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The Flooding Gradient Affects Seed Dispersal by Fruit-Eating Fishes in Amazonian Whitewater Floodplain Forests

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ABSTRACT

Seed dispersal by fish (ichthyochory) plays a key role in the structure of Amazonian floodplain forests. The hydrological regime creates broad variability in flooding depth and duration, and as a result, the tree species richness increases as the flooding depth and duration decrease. This flooding gradient leads to habitats, such as low várzea (LV) and high várzea (HV) forests, corresponding to flood durations of 50–230 and ≤ 50 days year^{-1}, respectively. Our study evaluated the fruit consumption by fish and the seed dispersal potential along the flood gradient. We tested the hypothesis that the role of fish as seed dispersers varies between LV and HV and that the seed dispersal network is modular and nested. We expect to find a greater contribution of fish to seed dispersal in LV forests. Based on fish collections from Paciência Island and a literature review, we identified 40 fish species that consumed fruits and seeds of 188 tree species in Amazon floodplains. Of these, 114 tree species were recorded on Paciência Island or in other floristic inventories along the flood gradient in várzea forests. When we considered only the tree species with distribution restricted to each forest type (LV or HV), the species richness of fruits and seeds consumed by fish was greater in LV forest. The ichthyochory network showed a significant nested structure. Although most forest inventories have found greater tree species richness in the HV, our study highlights the importance of fish consumption of fruit and seeds in LV forests.

RESUMO

A dispersão de sementes por peixes (ictiocoria) é fundamental para a estrutura das florestas alagáveis amazônicas. O regime hidrológico cria grande variabilidade na profundidade e duração das inundações, onde a riqueza de árvores aumenta com a diminuição da profundidade e duração das inundações. Esse gradiente de inundação leva à habitats, como as florestas de várzea baixa (VB) e várzea alta (VA), correspondendo a períodos de inundação de 50–230 e ≤ 50 dias por ano, respectivamente. Avaliamos o consumo de frutos pelos peixes e a potencial dispersão de sementes ao longo do gradiente de inundação. Testamos a hipótese de que o papel dos peixes como dispersores varia entre VB e VA, e que a rede de dispersão é modular e aninhada.

Esperamos encontrar maior contribuição dos peixes para a dispersão nas florestas de VB. Com base em coletas de peixes na Ilha da Paciência e em uma revisão da literatura, identificamos 40 espécies de peixes que consumiram frutos de 188 espécies arbóreas nas várzeas amazônicas. Destas, 114 espécies foram registradas na Ilha da Paciência ou em outros inventários florísticos ao longo do gradiente de inundação na várzea. Considerando apenas as espécies arbóreas com distribuição restrita a cada tipo de floresta (VB ou VA), a riqueza de espécies de frutos consumidos foi maior na floresta de VB. A rede de ictiocoria apresentou estrutura aninhada significativa. Embora a maioria dos inventários florísticos tenha encontrado maior riqueza de árvores na VA, destacamos a importância do consumo de frutos pelos peixes nas florestas de VB.

1 | Introduction

Many tropical trees produce fruits and seeds adapted for consumption by animals, and many tropical animals depend on these foods for at least part of the year (Howe 1984). In tropical forests, around 50%–90% of plant species have their seeds dispersed by animals (Howe and Smallwood 1982; Fleming et al. 1987). Seed dispersal, animal-mediated (zoochory) or otherwise, refers to the movement of seeds away from the parent plant (Howe and Smallwood 1982; Janzen 1983; Jordano 2000), and can play a key role in the structure and function of floodplain forests (Correa et al. 2015) as well as directly affect seed germination, plant establishment and gene flow (Traveset 1998; Bartel and Orrock 2022; Costa et al. 2023).

Floodplain forests occupy approximately 15% of the Amazon basin (Melack and Hess 2010). Only in the floodplain forests of the whitewater rivers of the Amazon basin ("várzea," sensu Junk et al. 2011), more than 1000 tree species found, making it the most species-rich floodplain forest in the world (Wittmann et al. 2006; Wittmann, Schöngart, and Junk 2010; Householder et al. 2024). These forests associated with whitewater rivers occupy an extensive area of approximately 450,000 km^2 (Wittmann and Junk 2016) and have experienced increases in the intensity of extreme flood and drought events (Fleischmann et al. 2023; Espinoza et al. 2024). In Amazonian floodplains, the hydrological regime is characterized by an annual, predictable, and long-lasting flood pulse of high amplitude (Junk et al. 1989; Schöngart and Junk 2007; Junk and Piedade 2010), where minor topographical variations determine significant differences in depth and duration of flooding (Junk 1989; Ferreira 1997). Floods can reach between 6 and 9 m in the western Amazon (Solimões-Marañon) and between 12 and 15 m of mean amplitude in the southern tributaries (Madeira, Purus, Juruá) of the Amazon River (Fassoni-Andrade et al. 2021). Differences in flood depth and duration determine the timing and duration of flowering and fruiting of many floodplain tree species (Ferreira 1997; Parolin et al. 2010). That is because the flood pulse synchronizes phenological rhythms, especially for flowering and fruit ripening (Worbes 1997; Schöngart et al. 2002).

Within a floodplain forest, trees at higher topographic elevations produce flowers several months after those at lower topographic elevations (Parolin et al. 2010). Although flowering may be more prolonged in higher areas, fruiting lasts shorter than at lower topographies, due to reduced flooding period (Parolin et al. 2002). These two topographic levels within floodplains lead to habitats, such as low várzea (LV) and high várzea (HV), which differ in both the depth and duration of flooding and, as a result, in the floristic structure, composition, and richness of tree species (Wittmann et al. 2002). In the Central Amazon, LV trees are subject to an average flood depth ranging from 3.0 to 7.5 m, corresponding to a flood duration of 50–230 days year^{-1}, respectively, while in the HV, the average flood depth is ≤ 3 m, with an average flood duration of ≤ 50 days year^{-1} (Wittmann et al. 2002).

Flood depth and duration determine the distribution of tree species along the flood gradient in Amazonian floodplain forests (Junk 1989; Worbes 1997; Householder et al. 2021). While most LV tree species have developed adaptations to long periods of flooding (Parolin et al. 2010), many of them are endemic species (Wittmann, Schöngart, and Junk 2010). HV tree species have developed fewer adaptations to flooding, and the phenology of many of these species can therefore be triggered by climatic factors unrelated to the annual flooding regime, such as precipitation and solar radiation (Parolin et al. 2010). As a result, species richness increases with decreasing flooding depth and duration (Ferreira 1997; Wittmann, Schöngart, and Junk 2010). Moreover, the central Amazonian LV and HV forests share only ≈17.5% of their tree species and differ in floristic and structural characteristics induced by the hydroperiod (Wittmann, Schöngart, and Junk 2010). For instance, LV forests have an average richness of 56.9 tree species ha^{-1} (with diameter at breast height—DBH, ≥ 10 cm), while HV forests have an average of 100.8 tree species ha^{-1} (Wittmann et al. 2006).

Adaptations of trees in Amazonian floodplain forests include seed dispersal mechanisms (Parolin et al. 2013). A critical adaptation for trees to disperse their seeds involves community-wide synchronicity of fruit maturation with the annual flood pulse (Haugaasen and Peres 2005; Hawes and Peres 2016). This adaptive strategy enables seed dispersal by water (hydrochory) and by fish (ichthyochory) (Parolin et al. 2013), since the flood pulse and the flood duration allow the access and permanence of frugivorous fishes in the flooded forest (Correa et al. 2015). In the Amazon basin, floodplain forests drive fruit-eating fish diversity (Correa et al. 2025), with 2716 known fish species (Dagosta and De Pinna 2019) and at least 93 consume fruits and seeds from flooded forests (Correa 2012). Among these, there is the group of migratory fish represented mainly by the orders Characiformes and Siluriformes (Goulding 1980, 1983; Mannheimer et al. 2003; Piedade et al. 2006; Correa et al. 2007; Costa, Weiss, and Piedade 2024), most of which are categorized as lateral migrants (Herrera-R et al. 2024). These species range from small and medium-sized characins (which feed mainly on aquatic and terrestrial invertebrates and occasionally consume fruits and seeds from marginal vegetation) to large omnivorous catfishes (Doradidae and Pimelodidae) and characins

(Serrasalmidae and Bryconidae) that consume considerable quantities of fruits (Correa et al. 2015; Costa et al. 2023). The interaction between frugivorous fishes and the tree community, form complex mutualistic networks (Correa et al. 2016; Araujo et al. 2021; Mateus et al. 2022; Pereyra et al. 2023), which lilkely influence natural forest regeneration through dispersal, germination, and establishment properties of many floodplain tree species (Correa et al. 2015; Costa et al. 2023). Those interactions may have played a significant role in the evolution of both, fishes and flowering plants (Gottsberger 1978; Correa et al. 2015).

Since the frequency of interactions between fish and plants depends on the abundance of fish and fruit produced in the environment (Costa, Weiss, Piedade, Ferreira, and Maltchik 2024), the LV and HV forests can impose temporal restrictions on interactions between fish and fruits, due to differences in depth and duration of flooding and, consequently, influence the structure of seed dispersal networks. The structure of complex networks of species interactions is important for the persistence and stability of the communities (Bascompte and Jordano 2007; Olesen et al. 2007; Mello et al. 2011b), and may present modularity and nestedness (Memmott et al. 2004; Burgos et al. 2007; Silva et al. 2023). Modular structures are formed by subgroups of species (modules) (Olesen et al. 2007; Mello et al. 2011a) that have many interactions among themselves and very few with species from other modules (Olesen et al. 2007). Nested structures are formed when specialist species (the less connected) interact with species that form perfect subsets of the species with which generalists (the highly connected) interact (Bascompte and Jordano 2007). Modular and nested structures increase the network stability and robustness against species loss (Memmott et al. 2004; Costa, Weiss, Piedade, Ferreira, and Maltchik 2024). Because anthropogenic impacts can cause modifications in aquatic ecosystems (Duponchelle et al. 2021; Schöngart et al. 2021) and potentially affect seed dispersal by fish, knowing the structure of mutualistic networks is essential to infer about the vulnerability of these interactions as a result of any changes in the ecosystem (Costa, Weiss, Piedade, Ferreira, and Maltchik 2024).

Considering the differences in floristic composition between the low and high várzea, we characterized fruit consumption by fish and seed dispersal potential along the flood gradient. We tested the hypothesis that the role of fish as seed dispersers varies between LV and HV and that the seed dispersal network is modular and nested. We expect to find a greater contribution of fish to seed dispersal in LV forests, as longer flooding times allow more time for fish–fruit interactions.

2 | Methods

2.1 | Study Area

This study was conducted in a stretch of floodplain forest of the Solimões River known as Ilha da Paciência (03°18′12″ S; 60°13′51″ W), Central Amazonia (Figure 1a). The Solimões River supports a typical "várzea" floodplain forest, is influenced by white waters with a pH close to neutral, which is rich in suspended matter (Irion et al. 2010). The annual rainfall in the region amounts to approximately 2100 mm year^{-1}, with a marked difference between the dry (June/October) and rainy (December/May) seasons (Parolin 2000). The average (±standard deviation) of the maximum water level is 28.14 ± 1.19 m (June), and the average of the minimum water level is 16.84 ± 2.70 m (November). The absolute maximum water level is 30 m (June), and the lowest recorded is 12.14 m (November). The annual mean amplitude (difference between the minimum and subsequent maximum water level) between 2020 and 2024 was 11.3 m (Figure 1b).

2.2 | Field Sampling and Collection of Fish and Seeds

A total of 12 biweekly collections were made, with six collections in HV and six in LV, with each place (HV and LV) separated by a distance of about 1000 m. The collections were carried out between April and July 2022 and February and March 2023, which correspond to the beginning of the rising-water period and the high-water period in the Solimões River, and the period of greater production and availability of fruits and seeds, respectively (Parolin et al. 2013). Fish were sampled using a set of nine gillnets (with mesh sizes ranging from 24 to 110 mm, 10 m long, 1.5–3.0 m high), which were joined together (90 m total length). Each sampling event lasted 60 h, with day and night sampling and gillnet inspections every 4 h. For each sampling event, the nine fishing nets were placed at point locations ($N = 12$) separated by ≈400 m. Captured fish were euthanized by immersion in an anesthetic (eugenol) solution for up to 10 min until the opercular movements ceased. While in the field, the standard length and weight of the individuals were recorded, and the digestive tracts (stomach and intestines) were removed for laboratory analysis of their contents. A representative specimen of each species was labeled, stored in a Styrofoam box with ice, and sent to the National Institute for Amazonian Research (INPA) in Manaus, for taxonomic confirmation with the help of specialists. The digestive tract analysis was performed in the laboratory using a stereomicroscope (10×) in the laboratory. Intact seeds found in the digestive tract were quantified and identified by comparison with herbarium samples at the National Institute for Amazonian Research (INPA). Permits for fish collection were obtained through the Biodiversity Authorization and Information System (SISBio; protocol no. 81822-1/2022) of the Chico Mendes Institute for Biodiversity Conservation (ICMBio). The INPA's Ethics Committee for the Use of Animals in research approved this research (CEUA; #67/2022).

2.3 | Tree Composition Along the Flood Gradient

A floristic survey of all trees with a diameter at breast height (DBH) ≥ 10 cm (using a tape measure) was carried out at each topographic level (LV and HV). At each location, three plots measuring 50 × 100 m (0.5 ha) were set up, separated by a distance of 200 m. The determination of LV and HV was based on water marks left on the tree trunks (measured with a hypsometer and tape measure), representing the maximum flood level of the previous year. Water marks varying between 3 and 7.5 m correspond to the LV, and water marks ≤ 3 m correspond to the HV (Wittmann et al. 2002). Botanical voucher samples (twigs, leaves, fruits, and bark) were obtained from tree species in the plots. These samples were placed in plastic bags and transported

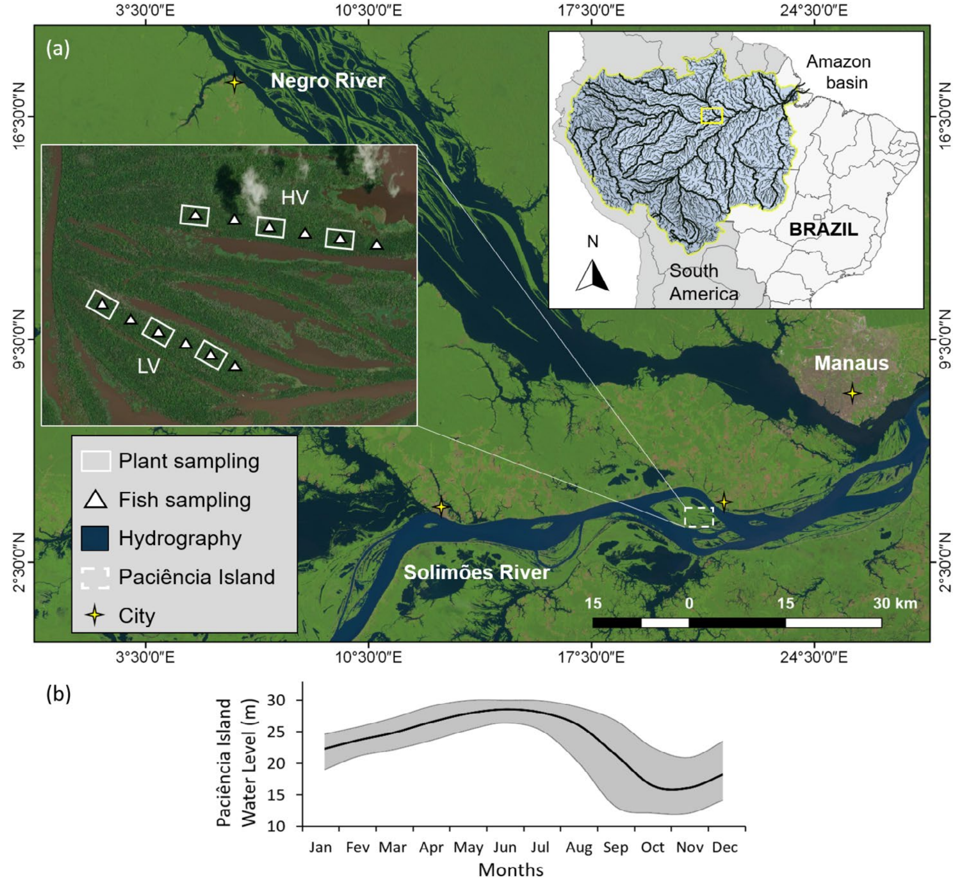

FIGURE 1 | Study area (a) located on Paciência Island in the Solimões River, showing the Low várzea (LV) and high várzea (HV). Flooding pattern on Paciência Island (b), data: Hidroweb/Brazilian National Water and Sanitation Agency—ANA; fluviometric station code 14990000 (Negro-Amazon confluence).

to the INPA's Herbarium for taxonomic identification with the help of a specialist.

2.4 | Additional Data Collection on Fruit and Seed Consumption by Fish From the Literature

To complement our field data, we compiled information from previous scientific studies on fruits and seeds of tree species consumed by fish in the Amazon basin, with occurrences (both fish and plants) in the Solimões/Amazon rivers. We searched the Web of Science database (WoS) for scientific articles on seed dispersal by fish. We used the search keyword "ichthyochory" and set the following filters: (i) only articles published in English and (ii) from 1970 to 2024. Our search resulted in a total of 64 scientific studies. Then, we manually checked each article to exclude works not carried out in the Amazon basin or in which the fruits and seeds consumed by the fish were not taxonomically identified. This reduced the number of studies to 24 (Honda 1974; Goulding 1980; Boujard et al. 1990; Kubitzki and Ziburski 1994; Maia and Chalco 2002; Knab-Vispo et al. 2003; Mannheimer et al. 2003; Silva et al. 2003a, 2003b; Claro-Jr et al. 2004; Lopes de Souza 2005; Piedade et al. 2006; Maia et al. 2007; Lucas 2008; Anderson et al. 2009; Correa et al. 2015; Weiss et al. 2016; Barbosa and Montag 2017; Freitas et al. 2018; Noronha 2018; Luque and Pinilla 2019; Lima 2023; Pereyra et al. 2023; Costa, Weiss, and Piedade 2024).

To verify the location of occurrence of tree species along the flood gradient, in addition to our field data, we used data from floristic inventories in whitewater flooded forests of the Japurá and Solimões/Amazon rivers, available in published books and articles (Ayres 2006; Assis and Wittmann 2011; Cattanio et al. 2002; Junk 1989; Lobo 2017; Parolin et al. 2010; Souza 2023; Wittmann et al. 2002, 2004, 2006, 2009, 2012; Wittmann, Parolin, et al. 2010). The validity of the scientific name for the fish species was verified in the Eschmeyer's Catalog of Fishes (http://researcharchive.calacademy.org/research/ichthyology/catalog/fishcatmain.asp) and for the tree species in the Global Biodiversity Information Facility—GBIF (https://www.gbif.org/species/6). We used only those records with a full scientific name for fruit species consumed by fish and for tree species recorded in floristic inventories. Species containing only the taxonomic genus or with a scientific name to be confirmed (e.g., "cf.") were not included in our study.

2.5 | Data Analysis

We performed a permutation *t*-test (with 9999 permutations) to assess differences between the species richness of fruits consumed by fish between LV and HV, with the *perm.t.test* function using the *MKinfer* package of R. Boxplots were generated with the *ggplot* function in the *ggpubr* package. We used a binary (presence/absence) and weighted interaction matrix, with 114 plant species (rows) and 40 fish species (columns), to construct bipartite networks, using the function *plotweb* of the *bipartite* package. Bipartite networks are important analytical tools for identifying which frugivores are most important for maintaining the structure of seed dispersal networks (Mello et al. 2011a, 2011b; Costa, Weiss, Piedade, Ferreira, and Maltchik 2024) and for quantifying and comparing network patterns statistically (Bascompte and Jordano 2007).

Network modularity analysis partitions large networks into distinct communities by optimizing subunit organization (Blondel et al. 2008). Using seeds and fruit species occurrence per fish species, we calculated modularity (Q) scores ranging from 0 to 1, where higher values indicate a stronger modular structure. The analysis was implemented using the *mod* function from the *bipartite* package in R. We set the method to implement the default Beckett algorithm, which automatically detects binary networks and applies the LPAb+ algorithm (Beckett 2016). Following Schleuning et al. (2014), we ran the *mod* function five times to obtain Q mean ± SD. To test significance, we compared observed modularity against two complementary null models, each run 1000 times. Patefield's algorithm (Patefield 1981) creates generalized networks allowing random species interactions while preserving the original number of interactions per species. Vázquez's algorithm (Vázquez et al. 2007) constrains networks by the proportion of realized links from the original network but does not retain original interaction counts. This dual approach tests whether observed modularity exceeds expectations from both randomized and structurally constrained networks. Statistical significance was determined using z-scores ($z = (Q_{\text{observed}} - \text{mean}\ (Q_{\text{NULL}}))/\text{SD}\ (Q_{\text{NULL}})$); absolute Z-score values ≥ 2 indicated significant modularity beyond random chance (Dormann and Strauss 2014).

To estimate the degree of nestedness of the binary network, we used the NODF (Nestedness based on Overlap and Decreasing Fill) metric, which ranges from 0 (not nested) to 100 (perfectly nested) (Almeida-Neto et al. 2008; Almeida-Neto and Ulrich 2011). The NODF was compared with a randomized null model 1000 times, via the *r2dtable* function of the *bipartite* package, which uses the Patefield algorithm to generate random contingency tables (Dormann et al. 2022). The significance of each network metric was further assessed using the *null.t.test* function, the real value of each metric was compared with the values from randomized networks 100 times (based on the Patefield algorithm; Dormann et al. 2022). Modularity and nestedness were considered significant when 95% or more of the random networks in the null model had values lower than those of the original network. To plot bipartite network graphs, we used the *plotModuleWeb* and *visweb* functions of the *bipartite* package. All statistical analyses were performed using the R platform (R version 4.3.1–2023).

3 | Results

Our field collections yielded a total of 5012 intact seeds from 49 tree morphotypes (34 were identified to the species level and the remaining 15 to the genus level), representing 33 tree families found in the digestive tracts of 241 frugivorous fish of 11 species. In our floristic inventories in the LV, we identified 22 tree species whose seeds are consumed by fish, whereas in the HV we identified only 13 tree species. Based on our fish collections on Paciência Island and through our literature review, we found a total of 40 fish species that consumed fruits and seeds of 188 tree species. Of these, 114 tree species were recorded on Paciência Island or in other floristic inventories along the flood gradient in várzea floodplain forests (Appendix S1). Of these tree species, 90 (57%) occurred in LV and 68 (43%) in HV, with 46 tree species (40%) exclusive to the LV, 44 species (39%) occurring in both habitats, and only 24 species (21%) exclusive to HV. The interaction networks between frugivorous fish and low and high várzea tree species (Figure 2) revealed that a few fish species consumed most fruit and seed species, including *Colossoma macropomum* ($N = 78$ species, 38%), *Piaractus brachypomus* ($N = 36$ species, 18%), and *Mylossoma albiscopum* ($N = 20$ species, 10%), all belonging to the Serrasalmidae family. The other fish species in the network ($N = 37$) consumed 34% ($N = 70$ species) of the fruit and seed species.

Although fish consumed most fruits and seeds from tree species occurring in LV, the species richness of fruits and seeds consumed by fish did not vary between LV and HV ($t = -1.039$, $\text{df} = 72$, $p = 0.322$; Figure 2a). Yet, when we considered only the tree species with restricted distribution to each forest type (LV or HV), the species richness of fruits and seeds consumed by fish was significantly higher in LV ($t = -2.170$, $\text{df} = 47$, $p = 0.015$; Figure 2b). Although the network is not significantly modular (mean observed $Q = 0.44 \pm 0.03$, $z\ \text{score}_{\text{PAT}} = 0.25$, null CI_{PAT} 2.5% and 97.5% = 0.43–0.47; $z\ \text{score}_{\text{VAZ}} = 3.95$, null CI_{VAZ} 2.5% and 97.5% = 0.41–0.44; Figure 3a), it presents a nested structure (mean observed NODF = 36.38, null CI_{PAT} 2.5% and 97.5% = 20.49–21.03; Figure 3b). No random network showed nestedness values higher than those observed in our networks.

4 | Discussion

This study presents the largest seed dispersal network for floodplain forests published to date. In addition, it demonstrates the relevance of flood depth and duration in shaping forest structure, species composition, and richness, and consequently potential fish-fruit interactions. This is relevant as the flooding regime of tropical rivers worldwide, including those in the Amazon basin, is increasingly affected by global change. Our results indicate that fish species consume a larger proportion of seeds from tree species that grow in higher and longer flooded LV. Many factors may cause a higher frequency of interaction between fish and plants restricted to LV, despite lower tree species richness compared to HV. Spatiotemporal variations in resource distribution can affect the probability of interactions (Vázquez et al. 2009; Dáttilo et al. 2014). Thus, a significant factor influencing fish-fruit interactions could be the longer flooding time experienced by tree species distributed in LV, with an average of 50–230 days year^{-1}, compared to ≥ 50 days year^{-1} for HV (Wittmann et al. 2002). After falling into the water, the fruits and seeds of many LV trees remain floating or submerged for extended periods without compromising seed germination viability (Lucas 2008). Some propagules may float for at least 2 months (Kubitzki 1985), increasing the likelihood of interactions with fish and dispersal through water and over long distances (Goulding 1983; Ziburski 1991).

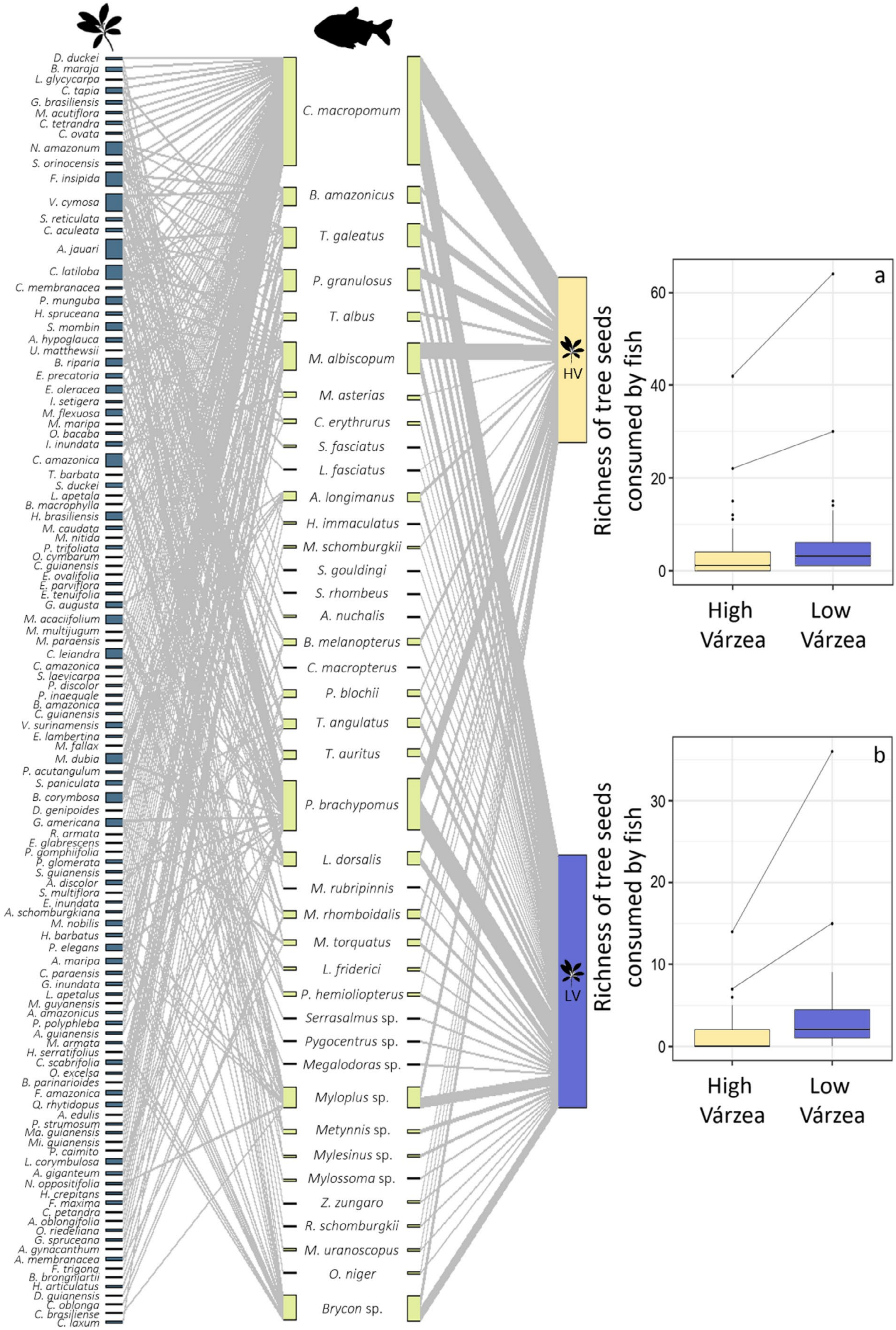

FIGURE 2 | Legend on next page.

FIGURE 2 | Network (binary) on the left showing the tree fruits and seeds consumed by each fish species, and on the right (weighted), showing the origin along the flood gradient of tree fruits and seeds consumed by fish in Amazonian floodplain forests: (a) all tree species recorded per flooded habitat, and (b) tree species with distribution restricted to each habitat (HV, high várzea; LV, low várzea).

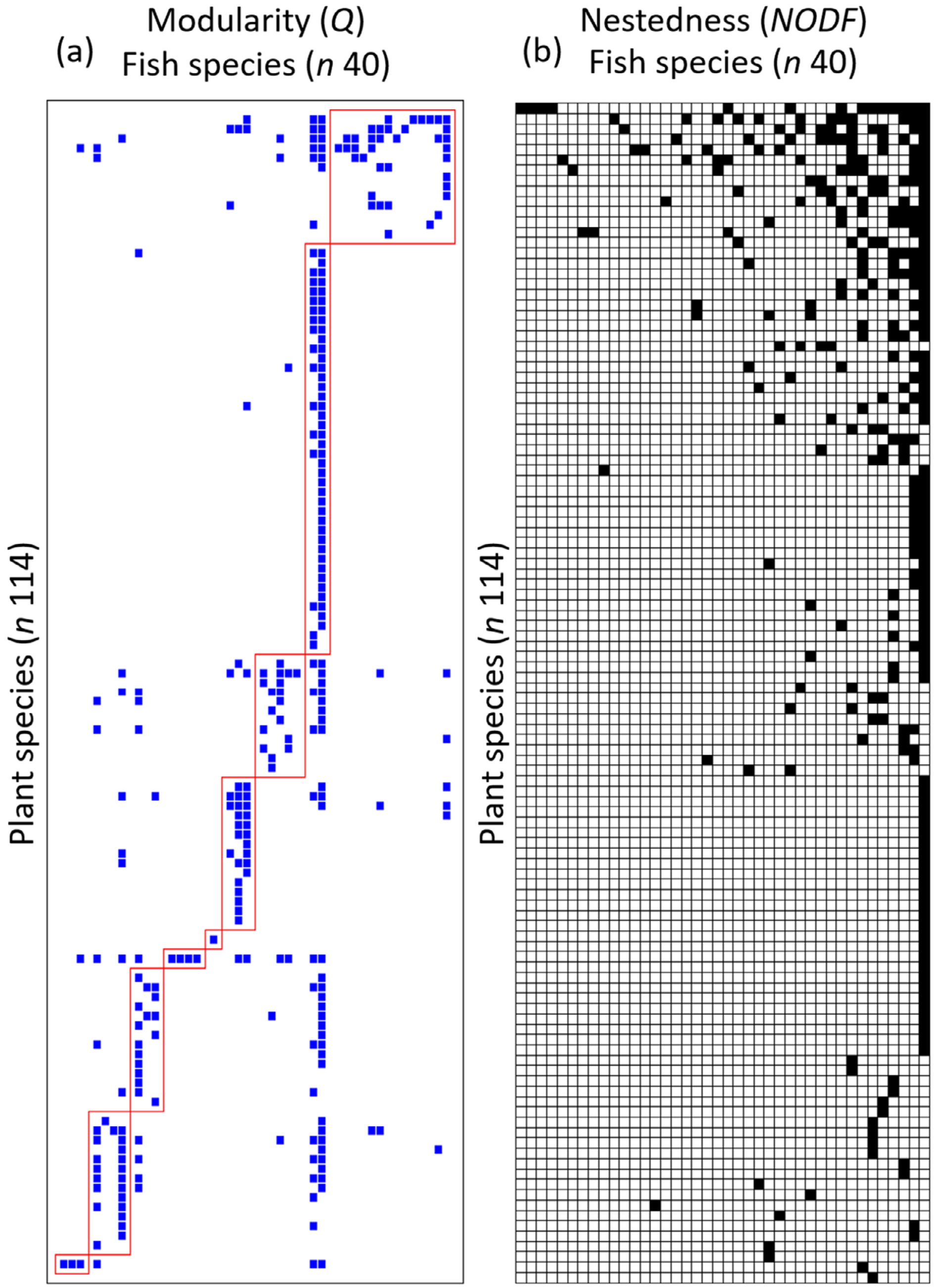

FIGURE 3 | Structure of the ichthyochory network.

Some tree species distributed in both habitats may present differences in the onset and average duration of flowering and fruiting (Ferreira 1998). For example, some tree species at lower elevations have longer flowering and fruiting period and this is better synchronized with higher inundation levels than individuals of the same species located at higher elevations within the same floodplain forest (Ferreira and Parolin 2007). To some extent, this may explain the large proportion of tree species whose seeds were ingested by fish shared between the low and high várzeas (39%), despite the relatively low number of shared tree species between both habitats (~17%), as demonstrated through floristic inventories (Wittmann et al. 2004; Wittmann, Schöngart, and Junk 2010; Householder et al. 2024). In general, floristic inventories carried out in flooded forests use abundance based indices (e.g., relative importance index) to quantify the importance of a given species across flood levels (Wittmann et al. 2006; Assis and Wittmann 2011). However, many tree species distributed across both habitats (low and high) exhibit different abundances at different locations along the gradient. For example, 76% of the individuals of *Garcinia brasiliensis* (Clusiaceae), 95% of the individuals of *Mabea nitida* (Euphorbiaceae), 88% of the individuals of *Pseudobombax munguba* (Malvaceae), and 89% of the individuals of *Symmeria paniculata* (Polygonaceae), among others, were found to occur in the LV (Assis and Wittmann 2011; Wittmann et al. 2012). Some fish species in our study ingested seeds of these species. Given the uneven distribution of tree individuals along the flooding gradient, many of these seeds are more likely to have been produced by individuals growing in LV.

Many tree species found mainly in the Amazonian floodplains also occur in adjacent “terra firme” (upland) forests, and many species typical of “terra firme” environments can be found, at least sporadically, in floodplain forests (Wittmann et al. 2012). Thus, tree species can be classified as floodplain specialists, generalists or “terra firme” specialists (Householder et al. 2024). In our study, of the 114 species of fruits and seeds recorded in fish, 67 (59%) are floodplain specialists, which are species with the most sophisticated adaptations to tolerate long floods, many of them being endemic to floodplains of Amazonian white waters (Wittmann et al. 2012; Householder et al. 2024). The endemism of many of these tree species (e.g., *Astrocaryum jauari*, *Piranhea trifoliata*, *Simaba multiflora*, *Symmeria paniculata*, *Tabebuia barbata*) consumed by fish in várzea areas may have contributed to the evolution of mutualism with frugivorous fish (e.g., Correa et al. 2018).

The evolutionary adaptations are also likely to influence fish–fruit interaction strength. Amazonian fish have evolved over tens of millions of years in flood pulse systems (Lundberg et al. 2010), where many, such as *Colossoma macropomum* and *Piaractus brachypomus*, are endemic to the Amazon and Orinoco basins and are considered important seed dispersal agents in flooded forests (Anderson et al. 2009). In our study, these two serrasalmids interacted with most of the plant species, consuming seeds mainly from tree species in the LV. Because they are specialist frugivores, they are adapted to exploit resources within the flooded forest, with their dentition adapted to break hard-shelled seeds (Goulding 1980). The fossil record of Serrasalmidae, which dates back to the Cretaceous-Paleocene, reveals dentition patterns similar to those of living taxa, suggesting that the diversification of trophic ecology occurred early in the evolution of serrasalmids (Kolmann et al. 2021). Considering that mutualistic interactions between frugivorous fish and tropical plants date back to the Late Cretaceous (~70 Ma) in South America (Thompson et al. 2014; Correa et al. 2015) and that before the establishment of the Amazon River (c. 11 Ma), the Amazon region already contained monomodal flood pulses (Hoorn et al. 1995; Figueiredo et al. 2009), it is possible that due to the longer time and height of flooding in lower topographies (Wittmann et al. 2002), these two species had more time to coevolve with tree species adapted to long-lasting inundations.

Seasonal floods in Amazonian floodplain forests affect the tree community along the flood gradient (Assis and Wittmann 2011; Wittmann et al. 2012), influencing the quantity and quality of food available within food webs (Junk 1980). As the position of a tree along the flood gradient can influence fruit production and availability (Ferreira 1998; Ferreira and Parolin 2007), the flood pulse plays a significant role in the reproduction and feeding strategies of the ichthyofauna (Bailly et al. 2008; Barbosa et al. 2018). Thus, the reproductive cycles and feeding plasticity of fish species may be important factors influencing their interaction with the tree flora. For example, fish species that migrate into flooded forests mainly at the beginning of the flooding season will have greater interaction with trees that grow on lower positions along the gradient, while fish species that occur mainly at the end of the flooding season or that enter the flooded forests later at the peak of the flood, may consume more seeds that originate from later and shorter flooded HV trees. In our study, we found many fish species ingesting seeds of a few plant species in their diet, which may result from low feeding specialization on fruits, an opportunistic strategy in which fish consume the most abundant fruit species (Horn et al. 2011), or a preference for those that taste better and provide more nutrients. Due to the ontogenetic, spatial, and individual changes in diet, combined with a vast repertoire of feeding tactics common to fish species (Abelha et al. 2001), it is challenging to recognize the relationships between fish and tree species along the flooding gradient.

The flood pulse in the Amazon floodplains is one of the main factors that influence the existence, productivity, and interactions among plants and animals (Junk et al. 1989). As a result, changes in the timing and predictability of floods can affect the evolutionary adaptations of both taxa (Lytle and Poff 2004). Currently, one of the main threats to flood regimes in the Amazon basin is climate change (Schöngart et al. 2024), and the construction of hydroelectric dams (Winemiller et al. 2016; Latrubesse et al. 2017; Timpe and Kaplan 2017; Anderson et al. 2018). Hydroelectric dams have changed the flow regime, especially the frequency and intensity of high and low pulses (Correa et al. 2022), significantly increasing the annual minimum levels and decreasing the annual amplitude in floodable areas downstream of the dam (Assahira et al. 2017). These abrupt changes in the hydrological regime can cause massive mortality of tree species and seedlings in the lower floodplain topographies due to several consecutive years of flooding along river stretches of up to 120 km downstream the dams (Assahira et al. 2017; Resende et al. 2019; Rocha et al. 2020). Similarly, flow regime regulation can reduce maximum water levels and affect higher floodplain topographies (Schöngart et al. 2021). Such changes could reduce the availability of fruits and seeds of tree species at higher elevations, such as those in the HV, and potentially affect the consumption and seed dispersal of these species by frugivorous fish. These interactions can also be influenced by changes in the hydrological cycle in different years, due to the intensification of extreme drought and flood events recently observed in the Amazon basin (Barichivich et al. 2018; Fleischmann et al. 2023; Espinoza et al. 2024; Schöngart et al. 2024). For example, in years with records of extreme floods, the fruits and seeds of trees species in the HV may remain available for fish for longer time, while in years in which the HV does not flood, the availability of fruits and seeds for fish may decrease.

Our analysis of the seed dispersal network revealed a significantly nested structure across LV and HV forests. In flooded forests, interactions between fish and plants often have a nested structure, in which a few frugivore species consume fruits and seeds of many plant species while most other frugivores consume less (Correa et al. 2016; Costa, Weiss, Piedade, Ferreira, and Maltchik 2024). The lack of modularity is not surprising, given that the three fish species (*C. macropomum*, *P. brachypomus*, and *M. albiscopum*) that consume the fruits of most species are distributed across both LV and HV (see Figure 2). Nevertheless, the observed nested pattern indicates that the mutualistic network between fish and flooded forests is generally robust to random species extinctions (Memmott et al. 2004; Pocock et al. 2012), although potentially susceptible to species loss, particularly of the most specialized fish (Araujo et al. 2021). In Amazonian aquatic environments, a myriad of perturbations produced by human activities, such as climate change (extreme drought and flood events), hydroelectric dams (Barichivich et al. 2018; Flecker et al. 2022; Schöngart et al. 2024), water pollution through mining and/or domestic and industrial wastewaters (Wittmann et al. 2015), and large-scale deforestation and selective logging of fruit-producing trees in floodplain forests (Renó et al. 2016; Renó and Novo 2019), can lead to local extinction or severe reductions in the abundance of species along the flood gradient (Castello and Macedo 2016; Duponchelle et al. 2021), hence altering the structure of seed dispersal networks.

In our study, we found 188 tree species whose seeds were ingested by fish, and for 40% of them, we were unable to determine the occurrence position along the flood gradient. Given the extent of the Amazonian floodplains, significant geographic gaps in floristic knowledge remain, including the Amazon/Solimões River, particularly along the main tributaries, such as the Madeira, Purus, and Juruá Rivers (Hopkins 2007). In addition, limitations in the complete taxonomic identification of tree species that occur along the flood gradient and the fruits and seeds consumed by fish make it difficult to carry out a more comprehensive analysis of the seed dispersal network in Amazonian floodplains. Although challenging, these floristic inventories are essential for generating detailed information on the complex spatial distribution of many of these species, which is still limited (Prance 1994; Cardoso et al. 2017).

Our results have important implications for the conservation of floodplain forests and frugivorous fish, as they indicate that changes in river flooding regimes caused by damming or climate change have the potential to negatively impact floodplain forests adapted to low and high várzeas and, consequently, the seed dispersal by frugivorous fish, which plays an important role in the recolonization and regeneration of these forests (Correa et al. 2015). Although most forest inventories have found greater tree richness in the HV (Assis and Wittmann 2011; Wittmann et al. 2012), our study highlights the importance of LV forests for ichthyochory and food webs.

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Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

The data and code that support the findings of this study are openly available in a public Figshare repository: https://doi.org/10.6084/m9.figshare.31906855.

References

Abelha, M. C. F., A. A. Agostinho, and E. Goulart. 2001. "Plasticidade trófica em peixes de água doce." *Acta Scientiarum* 23, no. 2: 425–434. https://doi.org/10.4025/actascibiolsci.v23i0.2696.

Almeida-Neto, M., P. Guimarães, P. R. Guimarães, R. D. Loyola, and W. Ulrich. 2008. "A Consistent Metric for Nestedness Analysis in Ecological Systems: Reconciling Concept and Measurement." *Oikos* 117: 1227–1239. https://doi.org/10.1111/j.0030-1299.2008.16644.x.

Almeida-Neto, M., and W. Ulrich. 2011. "A Straightforward Computational Approach for Measuring Nestedness Using Quantitative Matrices." *Environmental Modelling & Software* 26: 173–178. https://doi.org/10.1016/j.envsoft.2010.08.003.

Anderson, E. P., C. N. Jenkins, S. Heilpern, et al. 2018. "Fragmentation of Andes-to-Amazon Connectivity by Hydropower Dams." *Science Advances* 4, no. 1: eaao1642. https://doi.org/10.1126/sciadv.aao1642.

Anderson, J. T., J. Saldaña Rojas, and A. S. Flecker. 2009. "High-Quality Seed Dispersal by Fruit Eating Fishes in Amazonian Floodplain Habitats." *Oecologia* 161: 279–290. https://doi.org/10.1007/s00442-009-1371-4.

Araujo, J. M., S. B. Correa, J. Penha, J. Anderson, and A. Traveset. 2021. "Implications of Overfishing of Frugivorous Fishes for Cryptic Function Loss in a Neotropical Floodplain." *Journal of Applied Ecology* 58: 1499–1510. https://doi.org/10.1111/1365-2664.13891.

Assahira, C., A. F. Resende, S. E. Trumbore, F. Wittmann, B. B. L. Cintra, and E. S. Batista. 2017. "Tree Mortality of a Flood-Adapted Species in Response of Hydrographic Changes Caused by Na Amazonian River Dam." *Forest Ecology and Management* 396: 113–123. https://doi.org/10.1016/j.foreco.2017.04.016.

Assis, R. L., and F. Wittmann. 2011. "Forest Structure and Tree Species Composition of the Understory of Two Central Amazonian Várzea Forests of Contrasting Flood Heights." *Flora* 206: 251–260. https://doi.org/10.1016/j.flora.2010.11.002.

Ayres, J. M. C. 2006. *As matas de várzea do Mamirauá*. 3rd ed. MCT-CNPq-Programa do Trópico Úmido, Sociedade Civil de Mamirauá.

Bailly, D., A. A. Agostinho, and H. I. Suzuki. 2008. "Influence of the Flood Regime on the Reproduction of Fish Species With Different Reproductive Strategies in the Cuiabá River, Upper Pantanal, Brazil." *River Research and Applications* 24, no. 9: 1218–1229. https://doi.org/10.1002/rra.1147.

Barbosa, T. A. P., and L. F. A. Montag. 2017. "The Role of *Lithodoras dorsalis* (Siluriformes: Doradidae) as Seed Disperser in Eastern Amazon." *Neotropical Ichthyology* 15, no. 2: e160061. https://doi.org/10.1590/1982-0224-20160061.

Barbosa, T. A. P., D. C. O. Rosa, B. E. Soares, C. H. A. Costa, M. C. Esposito, and L. F. A. Montag. 2018. "Effect of Flood Pulses on the Trophic Ecology of Four Piscivorous Fishes From the Eastern Amazon." *Journal of Fish Biology* 93, no. 1: 30–39. https://doi.org/10.1111/jfb.13669.

Barichivich, J., E. Gloor, P. Peylin, et al. 2018. "Recent Intensification of Amazon Flooding Extremes Driven by Strengthened Walker Circulation." *Science Advances* 4: eaat8785. https://doi.org/10.1126/sciadv.aat8785.

Bartel, S. L., and J. L. Orrock. 2022. "The Important Role of Animal Social Status in Vertebrate Seed Dispersal." *Ecology Letters* 25: 1094–1109. https://doi.org/10.1111/ele.13988.

Bascompte, J., and P. Jordano. 2007. "Plant–Animal Mutualistic Networks: The Architecture of Biodiversity." *Annual Review of Ecology, Evolution, and Systematics* 38: 567–593. https://doi.org/10.1146/annurev.ecolsys.38.091206.095818.

Beckett, S. J. 2016. "Improved Community Detection in Weighted Bipartite Networks." *Royal Society Open Science* 3: 140536. https://doi.org/10.1098/rsos.140536.

Blondel, V. D., J. L. Guillaume, R. Lambiotte, and E. Lefebvre. 2008. "Fast UnFolding of Communities in Large Networks." *Journal of Statistical Mechanics: Theory and Experiment* 2008: 10008. https://doi.org/10.1088/1742-5468/2008/10/P10008.

Boujard, T., D. Sabatier, R. Rojas-Beltran, M. F. Prevost, and J. F. Renno. 1990. "The Food Habits of Three Allochthonous Feeding Characoids in French Guiana." *Revue d'Ecologie (La Terre et la Vie)* 45: 247–258.

Burgos, E., H. Ceva, R. P. J. Perazzo, et al. 2007. "Why Nestedness in Mutualistic Networks?" *Journal of Theoretical Biology* 249: 307–313. https://doi.org/10.1016/j.jtbi.2007.07.030.

Cardoso, D., T. Särkinen, S. Alexander, et al. 2017. "Amazon Plant Diversity Revealed by a Taxonomically Verified Species List." *Proceedings of the National Academy of Sciences of the United States of America* 114: 10695–10700. https://doi.org/10.1073/pnas.1706756114.

Castello, L., and M. N. Macedo. 2016. "Large-Scale Degradation of Amazonian Freshwater Ecosystems." *Global Change Biology* 22, no. 3: 990–1007. https://doi.org/10.1111/gcb.13173.

Cattanio, J. H., A. B. Anderson, and M. S. Carvalho. 2002. "Floristic Composition and Topographic Variation in a Tidal Floodplain Forest in the Amazon Estuary." *Revista Brasileira de Botânica* 25, no. 4: 419–430.

Claro-Jr, L., E. Ferreira, J. Zuanon, and C. Araujo-Lima. 2004. "O efeito da floresta alagada na alimentação de três espécies de peixes onívoros em lagos de várzea da Amazônia Central, Brasil." *Acta Amazonica* 34, no. 1: 133–137. https://doi.org/10.1590/s0044596720040001000018.

Correa, S. B., J. K. Araujo, J. Penha, C. Nunes da Cunha, K. E. Bobier, and J. T. Anderson. 2016. "Stability and Generalization in Seed Dispersal Networks: A Case Study of Frugivorous Fish in Neotropical Wetlands." *Proceedings of the Royal Society B: Biological Sciences* 283: 20161267. https://doi.org/10.1098/rspb.2016.1267.

Correa, S. B., K. V. Coronado-Franco, C. Jézéquel, et al. 2025. "Floodplain Forests Drive Fruit-Eating Fish Diversity at the Amazon Basin-Scale." *Proceedings of the National Academy of Sciences of the United States of America* 122, no. 3: e2414416122. https://doi.org/10.1073/pnas.2414416122.

Correa, S. B., R. Costa-Pereira, T. Fleming, M. Goulding, and J. T. Anderson. 2015. "Neotropical Fish–Fruit Interactions: Eco-Evolutionary Dynamics and Conservation." *Biological Reviews* 90, no. 4: 1263–1278. https://doi.org/10.1111/brv.12153.

Correa, S. B., P. C. de Oliveira, C. Nunes da Cunha, J. Penha, and J. T. Anderson. 2018. "Water and Fish Select for Fleshy Fruits in Tropical Wetland Forests." *Biotropica* 50, no. 2: 312–318. https://doi.org/10.1111/btp.12524.

Correa, S. B., P. Van Der Sleen, S. F. Siddiqui, et al. 2022. "Biotic Indicators for Ecological State Change in Amazonian Floodplains." *Bioscience* 72, no. 8: 753–768. https://doi.org/10.1093/biosci/biac038.

Correa, S. B., K. O. Winemiller, H. Lopez-Fernandez, and M. Galetti. 2007. "Evolutionary Perspectives on Seed Consumption and Dispersal by Fishes." *Bioscience* 57: 748–756. https://doi.org/10.1641/B570907.

Correa, S. B. 2012. *Trophic Ecology of Frugivorous Fishes in Floodplain Forests of the Colombian Amazon*. (Thesis), 167. Texas A&M University.

Costa, G., M. T. F. Piedade, E. J. Ferreira, and L. Maltchik. 2023. "The Effectiveness of Ichthyochoric Dispersal in Forested Wetlands of the Amazon Depends on the Species of Fish and Its Size." *Forest Ecology and Management* 549: 121481. https://doi.org/10.1016/j.foreco.2023.121481.

Costa, G., B. Weiss, and M. T. F. Piedade. 2024. "Larger Fish Disperse Larger Seeds in Oligotrophic Wetlands of the Central Amazon." *Wetlands* 44: 18. https://doi.org/10.1007/s13157-024-017797.

Costa, G., B. Weiss, M. T. F. Piedade, E. J. Ferreira, and L. Maltchik. 2024. "Structure and Vulnerability of the Ichthyochory Network in Wetland Forests of Central Amazonia." *Ecology of Freshwater Fish* 33: e12780. https://doi.org/10.1111/eff.12780.

Dagosta, F. C. P., and M. De Pinna. 2019. "The Fishes of the Amazon: Distribution and Biogeographical Patterns, With a Comprehensive List of Species." *Bulletin of the American Museum of Natural History* 2019: 1. https://doi.org/10.1206/0003-0090.431.1.1.

Dáttilo, W., R. Fagundes, C. A. Q. Gurka, et al. 2014. "Individual Based Ant-Plant Networks: Diurnal-Nocturnal Structure and Species-Area Relationship." *PLoS One* 9: e99838. https://doi.org/10.1371/journal.pone.0099838.

Dormann, C. F., J. Fruend, B. Gruber, et al. 2022. "Package 'bipartite'—Visualising Bipartite Networks and Calculating Some (Ecological) Indices." 181 p. https://cran.r-project.org/web/packages/bipartite/bipartite.pdf.

Dormann, C. F., and R. Strauss. 2014. "A Method for Detecting Modules in Quantitative Bipartite Networks." *Methods in Ecology and Evolution* 5: 90–98. https://doi.org/10.1111/2041210X.12139.

Duponchelle, F., V. J. Isaac, C. R. Da Costa Doria, et al. 2021. "Conservation of Migratory Fishes in the Amazon Basin." *Aquatic Conservation: Marine and Freshwater Ecosystems* 31: 1087–1105. https://doi.org/10.1002/aqc.3550.

Espinoza, J. C., J. C. Jimenez, J. A. Marengo, et al. 2024. "The New Record of Drought and Warmth in the Amazon in 2023 Related to Regional and Global Climatic Features." *Scientific Reports* 14: 8107. https://doi.org/10.1038/s41598-024-58782-5.

Fassoni-Andrade, A. C., A. S. Fleischmann, F. Papa, et al. 2021. "Amazon Hydrology From Space: Scientific Advances and Future Challenges." *Reviews of Geophysics* 59, no. 4: e2020RG000728. https://doi.org/10.1029/2020RG000728.

Ferreira, L. V. 1997. "Effects of the Duration of Flooding on Species Richness and Floristic Composition in Three Hectares in the Jaú National Park in Floodplain Forests in Central Amazonia." *Biodiversity and Conservation* 6: 1353–1363.

Ferreira, L. V. 1998. "Intraspecific Variation in Phenology in Relation to Flooding Duration in *Eschweilera parviflora* (Lecythidaceae) in Central Amazonian Floodplain Forest." *Anais da Academia Brasileira de Ciências* 70: 1–4.

Ferreira, L. V., and P. Parolin. 2007. "Tree Phenology in Central Amazonian Floodplain Forests: Effects of Water Level Fluctuation and Precipitation at Community and Population Level." *Pesquisas Botânica* 58: 139–156.

Figueiredo, J., C. Hoorn, P. van der Ven, and E. Soares. 2009. "Late Miocene Onset of the Amazon River and the Amazon Deep-Sea Fan: Evidence From the Foz do Amazonas Basin." *Geology* 37: 619–622. https://doi.org/10.1130/G25567A.1.

Flecker, A. S., Q. Shi, R. M. Almeida, et al. 2022. "Reducing Adverse Impacts of Amazon Hydropower Expansion." *Science* 375, no. 6582: 753–760. https://doi.org/10.1126/science.abj4017.

Fleischmann, A. S., F. Papa, S. K. Hamilton, et al. 2023. "Increased Floodplain Inundation in the Amazon Since 1980." *Environmental*

Research Letters 18, no. 3: 34024. https://doi.org/10.1088/1748-9326/acb9a7.

Fleming, T. H., R. Breitwish, and G. H. Whitesides. 1987. "Patterns of Tropical Vertebrate Frugivore Diversity." *Annual Review of Ecology and Systematics* 18: 91–109.

Freitas, T. M. S., V. H. C. Almeida, and L. F. A. Montag. 2018. "Evidence of Seed Dispersal of *Virola surinamensis* (Myristicaceae) by a Catfish in Eastern Amazonia, Brazil." *Boletim do Museu Paraense Emílio Goeldi, Ciências Naturais* 13, no. 2: 213–219.

Gottsberger, G. 1978. "Seed Dispersal by Fish in the Inundated Regions of Humaitá, Amazonia." *Biotropica* 10: 170–183.

Goulding, M. 1980. *The Fishes and the Forest: Explorations in Amazonian Natural History*. University of California Press.

Goulding, M. 1983. "The Role of Fish in Seed Dispersal and Plant Distribution in Amazonian Floodplains Ecosystems." In *Dispersal and Distribution*, edited by K. Kubitzki, 271–284. Verlag Paul Parey.

Haugaasen, T., and C. A. Peres. 2005. "Tree Phenology in Adjacent Amazonian Flooded and Unflooded Forests." *Biotropica* 37: 620–630.

Hawes, J. E., and C. A. Peres. 2016. "Patterns of Plant Phenology in Amazonian Seasonally Flooded and Unflooded Forests." *Biotropica* 48: 465–475.

Herrera-R, G. A., S. A. Heilpern, T. B. Couto, et al. 2024. "A Synthesis of the Diversity of Freshwater Fish Migrations in the Amazon Basin." *Fish and Fisheries* 25: 114–133. https://doi.org/10.1111/faf.12795.

Honda, E. M. S. 1974. "Contribuicão ao conhecimento da biologia de peixes do Amazonas: II. Alimentacão do tambaqui, *Colossoma bidens*." *Acta Amazonica* 4: 47–53.

Hoorn, C., J. Guerrero, G. A. Sarmiento, and M. A. Lorente. 1995. "Andean Tectonics as a Cause for Changing Drainage Patterns in Miocene Northern South America." *Geology* 23: 237–240. https://doi.org/10.1130/0091-7613(1995)023<0237:ATAACF>2.3.CO;2.

Hopkins, M. J. G. 2007. "Modelling the Known and Unknown Plant Biodiversity of the Amazon Basin." *Journal of Biogeography* 34: 1400–1411. https://doi.org/10.1111/j.1365-2699.2007.01737.x.

Horn, M., S. B. Correa, P. Parolin, et al. 2011. "Seed Dispersal by Fishes in Tropical and Temperate Fresh Waters: The Growing Evidence." *Acta Oecologica* 37: 561–577. https://doi.org/10.1016/j.actao.2011.06.004.

Householder, J. E., J. Schöngart, M. T. F. Piedade, et al. 2021. "Modeling the Ecological Responses of Tree Species to the Flood Pulse of the Amazon Negro River Floodplains." *Frontiers in Ecology and Evolution* 9: 628606. https://doi.org/10.3389/fevo.2021.628606.

Householder, J. E., F. Wittmann, J. Schöngart, et al. 2024. "One Sixth of Amazonian Tree Diversity Is Dependent on River Floodplains." *Nature Ecology & Evolution* 8: 901–911. https://doi.org/10.1038/s41559-024-02364-1.

Howe, H. 1984. "Implications of Seed Dispersal by Animals for Tropical Reserve Management." *Biological Conservation* 30, no. 3: 261–281. https://doi.org/10.1016/0006-3207(84)90087-9.

Howe, H. F., and J. Smallwood. 1982. "Ecology of Seed Dispersal." *Annual Review of Ecology and Systematics* 13: 201–228. https://doi.org/10.1146/annurev.es.13.110182.001221.

Irion, G., J. Mello, J. Morais, M. T. F. Piedade, W. J. Junk, and L. Garming. 2010. "Development of the Amazon Valley During the Middle to Late Quaternary: Sedimentological and Climatological Observations." In *Amazonian Floodplain Forest: Ecophysiology, Biodiversity and Sustainable Management*, edited by W. J. Junk, M. T. F. Piedade, F. Wittmann, J. Schöngart, and P. Parolin, 27–42. Springer.

Janzen, D. H. 1983. "Seed and Pollen Dispersal by Animals: Convergence in the Ecology of Contamination and Sloppy Harvest." *Biological Journal of the Linnean Society* 20, no. 1: 103–113. https://doi.org/10.1111/j.1095-8312.1983.tb01592.x.

Jordano, P. 2000. "Fruits and Frugivory." In *Seeds: The Ecology of Regeneration in Plant Communities*, edited by M. Fenner, 125–166. CABI.

Junk, W. J. 1980. "Áreas inundáveis: um desafio para a limnologia." *Acta Amazonica* 10, no. 4: 775–796.

Junk, W. J. 1989. "Flood Tolerance and Tree Distribution in Central Amazonian Floodplains." In *Tropical Forest: Botanical Dynamics, Speciation and Diversity*, edited by L. B. Holm-Nielsen, I. C. Nielsen, and H. Balslev, 47–64. Academic Press.

Junk, W. J., P. B. Bayley, and R. E. Sparks. 1989. "The Flood Pulse Concept in River Floodplain Systems." In *Proceedings of the International Large River Symposium*, edited by D. P. Dodge, 110–127. Canadian Special Publication in Fisheries and Aquatic Sciences.

Junk, W. J., and M. T. F. Piedade. 2010. "An Introduction to South American Wetland Forests: Distribution, Definitions and General Characterization." In *Amazon Floodplain Forests: Ecophysiology, Biodiversity and Sustainable Management*, edited by W. J. Junk, M. T. F. Piedade, F. Wittmann, J. Schöngart, and P. Parolin, 3–25. Ecological Studies 210. Springer Verlag.

Junk, W. J., M. T. F. Piedade, J. Schöngart, M. Cohn-Haft, J. M. Adeney, and F. Wittmann. 2011. "A Classification of Major Naturally-Occurring Amazonian Lowland Wetlands." *Wetlands* 31: 623–640. https://doi.org/10.1007/s13157-011-0190-7.

Knab-Vispo, C., F. Daza, C. R. Vispo, and N. González. 2003. "The Diet of Morocoto (*Piaractus brachypomus*) in the Lower Rio Caura in Relation to Its Ecological Role and Its Conservation." *Scientia Guaianae* 12: 367–391.

Kolmann, M. A., L. C. Hughes, L. P. Hernandez, et al. 2021. "Phylogenomics of Piranhas and Pacus (Serrasalmidae) Uncovers How Dietary Convergence and Parallelism Obfuscate Traditional Morphological Taxonomy." *Systematic Biology* 70: 576–592. https://doi.org/10.1093/sysbio/syaa065.

Kubitzki, K. 1985. "The Dispersal of Forest Plants." In *Amazonia-Key Environments*, edited by G. T. Prance and T. E. Lovejoy, 129–163. Pergamon.

Kubitzki, K., and A. Ziburski. 1994. "Seed Dispersal in Floodplain Forests of Amazonia." *Biotropica* 26: 30–43. https://doi.org/10.2307/2389108.

Latrubesse, E. M., E. Y. Arima, T. Dunne, et al. 2017. "Damming the Rivers of the Amazon Basin." *Nature* 546: 363–369. https://doi.org/10.1038/nature22333.

Lima, M. J. F. 2023. "Consumo e dispersão de sementes por peixes em floresta de igapó da reserva de desenvolvimento sustentável do tupé, Manaus, Amazonas—Brasil." Dissertação, Universidade Federal do Amazonas—UFAM. 77 p.

Lobo, G. S. 2017. "A alteração do regime hidrológico afeta a composição florística e estrutura de florestas de igapó? Um estudo comparativo entre um rio regulado e outro prístino na Reserva de Desenvolvimento Sustentável do Uatumã, Amazônia Central." Diss. Instituto Nacional de Pesquisas da Amazônia—INPA. 82 p.

Lopes de Souza, L. 2005. "Frugivoria e dispersão de sementes por peixes na reserva de desenvolvimento sustentável Amanã." *Uakari* 1: 9–17.

Lucas, C. M. 2008. "Within Flood Season Variation in Fruit Consumption and Seed Dispersal by Two Characin Fishes of the Amazon." *Biotropica* 40: 581–589. https://doi.org/10.1111/j.17447429.2008.00415.x.

Lundberg, J. G., M. H. Sabaj Pérez, W. M. Dahdul, and O. A. Aguilera. 2010. "The Amazonian Neogene Fish Fauna." In *Amazonia: Landscape and Species Evolution: A Look Into the Past*, edited by C. Hoorn and F. P. Wesselingh, 281–301. Blackwell Publishing.

Luque, F. J., and G. A. Pinilla. 2019. "Juveniles of the Overexploited Amazonian Fish *Colossoma macropomum* (Characiformes: Serrasalmidae) as Potential Seed Dispersers of *Cecropia* spp." *Revista de Biología Tropical* 67: 654–666. https://doi.org/10.15517/rbt.v67i3.34925.

Lytle, D. A., and N. L. Poff. 2004. “Adaptation to Natural Flow Regimes.” *Trends in Ecology and Evolution* 19: 94–100.

Maia, L. A., L. M. Santos, and P. Parolin. 2007. “Germinação de sementes de *Bothriospora corymbosa* (Rubiaceae) recuperadas do trato digestório de *Triportheus angulatus* (sardinha) no Lago Camaleão, Amazônia Central.” *Acta Amazonica* 37, no. 3: 321–326. https://doi.org/10.1590/S0044-59672007000300002.

Mannheimer, S., G. Bevilacqua, E. P. Caramaschi, and F. R. Scarano. 2003. “Evidence for Seed Dispersal by the Catfish *Auchenipterichthys longimanus* in an Amazonian Lake.” *Journal of Tropical Ecology* 19: 215–218. https://doi.org/10.1017/S0266467403003249.

Mateus, L., R. M. Rodrigues Costa, and J. Penha. 2022. “Spatiotemporal Diet Shifting in a Neotropical Fish Species: The Role of Riparian Vegetation and Seasonal Inundation.” *Frontiers in Environmental Science* 10: 883298. https://doi.org/10.3389/fenvs.2022.883298.

Melack, J. M., and L. L. Hess. 2010. “Remote Sensing of the Distribution and Extent of Wetlands in the Amazon Basin.” In *Central Amazonian Floodplain Forests: Ecophysiology, Biodiversity and Sustainable Management*, edited by W. J. Junk, M. T. F. Piedade, F. Wittmann, J. Schöngart, and P. Parolin, 43–59. Springer.

Mello, M. A. R., F. M. D. Marquitti, P. R. Guimarães Jr., E. K. V. Kalko, P. Jordano, and M. A. M. Aguiar. 2011a. “The Modularity of Seed Dispersal: Differences in Structure and Robustness Between Bat and Bird–Fruit Networks.” *Oecologia* 167: 131–140. https://doi.org/10.1007/s00442-011-1984-2.

Mello, M. A. R., F. M. D. Marquitti, P. R. Guimarães Jr., E. K. V. Kalko, P. Jordano, and M. A. M. De Aguiar. 2011b. “The Missing Part of Seed Dispersal Networks: Structure and Robustness of Bat-Fruit Interactions.” *PLoS One* 6: e17395. https://doi.org/10.1371/journal.pone.0017395.

Memmott, J., N. M. Waser, and M. V. Price. 2004. “Tolerance of Pollination Networks to Species Extinctions.” *Proceedings of the Royal Society B: Biological Sciences* 271: 2605–2611. https://doi.org/10.1098/rspb.2004.2909.

Noronha, F. A. 2018. “Assembleias de peixes consumidoras de frutos e dispersoras de sementes em uma área de igapó da Amazônia Central, Brasil.” Dissertação, Universidade Federal do Amazonas—UFAM. 71 p.

Olesen, J. M., J. Bascompte, Y. L. Dupont, and P. Jordano. 2007. “The Modularity of Pollination Networks.” *Proceedings of the National Academy of Sciences* 104: 19891–19896. https://doi.org/10.1073/pnas.0706375104.

Parolin, P. 2000. “Phenology and CO2-Assimilation of Trees in Central Amazonian Floodplains.” *Journal of Tropical Ecology* 16: 465–473. https://doi.org/10.1017/S0266467400001516.

Parolin, P., N. Armbrüster, F. Wittmann, L. V. Ferreira, M. T. F. Piedade, and W. J. Junk. 2002. “A Review of Tree Phenology in Central Amazonian Floodplains.” *Botanica* 52: 195–222.

Parolin, P., F. Wittmann, and L. V. Ferreira. 2013. “Fruit and Seed Dispersal in Amazonian Floodplain Trees—A Review.” *Ecotropica* 19: 15–32.

Parolin, P., F. Wittmann, and J. Schöngart. 2010. “Tree Phenology in Amazonian Floodplain Forests.” In *Central Amazonian Floodplain Forests: Ecophysiology, Biodiversity and Sustainable Management*, edited by W. J. Junk, M. T. F. Piedade, F. Wittmann, J. Schöngart, and P. Parolin, 61–102. Springer. https://doi.org/10.1007/978-90-481-8725-6_5.

Patefield, W. M. 1981. “Efficient Method of Generating Random R x C Tables With Given Row and Column Totals: Algorithm AS 159.” *Applied Statistics* 30, no. 1: 91–97.

Pereyra, P. E. R., G. Hallwass, A. Begossi, L. L. Giacomin, and R. A. M. Silvano. 2023. “Fishers' Knowledge Reveals Ecological Interactions Between Fish and Plants in High Diverse Tropical Rivers.” *Ecosystems* 26: 1095–1107. https://doi.org/10.1007/s10021-023-00818-4.

Piedade, M. T. F., P. Parolin, and W. J. Junk. 2006. “Phenology, Fruit Production and Seed Dispersal of *Astrocaryum jauari* (Arecaceae) in Amazonian Blackwater Foodplains.” *Revista de Biología Tropical* 54: 1171–1178. https://doi.org/10.15517/rbt.v54i4.3094.

Pocock, M. J. O., D. M. Evans, and J. Memmott. 2012. “The Robustness and Restoration of a Network of Ecological Networks.” *Science* 335: 973–977. https://doi.org/10.1126/science.1214915.

Prance, G. T. 1994. “A Comparison of the Efficacy of Higher Taxa and Species Numbers in the Assessment of Biodiversity in the Neotropics.” *Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences* 345: 89–99.

Renó, V., E. Novo, and M. Escada. 2016. “Forest Fragmentation in the Lower Amazon Floodplain: Implications for Biodiversity and Ecosystem Service Provision to Riverine Populations.” *Remote Sensing* 8, no. 11: 886. https://doi.org/10.3390/rs8110886.

Renó, V., and E. Novo. 2019. “Forest Depletion Gradient Along the Amazon Floodplain.” *Ecological Indicators* 98: 409–419. https://doi.org/10.1016/j.ecolind.2018.11.019.

Resende, A. F., J. Schöngart, A. S. Streher, J. Ferreira-Ferreira, M. T. F. Piedade, and T. S. F. Silva. 2019. “Massive Tree Mortality From Flood Pulse Disturbances in Amazonian Floodplain Forests: The Collateral Effects of Hydropower Production.” *Science of the Total Environment* 659: 587–598. https://doi.org/10.1016/j.scitotenv.2018.12.208.

Rocha, M., Y. O. Feitosa, F. Wittmann, M. T. F. Piedade, A. F. Resende, and R. L. Assis. 2020. “River Damming Affects Seedling Communities of a Floodplain Forest in the Central Amazon.” *Acta Botânica Brasílica* 34, no. 1: 192–203. https://doi.org/10.1590/0102-33062019abb0263.

Schleuning, M., L. Ingmann, R. Strauss, et al. 2014. “Ecological, Historical and Evolutionary Determinants of Modularity in Weighted Seed-Dispersal Networks.” *Ecology Letters* 17, no. 4: 454–463.

Schöngart, J., and W. J. Junk. 2007. “Forecasting the Floodpulse in Central Amazonia by ENSO Indices.” *Journal of Hydrology* 335: 124–132.

Schöngart, J., M. T. F. Piedade, S. Ludwigshausen, V. Horna, and M. Worbes. 2002. “Phenology and Stem-Growth Periodicity of Tree Species in Amazonian Floodplain Forests.” *Journal of Tropical Ecology* 18: 581–597. https://doi.org/10.1017/S0266467402002389.

Schöngart, J., F. Wittmann, W. J. Junk, et al. 2024. “Fate of Floodplain Forests in a Changing Amazon.” In *The Future of Amazonian Aquatic Biota*, edited by S. S. de Souza, S. Braz-Mota, and A. L. Val, 163–222. Springer. https://doi.org/10.1007/978-3-031-66822-7_7.

Schöngart, J., F. Wittmann, A. F. Resende, et al. 2021. “The Shadow of the Balbina Dam: A Synthesis of Over 35 Years of Downstream Impacts on Floodplain Forests in Central Amazonia.” *Aquatic Conservation* 31, no. 5: 1117–1135. https://doi.org/10.1002/aqc.3526.

Silva, G. G., M. A. Pizo, A. J. Green, E. Sebastián-González, L. Bugoni, and L. Maltchik. 2023. “A Waterfowl Seed-Dispersal Network From the Neotropical Region Is Nested and Modular.” *Biotropica* 55: 480–488. https://doi.org/10.1111/btp.13202.

Silva, J. A. M., M. Pereira-Filho, and M. I. Oliveria-Pereira. 2003a. “Frutos e sementes consumidos pelo Tambaqui, *Colossoma macrompum* (Cuvier, 1818) incorporados em rações. Digestibilidade e velocidade de trânsito pelo trato gastrointestinal.” *Revista Brasileira de Zootecnia* 32, no. 6: 1815–1824. https://doi.org/10.1590/S1516-35982003000800003.

Silva, J. A. M., M. Pereira-Filho, and M. I. Oliveria-Pereira. 2003b. “Valor nutricional e energético de espécies vegetais importantes na alimentação do Tambaqui.” *Acta Amazonica* 33, no. 4: 687–700. https://doi.org/10.1590/S0044-59672003000400014.

Souza, S. N. G. 2023. “Estrutura filogenética de comunidades arbóreas ao longo do gradiente de inundação em florestas de água preta na Amazônia Central e Oriental.” Dissertação. Instituto Nacional de Pesquisas da Amazônia—INPA. 84 p.

Thompson, A. W., R. Betancur-R, H. López-Fernández, and G. Ortí. 2014. "A Time-Calibrated, Multi-Locus Phylogeny of Piranhas, Pacus, and Allies (Characiformes: Serrasalmidae) and a Comparison of Species Tree Methods." *Molecular Phylogenetics and Evolution* 81: 242–257. https://doi.org/10.1016/j.ympev.2014.06.018.

Timpe, K., and D. Kaplan. 2017. "The Changing Hydrology of a Dammed Amazon." *Science Advances* 3: e1700611. https://doi.org/10.1126/sciadv.1700611.

Traveset, A. 1998. "Effect of Seed Passage Through Vertebrate Frugivores' Guts on Germination: A Review." *Perspectives in Plant Ecology, Evolution and Systematics* 1: 151–190. https://doi.org/10.1078/1433-8319-00057.

Vázquez, D. P., N. Blühgen, L. Cagnolo, and N. P. Chacoff. 2009. "Uniting Pattern and Process in Plant–Animal Mutualistic Networks: A Review." *Annals of Botany* 103: 1445–1457. https://doi.org/10.1093/aob/mcp057.

Vázquez, D. P., C. J. Melián, N. M. Williams, N. Blüthgen, B. R. Krasnov, and R. Poulin. 2007. "Species Abundance and Asymmetric Interaction Strength in Ecological Networks." *Oikos* 116: 1120–1127. https://doi.org/10.1111/j.2007.0030-1299.15828.x.

Weiss, B., J. A. S. Zuanon, and M. T. F. Piedade. 2016. "Viability of Seeds Consumed by Fishes in a Lowland Forest in the Brazilian Central Amazon." *Tropical Conservation Science* 9: 1–10. https://doi.org/10.1177/1940082916676129.

Winemiller, K. O., P. B. McIntyre, L. Castello, et al. 2016. "Balancing Hydropower and Biodiversity in the Amazon, Congo, and Mekong." *Science* 351, no. 6269: 128–129. https://doi.org/10.1126/science.aac7082.

Wittmann, A. O., P. Parolin, M. T. F. Piedade, W. J. Junk, and J. L. Guillaumet. 2010. *Manual of Trees From Central Amazonian Várzea Floodplains: Taxonomy, Ecology and Use/Manual de árvores de Várzea da Amazônia Central: Taxonomia, Ecologia e Uso*, edited by F. Wittmann, J. Schöngart, and J. M. de Brito, 286 p. Instituto Nacional de Pesquisas da Amazônia—INPA.

Wittmann, F., D. Anhuf, and W. J. Junk. 2002. "Tree Species Distribution and Community Structure of Central Amazonian Várzea Forests by Remote-Sensing Techniques." *Journal of Tropical Ecology* 8: 805–820. https://doi.org/10.1017/S0266467402002523.

Wittmann, F., E. Householder, A. de Oliveira Wittmann, A. Lopes, W. J. Junk, and M. T. Piedade. 2015. "Implementation of the Ramsar Convention on South American Wetlands: An Update." *Research and Reports in Biodiversity Studies* 4: 47–58. https://doi.org/10.2147/RRBS.S64502.

Wittmann, F., E. Householder, M. T. F. Piedade, et al. 2012. "Habitat Specifity, Endemism and the Neotropical Distribution of Amazonian White-Water Floodplain Trees." *Ecography* 36, no. 6: 690–707. https://doi.org/10.1111/j.1600-0587.2012.07723.x.

Wittmann, F., and W. J. Junk. 2016. "The Amazon River Basin." In *The Wetland Book II: Distribution, Description and Conservation*, edited by C. M. Finlayson, G. R. Milton, R. C. Prentice, and N. C. Davidson, 1–20. Springer.

Wittmann, F., W. J. Junk, and M. T. F. Piedade. 2004. "The Várzea Forests in Amazonia: Flooding and the Highly Dynamic Geomorphology Interact With Natural Forest Succession." *Forest Ecology and Management* 196: 199–212. https://doi.org/10.1016/j.foreco.2004.02.060.

Wittmann, F., J. Schöngart, and W. J. Junk. 2010. "Phytogeography, Species Diversity, Community Structure and Dynamics of Central Amazoian Floodplain Forests." In *Central Amazonian Floodplain Forests: Ecophysiology, Biodiversity and Sustainable Management*, edited by W. J. Junk, M. T. F. Piedade, F. Wittmann, J. Schöngart, and P. Parolin, 61–102. Springer.

Wittmann, F., J. Schöngart, J. C. Montero, et al. 2006. "Tree Species Composition and Diversity Gradients in White Water Forests Across the Amazon Basin." *Journal of Biogeography* 33: 1334–1347. https://doi.org/10.1111/j.1365-2699.2006.01495.x.

Wittmann, F., J. Schöngart, H. L. Queiroz, et al. 2009. "The Amazon Floodplain Demonstration Site: Sustainable Timber Production and Management of Central Amazonian White-Water Floodplains." *Ecohydrology & Hydrobiology* 9, no. 1: 41–54. https://doi.org/10.2478/v10104-009-0038-4.

Worbes, M. 1997. "The Forest Ecosystem of the Floodplains." In *The Central Amazon Floodplain: Ecology of a Pulsating System*, edited by W. J. Junk, 223–266. Springer. https://doi.org/10.1007/978-3-662-03416-3_11.

Ziburski, A. 1991. "Dissemination, Keimung und Etablierung einiger Baumarten der Überschwemmungswälder Amazoniens." In *Tropische und subtropische Pflanzenwelt*, edited by W. Rauh, 1–9. Akademie der Wissenschaften und der Literatur.

Maia, L. A., and F. P. Chalco. 2002. "Produção de frutos de espécies da floresta de Várzea da Amazônia Central importantes na alimentação de Peixes." *Acta Amazonica* 32, no. 1: 45–53. https://doi.org/10.1590/1809-43922002321054.

Supporting Information

Additional supporting information can be found online in the Supporting Information section. **Appendix S1:** Tree seed species consumed by different fish species (*) in distinct locations in the Amazon basin, and location of occurrence of tree species (**) in the flood gradient (Low Várzea—LV and High Várzea—HV), according to floristic inventories carried out in the Japurá and Solimões-Amazonas Rivers: Ayres (2006) (1); Assis and Wittmann (2011) (2); Cattanio et al. (2002) (3); Junk (1989) (4); Lobo (2017) (5); Parolin et al. (2010) (6); Souza (2023) (7); Wittmann et al. (2002) (8); Wittmann et al. (2004) (9); Wittmann et al. (2006) (10); Wittmann et al. (2009) (11); Wittmann, Parolin, et al. (2010) (12); Wittmann et al. (2012) (13); Our field.