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Fishery yields vary with land cover on the Amazon River floodplain

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Abstract

Inland fisheries underpin food security in many tropical countries. The most productive inland fisheries in tropical and subtropical developing countries occur in large river–floodplain systems that are often impacted by land cover changes. However, few studies to date have assessed the effects of changes in floodplain land cover on fishery yields. Here, we integrated fisheries and satellite-mapped habitat data to evaluate the effects of floodplain deforestation on fishery yields in 68 floodplain lake systems of the lower Amazon River, representing a wide range in relative amounts of woody, herbaceous and non-vegetated land cover. We modelled relative fish yields (fish capture per unit effort [CPUE]) in the floodplain lakes as a function of the relative amounts of forest, shrub, aquatic macrophyte and bare/herbaceous habitats surrounding them. We found that forest amount was positively related ($p = .0003$) to multispecies CPUE. The validity of these findings was supported by rejection of plausible alternative causative mechanisms involving habitat-related differences in amount of piscivores, fishing effort, lake area, and habitat effects on CPUE of the nine taxa dominating multispecies yields. Our results provide support to the idea that removal of floodplain forests reduces fishery yields per unit effort. Increased protection of floodplain forests is necessary to maintain the food, income and livelihood security services provided by large river–floodplain fisheries.

KEYWORDS

Amazon fish habitats, deforestation, inland fisheries, large tropical rivers, multispecies

1 | INTRODUCTION

Inland fisheries underpin food security in many tropical and subtropical countries (FAO 2014; Lynch et al., 2016), often sustaining the livelihoods of the poorest human populations (Béné, Steel, Luadia, & Gordon, 2009; Isaac et al., 2015; Neiland & Béné, 2006; Welcomme et al., 2010). The most productive inland fisheries occur in river floodplains (Bayley, 1995), which provide fish with critical vegetated habitats on the floodplains (Castello, Isaac, & Thapa, 2015; Fernandez, 1997). However, floodplain habitats worldwide are threatened by land cover changes (Tockner & Stanford, 2002), and the effects on fisheries of floodplain land cover change have not been assessed. How do changes in floodplain land cover affect fishery yields?

The importance of floodplains for fish is well established (Welcomme, 1985). Seasonally rising waters prompt fish to spawn and migrate laterally out of lakes and river channels into mosaics of flooded

shrub, forest and macrophyte habitats (Bayley, 1988; Fernandez, 1997). In these floodplain habitats, fish of all ages find protection from predators in the structural complexity provided by vegetation as well as abundant food resources that increase their rates of survival and body growth (Castello, 2008a; Gomes & Agostinho, 1997). C_3 plants (tree seeds, fruits and leaves and non-gramineous aquatic macrophytes) and algae (periphyton and phytoplankton) are the main sources of carbon supporting fish biomass (e.g. Carvalho et al., 2017; Davis, Blanchette, Pusey, Jardine, & Pearson, 2012; Hladyz, Nielsen, Suter, & Krull, 2012; Lewis, Hamilton, Rodriguez, Saunders, & Lasi, 2001; Mortillaro et al., 2015; Roach, 2013). For some species, such as the economically important tambaqui (*Colossoma macropomum*, Characidae), fruits and seeds constitute the major food source during high waters (Oliveira, Martinelli, Moreira, Soares, & Cyrino, 2006). C_4 grasses are generally unimportant food sources for fish despite their often-high productivity (Forsberg, Araujo-Lima, Martinelli, Victoria, & Bonassi, 1993; Jepsen & Winemiller, 2007). C_3 plants and algae have been found to support trophic pathways to river fishes of the Mekong basin in Asia (Ou & Winemiller, 2016), the Paraná and Amazon basins in South America (Forsberg et al., 1993; Hoeinghaus, Winemiller, & Agostinho, 2007; Oliveira, Soares, Martinelli, & Moreira, 2006) and the Brazos River in North America (Zeug & Winemiller, 2008). Accordingly, inundatable floodplain area is generally positively related to fish biomass and associated fishery yields (Castello, Isaac et al., 2015; Welcomme, 1985).

The vegetated habitats of tropical floodplains are often cleared as fishing communities engage in a range of economic activities including agriculture and animal husbandry (McGrath, Cardoso, Almeida, & Pezzuti, 2008). Land cover changes have already extensively modified most riparian corridors in Europe and densely populated regions of Asia (Tockner & Stanford, 2002; Tockner et al., 2008) and are increasingly affecting floodplains of the lower Mekong and Amazon basins through agricultural production and cattle ranching (Campbell, Poole, Giesen, & Valbo-Jorgensen, 2006; Renó, Novo, Suemitsu, Rennó, & Silva, 2011). Depending on land use and floodplain elevation, floodplain forests and shrubs may be cleared, and may regrow as forest or shrub, or persist as aquatic macrophyte or bare/herbaceous habitats (Renó et al., 2011). A literature review of the effects of changes in habitat cover on freshwater fish found varied and inconsistent evidence, although a meta-analysis of the data used in the same studies found a direct link between habitat and fish abundance or biomass (Smokorowski & Pratt, 2007). Studies based on fish diet and trophic modelling of the Amazonian river food web have predicted that loss of floodplain forests decreases fishery yields (Angelini, Fabre, & Silva, 2006; Goulding, 1980). The abundance and biomass of various fishes of Amazon floodplain lakes were found to be positively related to forest amount (Arantes et al., 2017; Lobón-Cerviá, Hess, Melack, & Araujo-Lima, 2015).

Although there seems to be a direct link between fish and floodplain forests, floodplain land cover changes could have negligible effects on fish. Many fishes regulate their population dynamics via limiting factors such as fishing and larval supply or by exhibiting compensatory responses (e.g. changes in growth; Caley

et al., 1996; Halls, Debnath, Kirkwood, & Payne, 2000; Arantes, Castello, Stewart, Cetra, & Queiroz, 2010; Petersen, Brum, Rossoni, Silveira, & Castello, 2016; Fabré, Castello, Isaac, & Batista, 2017). The diets of many freshwater fishes naturally vary with age, season and location within the system (Carvalho et al., 2017; Welcomme, Winemiller, & Cowx, 2006; Winemiller et al., 2014), potentially allowing fish to adapt their feeding behaviours to the habitats that replace natural vegetation. Habitat changes may also cause fish to exhibit compensatory responses at the community level (e.g. changing species composition; Smokorowski & Pratt, 2007). In line with these expectations, studies of riparian deforestation of streams have found varied effects on fish biomass but consistent changes in assemblage structure (Bojsen, 2005; Bojsen & Barriga, 2002; Dias, Magnusson, & Zuanon, 2010; Giam et al., 2015; Iwata, Nakano, & Inoue, 2003; Jones, Helfman, Harper, & Bolstad, 1999; Kouamé, Yao, Bi, Kouamélan, & N'Douba, 2008; Lorion & Kennedy, 2009; Sweeney et al., 2004; Teresa & Casatti, 2012; Wright & Flecker, 2004). Loss of stream canopy cover generally increases light intensity and decreases inputs of allochthonous materials, increasing the portion of the fish community that is supported by autochthonous food sources such as phytoplankton (Allan, 2004; Angermeier & Karr, 1983).

Here, we evaluated possible effects of changes in floodplain land cover on fishery yields by modelling relative fish yields (capture per unit effort [CPUE]) in floodplain lakes as a function of surrounding habitat types. We used unparalleled fisheries and habitat datasets for a 400 km reach of the lower Amazon River floodplain where 56% of floodplain forest has been lost to clearing for jute plantations and cattle ranching (Renó et al., 2011); floodplain lakes in this region occur within a gradient of land cover conditions. We tested the degree to which each floodplain habitat type affected lake CPUE and used the resulting estimates to infer the likely impacts on fishery yields of forest loss and replacement by non-forest habitats.

2 | METHODS

2.1 | Study area

We conducted this study in the lower Amazon River floodplain, in the state of Pará, Brazil (Figure 1). Here, the floodplain is classified as *várzea*: a complex mosaic of plant communities, lakes and channels that are adjacent to, and nearly completely seasonally inundated by, nutrient-rich river whitewaters (Irion, Junk, & de Mello, 1997; Junk & Piedade, 1997). River waters fluctuate seasonally by 5.7 m with a mean annual maximum in May–June and a minimum in November (Castello, Isaac et al., 2015). High waters cause fish populations and fishing activities to move from river channels and floodplain lakes to floodplain forest, shrub and aquatic macrophyte habitats, while low waters cause fish and associated fisheries to recede back to river channels and floodplain lakes (Isaac, Castello, Santos, & Ruffino, 2016). Fish yields comprise 42 fish taxa, but are highly dependent on a few taxa (Table S1).
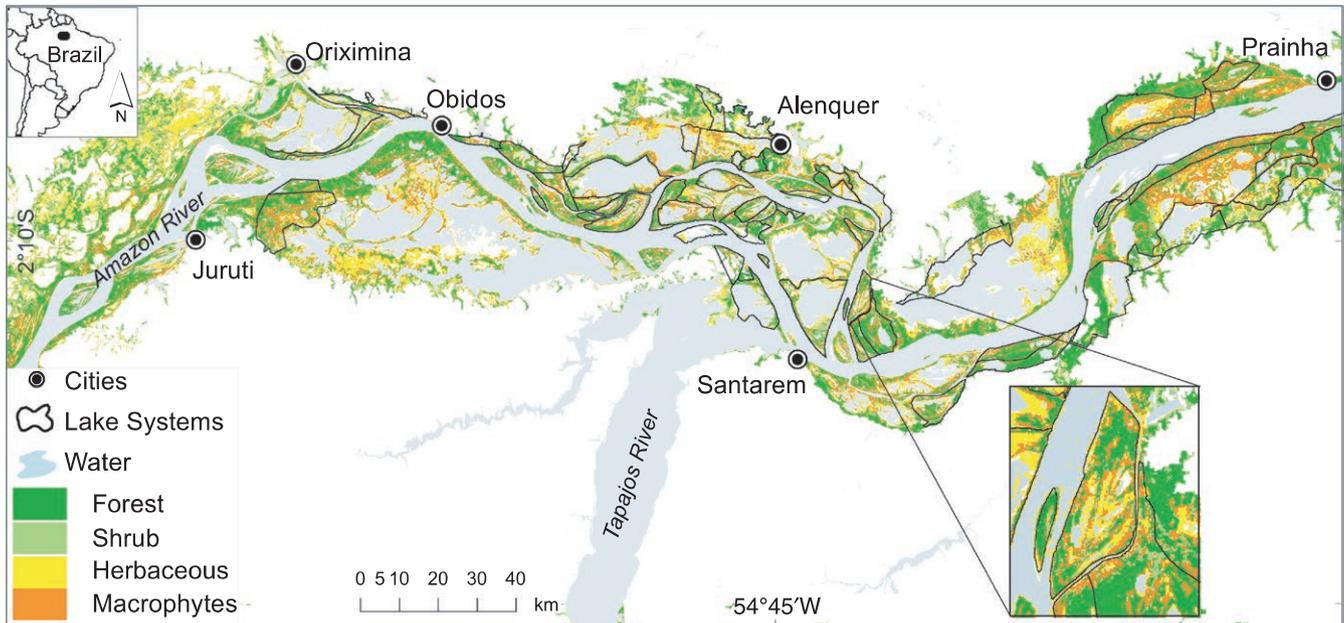
FIGURE 1 Study area, showing lake systems, habitat classes and cities in which fishery landing data were collected

2.2 | Lake systems as units of analysis

Linking changes in floodplain habitats to fish populations requires matching the spatial scales over which functional relationships occur with the scale of study (Smokorowski & Pratt, 2007). We organized fisheries and habitat data based on the concept of *lake systems*, which Amazonian fishers use to describe the principal range of fish movement within the floodplains. Our choice of lake systems as spatial units of analysis stemmed from unsuccessful preliminary analyses attempting to relate various forms of fish yield estimates in floodplain lakes (e.g. catch, CPUE) to habitat extent data within adjacent buffer zones of varying radii sizes (3, 5 and 10 km), as carried out in previous studies (e.g. Lobón-Cerviá et al., 2015). River channels, and floodplain channels wider than 100 m at low water, are excluded from lake systems because they differ markedly from floodplain channels in terms of depth and current. Although many fish taxa use river channels to migrate in and out of floodplains, and fish can migrate across lake systems during high waters, we found support for the lake system concept in previous studies. Fish populations and assemblages in Amazonian floodplains have been shown to differ across lake systems as a function of local fishing practices and habitat conditions (Castello, Arantes, Mcgrath, Stewart, & Sousa, 2015; Castello, McGrath, Arantes, & Almeida, 2013; Castello, McGrath, & Beck, 2011; Castello, Viana, Watkins, Pinedo-Vasquez, & Luzadis, 2009). A lake system-based (as opposed to lake-based or buffer-based) approach is consistent with recent views of Amazonian fish metapopulation dynamics as involving interacting local populations within a larger region of seasonally connected floodplain habitat (Hurd et al., 2016). We mapped 68 lake systems in the study area (Figure 1), guided by differences in floodplain geomorphology and hydrologic connectivity at mid-water stage as observed on Landsat Thematic Mapper imagery. We manually delineated lake system boundaries based on the following features: (i) floodplain

channels wider than 100 m at low water stage; (ii) levees forming the border between floodplain units with distinct geomorphologic types (e.g. scroll systems with differing orientations and curvatures; scroll vs. dish-shaped lakes); and (iii) sub-basins of large dish-shaped lakes. During high waters (~3 months per year), most parts of the floodplain are hydrologically connected; channel currents, fish swimming range and availability of suitable habitat corridors are the main constraints on fish movement. At intermediate water levels (~6 months per year), additional topographic constraints are imposed on movement between lake systems by non-flooded areas on and adjacent to levees. Within lake systems, ridges between scroll lakes increasingly limit hydrologic connectivity as water levels fall, and the open-water area of dish-shaped lakes is reduced as lake margins are exposed. At low water (~3 months per year), dish-shaped lakes within lake systems are further reduced in area, in many cases becoming fragmented into sub-basins. Our lake systems encompassed 3,841 km^2 and varied in size from 20 to 750 km^2, with a median area of 65 km^2.

2.3 | Fishery data

The fishery data were collected by a monitoring system based on standardized protocols (the IARA project; Ruffino, Isaac, & Milstein, 1998) that recorded yield, taxa, gear, effort and location of fishing trips that took place in the region between January 1993 and December 2004 (Figure 1). We excluded fishing data from river channels, which dominate yields of long-distance migrant taxa, in order to reliably assign floodplain lake fish yields to surrounding habitats. Our analysis focused on the main fishery type in the region, which is fishing by motorized boats using gillnets. We did not consider non-gillnet floodplain fishery data, to remove potential biases in catchability rates caused by habitat-related differences in the use of different gears and boat sizes. The analysed dataset included 36,984 fishing trips that were

responsible for 52% of the total fish yield in weight recorded in river and floodplain habitats in the region. The dataset comprised 62% of the catch and 76% of the effort performed in floodplain habitats, with the remainder of the fishing data for floodplain habitats comprising non-gillnet gears including long-lines and hook-and-line.

We calculated CPUE for every lake system and year in terms of kg fisher^{-1} days^{-1}, following studies indicating that alternative measures of fishing effort in Amazonian fisheries (e.g. number and size of nets) provide no additional information (e.g. Petrere, 1978). Because the variance of catch increased with effort, we estimated CPUE for lake system and year by dividing annual lake system catch by annual lake system effort (Petrere, Giacomini, & De Marco, 2010). We calculated CPUE for all 42 taxa together (i.e. multispecies) and separately for the 10 taxa contributing 85% of the total yield. The 10 taxa comprised a range of life history strategies (Isaac et al., 2016). Some taxa spend their entire life cycle in floodplain habitats (e.g. pescada; *Plagioscion squamosissimus*, Scianidae), while others utilize floodplains only during high waters and migrate hundreds (e.g. jaraqui; *Semaprochilodus taeniurus*, Prochilodontidae) and even thousands of kilometres (e.g. dourada; *Brachyplatystoma rousseauxii*, Pimelodidae) along river channels during low waters.

2.4 | Habitat data

Floodplain habitat extent was estimated using published land cover maps for low- and high-water conditions at 100 m scale, derived from mosaics of Japanese Earth Resources Satellite 1 (JERS-1) imagery acquired during October–November 1995 and May–June 1996 (Hess et al., 2015a, 2015b). We organized the dual-season floodplain habitat data into five classes (lake, forest, shrub, aquatic macrophyte and bare/herbaceous) to represent the main habitats available for fish (Table 1). Lake habitat was equivalent to open-water area during low waters; this class is primarily lakes but also includes floodplain channels narrower than 100 m. Bare/herbaceous habitat included areas with soil, fresh sediments, grasses or forbs during low waters, and without aquatic macrophyte cover during high waters; these areas transition to open water during high waters. Aquatic macrophyte habitat included areas with beds of emergent or floating grasses (primarily *Hymenachne amplexicaulis*, *Paspalum fasciculatum*, *Oryza perennis*,

P. repens and *Echinochloa polystachya*) or broad-leaved herbaceous plants (including *Eichhornia* spp., *Pistia* spp. *Salvinia* spp. and *Victoria* spp.) during high waters (Silva, Costa, & Melack, 2010). Shrubs included woody successional species such as *Salix* spp. and the aroid *Montrichardia arborescens*. Forest referred to closed-canopy tree cover greater than about 5 m in height. We calculated the percentage of each habitat within the boundaries of each lake system.

We considered the JERS-based estimates of habitat cover to be valid for the entire 1993–2004 fishery sampling period, and we did not account for minor land cover changes that occurred during that period. Fifty-six per cent of the floodplain forest cover in the study area was lost between the late 1970s and 2008, and 78% of the deforested area was replaced with non-forest vegetation, bare/herbaceous or open-water habitats, primarily as a result of clearing for jute plantations and cattle ranching, with smaller areas lost to channel erosion (Renó et al., 2011). Because land cover change data specific to the 1993–2004 fishery sampling period did not exist and significant land cover change during this period would affect our analyses, we estimated changes in land cover during the study period by comparing remote sensing data from 1995 (JERS images) with comparable data for 2007 (ALOS PALSAR images; see Supporting Information; Table S2). The median change of gain in forest extent minus loss in forest extent was +2.3% for all lake systems; it was less than +5% in 65% of the lake systems and <10% in 89% of the lake systems. Preliminary regression analyses indicated that variability between lake systems in the amount of land cover change during the study period did not affect the results reported below.

2.5 | Data analyses

We quantified the effect of floodplain habitat type on lake system CPUE through a spatially comparative approach, as the lake systems were distributed along a gradient of habitat conditions, with forest cover ranging from 0 to 60% (Figure S1). However, because our analysis is observational, the validity of possible floodplain habitat effects on multispecies CPUE should be supported via falsification of alternative causative mechanisms. Thus, we can only infer the impacts on fishery yields of forest loss once plausible alternative explanations have been discounted. Based on data availability and previous

Habitat	Importance for fish
Lake	Main habitat during low waters, as other habitats dry out; provides phytoplankton and detritus
Bare/herbaceous	Undocumented, but can be expected to provide feeding opportunities such as deposited detritus or insects
Aquatic macrophyte	Provides feeding opportunities (periphyton, insects, plant material, detritus) and protection for fish of all ages, particularly juveniles
Shrub	Undocumented, but may be similar to forest
Forest	Important carbon source for many fish species (e.g. fruits, seeds, leaves, periphyton, detritus) as well as spawning and nursery habitat

TABLE 1 Amazonian floodplain habitats available for fish; habitat classes based on Hess et al. (2015a). All habitat classes were used as candidate explanatory variables, except lake, which was used to standardize capture per unit effort per unit of lake area. Information on importance to fish is from Goulding (1980), Welcomme (1985), Benedito-Cecilio, Araujo-Liima, Forsberg, Bittencourt, and Martinelli (2000), Melack and Forsberg (2001), Oliveira, Martinelli et al. (2006), Castello (2008a) and Arantes et al. (2013)

large-scale studies evaluating the role of ecosystem degradation on fish communities (e.g. Mumby et al., 2004), we tested for four main plausible scenarios:

1. The first scenario was that habitat effects observed on CPUE were due to habitat-related differences in trophic structure of the catch. If fishing reduced the amount of piscivores in lake systems possessing greater amounts of certain habitats, those lake systems could have had greater multispecies CPUE through predatory release. To evaluate whether trophic structure of the catch could have explained habitat effects on multispecies CPUE, our analysis considered the percentage (in weight) of piscivores in the catch.

2. The second plausible scenario was that habitat effects on CPUE could have been due to habitat-related differences in non-gillnet fishing effort, which was not accounted for in our measure of CPUE. To evaluate whether non-gillnet fishing effort explained habitat effects on CPUE, our analysis considered non-gillnet fishing effort.

3. The third plausible scenario was that habitat effects on CPUE were due to habitat-related differences in lake area. Our study area possesses lakes and lake systems of different forms and sizes (e.g. dish-type lakes, scroll lakes), and lake system size can determine management regime (Isaac & Ruffino, 2007), having the potential to affect CPUE. To evaluate whether lake or lake system size could have explained habitat-related differences in CPUE, our analysis considered lake area.

4. The fourth plausible scenario was that habitat effects observed on multispecies CPUE were driven by one or a few taxa, even though most taxa were not affected by differences in habitat. To evaluate whether habitat effects observed on multispecies CPUE were driven by one or a few taxa, our analysis quantified the effect of floodplain habitat type on CPUE of each of the 10 taxa contributing 85% of the multispecies yield in weight.

We used multiple linear regression modelling to quantify the degree to which distinct floodplain habitats affected CPUE and assessed whether any of the four plausible scenarios explained possible floodplain habitat effects on CPUE. We developed 11 models with mean annual log-transformed CPUE (kg fisher^{-1} days^{-1}) as the response: one for all 42 taxa (referred to as multispecies) and 10 for the taxa contributing 85% of the multispecies yield in weight. The multispecies CPUE model included the following candidate explanatory variables: the percentages of forest, shrub, aquatic macrophyte and bare/herbaceous habitat area within each lake system, as well as estimates of lake area, non-gillnet fishing effort and the percentage of piscivores in the catch. The 10 taxa-specific CPUE models included the percentages of forest, shrub, aquatic macrophyte and bare/herbaceous habitat area within each lake system as candidate explanatory variables. We ran each of the 11 models to identify explanatory variables that were significant at α = 5% and then ran the models again including only the significant candidate explanatory variables. The model was assessed with respect to independent errors (Durbin–Watson test), normally distributed errors (visual inspection of

residual plots), and multicollinearity (variance inflation factor). The analyses were performed in R v. 3.3.3.

3 | RESULTS

Our models indicated that forest habitat was the principal variable explaining variability in fish yields. Percentage cover of forest habitat was positively related to multispecies CPUE at a significance of $p = .0003$, whereas other habitat variables were unrelated to multispecies CPUE (Table 2; Figure 2). The effect of forest habitat on multispecies CPUE could not be attributed to alternative causative mechanisms, as lake area, non-gillnet fishing effort and the percentage of piscivores in the catch were all unrelated to multispecies CPUE (Table 2). The coefficient of the forest habitat parameter had a 1:1 ratio with multispecies log CPUE. The multispecies model explained 18% of the variability in multispecies CPUE across lake systems ($R^2 = .18$), indicating that factors not accounted for in our analysis influenced multispecies fish yields in these lake systems.

The observed effect of forest habitat on multispecies CPUE was not driven by one or a few taxa, as forest amount also was positively related to CPUE of nine of the 10 taxa contributing 85% of the yield at a significance of $p < .03$ or lower (Table 2). Shrub amount was negatively related to CPUE of one taxa, at a significance of $p < .029$ (Table 2). The amount of variability explained by the nine significant taxa-specific models of CPUE across all lake systems varied from a minimum of 10% to a maximum of 34% ($R^2 = .10$ and $.34$, respectively; Table 2).

The assumptions of all regression models were met. The candidate explanatory variables were not autocorrelated ($r < [.5]$; Figure S1), and response observations were not spatially autocorrelated (Mantel test, $p = .5$). Durbin–Watson statistics varied between 1.7 and 2.1. Variance inflation factor values varied between 1.0 and 1.5. Inspection of residual plots indicated that errors were normally distributed.

4 | DISCUSSION

Our results provide inferential support to the idea that the yields provided by fish populations in the Amazon River depend on floodplain forests and that dependency cannot be replicated by alternative habitats. Although we employed a spatial analytical approach to understand a process that occurs over time, the results suggest that the removal of floodplain forests reduces multispecies fishery yields per unit effort (Figure 2). The validity of our results is supported by rejection of plausible alternative causative mechanisms involving habitat-related differences in lake size, amount of piscivores, non-gillnet fishing effort and habitat effects on CPUE of the taxa dominating multispecies yields (Table 2). Our results are based on extensive fisheries and land cover datasets encompassing a large geographical area and several thousand fishing trips over many years. CPUE was not spatially autocorrelated, so geographically related factors that were not included in our models (e.g. distance to cities) are unlikely to have affected our results.

TABLE 2 Model parameter estimates of log CPUE (kg fisher⁻¹ days⁻¹) as a function of the percentage amount of habitat types. Models of log CPUE include multispecies CPUE (including 42 taxa) and CPUE for each of the 10 taxa contributing 85% of the multispecies catch in weight (Table S1). Models of multispecies CPUE also include four other candidate explanatory variables testing for alternative causative mechanisms explaining possible habitat-related patterns

| Taxa	Intercept Coef. ± SE (p-value)	Bare/herbaceous Coef. ± SE (p-value)	Aquatic macrophyte Coef. ± SE (p-value)	Shrub Coef. ± SE (p-value)	Forest Coef. ± SE (p-value)	Lake area (km²) Coef. ± SE (p-value)	Non-gillnet effort (fisher days) Coef. ± SE (p-value)	Piscivores (%) Coef. ± SE (p-value)	R^2
Multispecies	2.446 ± 0.065 (.000)				0.010 ± 0.002 (.000)	—	—	—	.18
Mapará (*Hypophthalmus* spp., Pimelodidae)	1.767 ± 0.308 (.000)				0.340 ± 0.108 (.003)	—	—	—	.19
Dourada (*Brachyplatystoma rousseauxii*, Pimelodidae)	2.219 ± 0.086 (.000)				0.019 ± 0.003 (.000)	—	—	—	.33
Curimatá (*Prochilodus nigricans*, Characidae)	2.330 ± 0.093 (.000)				0.013 ± 0.004 (.001)	—	—	—	.17
Mandi-Moela (*Pimelodina flavipinnis*, Pimelodidae)	2.375 ± 0.143 (.000)				0.016 ± 0.006 (.020)	—	—	—	.16
Pescada (*Plagioscion* spp., Scianidae)	2.350 ± 0.103 (.000)				0.010 ± 0.004 (.001)	—	—	—	.18
Jaraqui (*Semaprochilodus* spp., Characidae)						—	—	—	
Acari (*Squaliforma emarginata, Pterygoplichthys pardalis*, Loricaridae)	2.461 ± 0.088 (.000)				0.009 ± 0.002 (.001)	—	—	—	.11
Surubim (*Pseudoplatystoma* spp., Pimelodidae)	2.412 ± 0.098 (.000)			-0.008 ± 0.003 (.029)	0.017 ± 0.003 (.000)	—	—	—	.34
Aracu (*Schizodon fasciatus, S. vittatus, Leporinus* spp., *Rhytiodus microlepis*, Anostomidae)	2.412 ± 0.113 (.000)				0.012 ± 0.005 (.030)	—	—	—	.10
Tambaqui (*Colossoma macropomum*, Characidae)	2.295 ± 0.094 (.000)				0.017 ± 0.004 (.000)	—	—	—	.20
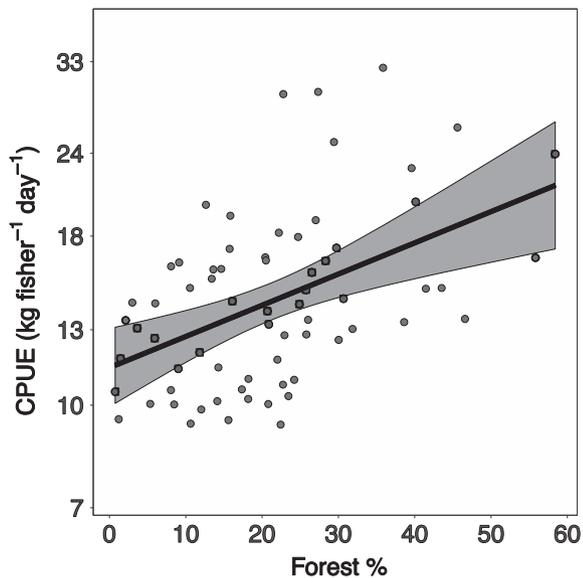
FIGURE 2 Floodplain forest habitat effects on multispecies capture per unit effort (CPUE). The data points plotted are observations in 68 lake systems (Figure 1). Solid line denotes predictions from the model (presented in Table 2) for the effects of forest habitat on multispecies CPUE. Grey bands represent 95% confidence intervals

Our results are consistent with previous studies showing that Amazon floodplain forests are important carbon sources for fish (Goulding, 1980; Oliveira, Martinelli et al., 2006; Oliveira, Soares et al., 2006) and that floodplain forest amount is directly related to fish abundance and biomass (Arantes et al., 2017; Lobón-Cerviá et al., 2015). Floodplain forests underpin fish production by possessing complex structures that protect fish and their offspring from predators (Bayley, 1988; Goulding, 1980) and provide habitat for terrestrial and aquatic insects, which are significant components of fish diets (Oliveira, Martinelli et al., 2006; Oliveira, Soares et al., 2006). These forests possess an abundance of C_3 plant materials as well as phytoplankton and periphyton on which many fish selectively feed (Melack & Forsberg, 2001).

We note, however, that our analysis lacks historical time series of floodplain land cover and fish yields, so it cannot conclusively demonstrate the effects of land cover change on fishery yields. Other factors not included in our analyses could potentially explain our results. Chief among these is the assumption in our analyses of constancy in gillnet catchability across lake systems with varying forest amounts. Forested habitats generally decrease the efficiency, and even impede the use, of most fishing gears including gillnets (Knight & Bain, 1996). The observed positive effect of forests on CPUE can thus be expected to be under-, not over-, estimated, and gillnet catchability is unlikely to have weakened our conclusions. Further support for our use of CPUE as an index of relative fish yields comes from studies in the same area showing that lake systems with higher multispecies CPUE possess fishes with greater body sizes and in higher densities (Castello et al., 2011; Castello, Arantes et al., 2015).

The low proportion of the variability explained in lake system CPUE indicates that factors not accounted for in our analysis also influence floodplain fish yields. The robustness of our analysis depends on the representativity of the land cover data for years 1995–1996 to that of the fishery data during years 1993–2004. The +2.3% change in forest extent in the lake systems between 1995–1996 and 2007 may be responsible for some of the unexplained variability in our models. Other factors not accounted for in our analysis include management efforts. CPUE in dish-type lakes, for example, has been shown to be lower than in other lakes, as the large size of these lakes (>100 km^2) makes it difficult for local fishers to impose and monitor local-level fishing restrictions (Isaac & Ruffino, 2007). Other possible sources of CPUE variation among lakes include lake depth and connectivity, which have been shown to affect fish biomass and abundance in the central Amazon region (Arantes, Castello, Cetra, & Schilling, 2013; Nolan, Fabré, & Batista, 2009). Large-scale spatial and temporal data on Amazonian floodplain land cover change, morphology and management efforts are necessary to enable more refined analyses that can further improve our understanding of how fish production and yields interact with land cover changes.

We suggest that floodplain deforestation can affect fish population dynamics via two main processes: altered patterns of habitat selection and decreased in situ fish production. When water levels rise, fish migrate out of river channels and floodplain lakes onto floodplain areas, and many display strong selection of forested habitats (e.g. Castello, 2008a, 2008b). As deforestation decreases availability of floodplain forests for fish, deforested areas could be expected to host decreased fish densities. The fewer fish inhabiting deforested areas could grow more slowly due to food scarcity and be more susceptible to predation owing to simplified habitat structure, thereby leading to decreased rates of in situ fish production. The extent to which floodplain deforestation alters patterns of habitat selection or decreases in situ fish production is unclear, and it is conceivable that both processes occur. Future research could reveal the processes by which floodplain land cover change affect fish populations and associated yields.

The results herein support the view that floodplain deforestation lowers fishery yields. Yet, relative to their coverage, floodplains worldwide are protected to a much lesser degree than upland environments (Tockner & Stanford, 2002). In the Amazon Basin, very few protected areas were designed to protect freshwater ecosystems (Castello & Macedo, 2016). Protection of floodplains in the Brazilian Amazon is mostly based on the Forest Code, which establishes the extent of protected riparian vegetation based on the width of river channels. For river channels wider than 600 m, a maximum of only 500 m of adjacent floodplain is protected by law, regardless of vegetation type and despite the fact that many floodplains in the basin are tens of kilometres wide (Melack & Hess, 2010). This level of protection appears to be insufficient given the escalating range and severity of natural and anthropogenic pressures on floodplain ecosystems. Maintaining the productivity of floodplain fisheries requires increasing current levels of protection for floodplain systems and their forests as well as educating fishing communities on the adverse fishery effects caused by floodplain land cover changes. The lower Amazon floodplain has already experienced high rates of deforestation and degradation (Harris, 2011;

Lucas et al., 2014; Renó et al., 2011). Our data suggest that continued loss of floodplain forest cover would cause serious detrimental effects for the functioning of floodplain ecosystems as well as the fisheries and livelihoods they sustain.

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CONFLICT OF INTEREST

The authors declare no conflicts of interest.

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