Article:

Phillips, O. orcid.org/0000-0002-8993-6168 and Baker, T. (2025) Floodplain forests drive fruit-eating fish diversity at the Amazon Basin-scale. Proceedings of the National Academy of Sciences, 122 (3). e2414416122. ISSN 0027-8424

https://doi.org/10.1073/pnas.2414416122

Main Manuscript for

Floodplain forests drive fruit-eating fish diversity at the Amazon Basin-scale

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Competing Interest Statement: The authors declare that they have no competing interests.

Classification: Biological sciences, Ecology.

Keywords: frugivory, flooded forest, flood pulse, Amazon River, maintenance of biodiversity

This PDF file includes:

Main Text
Figures 1 to 3
Tables 1 to 2

Abstract

Unlike most rivers globally, nearly all lowland Amazonian rivers have unregulated flow, supporting seasonally flooded floodplain forests. Floodplain forests harbor a unique tree species assemblage adapted to flooding and specialized fauna, including fruit-eating fish that migrate seasonally into floodplains, favoring expansive floodplain areas. Frugivorous fish are forest-dependent fauna critical to forest regeneration via seed dispersal and support commercial and artisanal fisheries. We implemented generalized mixed effects models to investigate drivers of species richness among specialized frugivorous fishes across the ~6,000,000 km^2 Amazon Basin, analyzing 29 species from 9 families (10,058 occurrences). Floodplain predictors per sub-basin included floodplain forest extent, tree species richness (309,540 occurrences for 2,506 species), water biogeochemistry, flood duration, and elevation, with river order controlling for longitudinal positioning along the river network. We observed heterogeneous patterns of frugivorous fish species richness, which were positively correlated with floodplain forest extent, tree species richness, and flood duration. The natural hydrological regime facilitates fish access to flooded forests and controls fruit production. Thus, the ability of Amazonian floodplain ecosystems to support frugivorous fish assemblages hinges on extensive and diverse seasonally flooded forests. Given the low functional redundancy in fish seed dispersal networks, diverse frugivorous fish assemblages disperse and maintain diverse forests; vice-versa, diverse forests maintain more fish species, underscoring the critically important taxonomic interdependencies that embody Amazonian ecosystems. Effective management strategies must acknowledge that access to diverse and hydrologically functional floodplain forests is essential to ensure the long-term survival of frugivorous fish and, in turn, the long-term sustainability of floodplain forests.

Significance statement

The Amazon River Basin has Earth’s most extensive seasonally flooded floodplain forests. These ecosystems harbor communities of trees and animals adapted to prolonged flooding, including fruit-eating fish. When fish eat fruits, they often swallow intact seeds and move them away from maternal trees, contributing to natural forest regeneration. Nevertheless, floodplain deforestation, hydrological and climatic changes, and overfishing threaten this interdependency. In a basinwide analysis of fruit-eating fish species richness patterns, we found floodplain forest extent, richness of tree species, and flood duration to be the most critical landscape and ecosystem features. We conclude that the long-term survival of fruit-eating fish and, in turn, the long-term sustainability of floodplain forests depend on having access to diverse and hydrologically functional floodplain forests.

Main Text

Introduction

Floodplains are vital ecosystems within riverscapes due to their enormous plant and animal biodiversity and the provision of multiple ecosystem services and processes (1). In temperate and tropical regions that receive high rainfall during wet seasons, floodplains typically support extensive forests subject to regular flooding (2). Flooding dynamics shape the ecology, physiology, and human use of floodplain forests, making them highly complex ecosystems susceptible to global change. In floodplain forest ecosystems, flooding drives soil nutrient supply (3), productivity (4), phenology (5), recruitment (6), plant species composition and zonation (7), community structure of resident and migratory animals (8, 9), and temporal dynamics of human use (10). Despite their importance for biodiversity and human wellbeing, floodplain forests are among the most threatened ecosystems globally, while land use change, hydrological infrastructure, and global climate change are among the main drivers (e.g., 11, 12).

The Amazon River Basin is the largest drainage basin on Earth and holds the most extensive floodplain forests in the world (i.e., 516,400 km^2 representing ~9% of the Amazon rainforest biome) (13). The predictable and long-lasting hydrological cycle in the Amazon Basin facilitates adaptations to annual flooding regimes, leading to unique and highly interdependent plant and animal species assemblages. Floodplain forests support one-sixth of Amazonian tree species, which are highly adapted to seasonal flooding and absent from adjacent non-flooded forests (14). Floodplain forests also support unique fish assemblages, as demonstrated through paired sampling in floodplain forests and floating meadows (15, 16). From arthropods (17) to top predators like jaguars (18), the temporal nature of flooded forests promotes seasonal vertical migrations of many ground-dwelling animals into the forest canopy during the flood season. Fish and other aquatic animals migrate laterally from river channels into flooded forests (19–21). The flood pulse subsidizes food webs within the aquatic-terrestrial transition zone (i.e., the moving littoral) (2). Tree communities, for instance, synchronize fruit production with the annual flood season (5), and numerous fish species have evolved morphological and physiological adaptations related to fruit consumption (22). For frugivorous fish, fruit consumption is at a maximum during the flood season, amounting to >90% of stomach contents, and seasonal diet shifts between fruit and alternative foods facilitate species coexistence (20). In turn, frugivorous fishes contribute to floodplain forest regeneration; they are considered the oldest seed dispersers in South American wetlands and disperse seeds of >500 plant species (22). Frugivorous fish maintain functionally diverse forests, as demonstrated by intra- and inter-specific differences in fruit selection (23) and low functional redundancy in seed dispersal and seed predation networks (24).

At a basin level, Amazonian frugivorous fish prefer areas with extensive floodplains (25). However, floodplain attributes that drive basinwide patterns of frugivorous fish species-richness and distribution remain unknown. The diets of frugivorous fishes generally follow a frugivory gradient ranging from high to low fruit consumption (25). Given this variability in their dependence on fruit, we focused on specialized frugivorous fish (i.e., those with >50% fruit in their diet) to test the hypothesis that floodplain ecosystem- and landscape-level attributes (i.e., forest extent, tree diversity, water color, flood duration, elevation) modulate frugivorous fish species-richness. We expect more extensive floodplain forests with higher tree diversity to provide a more variable fruit-based diet, thus supporting more frugivorous fish species. Water color in rivers (white, black, and clear) is an essential indicator of the basin's biogeochemistry, reflecting numerous characteristics such as origin, sediment and nutrient amount, water quality, and productivity (reviewed by 26). Várzea forests, typically associated with white-water river floodplains, host greater tree diversity than igapó forests, which grow on black-water and clear-water river floodplains (27, 28). White-water rivers are, therefore, expected to support more frugivorous fish species. Floodplains with longer flood duration allow fish to exploit food resources within flooded forests for a prolonged time. These areas are, therefore, expected to support more frugivorous fish species. Lastly, floodplain extent is related to elevation; thus, areas with high elevation are expected to support less diverse frugivorous fish assemblages.

Results

Mapping the spatial distribution of frugivorous fish species showed uneven distribution (the number of species within a sub-basin ranged between 0 and 27, mean = 11). Higher richness was found in the Amazon mainstem, northwestern subbasins, the Rio Negro of Central Amazonia, and Madeira and Tapajós of Southern Amazonia (Fig. 1A). A similar overall spatial distribution pattern emerged when weighted by inventory completeness, emphasizing well-sampled regions with high frugivorous richness (Fig. 1B; See *SI Appendix,* Table S1).

Supporting our hypotheses, the variable selection procedure, applied to the linear mixed effects model, revealed clear positive effects on frugivorous species richness of Strahler's river order, flood duration, flooded forest area, and forest tree diversity (Table 1, Fig. 2). Conversely, the model showed a negative effect of white-water proportion (Table 1, Fig. 2). Note that sub-basin area and elevation were not selected by the variable selection procedure and had no significant effect on frugivorous fish species richness after accounting for all other explanatory variables. The fixed effects portion of the model explained 32% of the variation in the data, while the random portion of the model, accounting for the major tributary grouping, explained 9% (Table 1). When restricting the dataset to the 25% best-sampled sub-basins for forest tree diversity (*SI Appendix,* Fig. S1), the variable selection procedure applied on the linear mixed effects model still revealed strong positive effects of Strahler's river order, forest tree diversity, and flooded forest area, and a slight negative effect of white-water proportion (Table 2). The outputs of this model and the corresponding partial regression plots (Fig. 3) support our hypotheses and show that restricting our dataset does not change our main findings. With this restricted dataset, the variation in the data explained by the model increased; the fixed effects portion of the model explained 36%, while the random portion of the model explained 17% (Table 2).

The distribution of species richness of serrasalmid frugivorous fish in the Amazon River Basin showed a very similar pattern to that of frugivorous species from all families (*SI Appendix,* Fig. S2). In accordance with our hypotheses, the complementary test restricted to the Serrasalmidae family provided overall similar results for frugivore richness, showing strong positive effects of Strahler's river order and flooded forest area, a positive effect of flood duration although less significant, and negative effects of white-water proportion and sub-basin area (*SI Appendix,* Table S2 and Fig. S3). In this model, the stepwise procedure did not select the random variable, and the model explained 47% of the variation in the data (*SI Appendix,* Table S2). When restricting the dataset to the 25% best-sampled sub-basins for forest tree diversity, species richness of serrasalmid frugivorous fish was related to four variables, positively to Strahler's river order, forest tree diversity, and flooded forest area, and negatively to white-water proportion (*SI Appendix,* Table S3 and Fig. S4). Here the random variable was again not selected by the stepwise procedure, and the model explained around 58% of the variation in the data (*SI Appendix,* Table S2). Finally, when applying the same analytical procedure to species richness of serrasalmid piscivorous fish, the mixed models, either considering all sub-basins or only those 25% best-sampled sub-basins for forest tree diversity, revealed no effect of any of the considered explanatory variables (*SI Appendix,* Tables S4 and S5).

Discussion

Understanding landscape and ecosystem factors that influence the maintenance of biodiversity is essential to improve conservation strategies in a time of rapid environmental changes. Across the Amazon Basin, the number of specialized frugivorous fish species is explained by the extent of floodplain forests and their tree diversity, and these relationships are robust throughout all the models tested. Tree richness is a proxy of food availability, while floodplain forest extent and flood duration are proxies of habitat availability. Our study goes beyond recent efforts to link forest cover to frugivore diversity (e.g., 29–31) by analyzing how forest diversity may influence frugivore diversity at such a scale. Since fish contribute to forest regeneration via seed dispersal and support commercial and artisanal fisheries, results from this study are relevant for landscape restoration planning (e.g., 32) and managing frugivorous fishes (33).

Seed dispersal is an essential ecological process in tropical forests where frugivorous animals move seeds away from the mother tree, directly influencing forest regeneration and community structure (34, 35). Seed dispersal networks are highly heterogeneous, often comprising multiple frugivore species interacting with a few or many plant species and characterized by divergent behavioral and morphological traits (36). As a result, frugivore species within networks have complementary ecological functions and may contribute differently to the qualitative and quantitative aspects of seed dispersal effectiveness (37). Asymmetric links (e.g., pairs of generalized frugivores that depend on many plant species and specialized plants that depend on one or few animal species) can compensate for decreases in the local abundance of specialized species and increase network robustness (36). In floodplain forests, seed dispersal networks include multiple species of frugivorous fishes, each playing unique roles. For instance, large-bodied species disperse a higher diversity of seed species and sizes than co-occurring small-bodied species; small fish disperse only a subset of small-seeded species (38). Passage through fish guts can speed up and enhance the success of seed germination, but fish and plant interspecific variability mediate these effects. A fish species can enhance the germination success of some plant species but not others within the same region (39). Likewise, passage through bigger fish increases germination success for some plant species but decreases or does not affect others (39, 40). Frugivorous fishes show preferential consumption for particular fruit species regardless of their availability in the landscape. They maintain fruit selectivity across years, where individuals of the same species are more similar in their fruit choice than individuals of other species (23). Overall, frugivorous fishes have more mutualistic (i.e., mostly seed dispersal) than antagonist relationships (i.e., seed predation), and fish disperse different sets of species than those predated (24). These lines of evidence suggest that, at a sub-basin scale, the richness of frugivorous fish species is an adequate diversity metric to capture the suitability of floodplain ecosystems to support diverse assemblages of frugivorous fishes. Our findings demonstrate that extensive and diverse floodplain forests are essential to maintaining diverse assemblages of frugivorous fishes. In turn, the seed dispersal by fish mutualism is critical to maintaining high tree species richness in flooded forests.

Deforestation and frugivore over-exploitation significantly threaten the persistence of floodplain forests. Along the Amazon River mainstem and Andean tributaries, sediment transport and deposition during flooding enhance floodplain soil fertility (41), making floodplain forests susceptible to large-scale agricultural deforestation. For instance, 70% of floodplain forests in lower Amazonia have been clear-cut for agriculture and cattle ranching (42). Like fish, arboreal and terrestrial frugivores migrate seasonally into flooded forests and contribute to forest regeneration. During the flood season, arboreal frugivores disperse seeds, while during the dry season, terrestrial frugivores and granivores predate upon non-dispersed seeds (8). However, due to their association with river networks, floodplain forests are readily accessible to hunters, leading to historically depleted populations of large-bodied vertebrates in floodplain forests compared to non-flooded forest interior populations (43). The absence of large frugivore vertebrates limits the dispersal of animal-dispersed species and exacerbates the effects of pre-dispersal seed predation on forest community structure (34).

Similarly, frugivorous fish of all sizes are heavily consumed in Amazonia, leading to overexploitation, population depletion, and loss of ecological function. The commercial exploitation of Tambaqui (*Colossoma macropomum*, Serrasalmidae), one of the largest frugivorous fish, started in the 1880s. By the mid-1970s, Tambaqui was the most exploited species in the Central Amazon, but landings dropped by 97% in just three decades (44). Nowadays, large Tambaqui individuals are rare near cities, creating a seed dispersal limitation for ~20% of large-seeded floodplain taxa (45). Small- and medium-sized frugivorous fish species are also heavily exploited and consumed by riverine households in the Amazon. For example, *Brycon melanopterus* (Bryconidae) and *Mylossoma albiscopus* (Serrasalmidae; formally recognized as M. *duriventre*) account for up to 80% and 64%, respectively, of locally consumed fish on the Colombian-Brazilian border (46). In the absence of large-bodied frugivorous fishes, the overexploitation of small- and medium-sized species will likely exacerbate seed dispersal limitation in floodplains (e.g., 38). Thus, the combined loss of fish and terrestrial frugivores can imperil vertebrate-mediated floodplain forest regeneration.

Changes to the natural flooding regime constitute another significant threat to floodplain forests and frugivorous fishes. Our study demonstrated that flood duration increases the richness of frugivorous fish species. This relationship was expected, given that more prolonged flooding facilitates extended access to fruits within the flooded forests by fish (20). Flood duration drives the zonation and structure of flooded forest tree assemblages (7). A variable flooding regime across the Amazon Basin (≈ 3 to 8 months) (47) creates a heterogeneous flooded forest distribution over Amazonia. For instance, centers of endemism occur in Western Amazonia with short floods and in Central Amazonia with prolonged floods (27). In central Amazonia, black-water floodplain forests flood longer and more profoundly (> 300 days year^{-1} and 9–9.5 m) than white-water floodplain forests (270 days year^{-1} and 7–7.5 m) (7, 48). Such regional differences may help explain the high richness of frugivorous fishes in the Rio Negro of Central Amazonia. However, flooding patterns in Amazonian floodplains are being altered by dams (49) and climate change (50, 51). Such changes negatively impact floodplain forest diversity and, therefore, frugivorous fishes. Permanent flooding resulting from reservoir construction causes massive tree mortality and shifts in species composition in floodplain forests (52). Climate-change-driven extreme drought benefits drought-resistant species and increases forest fires (11), while extreme flooding benefits tree species adapted to prolonged flooding and suppresses those distributed in higher ground with lower flooding tolerance (52). Moreover, changes to the flood pulse of Amazonia would likely impact the community-wide synchronization of fruit ripening with the flood, further reducing fruit availability to fish (47).

Contrary to our expectation, the richness of frugivorous fish species decreased in sub-basins dominated by Andean white-water rivers despite having fertile floodplain soils and productive forests. High yields of annual sediment deposition coupled with high channel erosion rates create highly productive and dynamic forests in white-water floodplains (28). Productivity in early successional white-water floodplains is 10-fold higher (31.8 Mg C ha^{-1} year^{-1}) compared to black-water floodplain forests (2.9 Mg C ha^{-1} year^{-1}) (53). For trees shared between both forest types, those in white-water floodplains grow two to five times faster (54). Floodplain forests of white-water rivers also have greater tree diversity than those associated with black-water rivers (mean ± S.E.: white-water: 82.11 ± 3.03 species/ha (N = 240 plots), black-water: 64.43 species/ha (N = 222 plots)) (55). Nevertheless, floodplain forests of black-water rivers have higher tree species turnover, fruit trait diversity, water transparency, and flood duration relative to white-water rivers, which may explain this unexpected pattern.

Black-water floodplain forests form more heterogeneous stands driven by high species turnover along riverine environmental gradients (i.e., soil texture, flood height, and flooding duration) (14, 56). Fruit traits like seed size vary more in black-water floodplains to offset soil nutrient limitations; trees of black-water floodplains have heavier seeds (mean biomass: black-water: 7.1 g, white-water: 1.2 g) (57). Interestingly, previous research demonstrated that the probability of floating and buoyancy time decreases with fruit density driven by seed mass (58). Thus, fish likely play a more critical role in the seed dispersal of heavier and large-seeded species in black-water flooded forests than water-mediated dispersal. High species turnover and fruit trait diversity contribute to a more diverse fruit offer for fish, likely supporting greater fruit-eating fish diversity. Nevertheless, limited data on plant functional diversity hinders our understanding of how fruit trait diversity in floodplains influences frugivorous fish diversity. There is a paucity of databases for tropical wetland forests in general (59) and, particularly, of databases at the species level that evaluate fruit traits relevant to frugivores. Besides seed size, fruit size, pulp yield, fruit density, nutrient composition, and toxins are critical traits that likely influence fruit selection by frugivorous fishes.

Lastly, water transparency is higher in black-water and clear-water than in white-water rivers (black-water: 0.6–4 m, clear-water: 1–3 m, white-water: 0.1–0.6 m) (26). Greater water transparency supports a greater diversity of visually oriented fish and may facilitate fruit detection. In a recent analysis of Amazonian fish assemblages, species belonging to orders with a more developed visual system, like Characiformes, were observed in higher proportion in black- and clear-water rivers in contrast with species in orders where the sensory system does not necessarily depend on light (i.e., Siluriformes) which proportion was higher in white waters (26). Our analyses included 29 fish species from 9 families, most of which are characiforms (exceptions are 6 species of siluriform catfishes; *SI Appendix,* Table S6). For instance, frugivorous serrasalmids (Characiformes) are diverse and abundant in black-water river floodplains (e.g., 20), and breeding individuals are colorful, suggesting that color vision plays a role in their behavioral ecology. However, how the light environment in flooded forests and whether variability in visual pigments among frugivorous fishes influence fruit detectability remains unknown. Further investigation is needed to assess how water transparency influences tradeoffs in fruit traits, fish vision, and seed dispersal ability, as well as the capability of black-water and clear-water flooded forests to support more diverse frugivorous fish assemblages.

In summary, the natural hydrological regime facilitates fish access to forests and controls fruit production. Nevertheless, the ability of Amazonian floodplain ecosystems to support speciose frugivorous fish assemblages hinges on having extensive and diverse seasonally flooded forests. Effective management and conservation strategies for frugivorous fish must acknowledge that access to diverse and hydrologically functional floodplain forests is pivotal to their long-term persistence. Across Amazonia, 36% of the rainforest biome has been degraded by timber extraction, fire, edge effects from deforestation, and extreme drought (60). In comparison, the extent of floodplain forest deforestation reaches 70% in some areas of Amazonia, where the remaining fragmented landscape has lower plant, bird, mammal, and insect abundance and diversity (42). Such reduction in floodplain forest cover also shrinks fish functional diversity (61) and fisheries yield at regional (62) and local scales (e.g., the loss of 1 km^2 of floodplain forest lowers catches by 9%) (63). Globally, levees have disconnected numerous lowland rivers from their floodplains, altering forest composition (12), while dams have caused the permanent inundation of floodplain forests, leading to massive tree mortality (52). As the need for alternative energy sources pushes dam development in large tropical rivers, decision-making should prioritize the persistence of functional lowland river floodplains (64). Given the high dependence of specialized frugivorous fishes on fruit from floodplain forests, they can serve as indicators of forest degradation and early warning signals of permanent floodplain forest loss (47). Lastly, as animal biodiversity, and particularly freshwater fish, rapidly declines worldwide (65), comprehending the impact of losing floodplain forests on biodiversity and ecosystem services is crucial for floodplain management and restoration.

Material and Methods

1. Frugivorous fish diversity

We estimated frugivorous fish species-richness based on a recent review of fruit-consuming fish in the Amazon Basin (66). We focused on the mid-high and highly specialized frugivorous fishes, those eating >50% of fruits in their diets, represented by 29 species from 9 families distributed across the basin (*SI Appendix,* Table S6). For these 29 fish species, we gathered 10,058 occurrences from the AmazonFish Project database (*SI Appendix,* Fig. S5). This collaborative and exhaustive database includes fish species occurrences for the entire Amazon Basin from 1834 to 2019, from published literature, biological collections, and field expeditions (67). We then assigned frugivorous fish occurrences into 144 sub-basin units covering the entire Amazon Basin based on the classification made by Jézéquel et al. (67). These 144 sub-basin units were based on the HydroBASINS framework (68), a subset of the HydroSHEDS database, combining levels 5 and 6 to delineate hydrological sub-basins > 20,000 km^2. An exception was made for sub-basins located in the Amazon River mainstem that were delineated based on the distance between two main tributaries entering the mainstem.

2. Fish inventory completeness assessment

Fish inventories are far from complete in tropical freshwaters, and the Amazon Basin is one example of heterogeneous distribution of sampling effort, potentially resulting in distorted and incomplete views of biodiversity patterns (67, 69). For this reason, we included a survey completeness evaluation in our modeling analyses based on the curvilinearity of smoothed species accumulation curves (SACs). SACs of poorly sampled regions tend to follow a straight line. In contrast, SACs of better-sampled regions have a higher curvature, and those from well-sampled areas reach a plateau (70). The mean slope of the last 10% of SACs (i.e., the last right-side portion of the SAC) reflects the degree of curvilinearity and was used as a proxy for inventory incompleteness (71). The inverse of this mean slope (1/slope) was used as a completeness index, as shallow slopes (values close to zero) indicate saturation in the sampling. In contrast, steep slopes (values close to or above one) reflect high levels of incompleteness (71). We applied this procedure to each sub-basin using the 'specaccum' function in the R (72) package *vegan* (73) and applying the commonly used "random" method, which calculates the mean SAC and its standard deviation from random permutations of the data (e.g., 71, 74). We used the entire AmazonFish species occurrence dataset (67), including records of all fish species from the Amazon Basin.

3. Floodplain forest tree diversity

To estimate the species richness of flooded forests per sub-basin, we first retrieved tree species composition from the Amazon Tree Diversity Network–ATDN. We filtered out plots/transects established within floodplain areas based on a high-resolution, gridded dataset of Earth's floodplains at 250-m resolution (GPLAIN250m; 75), resulting in 384 georeferenced vegetation plots and/or transects with 29,415 registers (*SI Appendix,* Fig. S5). We used the species recorded in ATDN floodplain plots to build a reference list of floodplain forest tree species. To increase the spatial extent, we then searched the occurrences of those species in the reference list using the Global Biodiversity Information Facility database–GBIF (*SI Appendix,* Fig. S5; GBIF tree species occurrence dataset: https://doi.org/10.15468/dl.fndaqe). We downloaded the GBIF data using the R package *rgbif* (76) and calculated the number of occurrences and the number of floodplain tree species per sub-basin. This effort resulted in 309,540 occurrences (from GBIF) for 2,506 tree species that were included in subsequent analyses. As a proxy of floodplain forest tree diversity per sub-basin and to account for the varying sampling effort between sub-basins, we used the residual values of the relationship between the number of sites with registers in the GBIF database (GBIF sites) and the number of tree species recorded per sub-basin (*SI Appendix,* Fig. S1). To further ensure that the differences in sampling effort (i.e., the number of GBIF sites) did not affect our results, we repeated our statistical analyses (see below), restricting the dataset to the 25% best-sampled sub-basins, where the tree diversity is not affected by an increase in sampling effort (*SI Appendix,* Fig. S1).

4. Floodplain and landscape variables

Besides forest tree diversity, we assessed the contribution of other variables related to environmental and floodplain conditions expected to explain the distribution of frugivorous fish species-richness in this highly dynamic system: flooded forest area, water color, flood duration, elevation, sub-basin area, and Strahler's river order. We calculated the flooded forest area per sub-basin using the flooded forest class in the satellite-derived product LBA- ECO LC- 07 Wetland Extent, Vegetation and Inundation: Lowland Amazon Basin (13). This dataset provides a map of the wetland extent, vegetation type, and dual-season flooding state of the entire lowland Amazon Basin acquired from satellite imagery during October–November 1995 and May–June 1996 (13). We used water color as a proxy for river biogeochemistry characterization (reviewed by 26). We retrieved water color data from the Science for Nature and People Partnership–SNAAP database (77) and estimated the white, black, and clear water proportion per sub-basin. From water color data, we used the white-water proportion area. The duration of the annual flood in Amazonian floodplains ranges between 3 to 8 months (47). To estimate flood duration per sub-basin, we used the GIS product Surface WAter Fraction High Resolution (SWAF- HR) for 2012, which contains monthly inundation areas at a 1 km spatial resolution (78). Flood duration was calculated by averaging pixel values (number of months flooded) per sub-basin. We extracted elevation data per sub-basin from a Digital Elevation Model with a 90 m spatial resolution (79) and computed mean values. Finally, we used the maximum Strahler river order within each sub-basin provided by Venticinque et al. (77) to control for the position of sub-basins along the longitudinal gradient of the river network because habitat size and sub-basin connectivity increase from up to downstream areas, potentially affecting species diversity.

5. Statistical analyses

To examine the effects of floodplain ecosystem and landscape characteristics on frugivorous fish species-richness (response variable), we performed linear mixed effects models using the 'lmer' function from the R package *lme4* (80) with flooded forest area, forest tree diversity, biogeochemistry/water color, flood duration, elevation, and Strahler's river order as explanatory fixed effects. We added major tributary groups (i.e., 21 main tributaries delineated by 67) as a categorical random effect to account for potential spatial autocorrelation from sub-basins belonging to the same major tributaries. We also added the sub-basin surface area as an explanatory variable to control for the potential effect of area on diversity (i.e., larger drainage basins usually have more species) (81). The fish inventory completeness index (see above) was included in the models as weights, giving more importance to well-sampled sub-basins. Finally, we applied a simple backward stepwise procedure using the 'step' function from the R package *lmerTest* (82) to select the most important variables affecting frugivorous species richness. All explanatory variables were scaled to provide comparable estimates. To reduce skewness and improve normality, sub-basin area and elevation were transformed to *log(x)*, frugivorous fish species richness to *log(x+1)* as some sub-basins had zero richness values, and flooded forest area to *x^(1/3)* (logarithmic and cube root are among the most commonly used transformation for reducing right skewness and improve normality). Before performing the models, we used the Variance Inflation Factor to evaluate collinearity among explanatory variables and obtained values below 2.5 for all the predictors included in all the models using the 'vif' function from the R package *car* (83).

6. The Serrasalmidae family

As a complementary test of our expected relationships between frugivorous fish diversity, floodplain and landscape variables, we re-ran the above-described procedures and analyses, restricting our fish diversity dataset to the Serrasalmidae family (i.e., 12 frugivorous species and 19 piscivorous species distributed in the Amazon Basin). This specific family offers an ideal model for testing the robustness of our results, being composed of well-known trophically specialized clades ranging from frugivory to piscivory (84) and widely distributed across the Amazon Basin. These features allow for a balanced comparison of two very contrasted feeding habits that should, in turn, provide equally contrasted patterns in terms of the relationships between diversity and floodplain and landscape characteristics. The analysis of frugivorous serrasalmid diversity, which functions as a sensitivity test, should provide similar results as for the all-frugivore-clades diversity (i.e., 29 species in 9 families of mid-high and highly specialized frugivores distributed in the Amazon Basin; see above) and opposite results for the piscivorous serrasalmid diversity (i.e., no relationship with flooded forest area, forest tree diversity, flood duration or white-water proportion). The piscivorous species were defined according to the trophic guilds determined by Coronado-Franco et al. (25) for the whole Serrasalmidae family.

Data on fish distributions across Amazonia and sub-basin-level data for frugivorous fish species richness (all taxa and serrasalmids) and trees included in regression models and code for analyses, plots, and tables included in the manuscript and appendices will be archived on the Mississippi State University Scholars Junction and made publically available upon manuscript acceptance.

Acknowledgements

C. Jézéquel and P.A. Tedesco were funded through the AMAZONFISH project (ERANet-LAC: ELAC2014/DCC-0210), and ForestFisher project through the 2020–2021 Biodiversa and Water JPI joint call for research projects, under the BiodivRestore ERA-NET Cofund (GA N◦101003777), with the EU and the funding organizations ANR, FCT, FAPEAM, DFG and FUNDECT. C. Jézéquel and P.A. Tedesco were also supported by the CRBE Laboratory through the LABEX TULIP and CEBA (ANR-10-LABX-41, ANR-10-LABX-25-01). S.B. Correa and K. Coronado-Franco were supported by the

Forest and Wildlife Research Center of Mississippi State University, USA (McIntire Stennis project #1026075 to S.B. Correa).

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Figures and Tables

Figure 1. (A) Map of the frugivorous fish diversity (i.e., number of species classified as mid-high or highly specialized frugivores, see methods) in the Amazon River Basin for 144 sub-basins. (B) Map of the frugivorous fish diversity weighted by the completeness index of fish taxonomic knowledge for each sub-basin (i.e., computed as richness values multiplied by the completeness index; see the Material and Methods, section 2, for details about the index). Black lines show boundaries between major tributaries.

Figure 2. Partial regression plots based on the best model resulting from the stepwise procedure (see Table 1) on the linear mixed model for frugivorous fish richness (from all fish families). Plotted points represent partial residuals. The size of the circles represents weights related to the fish inventory completeness index. Shaded areas indicate 95% confidence bands.

Figure 3. Partial regression plots based on the best model resulting from the stepwise procedure and restricting the dataset to the 25% best-sampled sub-basins for forest tree diversity (see Table 2). Plotted points represent partial residuals. The size of the circles represents weights related to the inventory completeness index. Shaded areas indicate 95% confidence bands.