara	*Phractocephalus hemioliopteracus*	Mid	Piscivore	Local	Periodic-large	Benthic-fast
Mandi	*Pimelodus blochii*	Mid	Omnivore	Local	Periodic-small	Benthic-fast

Common name	Family Species	Fishery importance	Trophic	Migratory	Life history	Habitat use
Piranambu	*Pinirampus pirinampu*	Mid	Piscivore	Local	Periodic-large	Benthic-fast
Cara de gato	*Platynematichthys notatus*	Mid	Piscivore	Local	Periodic-large	Benthic-fast
	Potamotrygonidae					
Arraia	*Potamotrygon motoro*	Mid	Pisc./MacInv	Local	Equilibrium-large	Benthic-fast
	Potamotrygon sp.	Mid	Pisc./MacInv	Local	Equilibrium-large	Benthic-fast
	Pristigasteridae					
Apapa	*Ilisha amazonica*	Mid	Planktivore	Local	Periodic-small	Nekt maneuv
	Pellona castelnaeana	Mid	Piscivore	Local	Periodic-large	Nekt maneuv
	Pellona flavipinnis	Mid	Piscivore	Local	Periodic-large	Nekt maneuv
	Serrasalmidae					
Pacu	*Metynnis argenteus*	Mid	Herbivore	Local	Intermediate	Nekt maneuv
	Metynnis hypsauchen	Mid	Herbivore	Local	Intermediate	Nekt maneuv
	Metynnis luna	Mid	Herbivore	Local	Intermediate	Nekt maneuv
	Myleus rubripinnis	Mid	Herbivore	Local	Intermediate	Nekt maneuv
	Myloplus torquatus	Mid	Herbivore	Local	Intermediate	Nekt maneuv
	Mylossoma aureum	Mid	Herbivore	Local	Periodic-small	Nekt maneuv
	Mylossoma duriventre	Mid	Herbivore	Local	Periodic-small	Nekt maneuv

Common name	Family Species	Fishery importance	Trophic	Migratory	Life history	Habitat use
	Serrasalmidae					
Pirapitinga	*Piaractus brachypomus*	Mid	Herbivore	Regional	Periodic-large	Surf dweller
Piranha	*Catoprion mento*	Mid	Piscivore	Local	Intermediate	Epib maneuv
	Pristobrycon sp.	Mid	Omnivore	Local	Intermediate	Nekt maneuv
	Pristobrycon striolatus	Mid	Omnivore	Local	Intermediate	Nekt maneuv
	Pygocentrus nattereri	Mid	Piscivore	Local	Intermediate	Nekt maneuv
	Serrasalmus eigenmanni	Mid	Piscivore	Local	Intermediate	Nekt maneuv
	Serrasalmus elongatus	Mid	Piscivore	Local	Intermediate	Nekt maneuv
	Serrasalmus maculatus	Mid	Piscivore	Local	Intermediate	Nekt maneuv
	Serrasalmus rhombeus	Mid	Piscivore	Local	Intermediate	Nekt maneuv
	Serrasalmus serrulatus	Mid	Omnivore	Local	Intermediate	Nekt maneuv
	Serrasalmus spilopleura	Mid	Piscivore	Local	Intermediate	Nekt maneuv
	Acestrorhynchidae					
Dentudo/ Peixe-cachorro	*Acestrorhynchus abbreviatus*	None	Piscivore	Local	Periodic-small	Nekt swim
	Acestrorhynchus falcatus	None	Piscivore	Local	Periodic-small	Nekt swim
	Acestrorhynchus falcirostris	None	Piscivore	Local	Periodic-small	Nekt swim
	Acestrorhynchus heterolepis	None	Piscivore	Local	Periodic-small	Nekt swim
	Acestrorhynchus nasutus	None	Piscivore	Sedentary	Periodic-small	Nekt swim

Common name	Family Species	Fishery importance	Trophic	Migratory	Life history	Habitat use
	Apteronotidae					
Sarapó	*Parapteronotus hasemani*	None	Invertivore	Local	Periodic-small	Gymnotif
	Sternarchella schotti	None	Invertivore	Local	Periodic-small	Gymnotif
	Auchenipteridae					
Mandubé	*Ageneiosus ucayalensis*	None	Piscivore	Local	Intermediate	Benthic-slow
	Ageneiosus vittatus	None	Piscivore	Local	Intermediate	Benthic-slow
	Epapterus dispilurus	None	Invertivore	Sedentary	Intermediate	Benthic-slow
	Tympanopleura atronasus	None	Piscivore	Local	Intermediate	Benthic-slow
	Tympanopleura piperata	None	Piscivore	Local	Intermediate	Benthic-slow
Mandii de boto	*Centromochlus heckelii*	None	Omnivore	Sedentary	Intermediate	Benthic-slow
Cangati	*Parauchenipterus sp. porosus*	None	Omnivore	Sedentary	Intermediate	Benthic-slow
	Trachelyopterus galeatus	None	Omnivore	Sedentary	Intermediate	Benthic-slow
	Belonidae					
Agulhão prata	*Pseudotylosurus microps*	None	Pisc./MacInv	Local	Periodic-small	Nekt swim
	Characidae					
Sardinha dentuda	*Agoniates anchovia*	None	Piscivore	Local	Periodic-small	Nekt maneuv
Piabão	*Astyanax abramis*	None	Omnivore	Local	Periodic-small	Nekt maneuv

Common name	Family Species	Fishery importance	Trophic	Migratory	Life history	Habitat use
	Charax gibbosus	None	Piscivore	Local	Periodic-small	Epib maneuv
Peixe cão	*Charax michaeli*	None	Piscivore	Local	Periodic-small	Epib maneuv
	Charax tectifer	None	Piscivore	Local	Periodic-small	Epib maneuv
Piaba	*Moenkhausia cf.megalops*	None	Omnivore	Sedentary	Opportunistic	Nekt maneuv
Zé-do-ó	*Roeboides affinis*	None	Pisc./MacInv	Sedentary	Opportunistic	Epib maneuv
	Roeboides myersii	None	Pisc./MacInv	Local	Periodic-small	Epib maneuv
-	*Stichonodon insignis*	None	Invertivore	Sedentary	Opportunistic	Nekt maneuv
Matupiri	*Tetragonopterus argenteus*	None	Omnivore	Local	Periodic-small	Epib maneuv
-	*Stethaprion erythrops*	None	Invertivore	Local	Periodic-small	Nekt maneuv
	Chilodontidae					
Cabeça-dura	*Caenotropus labyrinthicus*	None	Omnivore	Local	Periodic-small	Nekt maneuv
	Cichlidae					
Papa terra	*Acarichthys heckelii*	None	Invertivore	Sedentary	Equilibrium-small	Epib maneuv
Acará lanterna	*Acaronia nassa*	None	Pisc./MacInv	Sedentary	Equilibrium-small	Epib maneuv
Rabo de fogo	*Chalceus macrolepidotus*	None	Invertivore	Local	Periodic-small	Nekt maneuv
Acará cascudo	*Cichlasoma amazonarum*	None	Omnivore	Sedentary	Equilibrium-small	Epib maneuv
Acará bandeira	*Pterophyllum scalare*	None	Invertivore	Sedentary	Equilibrium-small	Epib maneuv
	Ctenoluciidae					
Bicuda	*Boulengerella maculata*	None	Piscivore	Local	Periodic-large	Nekt swim

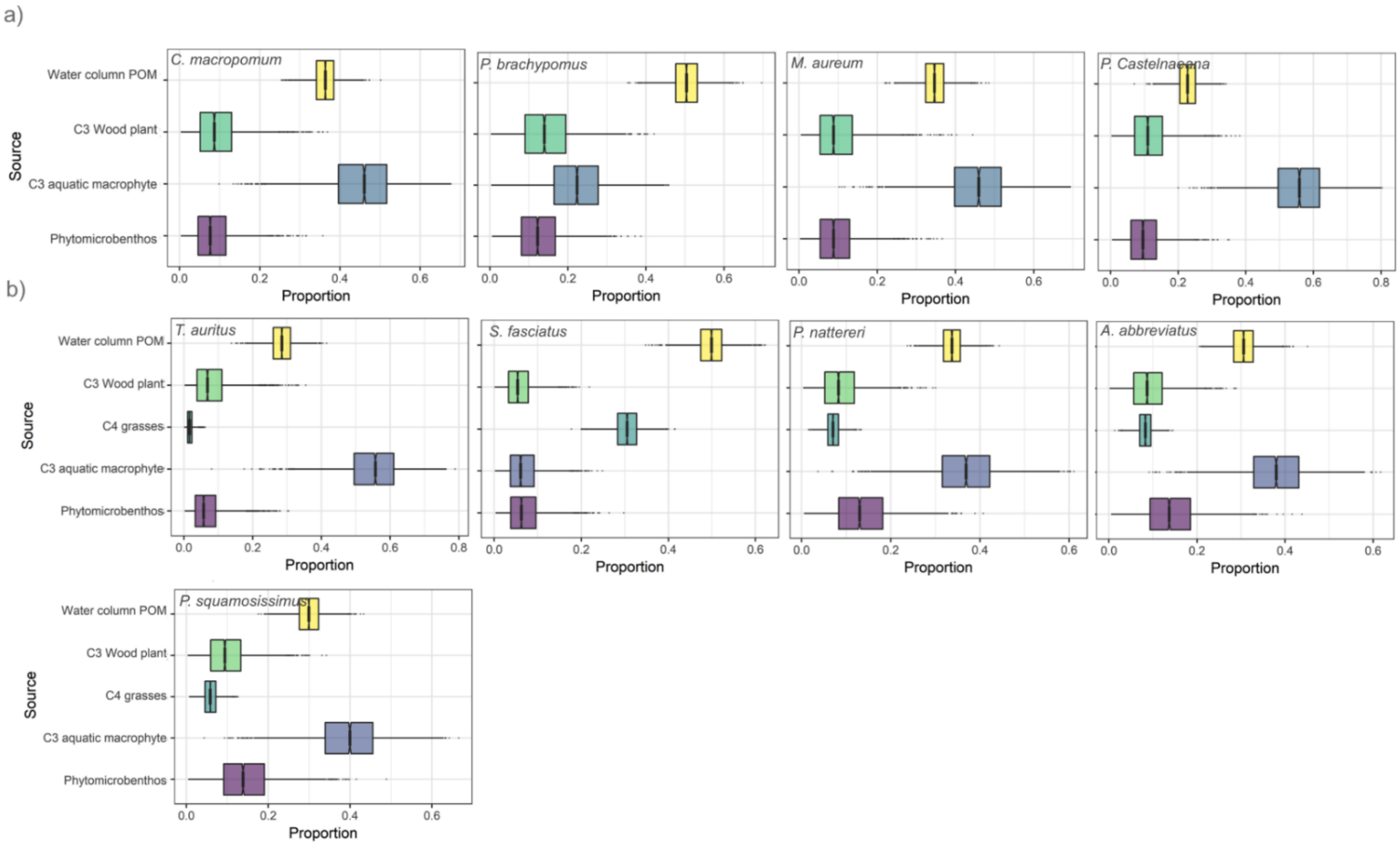
Common name	Family Species	Fishery importance	Trophic	Migratory	Life history	Habitat use
	Curimatidae					
Peito de aço	*Cyphocharax abramoides*	None	Detritivore	Local	Periodic-small	Epib maneuv
Curimatai	*Cyphocharax spiluropsis*	None	Detritivore	Local	Periodic-small	Epib maneuv
	Steindachnerina bimaculata	None	Detritivore	Local	Periodic-small	Epib maneuv
	Doradidae					
Reque-reque	*Agamyxis pectinifrons*	None	Omnivore	Sedentary	Periodic-small	Benthic-slow
	Amblydoras affinis	None	Omnivore	Sedentary	Periodic-small	Benthic-slow
	Amblydoras spinossissimus	None	Omnivore	Sedentary	Periodic-small	Benthic-slow
	Anadoras grypus	None	Omnivore	Sedentary	Periodic-small	Benthic-slow
	Nemadoras sp.	None	Omnivore	Local	Periodic-small	Benthic-fast
	Opsodoras stuebelii	None	Invertivore	Local	Periodic-small	Benthic-slow
	Ossancora punctata	None	Invertivore	Sedentary	Intermediate	Benthic-slow
	Tenellus leporhinus	None	Omnivore	Local	Periodic-small	Benthic-fast
	Tenellus ternetzi	None	Invertivore	Local	Periodic-small	Benthic-slow
	Trachydoras nattereri	None	Invertivore	Sedentary	Intermediate	Benthic-slow
	Trachydoras steindachneri	None	Invertivore	Sedentary	Intermediate	Benthic-slow
Bacui	*Platydoras costatus*	None	Omnivore	Sedentary	Periodic-small	Benthic-slow
	Engraulidae					
Sardinha	*Jurengraulis juruensis*	None	Planktivore	Local	Periodic-small	Nekt maneuv
	Anchoviella guianensis	None	Planktivore	Sedentary	Opportunistic	Nekt maneuv
	Lycengraulis batesii	None	Pisc./MacInv	Local	Periodic-small	Nekt maneuv

Common name	Family Species	Fishery importance	Trophic	Migratory	Life history	Habitat use
	Gasteropelecidae					
Sardinha papuda	*Thoracocharax securis*	None	Omnivore	Local	Periodic-small	Epib maneuv
	Gymnotidae					
Poraque	*Electrophorus electricus*	None	Piscivore	Sedentary	Equilibrium-large	Benthic-slow
Sarapó	*Gymnotus arapaima*	None	Pisc./MacInv	Sedentary	Equilibrium-small	Gymnotif
	Hemiodontidae					
Reque-reque	*Hemidoras morrisi*	None	Omnivore	Local	Periodic-small	Benthic-fast
	Loricariidae					
Cascudo/ acarizinho/ bodozinho	*Hypostomus plecostomus*	Mid	Detritivore	Sedentary	Equilibrium-large	Benthic-slow
	Hypostomus carinatus	None	Detritivore	Sedentary	Equilibrium-large	Benthic-slow
	Hypostomus oculeus	None	Detritivore	Sedentary	Equilibrium-large	Benthic-slow
	Dekeyseria amazonica	None	Detritivore	Sedentary	Equilibrium-small	Benthic-slow
	Hypoptopoma gulare	None	Detritivore	Sedentary	Intermediate	Benthic-slow
	Limatulichthys griseus	None	Omnivore	Sedentary	Equilibrium-large	Benthic-slow
Acari chato	*Loricaria cf. nickeriensis*	None	Detritivore	Sedentary	Equilibrium-small	Benthic-slow
	Loricaria sp.	None	Detritivore	Sedentary	Equilibrium-small	Benthic-slow

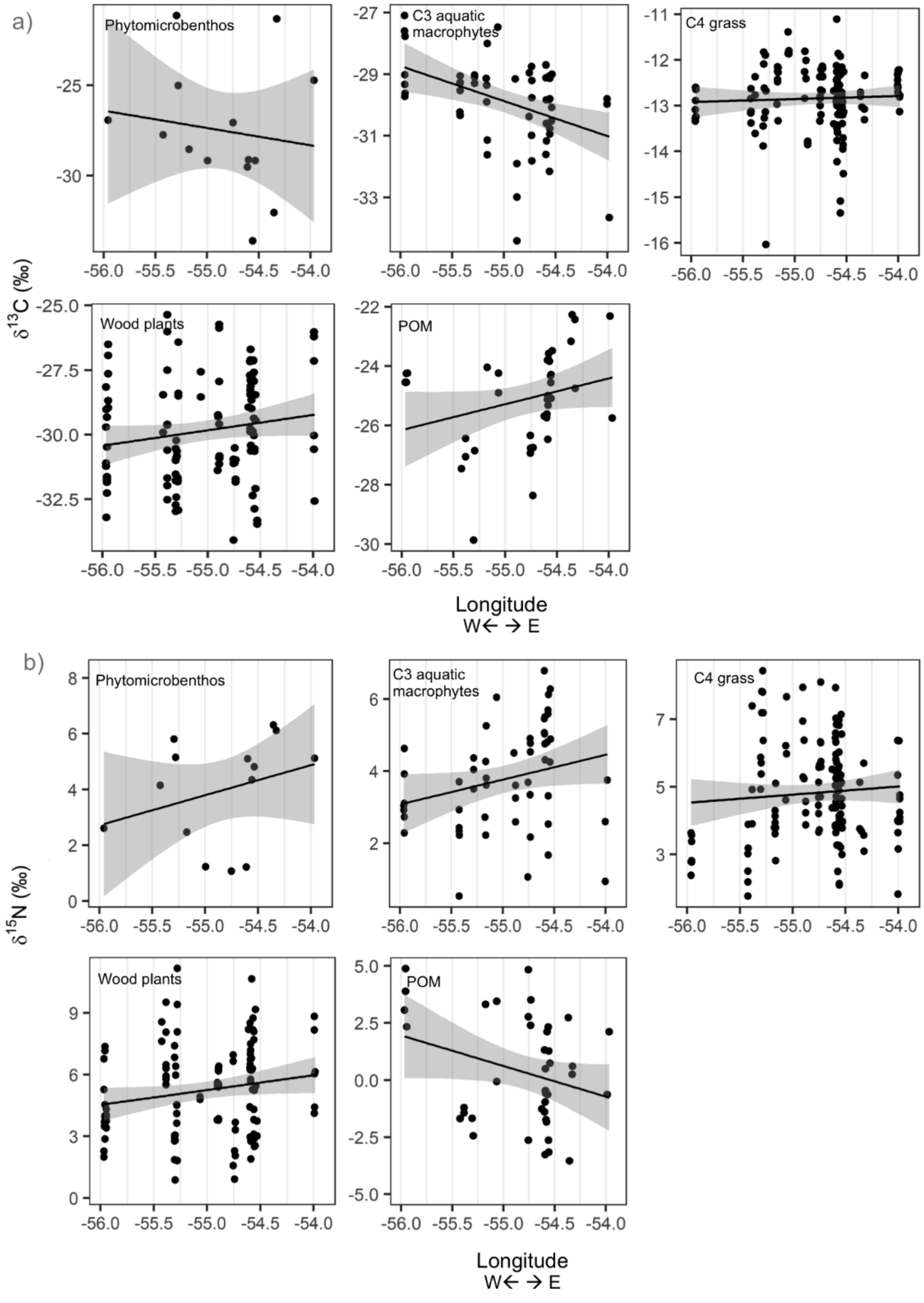
	Family Species	Fishery importance	Trophic	Migratory	Life history	Habitat use
	Loricariichthys sp.	None	Omnivore	Sedentary	Equilibrium-large	Benthic-slow
Limpa Vidro	*Otocinclus sp.*	None	Detritivore	Sedentary	Opportunistic	Benthic-slow
Braço-de-moça	*Hemisorubim platyrhynchos*	None	Piscivore	Local	Periodic-large	Benthic-fast
Bico de pato	*Sorubim lima*	None	Piscivore	Local	Periodic-large	Benthic-fast
	Pristigasteridae					
Sardinha papuda	*Pristigaster cayana*	None	Planktivore	Local	Periodic-small	Epib maneuv
	Rhamphichthyidae					
Sarapó	*Gymnorhamphichthys sp.*	None	Invertivore	Sedentary	Periodic-small	Gymnotif
	Rhamphichthys marmoratus	None	Invertivore	Local	Periodic-large	Gymnotif
	Rhamphichthys rostratus	None	Invertivore	Local	Periodic-large	Gymnotif
	Sternopygidae					
	Eigenmannia limbata	None	invertivore	Local	Periodic-small	Gymnotif
	Sternopygus macrurus	None	Invertivore	Local	Periodic-large	Gymnotif
	Tetraodontidae					
Baiacu	*Colomesus asellus*	None	Omnivore	Sedentary	Periodic-small	Benthic-slow

APENDIX C

CHAPTER IV APPENDICES



Appendix C.1. Mixing model results showing proportional contributions of major production sources to the biomass of nine fish species in the Lower Amazon. Species names are indicated at the top left in each plot; plots in (a) exclude grasses based on implausibility assessed via C vs. N stable isotope ratio scatterplots, and plots in (b) include grasses.



Appendix C.1. Exploratory relationships between a) δ13C and b) δ15N of production sources and longitude in the floodplain of the lower Amazon River. W=West (upper-river direction), E=East (down-river direction). Regression lines were included to illustrate trends in isotopic composition along the river longitudinal gradient.