



Universidade Federal do Rio Grande
Instituto de Ciências Biológicas
Pós-graduação em Biologia de
Ambientes Aquáticos Continentais



Influência do gradiente de inundação na dispersão de sementes por peixes frugívoros em áreas de várzea, Amazônia Central

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Orientador: Dr. Leonardo Maltchik Garcia
Coorientadora: Dra. Maria Teresa Fernandez Piedade
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Rio Grande
2026



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Tese apresentada ao Programa de Pós-graduação em Biologia de Ambientes Aquáticos Continentais como requisito parcial para a obtenção do título de Doutor em Biologia de Ambientes Aquáticos Continentais.

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ATA DE DEFESA DE TESE DE DOUTORADO EM BIOLOGIA DE AMBIENTES AQUÁTICOS CONTINENTAIS – Nº 001/2026

Às 14h00 (quatorze horas) do dia 12 (doze) do mês de janeiro de 2026 (dois mil e vinte e seis), reuniram-se docentes, discentes e comunidade em geral, para a Defesa Pública da Tese de Doutorado do acadêmico Gilvan da Silva Costa, que ocorreu de forma híbrida. A Tese intitulada **“Influência do gradiente de inundação na dispersão de sementes por peixes frugívoros em áreas de várzea, Amazônia Central”** foi avaliada pela Banca Examinadora composta pelo Prof^o. Dr. Leonardo Maltchik Garcia (Orientador); Prof^a. Dr^a. Adriana Gava (PPGBAC/FURG), Prof. Dr. Alexandre Miranda Garcia (PPGBAC/FURG) e Prof^a. Dr^a. Lucia Helena Rapp Py-Daniel (INPA). Após a defesa e arguição pública, a Banca Examinadora reuniu-se, para deliberação final, e considerou o acadêmico **APROVADO**. Desta forma, o acadêmico concluiu mais umas etapas necessárias para a obtenção do grau de **DOUTOR EM BIOLOGIA DE AMBIENTES AQUÁTICOS CONTINENTAIS**. Nada mais havendo a tratar, às 18h00h (dezoito horas) foi lavrada a presente ata, que lida e aprovada, foi assinada pelos membros da Banca Examinadora, pelo Acadêmico e pela Coordenadora do Curso.

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RESUMO

Nas áreas alagáveis amazônicas, os regimes de cheias e secas criam gradientes de inundação que influenciam a ocorrência e distribuição da floresta alagada e desencadeiam ritmos de crescimento e ciclos reprodutivos das espécies de árvores. A floração e maturação dos frutos ocorre em sincronia com o aumento no nível da água dos rios. Essa é uma importante adaptação, que possibilita a dispersão das sementes pela água (hidrocoria) e por peixes frugívoros (ictiocoria). A ictiocoria em florestas alagáveis da Amazônia tem sido reconhecida como um importante mecanismo de dispersão para muitas espécies arbóreas, e tem o potencial de influenciar a composição de espécies e a estrutura desses ecossistemas, pois ao consumir e em sementes viáveis os peixes podem transportá-las para locais adequados à sua germinação e estabelecimento. Esta Tese investiga alguns fatores que podem afetar a dispersão de sementes por peixes, incluindo a viabilidade e velocidade de germinação das sementes após passagem pelo trato digestório dos peixes e a relação entre o tamanho dos peixes e o tamanho das sementes encontradas nos seus tratos digestórios; a estrutura e vulnerabilidade (modularidade, aninhamento, especialização e robustez) da rede de dispersão de sementes; e a influência do gradiente de inundação (várzea baixa e várzea alta) na dispersão de sementes pelos peixes e na estrutura da rede de dispersão. Realizamos coletas de peixes e plantas em campo e complementamos essas informações com dados obtidos da literatura científica. Encontramos que o comprimento e o peso dos peixes frugívoros estavam positivamente relacionados ao tamanho das sementes no trato digestório, embora a passagem das sementes pelos tratos digestórios não tenha aumentado a velocidade de germinação. Observamos uma estrutura de rede modular e aninhada, conferindo relativa robustez a rede de dispersão, e que o comprimento e peso dos peixes e o tamanho das sementes não mostrou diferenças significativas em relação à especialização. Ainda, encontramos que a riqueza de frutos e sementes consumidas pelos peixes foi maior nas florestas de várzea baixa, quando consideradas somente espécies de árvores restritas a cada gradiente, e que a rede apresentou estrutura aninhamento. Esses resultados aumentam a compreensão geral de como as interações entre peixes e plantas podem ser influenciadas por impactos antropogênicos nesses ecossistemas e auxiliam na elaboração de medidas de conservação para peixes frugívoros e florestas alagáveis tropicais.

Palavras-chave: Ecologia de redes, ictiocoria, florestas alagáveis, pulso de inundação, viabilidade de sementes.

ABSTRACT

In the Amazonian floodplains, flood and drought regimes create flooding gradients that influence the occurrence and distribution of flooded forests and trigger growth rhythms and reproductive cycles in tree species. The flowering and ripening of the fruit occurs in synchronism with the rise in river water levels. This is an important adaptation, which enables seeds to be dispersed by water (hydrochory) and by frugivorous fish (ichthyochory). The ichthyochory in flooded forests of the Amazon has been recognized as an important dispersal mechanism for many tree species and has the potential to influence the species composition and structure of these ecosystems, since by consuming viable seeds, fish can transport them to locations suitable for germination and establishment. This Thesis investigates some factors that may affect seed dispersal by fish, including seed viability and germination speed after passing through the digestive tract of fish, and the relationship between fish size and the size of seeds found in their digestive tracts; the structure and vulnerability (modularity, nestedness, specialization and robustness) of the seed dispersal network; and the influence of the flood gradient (low várzea and high várzea) on seed dispersal by fish and on the structure of the dispersal network. We collect fish and plants in the field and supplement this information with data obtained from scientific literature. We found that the length and weight of frugivorous fish were positively related to seed size in the digestive tract, although the passage of seeds through the digestive tract did not increase germination speed. We observed that the network structure was modular and nested, giving the dispersal network relative robustness, and that the length and weight of the fish and the size of the seeds did not show significant differences in relation to specialization. Furthermore, we found that the abundance of fruits and seeds consumed by fish was greater in low várzea forests when considering only tree species restricted to each gradient, and that the network presented a nested structure. These results increase the overall understanding of how interactions between fish and plants can be influenced by anthropogenic impacts in these ecosystems and assist in the development of conservation measures for frugivorous fish and tropical floodplain forests.

Keywords: Network ecology, ichthyochory, floodplain forests, flood pulse, seed viability.

APRESENTAÇÃO

Esta Tese segue os padrões de formatação do Programa de Pós-graduação em Biologia de Ambientes Aquáticos Continentais (PPGBAC) da Universidade Federal do Rio Grande (FURG). A Introdução Geral contém o corpo teórico do tema em estudo, bem como os objetivos que serão investigados nos capítulos; esta seção segue as normas de formatação da Associação Brasileira de Normas Técnicas (ABNT). O primeiro capítulo da tese tem como título “*The effectiveness of ichthyochoric dispersal in forested wetlands of the Amazon depends on the species of fish and its size*” e está publicado no periódico *Forest Ecology and Management* (Qualis Capes: A1), e sua formatação segue as normas da revista. Neste capítulo, investigamos a dispersão de sementes por peixes frugívoros em uma floresta alagada por águas barrentas (várzea) na Amazônia Central, onde avaliamos a velocidade de germinação das sementes após a passagem pelo trato digestório dos peixes e como o tamanho dos peixes e das sementes pode influenciar a dispersão das sementes de árvores das várzeas. O segundo capítulo, “*Structure and vulnerability of the ichthyochory network in wetland forests of Central Amazonia*” segue as normas de formatação e está publicado no periódico *Ecology of Freshwater Fish* (Qualis Capes: A2). Neste capítulo avaliamos a estrutura (modularidade, aninhamento, especialização e robustez) da rede de dispersão de sementes por peixes frugívoros em uma floresta de várzea na Amazônia Central. No terceiro capítulo, intitulado “*The flooding gradient affects seed dispersal by fruit-eating fishes in Amazonian whitewater floodplain forests*”, avaliamos o consumo de frutos pelos peixes e o potencial de dispersão de sementes ao longo do gradiente de inundação (várzea baixa e várzea alta), e a estrutura da rede de dispersão. Este capítulo segue as normas e está em revisão no periódico *Biotropica* (Qualis Capes: A2). Finalizamos com a seção de Considerações Finais e Perspectivas, onde as citações e referências bibliográficas seguem as normas da ABNT.

SUMÁRIO

AGRADECIMENTOS	iii
RESUMO	iv
ABSTRACT	v
LISTA DE FIGURAS	ix
LISTA DE TABELAS	x
INTRODUÇÃO GERAL	12
Referências	18
Capítulo 1 – The effectiveness of ichthyochoric dispersal in forested wetlands of the Amazon depends on the species of fish and its size	28
Abstract	29
Introduction	30
Methods	33
Results	38
Discussion	43
Conclusion	49
References	50
Capítulo 2 – Structure and vulnerability of the ichthyochory network in wetland forests of Central Amazonia	60
Abstract	61
Introduction	62
Methods	64
Results	68
Discussion	75
References	79
Capítulo 3 – The flooding gradient affects seed dispersal by fruit-eating fishes in Amazonian whitewater floodplain forests	89
Abstract	90
Introduction	91
Methods	94
Results	100
Discussion	104
References	109

Appendix	125
CONSIDERAÇÕES FINAIS E PERSPECTIVAS	135
Referências	136
ANEXOS	139

LISTA DE FIGURAS

Capítulo 1

Figure 1. Study area located on Paciência Island in the Solimões River.

Figure 2. Relationship between the length and weight of 11 species of frugivorous fish and the size of the seeds found in their digestive tracts. Fish code, top to down: Ba – *B. amazonicus*, Ce – *C. erytrutus*, Cm – *C. macropomum*, Lf – *L. fasciatus*, Ma – *M. asterias*, Mal – *M. albiscopum*, Pg – *P. granulosus*, Rm – *R. microlepis*, Sf – *S. fasciatus*, Ta – *T. albus*, Tg – *T. galeatus*.

Figure 3. Proportion of germinated seeds over time, for seeds removed from the digestive tracts in relation to the control treatment. Each curve is surrounded by a 95% confidence interval.

Capítulo 2

Figure 1. Binary (left) and weighted (right) bipartite network among frugivorous fish species and consumed seeds. Fish code: Ba – *B. amazonicus*, Ce – *C. erytrutus*, Cm – *C. macropomum*, Lf – *L. fasciatus*, Ma – *M. asterias*, Mal – *M. albiscopum*, Pg – *P. granulosus*, Rm – *R. microlepis*, Sf – *S. fasciatus*, Ta – *T. albus*, Tg – *T. galeatus*.

Figure 2. Binary (left) and weighted modular (right) network structure among frugivorous fish species and consumed seeds. Fish code: Ba – *B. amazonicus*, Ce – *C. erytrutus*, Cm – *C. macropomum*, Lf – *L. fasciatus*, Ma – *M. asterias*, Mal – *M. albiscopum*, Pg – *P. granulosus*, Rm – *R. microlepis*, Sf – *S. fasciatus*, Ta – *T. albus*, Tg – *T. galeatus*.

Figure 3. Relationship between length and weight of fish species and size of seeds as a function of specialization (d').

Figure 4. Robustness of the network against extinctions: by fish species removed (a–f), with all species (g), and cumulative removal of frugivorous fish (h–i). Fish code: Tg – *T. galeatus*, Pg – *P. granulosus*, Ta – *T. albus*, Ba – *B. amazonicus*, Mal – *M. albiscopum*, Cm – *C. macropomum*.

Capítulo 3

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).

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 (LV - Low Várzea and HV - High Várzea).

Figure 3: Structure of the ichthyochory network.

LISTA DE TABELAS

Capítulo 1

Table 1: Plant species consumed by fish. Mean seed size by species, number of seeds, fleshy (1) or non-fleshy (0) fruit, fish species and code: Ba – *B. amazonicus*, Ce – *C. erythrus*, Cm – *C. macropomum*, Lf – *L. fasciatus*, Ma – *M. asterias*, Mal – *M. albiscopum*, Pg – *P. granulosus*, Rm – *R. microlepis*, Sf – *S. fasciatus*, Ta – *T. albus*, Tg – *T. galeatus*.

Table 2: Species of frugivorous fish that consumed fruits. Mean of standard length ($\pm$ SL mm) and weight ($\pm$ W g) of fish and number of seeds and species of seeds consumed.

Table 3: Germination parameters: number of germinated seeds (NSG), germination percentage (GP%), mean germination time in days (MGT), mean germination rate (MGR).

Capítulo 2

Table 1: Species of frugivorous fish that consumed fruits. Number of fish, mean of standard length ($\pm$ SL mm) and weight ($\pm$ W g) of fish and species of seeds consumed.

Material suplementar do capítulo 3

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 et al. 2010b (12); Wittmann et al. 2012 (13); Our field collections (14).

INTRODUÇÃO GERAL

A bacia amazônica compreende a maior e mais complexa rede de canais fluviais do mundo (LATRUBESSE *et al.*, 2017). Nessa região, merecem destaque as áreas úmidas, consideradas como os ambientes de "transição entre sistemas terrestres e aquáticos" (COWARDIN *et al.*, 1979), também chamadas por Junk e colaboradores em 1989 como as zonas de transição aquático-terrestre "ATTZ". As áreas úmidas associadas aos grandes rios amazônicos constituem as áreas alagáveis, ecossistemas onde o pulso de inundação é a principal força motriz responsável pela existência, produtividade e interações da biota (JUNK *et al.*, 1989), pois desencadeiam ciclos biogeoquímicos, ritmos de crescimento e ciclos de vida da biota associada (JUNK, 1997). De acordo com suas características físico-químicas, que refletem a geologia das áreas de captação, as áreas alagáveis podem ser formadas por rios de águas pretas ou claras, denominadas de igapós, ou por rios de águas brancas, denominadas de várzeas (SIOLI, 1965; PRANCE, 1979; JUNK *et al.*, 2011). Os rios de águas pretas (como o rio Negro) drenam o escudo pré-cambriano da Guiana, que se caracteriza por grandes áreas de areias brancas (podzols); os rios de águas claras (como os rios Tapajós, Xingu e Tocantins) têm suas origens principalmente no escudo central brasileiro; enquanto os rios de águas brancas (como o curso principal do Amazonas e os rios Juruá, Japurá, Purus e Madeira) se originam nos Andes, de onde transportam grandes quantidades de sedimentos ricos em nutrientes (IRION *et al.*, 1997; JUNK *et al.*, 2011). Esses grandes rios, apresentam um pulso de inundação anual, monomodal, previsível, de longa duração e de alta amplitude, que resulta da sazonalidade das estações secas e chuvosas pronunciadas em suas bacias hidrográficas, possibilitando trocas laterais entre o rio e suas planícies de inundação (JUNK *et al.*, 1989; SCHÖNGART & JUNK, 2007; JUNK & PIEDADE, 2010).

Os ecossistemas naturais são geralmente muito complexos e existem em séries de coordenadas espaciais, temporais ou espaço-temporais, que podem apresentar gradientes de estrutura e função (MÜLLER, 1998; FIEDLER & BECK, 2008), que podem ocorrer devido à temperatura, precipitação, características do solo ou inundações sazonais (SCHWEITZER *et al.*, 2014; MARKS *et al.*, 2020; MYSTER, 2025). Gradientes referem-se à inclinação de uma curva (e.g. curva de riqueza em função de alguma característica ambiental), e apresentam um ou mais recursos ou condições que diferem no espaço ou no tempo (FOX *et al.*, 2011), onde a biota se adaptou e continua a responder a esses gradientes (MYSTER, 2002). Nos ecossistemas aquáticos, a dinâmica e alta variabilidade dos cursos de água, geram gradientes espaciais e temporais nas características abióticas e bióticas (ALLAN & CASTILLO, 2007). Por exemplo,

a profundidade da água forma um gradiente ambiental complexo (TITUS, 2009), que determina padrões de ocorrência e distribuição de espécies (MYSTER, 2025) e influencia a heterogeneidade dos rios e suas planícies de inundação (RAYBURG *et al.*, 2023). A heterogeneidade ambiental é um dos principais fatores que influenciam a estrutura e a dinâmica de populações e comunidades (YANG *et al.*, 2015), e está intrinsecamente ligado à estrutura das redes ecológicas nas mais diversas escalas (TYLIANAKIS & MORRIS, 2017).

Nas áreas alagáveis amazônicas, as variações topográficas podem resultar em diferenças na amplitude e tempo de inundação anual, mudando ao longo do curso do rio (JUNK, 1989; FERREIRA, 1997). Dependendo da topografia local, as inundações sazonais podem durar de várias semanas a vários meses por ano, e criam um gradiente espacial de diminuição da duração das inundações e da profundidade máxima com o aumento da distância do rio (WITTMANN *et al.*, 2002; MYSTER, 2018), que controla o estabelecimento, a distribuição e o crescimento das espécies arbóreas (JUNK *et al.*, 1989). As florestas de várzea da Amazônia têm sido foco de diversos estudos que buscam entender como o pulso de inundação influencia as comunidades arbóreas ao longo do gradiente de inundação (ASSIS & WITTMANN, 2011; WITTMANN *et al.*, 2012; LUIZE *et al.*, 2015, 2018). O monitoramento e os diversos inventários florísticos realizados nas várzeas representam um importante avanço para a compreensão desses efeitos e têm demonstrado que a riqueza de espécies aumenta das áreas mais próximas ao canal do rio (várzea baixa) em direção às partes mais elevadas (várzea alta), com poucas espécies sendo encontradas ao longo de todo o gradiente (WORBES *et al.*, 1992; FERREIRA, 1997; WITTMANN *et al.*, 2006, 2010). Esse gradiente, portanto, estrutura as florestas alagáveis (MYSTER, 2025), pois a duração e a altura da inundação determinam a elevação na qual uma árvore ocorre (JUNK, 1989).

As florestas de várzea, associadas aos rios de águas brancas, ocupam uma extensa área na bacia fluvial amazônica, estimada em aproximadamente 450.000 km², e cobrem entre 70–90% das áreas de várzea (MELACK & HESS, 2010). São normalmente inundadas a uma profundidade de até 7,5 m por até 230 dias por ano (JUNK *et al.*, 2011). Embora a inundação represente um fator limitante ao estabelecimento das espécies de árvores (JUNK *et al.*, 1989), devido à hipóxia ou anóxia sazonais (FURCH, 1984; PAROLIN, 2009), as várzeas possuem as florestas alagáveis mais diversas do mundo (WITTMANN *et al.*, 2006). Para sobreviver nesses ambientes, as comunidades vegetais desenvolveram uma série de adaptações estruturais, bioquímicas, fisiológicas e fenológicas desencadeadas pela pressão seletiva dos ciclos anuais de cheias e secas (SCHÖNGART *et al.*, 2002; PAROLIN *et al.*, 2004; PIEDADE *et al.*, 2010), que levam a uma zonação bem definida das espécies ao longo dos gradientes de inundação

(FERREIRA, 1997; WITTMANN *et al.*, 2002, 2010). Entre essas adaptações, a sincronização do período reprodutivo das espécies arbóreas com o aumento do nível da água dos rios (GOULDING, 1983; PAROLIN *et al.*, 2013), representa um importante mecanismo que possibilita a dispersão de frutos e sementes (CORREA *et al.*, 2015).

De modo geral, sementes podem ser dispersadas pelo vento (anemocoria), pela água (hidrocoria), pela gravidade (barocoria) e por uma grande variedade de animais (zoocoria), através da ingestão de frutos e sementes, bem como pelo transporte de sementes através de suas patas, plumagem ou pelos (PIEPALE *et al.*, 2006; PAROLIN *et al.*, 2013; TRAVESET *et al.*, 2014; HOFFMANN *et al.*, 2024). Embora a dispersão de muitas árvores das planícies de inundação esteja ligada às águas do rio, a germinação das sementes e o estabelecimento das árvores são sincronizadas com a fase terrestre (OLIVEIRA WITTMANN *et al.*, 2010). Para espécies de sementes que não flutuam, são esperadas condições de hipoxia após a submersão, inadequadas à germinação, que podem levar a períodos mais longos de dormência (FRANKLAND *et al.*, 1987; KOZLOWSKI & PALLARDY, 1997). A dormência é o estado de inatividade metabólica das sementes, que impede o embrião de crescer e a semente de germinar (CONSIDINE & CONSIDINE, 2016). Em florestas de várzea, embora uma maior proporção de plantas produza sementes dispersadas por agentes abióticos, em particular pela água (KUBITZKI & ZIBURSKI 1994; PAROLIN *et al.*, 2013), a dispersão de sementes por peixes (ictiocoria) tem sido reconhecida como um dos mecanismos fundamentais (GOULDING 1980; HAWES & PERES, 2014), que ajuda a dispersar as sementes de muitas espécies de plantas (WEISS *et al.*, 2016; ARAUJO *et al.*, 2021; COSTA *et al.*, 2023; PEREYRA *et al.*, 2023). Dependendo do consumidor, as sementes reagem de maneira diferente após serem ingeridas, de modo que ao passarem pelo trato digestório do animal a germinação pode aumentar, atrasar ou não ser afetada (TRAVESET, 1998; YULE *et al.*, 2015). Nesse sentido, alguns estudos têm sido realizados na tentativa de se compreender a importância dos peixes na quebra de dormência e germinação das sementes após a passagem por seus tratos digestórios (HORN, 1997; MANNHEIMER *et al.*, 2003; POLLUX *et al.*, 2006; WEISS *et al.*, 2016, 2022), pois ao consumirem sementes viáveis, os peixes podem transportá-las por longas distâncias, depositando-as em habitats adequados à sua germinação e estabelecimento (ANDERSON *et al.*, 2009, 2011).

Os peixes consumidores de sementes (frugívoros) ocorrem em todas as regiões biogeográficas, incluindo os Neotrópicos (HORN *et al.*, 2011), onde aproximadamente 150 espécies de peixes consomem frutos e sementes de quase 600 espécies de plantas (HORN *et al.*, 2011; CORREA *et al.*, 2015). Na bacia amazônica, as espécies de peixes que consomem

frutos de florestas alagáveis, pertencem às ordens Characiformes e Siluriformes (GOULDING, 1980, 1983; SOUZA-STEVAUX, 1994; MANNHEIMER *et al.*, 2003; PIEDADE *et al.*, 2006; CORREA *et al.*, 2007), e estão distribuídos principalmente entre as famílias Doradidae, Pimelodidae, Serrasalminidae e Bryconidae (CORREA *et al.*, 2015; COSTA *et al.*, 2023). Essa diversidade de espécies de peixes e plantas em áreas alagáveis forma complexas redes de interações mutualísticas, que moldam a estrutura das comunidades (STRAUSS e IRWIN, 2004; CORREA *et al.*, 2016; ARAUJO *et al.*, 2021). Nos últimos anos, os estudos sobre dispersão de sementes têm se diversificado, principalmente no sentido de descrever a estrutura das redes de interações (BASCOMPTE & JORDANO, 2007; CORREA *et al.*, 2016), e de entender como a estrutura das redes varia ao longo dos gradientes ambientais (TYLIANAKIS & MORRIS, 2017). Por isso, além das interações (e.g. presença/ausência ou frequência), os estudos sobre redes ecológicas têm levado em conta a distribuição das espécies (SCHLEUNING *et al.*, 2015), pois os gradientes naturais podem influenciar a estrutura das redes, em função de mudanças na abundância e riqueza de espécies, que influenciam a probabilidade ou a frequência com que as interações ocorrem (TYLIANAKIS & MORRIS, 2017). A comparação de redes ecológicas entre gradientes é necessária para se compreender os processos que moldam sua estrutura e distribuição ao longo do tempo e do espaço (PELLISSIER *et al.*, 2017).

O reconhecimento de padrões em comunidades ecológicas é um dos mais persistentes desafios da ciência ecológica (LEWINSOHN *et al.*, 2006), e o estudo das redes ecológicas fornecem maneiras de quantificar e comparar alguns desses padrões entre comunidades (BASCOMPTE & JORDANO, 2007). De forma geral, para redes ecológicas (e.g. polinização, parasitismo e dispersão de sementes), dois padrões podem ser observados: o aninhamento e a modularidade (OLESEN *et al.*, 2007; FORTUNA *et al.*, 2010; CORREA *et al.*, 2016). O aninhamento envolve ligações entre espécies especialistas e generalistas (NIELSEN & BASCOMPTE, 2007), onde as espécies de plantas e animais mais generalistas interagem entre si, gerando um núcleo denso de interações ao qual o restante da comunidade está conectado (BASCOMPTE *et al.*, 2003). Redes que apresentam modularidade consistem em módulos interconectados, onde cada módulo é um grupo de espécies que estão mais intimamente conectadas entre si do que com espécies em outros módulos (OLESEN *et al.*, 2007). Apesar da importância do aninhamento e da modularidade para a estabilidade e persistência das comunidades, a relação entre esses padrões estruturais permanece desconhecida (FORTUNA *et al.*, 2010). Como a estrutura das redes tem implicações importantes para a estabilidade das espécies (BASCOMPTE & JORDANO, 2007), detectar esses padrões e entender a estrutura

das redes de interações mutualísticas é fundamental para inferir sua robustez diante das mudanças ambientais (BASCOMPTE & JORDANO, 2014).

A dispersão de sementes mediada por animais é considerada um mutualismo, no qual uma espécie de planta pode ser dispersada por muitas espécies de frugívoros (SCHUPP *et al.*, 2010). Assim como outros grupos de frugívoros, os peixes podem atuar como predadores (interações antagonísticas) ou dispersores (interações mutualísticas) de sementes (ANDERSON *et al.*, 2011; DRACXLER & KISSLING, 2021), onde algumas espécies possuem adaptações que facilitam sua atividade como predadores ou dispersores de sementes (GOULDING, 1980; CORREA *et al.*, 2007, 2015). Entre elas, o tipo de dentição é um fator determinante, que influencia a dispersão de sementes (GOULDING, 1980). Por exemplo, muitos Characiformes Neotropicais, alguns dos gêneros *Colossoma* e *Piaractus*, têm dentes multicuspidados e molariformes que facilitam a quebra de frutos e sementes com casca dura. Outros gêneros de Characiformes como *Brycon*, *Pristobrycon* e *Serrasalmus* têm dentes multicuspidados afiados que podem cortar sementes (GOULDING, 1980), causando danos variáveis às sementes durante a ingestão (CORREA *et al.*, 2007). Quando mutualísticas, as interações entre frutos e frugívoros representam uma relação mutuamente benéfica entre vertebrados e plantas (FLEMING & KRESS, 2011), que é um componente crucial para a ecologia florestal e funcionamento de um ecossistema (HOWE & SMALLWOOD, 1982; LEVIN *et al.*, 2003; NATHAN & MULLER-LANDAU, 2000), bem como para recuperação de ambientes degradados, pois transportam sementes que, quando dispersas em locais adequados, podem iniciar processos de sucessão (WUNDERLE JUNIOR, 1997; GALETTI *et al.*, 2004; TRAVESET *et al.*, 2014). Contudo, com a degradação dos habitats e a sobreexploração das espécies, têm havido um declínio das populações de plantas e animais, bem como a extinção de frugívoros de grande e médio porte (PÉREZ-MÉNDEZ *et al.*, 2016; COSTA-PEREIRA *et al.*, 2018; GALETTI *et al.*, 2021).

O tamanho dos animais, além de outras características, é um importante fator que pode influenciar a efetividade da dispersão (GALETTI *et al.*, 2008; POLLUX, 2011), que é definida como o número de novas plantas adultas produzidas pelas atividades de dispersão dos dispersores (FEDRIANI *et al.*, 2023). Na região amazônica, devido à pressão da pesca, principalmente próximo aos centros urbanos, os grandes peixes frugívoros (e.g. *Colossoma macropomum* e *Piaractus brachypomus*) estão ameaçados pela exploração excessiva contínua (ISAAC & RUFFINO, 1996; COSTA-PEREIRA *et al.*, 2018). Em espécies de peixes consumidores de frutos, indivíduos maiores aumentam a eficácia da dispersão, porque consomem mais sementes em termos de diversidade, número e biomassa, e as dispersam para

mais longe da sua origem devido aos longos tempos de retenção nos seus tratos digestórios (GALETTI *et al.*, 2008; ANDERSON *et al.*, 2009, 2011; CORREA *et al.*, 2015). O desaparecimento de grandes dispersores de sementes devido à sobreexploração ou à perda de habitat, se traduz em uma redução da dispersão de sementes (DIRZO & MIRANDA, 1990; WRIGHT, 2003), e diminui o papel ecológico que as espécies desempenham nos ecossistemas (FRICKE *et al.*, 2025). Apesar de sua importância para a biodiversidade, as florestas alagáveis da Amazônia estão entre os ecossistemas mais ameaçados globalmente, sendo as mudanças no uso do solo, a construção de hidrelétricas e as mudanças climáticas globais alguns dos principais fatores (CASTELLO *et al.*, 2013; RENÓ & NOVO, 2019), que juntamente com a exploração excessiva dos peixes frugívoros ameaçam significativamente a persistência das interações entre a ictiofauna e as florestas alagáveis (ISAAC & RUFFINO, 1996; COSTA-PEREIRA *et al.*, 2018; CORREA *et al.*, 2025). Por isso, compreender a complexidade das interações entre peixes consumidores de frutos e as florestas alagáveis da Amazônia, é de vital importância para o manejo e conservação dessas espécies frente às crescentes ameaças antrópicas nessa região.

Objetivos

Objetivo geral

O objetivo geral desta Tese é investigar a influência do gradiente de inundação no consumo e dispersão de frutos e sementes por peixes e avaliar a estrutura da rede de dispersão em uma área de várzea na Amazônia central.

Objetivos específicos

- No primeiro capítulo, examinamos os efeitos da passagem das sementes pelos tratos digestórios dos peixes na germinação e a relação entre o tamanho dos peixes e o tamanho das sementes encontradas em seus tratos digestórios;
- No segundo capítulo, avaliamos a estrutura (modularidade, aninhamento, especialização e robustez) e a vulnerabilidade da rede de dispersão de sementes entre peixes e as florestas de várzea da Amazônia central;

- No terceiro capítulo, investigamos como a distribuição da vegetação ao longo do gradiente de inundação (várzea baixa e várzea alta) influencia a comunidade de peixes consumidores de sementes e a estrutura da rede de interação em áreas de várzea.

Referências

ANDERSON, J. T.; SALDANA-ROJAS, J.; FLECKER, A. S. High-quality seed dispersal by fruit-eating fishes in Amazonian floodplain habitats. **Oecologia**, v. 161, p. 279–290, 2009.

ANDERSON, J. T.; NUTTLE, T.; SALDANÃ-ROJAS, J. S.; PENDERGAST, T. H.; FLECKER, A. S. Extremely long-distance seed dispersal by an overfished Amazonian frugivore. **Proceedings of the Royal Society B: Biological Sciences**, v. 278, p. 3329–3335, 2011.

ARAUJO, J. M.; CORREA, S. B.; PENHA, J.; ANDERSON, J.; TRAVESET, A. Implications of overfishing of frugivorous fishes for cryptic function loss in a Neotropical floodplain. **Journal of Applied Ecology**, v. 58, p. 1499–1510, 2021.

ASSIS, R. L.; WITTMANN, F. Forest structure and tree species composition of the understory of two central Amazonian várzea forests of contrasting flood heights. **Flora**, v. 206, p. 251–260, 2011.

BASCOMPTE, J.; JORDANO, P.; MELIAN, C. J.; OLESEN, J. M. The nested assembly of plant animal mutualistic networks. **Proceedings of the National Academy of Sciences of the United States of America**, v. 100, p. 9383–9387, 2003.

BASCOMPTE, J.; JORDANO, P. Plant-animal mutualistic networks: The architecture of biodiversity. **Annual Review of Ecology, Evolution, and Systematics**, v. 38, p. 567–593, 2007.

BASCOMPTE, J.; JORDANO, P. Mutualistic networks. *Monographs in Population Biology*, Princeton University Press, Princeton, New Jersey, p. 292, 2014.

CASTELLO, L.; MCGRATH, D. G.; HESS, L. L.; COE, M. T.; LEFEBVRE, P. A.; PETRY, P.; MACEDO, M. N.; RENO, V. F.; ARANTES, C. C. The vulnerability of Amazon freshwater ecosystems. **Conservation Letters**, v. 6, p. 217–229, 2013.

- CONSIDINE, M. J.; CONSIDINE, J. A. On the language and physiology of dormancy and quiescence in plants. **Journal of Experimental Botany**, v. 67, n. 11, p. 3189–3203, 2016.
- CORREA, S. B.; WINEMILLER, K. O.; LÓPEZ-FERNÁNDEZ, H.; GALETTI, M. Evolutionary perspectives on seed consumption and dispersal by fishes. **BioScience**, v. 57, p. 748–756, 2007.
- CORREA, S. B.; COSTA-PEREIRA, R.; FLEMING, T.; GOULDING, M.; ANDERSON, J. T. Neotropical fish-fruit interactions: eco-evolutionary dynamics and conservation. **Biological Reviews**, v. 1267, p. 1263–1278, 2015.
- CORREA, S. B.; ARAUJO, J. K.; PENHA, J.; NUNES DA CUNHA, C.; BOBIER, K. E.; ANDERSON, J. T. Stability and generalization in seed dispersal networks: a case study of frugivorous fish in Neotropical wetlands. **Proceedings of the Royal Society B: Biological Sciences**, v. 283, p. 20161267, 2016.
- CORREA, S. B.; CORONADO-FRANCO, K. V.; JÉZÉQUEL, C.; RODRIGUES, A. C. et al. Floodplain forests drive fruit-eating fish diversity at the Amazon Basin-scale. **Proceedings of the National Academy of Sciences**, v. 122, n. 3, p. e2414416122, 2025.
- COSTA, G.; PIEDADE, M. T. F.; FERREIRA, E. J.; MALTCHIK, L. The effectiveness of ichthyochoric dispersal in forested wetlands of the Amazon depends on the species of fish and its size. **Forest Ecology and Management**, v. 549, p. 121481, 2023.
- COSTA-PEREIRA, R.; LUCAS, C.; CROSSA, M.; ANDERSON, J. T.; WEISS, B. A.; DARY, E. P.; PIEDADE, M. T. F.; DEMARCHI, L. O.; REBOUÇAS, E. R.; COSTA, G. S.; GALETTI, M.; CORREA, S. B. Defaunation shadow on mutualistic interactions. **Proceedings of the National Academy of Sciences**, v. 115, p. E2673–E2675, 2018.
- COWARDIN, L. M.; CARTER, V.; GOLET, F. C.; LAROE, E. T. Classification of wetlands and deepwater habitats of the United States. U.S. Fish and Wildlife Service, Office of Biological Services, Washington, DC, USA. FWS/OBS-79/31, 1979.
- DIRZO, R.; MIRANDA, A. Contemporary neotropical defaunation and forest structure, function, and diversity. **Conservation Letters**, v. 4, p. 444–447, 1990.
- DRACXLER, C.; KISSLING, W. D. The mutualism–antagonism continuum in Neotropical

palm–frugivore interactions: from interaction outcomes to ecosystem dynamics. **Biological Reviews**, v. 97, n. 2, p. 527-553, 2021.

FEDRIANI, J. M.; WIEGAND, T.; GARROTE, P. J.; LEIVA, M. J.; AYLLÓN, D. Seed dispersal effectiveness in fragmented and defaunated landscapes. **Ecosphere**, v. 14, n. 9, p. e4658, 2023.

FERREIRA, L. V. 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**, v. 6, p. 1353–1363, 1997.

FORTUNA, M. A.; STOUFFER, D. B.; OLESEN, J. M.; JORDANO, P.; MOUILLOT, D.; KRASNOV, B. R.; POULIN, R.; BASCOMPTE, J. Nestedness versus modularity in ecological networks: two sides of the same coin? **Journal of Animal Ecology**, v. 79, p. 811-817, 2010.

FOX, G. A.; SCHEINER, S. M.; WILLIG, M. R. A theory of ecological gradients: a framework for aligning data and models. In: SCHEINER, S. M.; WILLIG, M. R., The theory of ecology. London: University of Chicago Press, pp. 283–307, 2011.

FURCH, B. Untersuchungen zur Überschwemmungs-toleranz von Baumen de várzea und igapó. Blattpigmente. **Biogeographica**, v. 19, p. 77–83, 1984.

FLEMING, T. H.; KRESS, W. J. A brief history of fruits and frugivores. **Acta Oecologica**, v. 37, p. 521–530, 2011.

FRANCKLAND, B.; BARTLEY, M. R.; SPENCE, D. H. N. Germination under the water. In: CRAWFORD, R. M. M. (Ed.). Plant life in aquatic and amphibious habitats. Special publication series of the British Ecological Society. Blackwell Scientific Publications, Oxford, England, n. 5, pp. 167–178, 1987.

FRICKE, E. C.; COOK-PATTON, S. C.; HARVEY, C. F.; TERRER, C. Seed dispersal disruption limits tropical forest regrowth, **Proceedings of the National Academy of Sciences of the United States of America**, v. 122, n. 30, p. e2500951122, 2025.

GALETTI, M.; PIZO, M. A.; MORELLATO, L. P. C. Fenologia, frugivoria e dispersão de sementes. In: CULLEN JUNIOR, L.; RUDRAN, R.; VALLADARES-PÁDUA, C. Métodos de estudos em Biologia da conservação & manejo da vida silvestre. Paraná: UFPR, pp. 395-422,

2004.

GALETTI, M.; DONATTI, C. I.; PIZO, M. A.; GIACOMINI, H. C. Big fish are the best: seed dispersal of *Bactris glaucescens* by the Pacu fish (*Piaractus mesopotamicus*) in the Pantanal, Brazil. **Biotropica**, v. 40, p. 386–389, 2008.

GALETTI, M.; GONÇALVES, F.; VILLAR, N.; ZIPPARRO, V. B.; PAZ, C.; MENDES, C.; LAUTENSCHLAGER, L.; SOUZA, Y. *et al.* Causes and consequences of large-scale defaunation in the atlantic forest MARQUES, M.C.M.; GRELLE, C.E.V. (Eds.), The Atlantic Forest. History, biodiversity, threats and opportunities of the mega-diverse forest, Springer Nature Switzerland AG, Cham, pp. 297–324, 2021.

GOULDING, M. The fishes and the forest: explorations in Amazonian natural history. Berkeley and Los Angeles, CA: University of California Press, p. 292, 1980.

GOULDING, M. The role of fish in seed dispersal and plant distribution in Amazonian floodplains ecosystems. In: KUBITZKI, K. (Ed.). Dispersal and distribution. Hamburg, Germany: Verlag Paul Parey, pp. 271–284, 1983.

HAWES, J. E.; PERES, C. A. Fruit–frugivore interactions in Amazonian seasonally flooded and unflooded forests. **Journal of Tropical Ecology**, v. 30, n. 5, p. 381–399, 2014.

HOFFMANN, P. H. O.; ADOLFO, A.; GREEN, A. J.; STENERT, C.; SILVA, G. G.; WEBER, V.; MALTCHIK, L. Big rodents disperse small seeds and spores in Neotropical wetlands. **Journal of Ecology**, v. 00, p. 1–15, 2024.

HORN, M. H. Evidence for dispersal of fig seeds by the fruit-eating characid fish *Brycon guatemalensis* Regan in a Costa Rican tropical rain forest. **Oecologia**, v. 109, p. 259–264, 1997.

HORN, M.; CORREA, S. B.; PAROLIN, P.; POLLUX, B. J. A.; ANDERSON, J. T.; LUCAS, C.; WIDMANN, P.; TJIU, A.; GALETTI, M.; GOULDING, M. Seed dispersal by fishes in tropical and temperate fresh waters: The growing evidence. **Acta Oecologica**, v. 37, p. 561–577, 2011.

HOWE, H. F.; SMALLWOOD, J. Ecology of seed dispersal. **Annual Review of Ecology, Evolution, and Systematics**, v. 13, p. 201–228, 1982.

IRION, G.; JUNK, W. J.; MELLO, J. A. S. N. The large central Amazonian river floodplains

near Manaus: geological, climatological, hydrological and geomorphological aspects. In: JUNK, W. F. (Ed.). *The Central Amazon Floodplain Ecological Studies*. Berlin Heidelberg, Springer, pp. 23–46, 1997.

ISAAC, V. J.; RUFFINO, M. L. Population dynamics of tambaqui, *Colossoma macropomum* Cuvier, in the lower Amazon, Brazil. **Fisheries Management and Ecology**, v. 3, n. 4, p. 315–333, 1996.

JUNK, W. J. Flood tolerance and tree distribution in central Amazonian floodplains. In: HOLM-NIELSEN, L. B.; NIELSEN, I. C.; BALSLEV, H. (Eds.). *Tropical Forests: Botanical Dynamics, Speciation and Diversity*. London: Academic Press, pp. 47–64, 1989.

JUNK, W. J.; BAYLEY, P. B.; SPARKS, R. E. The flood pulse concept in river floodplain systems. In: DODGE, D. P. (Ed.), *Proceedings of the International Large River Symposium*. Canadian Special Publication in Fisheries and Aquatic Sciences, Ontario, pp. 110–127, 1989.

JUNK, W. J. *The Central Amazon Floodplain: Ecology of a Pulsing System*. Springer, Berlin, Heidelberg, New York, p. 556, 1997.

JUNK, W. J.; PIEDADE, M. T. F. An Introduction to South American Wetland Forests: Distribution, Definitions and General Characterization. In: JUNK, W. J., PIEDADE, M. T. F., WITTMANN, F., SCHÖNGART, J., PAROLIN, P. (Eds.). *Amazon floodplain forests: Ecophysiology, biodiversity and sustainable management*. Ecological Studies 210, Springer Verlag, Berlin Heidelberg-New York, pp. 3–25, 2010.

JUNK, W. J.; PIEDADE, M. T. F.; SCHÖNGART, J.; COHN-HAFT, M.; ADENEY, J. M.; WITTMANN, F. A classification of major naturally-occurring Amazonian lowland wetlands. **Wetlands**, v. 31, p. 623–640, 2011.

KOZLOWSKI, T. T.; PALLARDY, S. G. *Growth Control in Woody Plants*, Academic Press, San Diego, CA, 1997.

KUBITZKI, K.; ZIBURSKI, A. Seed dispersal of floodplain forest in Amazonia. **Biotropica**, v. 26, p. 30–43, 1994.

LATRUBESSE, E. M.; ARIMA, E. Y.; DUNNE, T.; PARK, E.; BAKER, V. R.; D'HORTA, F. M. *et al.* Damming the rivers of the Amazon basin. **Nature**, v. 546, p. 363–369, 2017.

LEVIN, S. A.; MULLER-LANDAU, H. C.; NATHAN, R.; CHAVE, J. The ecology and evolution of seed dispersal: a theoretical perspective. **Annual Review of Ecology, Evolution, and Systematics**, v. 34, p. 575–604, 2003.

LEWINSOHN, T. M.; LOYOLA, R. D.; PRADO, P. I. Matrízes, redes e ordenações: a detecção de estrutura em comunidades interativas. **Oecologia Brasiliensis**, v. 10, n. 1, p. 90–104, 2006.

LUIZE, B. G.; SILVA, T. S. F.; WITTMANN, F.; ASSIS, R. L.; VENTICINQUE, E. M. Effects of the Flooding Gradient on Tree Community Diversity in Várzea Forests of the Purus River, Central Amazon, Brazil. **Biotropica**, v. 47, n. 2, p. 137–142, 2015.

LUIZE, B. G.; MAGALHÃES, J. L. L.; QUEIROZ, H.; LOPES, M. A.; VENTICINQUE, E. M.; DE MORAES NOVO, E. M. L.; SILVA, T. S. F. The tree species pool of Amazonian wetland forests: Which species can assemble in periodically waterlogged habitats? **PLoS ONE**, v. 13, p. e0198130, 2018.

MANNHEIMER, S.; BEVILACQUA, G.; CARAMASCHI, E. P.; SCARANO, F. R. Evidence for seed dispersal by the catfish *Auchenipterichthys longimanus* in an Amazonian lake. **Journal of Ecology**, v. 19, p. 215–218, 2003.

MARKS, C. O.; YELLEN, B. C.; WOOD, S. A.; MARTIN, E. M.; NISLOW, K. H. Variation in Tree Growth along Soil Formation and Microtopographic Gradients in Riparian Forests. **Wetlands**, v. 40, p. 1909–1922, 2020.

MELACK, J. M.; HESS, L. L. Remote Sensing of the Distribution and Extent of Wetlands in the Amazon Basin. In: JUNK, W. J.; PIEDADE, M. T. F.; WITTMANN, F.; SCHÖNGART, J.; PAROLIN, P. (Eds.). Central Amazonian Floodplain Forests: Ecophysiology, Biodiversity and Sustainable Management. Berlin/Heidelberg/New York: Springer, pp. 43–59, 2010.

MÜLLER, F. Gradients in ecological systems. **Ecological Modelling**, v. 108, p. 3–21, 1998.

MYSTER, R. W. Mechanisms of plant response to gradients and after disturbances. **Botanical Review**, v. 67, p. 441–452, 2002.

MYSTER, R. W. Igapó (black-water) forests of the Amazon Basin. Springer, Berlin, 2018.

MYSTER, R. W. A Rank Correlative Comparison of Várzea (White-Water) Vs. Igapó (Black-Water) Floodplain Forest Gradients in the Amazon. **Wetlands**, v. 45, n. 43, 2025.

- NATHAN, R.; MULLER-LANDAU, H.C. Spatial patterns of seed dispersal, their determinants and consequences for recruitment. **Trends in Ecology & Evolution**, v. 15, p. 278–285, 2000.
- NIELSEN, A.; BASCOMPTE, J. Ecological networks, nestedness and sampling effort. **Journal of Ecology**, v. 95, p. 1134–1141, 2007.
- OLESEN, J. M.; BASCOMPTE, J.; DUPONT, Y. L.; JORDANO, P. The modularity of pollination networks. **Proceedings of the National Academy of Sciences**, v. 104, p. 19891–19896, 2007.
- OLIVEIRA-WITTMANN, A.; LOPES, A.; CONSERVA, A. D. S.; WITTMANN, F., PIEDADE, M. T. F. Seed Germination and Seedling Establishment of Amazonian Floodplain Trees. In: JUNK, W. J.; PIEDADE, M. T. F.; WITTMANN, F.; SCHÖNGART, J.; PAROLIN, P. (Eds.). Central Amazonian Floodplain Forests: Ecophysiology, biodiversity and sustainable management. Berlin/Heidelberg/New York: Springer, pp. 260–279, 2010.
- PAROLIN, P.; DE SIMONE, O.; HAASE, K. et al. Central Amazonian floodplain forests: tree adaptations in a pulsing system. **Botanical Review**, v. 70, p. 357–380, 2004.
- PAROLIN, P. Submerged in darkness: adaptations to prolonged submergence by woody species of the Amazonian floodplains. **Annals of Botany**, v. 103, p. 359–376, 2009.
- PAROLIN, P., WITTMANN, F., FERREIRA, L. V. Fruit and seed dispersal in Amazonian floodplain trees – a review. **Ecotropica**, v. 19, p. 15–32, 2013.
- PELLISSIER, L.; ALBOUY, C.; BASCOMPTE, J.; FARWIG, N.; GRAHAM, C.; LOREAU, M. et al. Comparing species interaction networks along environmental gradients. **Biological Reviews**, v. 93, n. 2, p. 785–800, 2018.
- PÉREZ-MÉNDEZ, N.; JORDANO, P.; GARCÍA, C.; VALIDO C. The signatures of anthropocene defaunation: cascading effects of the seed dispersal collapse. **Scientific Reports**, v. 6, n. 1, p. 24820, 2016.
- PEREYRA, P. E. R.; HALLWASS, G.; BEGOSSI, A.; GIACOMIN, L. L.; SILVANO, R. A. M. Fishers' knowledge reveals ecological interactions between fish and plants in high diverse tropical Rivers. **Ecosystems**, v. 26, p. 1095–1107, 2023.

- PIEADADE, M. T. F.; PAROLIN, P.; JUNK, W. J. Phenology, fruit production and seed dispersal of *Astrocaryum jauari* (Arecaceae) in Amazonian blackwater Foodplains. **Revista de Biologia Tropical**, v. 54, p. 1171–1178, 2006.
- PIEADADE, M. T. F.; FERREIRA, C. S.; WITTMANN, A. O.; BUCKERIDGE, M. S.; PAROLIN, P. Biochemistry of Amazonian Floodplain Trees. In: JUNK, W.; PIEADADE, M. T. F.; WITTMANN, F.; SCHÖNGART, J.; PAROLIN, P. (Eds.). Central Amazonian Floodplain Forests: Ecophysiology, Biodiversity and Sustainable Management. Berlin/Heidelberg/New York: Springer, pp. 123–134, 2010.
- POLLUX, B. J. A.; DE JONG, M.; STEEGH, A.; OUBORG, N. J.; VAN GROENENDAEL, J. M.; KLAASSEN, M. The effect of seed morphology on the potential dispersal of aquatic macrophytes by the common carp (*Cyprinus carpio*). **Freshwater Biology**, v. 51, p. 2063–2071, 2006.
- POLLUX, B. J. A. The experimental study of seed dispersal by fish (ichthyochory). **Freshwater Biology**, v. 56, p. 197–212, 2011.
- PRANCE, G. T. Notes on the vegetation of Amazonia. The terminology of Amazonian forest types subject to inundation. **Brittonia**, v. 31, p. 26–38, 1979.
- RAYBURG, S.; NEAVE, M.; THOMPSON-LAINING, J. The Impact of Flood Frequency on the Heterogeneity of Floodplain Surface Soil Properties. **Soil Systems**, v. 7, p. 63, 2023.
- RENÓ, V.; NOVO, E. Forest depletion gradient along the Amazon floodplain. **Ecological Indicators**, v. 98, p. 409–419, 2019.
- SIOLI, H. Bemerkung zur Typologie amazonischer Flüsse. **Amazoniana**, v. 1, p. 74–83, 1965.
- SOUZA-STEVEAUX, M. C.; NEGRELLE, R. R. B.; CITADINI-ZANETTE, V. Seed dispersal by the fish *Pterodorus granulosus* in the Paraná River basin, Brasil. **Journal of Tropical Ecology**, v. 10, p. 621–626, 1994.
- SCHONGART, J.; PIEADADE, M. T. F.; LUDWIGSHAUSEN, S.; HORNA, V.; WORBES, M. Phenology and stem-growth periodicity of tree species in Amazonian floodplain forests. **Journal of Tropical Ecology**, v. 18, p. 581–597, 2002.

SCHÖNGART, J.; JUNK, W. J. Forecasting the flood-pulse in Central Amazonia by ENSO indices. **Journal of Hydrology**, v. 335, p. 124–132, 2007.

SCHUPP, E. W.; JORDANO, P.; GÓMEZ, J. M. Seed dispersal effectiveness revisited: a conceptual review. **New Phytologist**, v. 188, p. 333–353, 2010.

SCHLEUNING, M.; FRÜND, J.; GARCÍA, D. Predicting ecosystem functions from biodiversity and mutualistic networks: an extension of trait-based concepts to plant-animal interactions. **Ecography**, v. 38, p. 380–392, 2015.

SCHWEITZER, J. A., JURIC, I., VAN DE VOORDE, T. F. J., CLAY, K., VAN DER PUTTEN, W. H., BAILEY, J. K. Are there evolutionary consequences of plant–soil feedbacks along soil gradients? **Functional Ecology**, v. 28, p. 55–64, 2014.

STRAUSS, S. Y., IRWIN, R. E. Ecological and evolutionary consequences of multispecies plant– animal interactions. **Annual Review of Ecology, Evolution, and Systematics**, v. 35, p. 435–466, 2004.

TITUS, J. E. Encyclopedia of Inland Waters - Aquatic Plants: A General Introduction. p. 43–51, 2009.

TRAVESET, A. Effect of seed passage through vertebrate frugivores' guts on germination: a review. **Perspectives in Plant Ecology, Evolution and Systematics**, v. 1, p. 151–190, 1998.

TRAVESET, A.; HELENO, R.; NOGALES, M. The ecology of seed dispersal. In: GALLAGHER, R. S. (Ed.). Seeds: the ecology of regeneration of plants communities, CAB International, Oxon, UK, pp. 62–93, 2014.

TYLIANAKIS, J. M.; R. J. MORRIS. Ecological networks across environmental gradients. **Annual Review of Ecology, Evolution, and Systematics**, v. 48, p. 25–48, 2017.

WEISS, B.; ZUANON, J. A. S.; PIEDADE, M. T. F. Viability of seeds consumed by fishes in a lowland forest in the Brazilian Central Amazon. **Tropical Conservation Science**, p. 1–10, 2016.

WEISS, B.; COSTA, G.; CORREA, S. B.; ZUANON, J.; PIEDADE, M. T. F. Does the consumption of pioneer-tree seeds from flooded forests by freshwater sardines affect seed germination? **Acta Oecologica**, v. 117, p. 103850, 2022.

WITTMANN, F.; ANHUF, D.; JUNK, W. J. Tree species distribution and community structure of central Amazonian várzea forests by remote-sensing techniques. **Journal of Tropical Ecology**, v. 8, p. 805–820, 2002.

WITTMANN, F.; SCHÖNGART, J.; MONTERO, J. C.; MOTZER, M.; JUNK, W. J.; PIEDADE, M. T. F.; QUEIROZ, H. L.; WORBES, M. Tree species composition and diversity gradients in white water forests across the Amazon Basin. **Journal of Biogeography**, v. 33, p. 1334–1347, 2006.

WITTMANN, F.; SCHÖNGART, J.; JUNK, W. J. Phytogeography, species diversity, community structure and dynamics of central Amazonian floodplain forests. In: JUNK, W. J.; PIEDADE, M. T. F.; WITTMANN, F.; SCHÖNGART, J.; PAROLIN, P. (Eds.). Central Amazonian Floodplain Forests: Ecophysiology, biodiversity and sustainable management Berlin/Heidelberg/New York: Springer, pp. 61–102, 2010.

WITTMANN, F.; HOUSEHOLDER, E.; PIEDADE, M. T. F.; DE ASSIS, R. L.; SCHÖNGART, J.; PAROLIN, P.; JUNK, W. J. Habitat specificity, endemism and the neotropical distribution of Amazonian white-water floodplain trees. **Ecography**, v. 36, p. 690–707, 2012.

WORBES, M.; KLINGE, H.; REVILLA, J. D.; MARTIUS, C. On the dynamics, floristic subdivision and geographical distribution of varzea forests in Central Amazonia. **Journal of Vegetation Science**, v. 3, p. 553–564, 1992.

WUNDERLE JUNIOR, J. M. The role of animal seed dispersal in accelerating native forest regeneration on degraded tropical lands. **Forest Ecology and Management**, v. 99, n. 1/2, pp. 223–235, 1997.

WRIGHT, S. J. The myriad consequences of hunting for vertebrates and plants in tropical forests. **Perspectives in Plant Ecology, Evolution and Systematics**, v. 6, p. 73–86, 2003.

YULE, T. S.; SEVERO-NETO, F.; TINTI-PEREIRA, A. P.; COSTA, L. B. L. C. Freshwater sardines of the pantanal delay seed germination in a floodplain tree species. **Wetlands**, v. 36, p. 195–199, 2015.

Capítulo 1

The effectiveness of ichthyochoric dispersal in forested wetlands of the Amazon depends on the species of fish and its size

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The effectiveness of ichthyochoric dispersal in forested wetlands of the Amazon depends on the species of fish and its size

Abstract

The interaction between fish and plants in Amazon floodplain is fundamental for the maintenance of frugivorous fish and tree communities. The viability of seeds after passing through the digestive tract of fish is a central factor for seed dispersal since it can influence colonization and regeneration of these environments. Our study investigated the seed dispersal by frugivorous fish in a flooded forest in the Central Amazon. We also evaluated the seed germination speed after passage of the digestive tract of fish and how the size of fish and the seeds can influence the dispersion of tree seeds in floodplains. A total of 5,012 seeds from 49 plant species were found in the digestive tracts of 11 frugivorous fish species. The length and weight of the frugivorous fish were positively related to the size of seeds in the digestive tract. The germination of the seeds removed from the fish varied between species. The passage of the seeds of the different plant species through the digestive tracts of the fish did not significantly increase the germination speed. Considering the anthropogenic pressures present in these environments, we can expect that a reduction in body size for some species of fish, due to overexploitation, may have negative consequences for some tree species that are dispersed mainly via ichthyochory.

Keywords: Fish size, floodplain forests, frugivory, ichthyochory, seed size, seed viability.

Introduction

Seed production, dispersal and germination are important ecological processes for plant survival and growth (Eriksson and Ehrlén, 2008; Anderson et al., 2009; Weiss et al., 2016, 2022). Fruit and seed dispersal determine species composition and influences ecosystem structure (Howe and Smallwood, 1982; Correa et al., 2015a), and frugivory is a key process in plant dynamics and natural habitat regeneration (Jordano, 2000). Regeneration is essential for maintaining forest biodiversity and the functions of ecosystems (Neuschulz et al., 2016). In the Amazon region, the hydrological regime plays a key role in the structure and functions of aquatic ecosystems (Junk et al., 1989), as well as in the composition of plant species in the floodplains (Kubitzki and Ziburski, 1994; Worbes, 1997; Parolin et al., 2004; Piedade et al., 2006; Ferreira et al., 2010). Fruit maturation occurs mainly at high-water levels, and the flood pulse favors dispersal of seeds via water (hydrochory) and fish (ichthyochory) (Ferreira, 1998; Parolin et al., 2013). These two mechanisms are the main forms of seed dispersal in floodable areas of the Amazon (Horn, 1997).

Seasonal flooding in Amazonian floodplain areas allows fish populations to exploit allochthonous resources from the flooded forests (Goulding, 1980), with lateral migrations during rising waters as they go in search of food and shelter (Castello, 2008). In these environments, the consumption of fruits by fish contributes to seed dispersal, which influences the structure (Howe, 1993; Pollux et al., 2006; Anderson et al., 2009; Pollux, 2011) and diversity of plants along the rivers (Hulme and Benkman, 2002; Correa et al., 2007). Although hydrochory is considered the main dispersal mechanism for riparian and aquatic vegetation (Nilsson et al., 1991; Malanson, 1993; Cain et al., 2000; Pollux et al., 2009), it operates almost exclusively along the river continuum (Williamson and Costa, 2000). On the other hand, seeds can be dispersed by fish upstream and downstream, laterally within the floodplain (Horn, 1997; Anderson et al., 2011), and for much greater distances than those reached by terrestrial

vertebrates such as monkeys, rodents and even birds (Cain et al., 2000). In flooded forests, fish consume most of the fruit and seed biomass, even surpassing birds and monkeys that eat propagules and leaves (Goulding, 1983).

The tropical wetlands of the planet are inhabited by a high diversity and abundance of frugivorous fish (Horn et al., 2011), with approximately 280 species, that consume fruit at least some period of their lives. In the Neotropical region, there are approximately 150 species of fruit-eating fish, which are distributed in 75 genera and 17 families (Horn et al., 2011). These species consume fruits and seeds of at least 566 plant species from 295 genera and 82 families (Correa et al., 2015a). In the Amazon basin, there are more than 3,000 species of fish (Van der Sleen and Albert, 2018), of which at least 93 are consumers of fruits and seeds from floodable forests (Correa, 2012), though this number can reach 200 species (Goulding, 1980).

Frugivorous fish have adaptations that facilitate their foraging activities and their dispersal of seeds (Goulding, 1980; Correa et al., 2007, 2015a). Since they do not have strong teeth, most frugivorous catfish are able to swallow whole fruits, and most seeds can pass intact through the intestine and later germinate (Goulding, 1980; Mannheimer et al., 2003; Weiss et al., 2016). However, not all fruit-eating fish species act as dispersers (Prudente et al., 2016), since the effectiveness of a frugivore as a seed dispersal agent depends either on the quantity and quality of the dispersion, or on the likelihood that the seeds will be deposited unharmed in places with high prospects for establishment (Jordano and Schupp, 2000). These quantitative and qualitative variables include the amount of seeds ingested, the mechanics of ingestion, the effects on germination due to the seed's passage through the digestive tract, fish movement patterns (Schupp, 1993), and the size and weight of the disperser (Galetti et al., 2008; Costa-Pereira and Galetti, 2015).

Approximately 15% of the Amazon basin is covered by floodable forests (Melack and Hess, 2010), and only in the fertile floodplain forests of the white-water rivers of the Amazon

basin (“várzea”, *sensu* Junk et al., 2011), more than 1,000 tree species are found (Wittmann et al., 2006, 2010). While seed dispersal of many of these species is linked to hydrochory and aquatic dispersers, seedling establishment is restricted to the terrestrial phase (Oliveira-Wittmann et al., 2010). After a seed is released from the plant, the duration and timing of germination are key processes for its establishment (Oliveira-Wittmann et al., 2010). The characteristics of the seeds are of great importance for their germination and, consequently, for the regeneration of floodable forests (Parolin et al., 2010). In this way, fish can play an important role in this process, since the ingestion of seeds by frugivores is an advantage that can increase germination percentages and speeds (Van der Pijl, 1982; Maia et al., 2007; Lehouck et al., 2011; Reid and Armesto, 2011). The passage of seeds through the digestive tract can promote chemical or physical scarification, which can remove parts of the fruit responsible for mechanical and chemical dormancy (Baskin and Baskin, 2004), thus eliminating inhibiting factors for germination and facilitating the activation of metabolic processes (Traveset and Verdú, 2002). This process may have implications for plant recruitment and establishment, since early germination may increase competitive fitness (Verdú and Traveset, 2005; Traveset et al., 2007; De Luis et al., 2008).

Several studies on the viability of seeds after their passage through the digestive tract of fish have been conducted (Horn, 1997; Mannheimer et al., 2003; Pollux et al., 2006; Maia et al., 2007; Weiss et al., 2016, 2022). However, there is still a large gap in the understanding of the mechanisms of the effects of seed ingestion by fish on germination and its potential for future plant recruitment (Santos et al., 2020). It is possible that the interaction between fish and plants is one of the most threatened mutualisms (Galetti et al., 2008), mainly due to the loss of floodable forests (Junk et al., 2000; Renó et al., 2016; Renó and Novo, 2019) and overfishing of frugivores (Castelo et al., 2013; Tregidgo et al., 2017; Costa-Pereira et al., 2018; Araujo et al., 2021) since large species remain the main target of fishing activities in the Neotropics

(Correa et al., 2015a), thus endangering the dispersal of large seeds (Costa-Pereira et al., 2018). Similarly, seed dispersal in upland (terra firme) forests can be affected by the removal of large mammals (Fragoso, 1997). In this sense, it is essential to understand the role of frugivorous fish as seed dispersers to predict the impact of their decline on the populations of plants dispersed by them (Galetti et al., 2008).

Here, we identified the species of seeds dispersed by frugivorous fish in floodplains of the Amazon basin. We tested whether the germination speed vary with the passage through the digestive tract of fish and whether the seed size varies with the weight and length of frugivorous fish. We expect to find that: (a) the passage of seeds through the digestive tract increases germination speed, and (b) the size of the seeds found in the digestive tracts is greater in larger fish.

Material and Methods

Study area

The study was carried out in a stretch of flooded forest of the Solimões River known as Paciência Island (03° 18'12" S; 60° 13' 51" W), in the central Amazon (Figure 1).

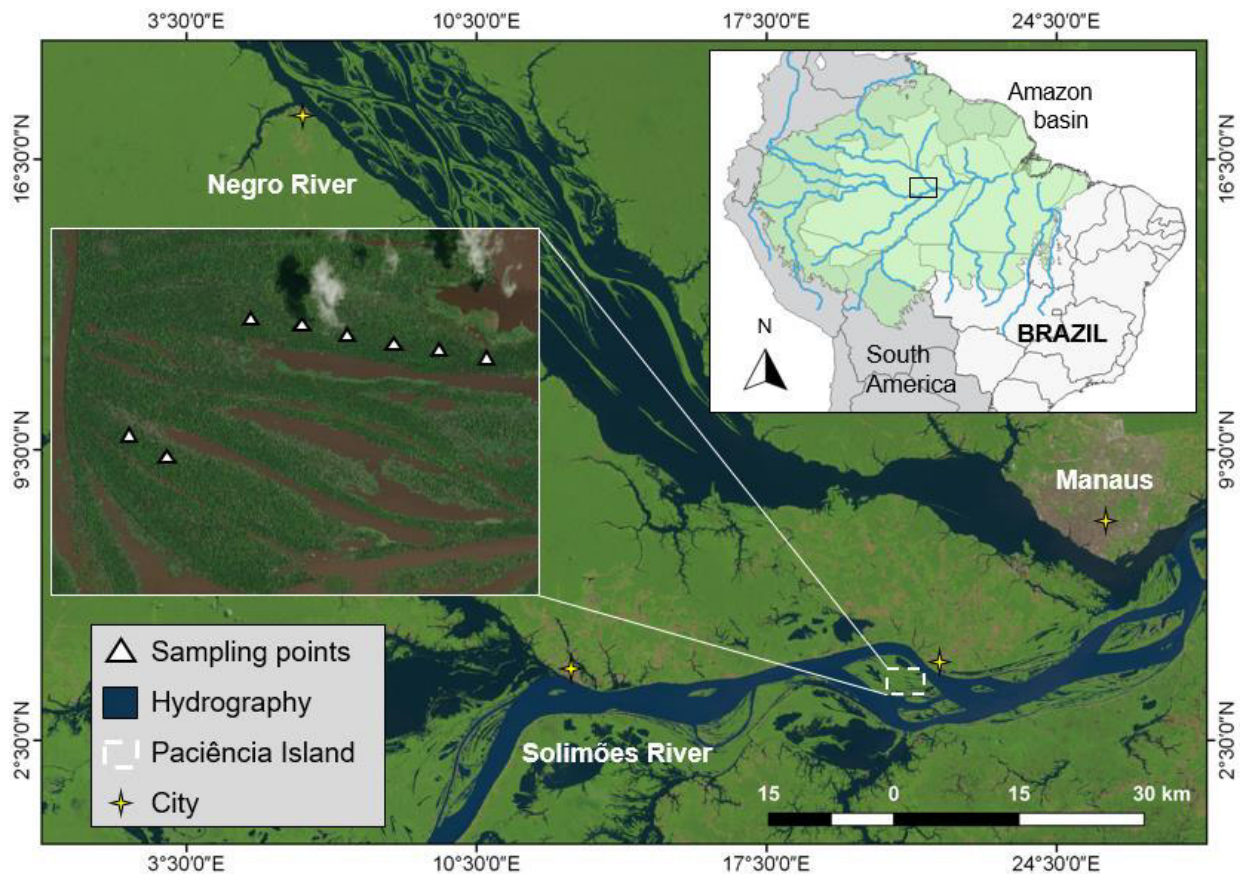


Figure 1. Study area located on Paciência Island in the Solimões River.

The annual rainfall in the region is approximately 2,100 mm/year, with a marked difference between the dry (June/October) and rainy (December/May) seasons (Parolin, 2000). The fluctuation of the water level in the stretch of flooded forest is of approximately 10 m, thus distinguishing the two hydrological phases, i.e., the aquatic phase, with the peak of the high-water period in June/July and the terrestrial phase, with the peak of the low-water period in October/November (Junk, 1989; Junk et al., 1989). The Solimões River is a typical “várzea” floodplain river, and has white waters, with a pH close to neutral, and is rich in suspended matter that carries clay minerals and releases nutrients to the alluvial soils (Irion et al., 2010).

Sampling design and collection of fish

A total of eight collections were carried out fortnightly between April and July 2022, which corresponds to the beginning of the rising-water period and high-water period of the

Solimões River, a period of greater production and availability of fruits and seeds. A set of nine gill nets (with meshes sizes from 24 to 110 mm, 10 m long, between 1.5 to 3.0 m in height) that were joined to each other was used for the collection of fish. The collection period was 24 hours, with inspections every four hours. For each collection, the nine fishing nets were placed at a subsequent point (n=8), separated by a distance of about 400 meters.

The captured fish were immersed in an anesthetic (eugenol) dissolved in water, and kept in the solution for up to 10 minutes after the opercular movements ceased. While in the field, the standard weight and length of the subjects were obtained and the digestive tracts (stomach and intestine) were removed for further analysis in the laboratory. One representative of each species was labeled and stored in a Styrofoam box and transported to the National Institute for Amazonian Research (INPA) for confirmation of the identity of the species with the help of specialists. In the laboratory, the analysis of the digestive tracts was carried out with the aid of a magnifying glass (10x). The seeds found intact in the digestive tract were quantified and stored to be identified by a parobotanist, and their identification confirmed at the INPA herbarium. The licenses for fish collections were obtained via the Biodiversity Authorization and Information System (SISBio; protocol number 81822-1/2022) of the Chico Mendes Institute for Biodiversity Conservation (ICMBio). The research was approved by the INPA Ethics Committee on the Use of Animals (CEUA; number 67/2022).

Morphometry of fish and seeds

The standard length (SL) of the fish was obtained from the tip of the nose to the end of the caudal peduncle with the aid of a millimeter ruler, and weighed on a precision digital scale. The size of the seeds was obtained at the points of greater width or length of the seeds with the aid of a digital caliper. The seed species found in large quantities in the digestive tracts were randomly limited to a number of ten seeds per species to obtain an mean value. The relationship

between length and weight of fish with seed size was evaluated together for all frugivorous species.

Sowing and germination of seeds

Seeds were collected in the field from trees in different individuals of each plant species and mixed to produce a homogenized sample (control treatment). The goal of collecting from multiple individuals was to eliminate dependence on seeds from the same individual. The seeds identified in the digestive tracts of the fish and collected directly from the trees remained immersed (10 cm deep) in water for 10 days before sowing in “várzea” floodplain soil, with monitoring and daily watering. All seeds from the digestive tracts were sown when the n was equal to or greater than 30 seeds per species of fish. The criterion for establishing seed germination was the protrusion of the radicle from the embryo. Each experiment was followed up for a period of 60 days. Germination was monitored in a greenhouse of the Ecology, Monitoring and Sustainable Use of Wetlands group (MAUA/INPA). During the period of the germination experiment, the temperature ranged from 24 °C to 37 °C, the relative humidity ranged from 35% to 95%, the accumulated precipitation in this period was 241 mm, and mean photosynthetic active radiation was $470.23 \mu\text{mol}\cdot\text{s}^{-1}\text{m}^{-2}$.

Design of germination experiments

The germination potential of the seeds was evaluated for three tree species: *Bothriospora corymbosa* (Rubiaceae), *Crataeva tapia* (Brassicaceae) and *Cecropia latiloba* (Urticaceae), which were taken from the digestive tracts of five fish species: *Trachelyopterus galeatus* (Auchenipteridae), *Chalceus erythrurus* (Chalceidae), *Colossoma macropomum* (Serrasalminidae), *Triportheus albus* (Triportheidae) and *Schizodon fasciatus* (Anostomidae). These five species of fish were the ones that contained seeds in large number of a given tree species. For the germination experiment, tree species with relatively high abundance found in

the digestive tract of fish and in the trees of the environment were used. A total of six comparison experiments between seeds removed from the digestive tracts versus seeds collected from the trees (control) were performed. For each treatment, the same amount of seeds was used in the respective controls, but the number of seeds was different in each treatment. For the plant species *C. latiloba* taken from *C. macropomum*, *T. albus* and *S. fasciatus*, a single control was used. They were organized as follows: treatment T1 - *B. corymbosa* seeds removed from *T. galeatus* (N = 130) versus control; treatment T2 - *B. corymbosa* seeds removed from *C. erythrurus* (N = 150) versus control; treatment T3 - *C. tapia* seeds removed from *C. macropomum* (N = 35) versus control; treatment T4 - *C. latiloba* seeds removed from *C. macropomum* (N = 200) versus control; T5 treatment - *C. latiloba* seeds removed from *T. albus* (N = 200) versus control and treatment T6 - *C. latiloba* seeds taken from *S. fasciatus* (N = 200) versus control.

Data analysis

A Generalized Mixed Effects Model was performed to assess the relationships between the size of the seeds found in the digestive tract (response variable) and the length and weight of the fish (predictor variable), using fish as a random factor. This analysis was carried out with *lme4* and *ggplot2* packages in R. By using the *GerminaQuant* function of the *GerminaR* package (Lozano-Isla et al., 2019), the main germination indices were obtained for seeds found in the digestive tracts of fish and seeds of control treatments: number of germinated seeds (NGS), germination percentage (GP%), mean germination time (MGT), mean germination rate (MGR).

To assess differences in the speed of germination between seeds removed from the digestive tract and the control treatment, we performed a Cox proportional hazards survival model, assessing the proportion of germinated seeds (response variable) as a function of time in days (predictor variable). This analysis was carried out with the *coxph*, *survfit* and *ggsurvplot*

functions of the *survival* (Therneau, 2023) and *survminer* (Kassambara and Kosinski, 2017) packages in R. The results were accessed using Wald chi-square (χ^2) tests for significance. All analyses were performed using the R software (R version 4.3.1-2023).

Results

A total of 5,012 intact seeds from 49 species and 33 families were found in the digestive tracts of 241 frugivorous fish of 11 species.

The most abundant and most consumed fruits by fish were of three species: *C. latiloba* (N = 2,503), *B. corymbosa* (N = 1,277) and *Ficus amazonica* (N = 792), totaling 90% of the seeds found. The size of the seeds found in the fish ranged between 1.2 and 44.9 mm (± 1.27 SE) (Table 1). The three species of seeds that had the largest size were *Swartzia argentea* (44.9 mm), *Simaba multiflora* (37.09 mm) and *Astrocaryum jauari* (32.5 mm). The majority of the species of seeds were found in the digestive tract of only one species of fish. Four species of seeds were found in the digestive tracts of at least five fish species: *C. latiloba*, *Rhigospira* sp., *Bactris riparia* and *B. corymbosa*. Fleshy and indehiscent fruits were found in 34 species (69.3%) and non-fleshy and dehiscent fruits in 15 species (30.6%) (Table 1).

Table 1: Plant species consumed by fish. Mean seed size by species, number of seeds, fleshy (1) or non-fleshy (0) fruit, fish species and code: Ba – *B. amazonicus*, Ce – *C. erythritus*, Cm – *C. macropomum*, Lf – *L. fasciatus*, Ma – *M. asterias*, Mal – *M. albiscopum*, Pg – *P. granulosus*, Rm – *R. microlepis*, Sf – *S. fasciatus*, Ta – *T. albus*, Tg – *T. galeatus*.

Family	Plant species	$\pm$ Seed size (mm)	Total seeds	Fruit type	Fish species / code
Annonaceae	<i>Guatteria inundata</i>	21.33	4	1	Tg. Pg. Ba.
	<i>Pseudoxandra polyphleba</i>	12.64	10	1	Tg. Pg.
Apocynaceae	<i>Odontadenia puncticulosa</i>	19.03	1	1	Tg.
	<i>Rhigospira</i> sp.	11.48	33	1	Tg. Pg. Ta. Sf. Rm.
Aquifoliaceae	<i>Ilex inundata</i>	5.6	8	1	Mal. Ma.
Arecaceae	<i>Astrocaryum jauari</i>	32.5	3	1	Tg. Pg. Cm.

	<i>Bactris riparia</i>	12.16	61	1	Tg. Pg. Ba. Cm. Ce.
Burseraceae	<i>Protium strumosum</i>	11.3	1	0	Pg.
Capparaceae	<i>Crataeva tapia</i>	10.16	40	1	Cm.
Celastraceae	<i>Salacia multiflora</i>	13.41	1	1	Tg.
Chrysobalanaceae	<i>Leptobalanus apetalus</i>	20.75	3	1	Ba.
	<i>Leptobalanus</i> sp.	12.45	1	1	Pg.
Combretaceae	<i>Combretum laxum</i>	12.28	1	0	Pg.
Connaraceae	<i>Connarus perrottetii</i>	9.47	10	0	Pg. Ba. Mal.
Dilleniaceae	<i>Davilla</i> sp.	7.04	5	0	Mal.
	<i>Tetracera</i> sp.	6.63	8	0	Tg.
Dioscoreaceae	<i>Dioscorea</i> sp.	4.47	1	0	Ta.
Euphorbiaceae	<i>Hevea brasiliensis</i>	22.78	1	0	Cm.
	<i>Maprounea guianensis</i>	6.1	1	0	Pg.
	<i>Sapium</i> sp.	5.46	8	0	Ta.
Fabaceae	<i>Ormosia excelsa</i>	19.3	3	0	Tg. Pg.
	<i>Swartzia argentea</i>	44.9	1	0	Tg.
Humiriaceae	<i>Schistostemon</i> sp.	16.46	1	1	Pg.
Lamiaceae	<i>Vitex cymosa</i>	14.94	6	1	Mal. Ma.
Lauraceae	<i>Nectandra amazonum</i>	15.67	2	1	Ma.
	<i>Ocotea</i> sp.	9.06	1	1	Ta.
Linaceae	<i>Roucheria columbiana</i>	7.78	1	1	Tg.
Lythraceae	<i>Cuphea</i> sp.	3.17	1	0	Pg.
Malpighiaceae	<i>Byrsonima</i> sp.	9.81	2	1	Tg.
Malvaceae	<i>Pseudobombax munguba</i>	5.35	11	0	Mal. Lf.
Moraceae	<i>Brosimum parinarioides</i>	3.53	34	1	Tg.
	<i>Ficus amazonica</i>	1.2	792	1	Tg. Ta. Mal.
	<i>Sorocea duckei</i>	14.4	16	1	Tg.
Myrtaceae	<i>Myrciaria dubia</i>	12.54	6	1	Tg. Pg. Ta.
Ochnaceae	<i>Sauvagesia</i> sp.	3.49	5	0	Tg. Ta.
Olacaceae	<i>Minquartia guianensis</i>	21.07	1	1	Pg.
Passifloraceae	<i>Passiflora</i> sp.	5.5	1	1	Ta.
Quinaceae	<i>Quiina rhytidopus</i>	13.53	62	1	Tg. Pg. Mal.
Rubiaceae	<i>Alibertia edulis</i>	6.4	25	1	Tg.

	<i>Bothriospora corymbosa</i>	1.58	1.277	1	Tg. Pg. Ta. Ba. Ce.
	<i>Faramea capillipes</i>	9.88	2	1	Tg.
	<i>Faramea</i> sp.	10.17	6	1	Tg. Ta.
	<i>Psychotria</i> sp.	4.41	40	1	Ba.
Sapotaceae	<i>Micropholis guyanensis</i>	13.96	1	1	Ba.
	<i>Pouteria caimito</i>	23.19	6	1	Pg.
Sapindaceae	<i>Paullinia cupana</i>	7.25	2	0	Ba.
Simaroubaceae	<i>Simaba multiflora</i>	37.09	2	1	Cm.
Smilacaceae	<i>Smilax</i> sp.	7.51	1	1	Ta.
Urticaceae	<i>Cecropia latiloba</i>	2.29	2.503	1	Tg. Ta. Ba. Mal. Cm. Sf.

The most abundant fish species were *T. galeatus* (N = 68), *Mylosoma albiscopum* (N = 44) and *T. albus* (N = 43). The length of the fish ranged between 145 and 276 mm (± 13.3 SE) and the weight between 76.6 and 386 g (± 26.7 SE) (Table 2). The fish species that consumed the most fruit species were *T. galeatus* (N = 23), *Pterodoras granulosus* (N = 18) and *T. albus* (N = 12). The fish species found with the greatest number of seeds were *S. fasciatus* (N = 1,281), *T. galeatus* (N = 1,238) and *T. albus* (N = 997). The fish species found with the least seeds were *Leporinus fasciatus* (N = 4) and *Rhytiodus microlepis* (N = 1) (Table 2).

Table 2: Species of frugivorous fish that consumed fruits. Mean of standard length ($\pm$ SL mm) and weight ($\pm$ W g) of fish and number of seeds and species of seeds consumed.

Family	Fish species	Total Fish	$\pm$ SL (mm)	$\pm$ W (g)	Total seeds	Plant species
Anostomidae	<i>Leporinus fasciatus</i>	1	270	386	4	1
	<i>Rhytiodus microlepis</i>	12	276	301.8	1	1
	<i>Schizodon fasciatus</i>	15	216	205	1,281	2
Auchenipteridae	<i>Trachelyopterus galeatus</i>	68	153	112.4	1,238	23
Bryconidae	<i>Brycon amazonicus</i>	18	184	168.3	84	9
Chalceidae	<i>Chalceus erythrurus</i>	18	192	149.6	410	2
Doradidae	<i>Pterodoras granulosus</i>	12	176	246.9	92	18

Serrasalminidae	<i>Colossoma macropomum</i>	8	210	210.1	729	6
	<i>Myloplus asterias</i>	2	157	179	13	3
	<i>Mylossoma albiscopum</i>	44	145	130	163	8
Triportheidae	<i>Triportheus albus</i>	43	171	76.6	997	12

Relationship between size of fish and size of seeds

The Generalized Mixed Effects Model revealed that length (Wald's test, $X^2 = 20.247$, $df = 1$, $p < 0.001$) and weight (Wald's test, $X^2 = 24.911$, $df = 1$, $p < 0.001$) of the frugivorous fish were positively related to the size of the seeds found in the digestive tracts (Figure 2). The longer the length and weight of the fish, the larger the size of the seeds observed.

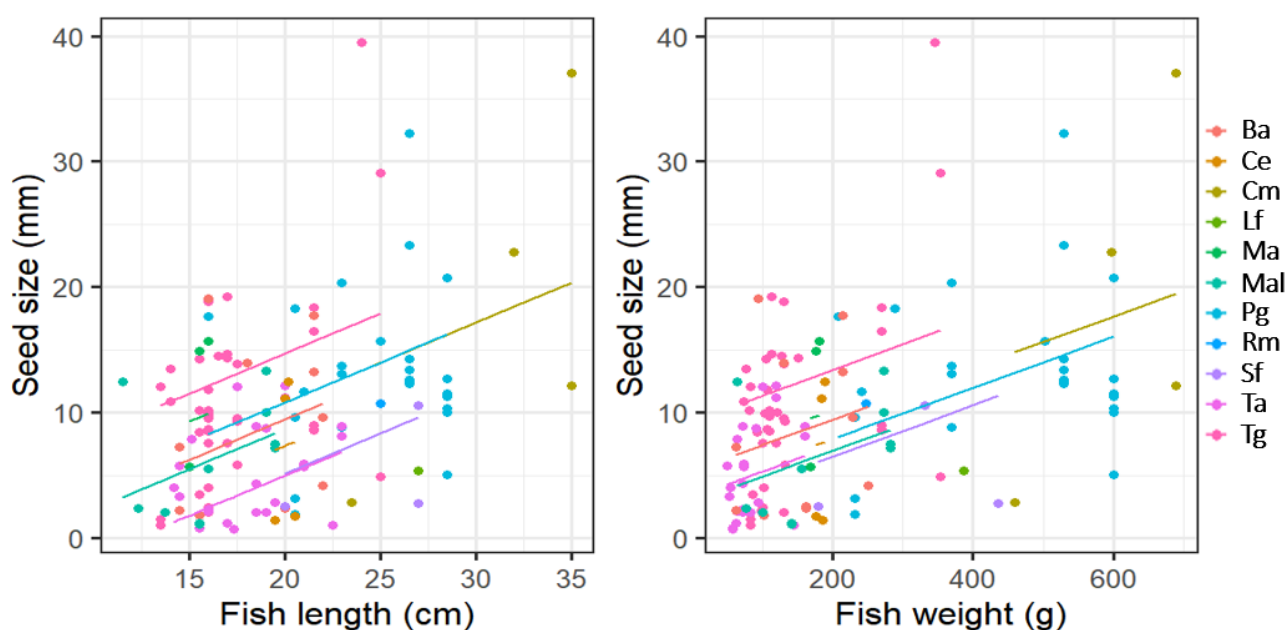


Figure 2: Relationship between the length and weight of 11 species of frugivorous fish and the size of the seeds found in their digestive tracts. Fish code, top to down: Ba – *B. amazonicus*, Ce – *C. erytrutus*, Cm – *C. macropomum*, Lf – *L. fasciatus*, Ma – *M. asterias*, Mal – *M. albiscopum*, Pg – *P. granulosus*, Rm – *R. microlepis*, Sf – *S. fasciatus*, Ta – *T. albus*, Tg – *T. galeatus*.

Viability of seeds

The germination of the seeds found in the digestive tract of fish varied between species and began between 4 and 12 (± 0.79 SE) days after sowing. The Cox regression model revealed a significant effect of fish consumption on the germination speed only for seeds of *B. corymbosa* removed from the digestive tract of *T. galeatus* (T1; Wald's test, $X^2 = 14.61$, $df = 1$, $p < 0.001$, Fig. 3a), compared to the control treatment. The passage of seeds through the digestive tracts of *T. galeatus* reduced the germination speed (Figure 3).

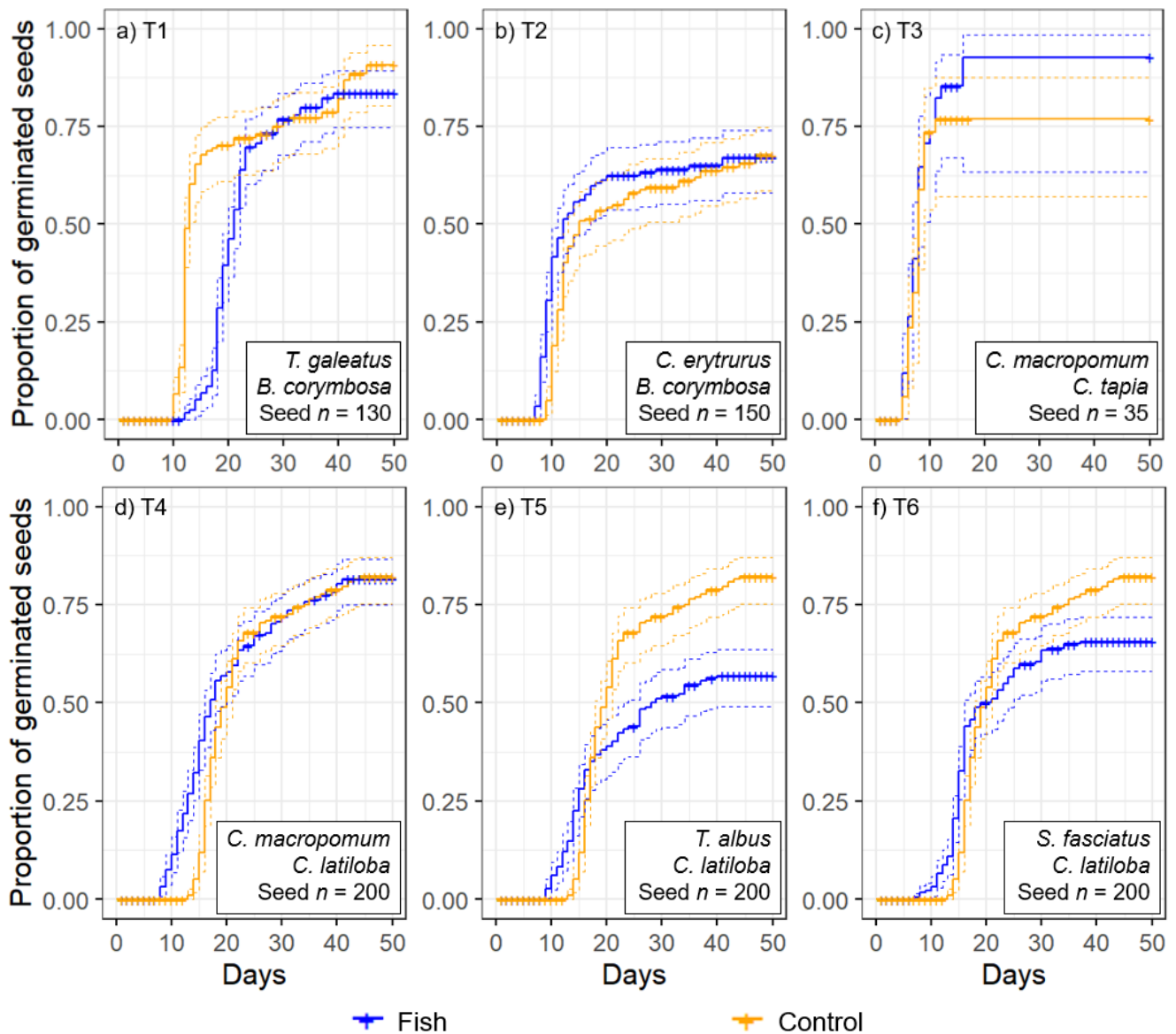


Figure 3: Proportion of germinated seeds over time, for seeds removed from the digestive tracts in relation to the control treatment. Each curve is surrounded by a 95% confidence interval.

With the exception of the *C. latiloba* seeds consumed by *T. albus* (T5), all other treatments showed germination percentages of over 60%. The highest percentage of germination was observed in the *C. tapia* seeds recovered from the digestive tract of *C. macropomum* (T3) (GP = 85.7%), and the lowest percentage of germination was observed in the *C. latiloba* seeds consumed by *T. albus* (GP = 51.5%). The highest mean germination time was observed for the *B. corymbosa* seeds consumed by *T. galeatus* (T1) (MGT = 20.4), and the lowest mean germination time was for the *C. tapia* seeds of the control treatment (MGT = 7.6) (Table 3).

Table 3: Germination parameters: number of germinated seeds (NSG), germination percentage (GP%), mean germination time in days (MGT), mean germination rate (MGR).

Treatments	Total seeds	NSG	GP%	MGT	MGR	Germination speed Wald's test, X^2
<i>T. galeatus</i>	130	97	74.6	20.4	0.05	$p < 0.001$
<i>B. corymbosa</i> (control)	130	100	76.9	13.3	0.069	
<i>C. erythrurus</i>	150	95	63.3	10.8	0.093	$p > 0.114$
<i>B. corymbosa</i> (control)	150	93	62	13.8	0.069	
<i>C. macropomum</i>	35	30	85.7	7.8	0.144	$p > 0.399$
<i>C. tapia</i> (control)	35	26	74.2	7.6	0.154	
<i>C. macropomum</i>	200	148	74	17.1	0.059	$p > 0.143$
<i>C. latiloba</i> (control)	200	144	72	19.3	0.052	
<i>T. albus</i>	200	103	51.5	17.6	0.058	$p > 0.05$
<i>C. latiloba</i> (control)	200	144	72	19.3	0.052	
<i>S. fasciatus</i>	200	120	60	16.8	0.062	$p > 0.154$
<i>C. latiloba</i> (control)	200	144	72	19.3	0.052	

Discussion

Our study showed a high number and high diversity of seeds in the digestive tracts of frugivorous fish. This result demonstrates the importance of fruits as a food source for fish and the role of fish in seed dispersal in Amazon floodplains. Other studies in Neotropical regions

have shown a high number of seeds dispersed by frugivorous fish (Correa et al., 2015a), and our work shows a high variation in the size of dispersed seeds (1 to 45 mm), which indicates the complexity of ichthyochory in the Amazon floodplains.

Neotropical wetlands are home to a high diversity of frugivorous fish, with approximately 150 known species (Horn et al., 2011), and at least 93 species are known from the Amazon basin (Correa, 2012). Our study showed 11 species that feed on fruits in an Amazon floodplain during the flood period, and indicated that there is a positive relationship between size of frugivorous fish and size of dispersed seeds. This result showed the importance of the size of frugivorous fish in the dispersal of large seeds from the Amazonian floodplains. However, the results also indicated that large species also carry small seeds, which may have occurred due to the consumption of whole fruits. In general, small-sized seeds are produced in polyspermic fruits. For example, fruits of *F. amazonica* (~ 1 cm), *B. corymbosa* (~ 0.7 cm) and even *C. tapia* (~ 7 cm) can contain dozens or hundreds of seeds. While *C. latiloba* (~ 15 cm long) can contain an average of 5,000 seeds per fruit (Parolin, 1997). Therefore, it is important to highlight that there may be an underestimation of the ability of some fish species to transport seeds of certain sizes, as seeds found in the digestive tract may have been ingested with the whole fruit.

Some studies have shown that larger fish consume a greater quantity and diversity of fruits (Galetti et al., 2008; Correa et al., 2015b), and transport them over longer distances (Anderson et al., 2011). In terms of conservation, this result shows that the overexploitation of larger fish in floodplain forests could compromise the dispersion of relatively large seeds, such as those of *S. argentea* (44.9 mm), *S. multiflora* (37.09 mm), *A. jauari* (32.5 mm), *Pouteria caimito* (23.19 mm) and *Hevea brasiliensis* (22.78 mm). In addition, the overexploitation of large fish currently occurring in the Amazonian floodplains (Tregidgo et al., 2017; Costa-Pereira et al., 2018) could prioritize the dispersion of smaller seeds, such as those of *F.*

amazonica (1.2 mm), *B. corymbosa* (1.58 mm) and the pioneer *C. latiloba* (2.29 mm). Since these small seed species are produced in large quantities in these environments, there could be a dominance of these plants in these ecosystems over time. For example, pioneer species from the Amazonian floodplain such as *C. latiloba*, *Pseudobombax munguba* and *Salix martiana* have fast growth (Junk et al., 2020). During the initial secondary succession process *C. latiloba* can form monospecific clusters (Worbes et al., 1992) with up to 1,000 individuals/ha (≥ 10 cm DAP) (Schöngart, 2003). The high seed production and fast growth of some pioneer species are essential for the regeneration of floodplain forests degraded by deforestation, and frugivorous fish can play an important role in the dispersal process for many of these pioneer species.

In our study we observed that larger fish individuals in the community also tend to transport a greater variety of seed sizes than smaller individuals; however, they also transport small seeds. Araujo et al. (2021) observed that large individuals tend to be less specialized, dispersing seeds of different sizes, thus filling a unique seed dispersal niche that small individuals cannot occupy. In addition, the capture of large individuals through overfishing has directed populations towards smaller size classes (Tregidgo et al., 2017), which makes individuals more predators than seed dispersers (Correa et al., 2007). These impacts have recently been reported for the species *C. macropomum* in the central Amazon (Tregidgo et al., 2017; Costa-Pereira et al., 2018), where pressure, mainly from commercial fishing close to large urban centers, has caused a decline in the abundance and size of individuals.

An important predictor for seed dispersal is related to dispersion quality (Jordano and Schupp, 2000). Fruit processing by frugivores determines how many seeds are deposited unharmed in potentially safe places (Jordano, 2000). Some species of frugivorous fish can carry seeds in large quantities, but destroy most of them. Many species of Neotropical Characiformes, some of the genera *Colossoma* and *Piaractus*, have multicuspid, molariform teeth that facilitate the breaking of hard-shelled fruits and seeds. Others of the genera *Brycon*, *Pristobrycon* and

Serrasalmus have sharp multicuspid teeth that can cut fruits and seeds (Goulding, 1980), causing variable damage to seeds during ingestion (Correa et al., 2007). In the Neotropics, in addition to the Characiformes, the order Siluriformes has many species that consume fruits, especially the families Auchenipteridae, Doradidae and Pimelodidae (Mannheimer et al., 2003; Horn et al., 2011). In our study, the fish species carrying more seed species were the catfish *T. galeatus* (N = 23) and *P. granulosus* (N = 18). Since these species are not strictly fruit consumers, they may have a wide variation in their food spectrum (Agostinho et al., 2009; Sousa et al., 2017), this result may be related to the fact that these species have villiform teeth, increasing the likelihood of ingesting whole fruits and seeds (Goulding, 1980). Although *T. galeatus* was one of the smallest species (± 153 mm), it was the main fruit consumer. Catfish that feed on fruits tend to be large species with larger stomach volume. The seven species of Neotropical catfish of the families Pimelodidae and Doradidae that were found with fruits in their digestive tract were relatively large (> 50 cm) (Correa et al., 2007), and a reduction in the size of the individuals of these species could compromise the dispersion of large seeds in the region.

For tree species that occur in floodplain areas of the Amazon, the ability of fruits and seeds to float can be extremely important for dispersal over long distances via hydrochory. However, not all tree species possess this ability; for example, species of the families Arecaceae (*B. riparia* and *A. jauari* palms) consumed by *T. galeatus*, *P. granulosus* and *C. macropomum*, and Lauraceae (*Nectandra amazonum*), consumed by *M. asterias*, are relatively large ($\sim 1-3$ cm) and heavy and without well-developed structures for buoyancy (Kubitzki and Ziburski, 1994; Piedade et al., 2003, 2006). In our study, most of the seed species that are recorded in the digestive tracts of fish tend to sink when they fall into the water, which may benefit fish with benthic habits such as *T. galeatus* and *P. granulosus* (Agostinho et al., 2009; Rocha et al., 2021). In addition, hydrochoric dispersion distances for floating seeds may vary depending on the

location and habitat characteristics where the seeds fall into the water (Hyslop and Trowsdale, 2012; Zamorano et al., 2022). Floating seeds deposited in floodplain lake systems, for example, where the speed of the current is reduced, will not be favored by hydrochory, unlike those floating ones that are deposited in the riverbed. In this way, ichthyochory can be very important for plant species that produce seeds that do not float, but also for those that do float. For species that do not float, the retention time of the seeds in the digestive tracts and the habit of life of the fish, whether sedentary or migrating, are crucial factors that determine the distances traveled in the time between their ingestion and their deposition in the environment.

Viability of seeds

The seeds removed from the digestive tracts showed germination percentages between 51 and 85% in all treatments. The passage of *B. corymbosa* seeds through the digestive tracts of *T. galeatus* and *C. erythrurus*, *C. tapia* by *C. macropomum*, and *C. latiloba* by *C. macropomum*, *T. albus* and *S. fasciatus* did not increase the germination speed. Some studies point out that the passage of seeds through the digestive tract of fish does not always increase the likelihood of germination (Smits et al., 1989; Anderson et al., 2009; Boedeltje et al., 2015), but can reduce it (Pollux et al., 2006; Boedeltje et al., 2015; Weiss et al., 2022) or even have no effects (Adams et al., 2007). Our study showed that these frugivorous species disperse the seeds of tree species in the Amazon floodplains, and increase their dispersion to areas further away from their mother plant, but this does not increase their germination speed. This result may be related to the characteristics of the seeds, the retention time of the seeds in the digestive tracts and the ability to digest seeds (Kubitzki and Ziburski, 1994). The retention time of seeds in the digestive tracts is an important factor (Schupp, 1993) as it determines the dispersion distance of seeds (Pollux, 2011) and their probability of germination (Traveset, 1998). However, many species of seeds are transported with the fruit or with pulp by the fish. For example, in our

study, the majority of fruits consumed by fish were fleshy (69.3%), and even some non-fleshy dehiscent fruits such as the species *Connarus perrottetii*, *Maprounea guianensis*, *Paullinia cupana*, *Protium strumosum* and *S. argentea* have seeds with aril. This could reduce or even prevent seed scarification by the fish gastric acids, even considering a long retention time. Another point to be noted is that the seeds may not have spent adequate time in the digestive tracts to suffer any significant effect of scarification, since the seeds were recovered from the fish during the digestion process. In studies with field collections of fish, it is difficult to determine the time when the fruits were consumed, and thus the length of time that these seeds remained in the digestive tracts of the fish.

In flooded forests of the Amazon, germination for many species does not occur until the emergence of dry land (Kubitzki and Ziburski, 1994). This may have an implication for some plant species, in which the previous break in dormancy or increase in germination speed may be unfavorable to their establishment. In general, seeds may exhibit endogenous (physiological, morphological or morphophysiological) or exogenous (physical, chemical or mechanical) dormancy (Nikolaeva, 1977). In endogenous dormancy, some characteristic of the embryo prevents germination, while in exogenous dormancy some chemical substance or seed structure such as the endosperm and tegument, which cover the embryo, can prevent germination (Baskin and Baskin, 2014). Some species, in our study, exhibit morphophysiological dormancy as in seeds of *Astrocaryum jauri* and *Minquatia guianensis*, physical dormancy as in *Vitex cymosa*, and others such as *C. latiloba*, *Hevea brasiliensis*, *Ormosia excelsa*, *Pouteria caimito* and *Sorocea duckei* do not show dormancy (Parolin, 2002; Baskin and Baskin, 2014). Dormancy can maximize plant survival by preventing germination under unfavorable conditions (Vasconcelos et al., 2011), for example, anoxic conditions as the floodwaters recede from the forest floor (Kubitzki and Ziburski, 1994). As a result, an increase in germination speed may not be an evolutionary advantage for some species in floodplain forests. Therefore, depending

on the plant species, the fact that the seeds of some species do not have an increase in germination speed would not imply negative effects, since dormancy can help in the dispersion of seeds over greater geographical distances (Kaye et al., 1997). A decrease in germination speed, as verified for seeds of *B. corymbosa* removed from *T. galeatus* (T1) in relation to the control, can allow the temporal germination of tropical seeds in different periods, making it possible for many seedlings to survive when the water level is low and, in turn, have a positive effect on recruitment (Yule et al., 2015).

It is important to note that, although there was no significant increase in the germination speed of the *B. corymbosa*, *C. tapia* and *C. latiloba* species consumed by fish, the germination percentages after passage through the digestive tracts remained above 50%. When considering the high abundance of seeds of these species in the environment (Parolin, 1997; Wittmann et al., 2002), especially *B. corymbosa* and *C. latiloba*, even a low potential of germination after passing through the digestive tract can be compensated by the large number of seeds of these species that are produced. Additionally, non-germinated seeds after passage through the digestive tract may represent a considerable proportion of ingested seeds, for example, 50% of *C. latiloba* seeds removed from *T. albus* did not germinate. Thus, we recommend that future studies use the tetrazolium test approach to determine the viability of non-germinated seeds after passage through the digestive tract of fish (Weiss et al., 2023).

Conclusions

The importance of fruits and seeds in the diet of fish is strongly associated with their availability (Correa et al., 2007). Thus, our results suggest that changes in ecosystems caused by anthropogenic activities, such as deforestation in floodplain forests (Junk et al., 2000; Renó et al., 2016; Renó and Novo, 2019), which reduces the amount and variety of fruits and seeds available to ichthyofauna, associated with overfishing of frugivores (Castelo et al., 2013;

Tregidgo et al., 2017; Costa-Pereira et al., 2018), which decreases the ability of certain species to consume fruits and disperse seeds of certain plant species, could have serious consequences for the recruitment and establishment of some plant species in the floodplains of the Amazon region. Our results are fundamental for obtaining a general understanding of these impacts on ecosystems and for formulating conservation measures for frugivorous fish and tropical trees.

References

- Adams, SB, Hamel, PB, Connor, K, Burke, B, Gardiner, ES, Sage, D, 2007. Potential roles of fish, birds and water in swamp privet (*Forestiera acuminata*) seed dispersal. *Southwest. Nat.* 6, 669–682. [https://doi.org/10.1656/1528-7092\(2007\)6\[669:PROFBA\]2.0.CO;2](https://doi.org/10.1656/1528-7092(2007)6[669:PROFBA]2.0.CO;2)
- Agostinho, CS, Marques, EE, Oliveira, RJ, Braz, PS, 2009. Feeding ecology of *Pterodoras granulosus* (Siluriformes, Doradidae) in the Lajeado Reservoir, Tocantins, Brazil. *Iheringia, Ser. Zool.* 99, 301–306. <https://doi.org/10.1590/S0073-47212009000300012>
- Anderson, JT, Saldaña Rojas, J, Flecker, AS, 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>
- Anderson, JT, Nuttle, T, Rojas, JS, Pendergast, TH, Flecker, AS, 2011. Extremely long-distance seed dispersal by an overfished Amazonian frugivore. *Proc. R. Soc. B.* 278, 3329–3335. <https://doi.org/10.1098/rspb.2011.0155>
- Araujo, JM, Correa, SB, Penha J, Anderson J, Traveset, A, 2021. Implications of overfishing of frugivorous fishes for cryptic function loss in a Neotropical floodplain. *J. Appl. Ecol.* 58, 1499–1510. <https://doi.org/10.1111/1365-2664.13891>
- Baskin, JM, Baskin, CC, 2004. A classification system for seed dormancy. *Seed Sci. Res.* 14, 1–16. <https://doi.org/10.1079/SSR2003150>
- Baskin, JM, Baskin, CC, 2014. Seeds: Ecology, biogeography, and evolution of dormancy and germination. Amsterdam: Elsevier, 1–1586 p. <http://dx.doi.org/10.1016/B978-0-12-416677-6.00002-0>

- Boedeltje, G, Spanings, T, Flik, G, Pollux, BJA, Sibbing, FA, Verberk, WCEP, 2015. Effects of seed traits on the potential for seed dispersal by fish with contrasting modes of feeding. *Freshwater Biol.* 60, 944–959. <https://doi.org/10.1111/fwb.12550>
- Cain, ML, Milligan, BG, Strand, AE, 2000. Long-distance seed dispersal in plant populations. *Am. J. Bot.* 87, 1217–1227. <https://doi.org/10.2307/2656714>
- Castello, L, 2008. Lateral migration of *Arapaima gigas* in floodplains of the Amazon. *Ecol. Freshw. Fish* 17, 38–46. <https://doi.org/10.1111/j.1600-0633.2007.00255.x>
- Castello, L, Mcgrath, DG, Hess, LL, Coe, MT, Lefebvre, PA, Petry, P, Macedo, MN, Reno, VF, Arantes, CC, 2013. The vulnerability of Amazon freshwater ecosystems. *Conserv. Lett.* 6, 217–229. <https://doi.org/10.1111/conl.12008>
- Correa, SB, Winemiller, KO, López-Fernández, H, Galetti, M, 2007. Evolutionary perspectives on seed consumption and dispersal by fishes. *BioScience* 57, 748–756. <https://doi.org/10.1641/B570907>
- Correa, SB, 2012. Trophic Ecology of Frugivorous Fishes in Floodplain Forests of the Colombian Amazon. (Thesis). Texas A&M University, 167 p.
- Correa, SB, Costa-Pereira, R, Fleming, T, Goulding, M, Anderson, JT, 2015a. Neotropical fish–fruit interactions: eco-evolutionary dynamics and conservation. *Biol. Rev.* 90, 1263–1278. <https://doi.org/10.1111/brv.12153>
- Correa, SB, Araújo, JK, Penha, JM, Cunha, CN, Stevenson, PR, Anderson, JT, 2015b. Overfishing disrupt an ancient mutualism between frugivorous fish and plants in Neotropical wetlands. *Biol. Conserv.* 191, 159–167. <https://doi.org/10.1016/j.biocon.2015.06.019>
- Costa-Pereira, R, Galetti, M, 2015. Frugivore downsizing and the collapse of seed dispersal by fish. *Biol. Conserv.* 191, 809–811. <https://doi.org/10.1016/j.biocon.2015.07.011>
- Costa-Pereira, R, Lucas, C, Crossa, M, Anderson, JT, Weiss, BA, Dary, EP, Piedade, MTF, Demarchi, LO, Rebouças, ER, Costa, GS, Galetti, M, Correa, SB, 2018. Defaunation shadow on mutualistic interactions. *P. Natl. Acad. Sci-Biol.* 115, E2673–E2675. <https://doi.org/10.1073/pnas.1801106115>
- De Luis, M, Verdú, M, Ravento, J, 2008. Early to rise makes a plant healthy, wealthy and wise.

Ecology 89, 3061–3071. <https://doi.org/10.1890/07-1828.1>

Eriksson, O, Ehrlén, J, 2008. Seedling recruitment and population ecology. In: Leck, MA, Parker, VT, Simpson, RL (Eds.), *Seedling Ecology and Evolution*, 239–254. Cambridge University Press, Cambridge, UK.

Ferreira, LV, Prance, GT, 1998. Species richness and floristic composition in four hectares in the Jaú National Park in upland forest in Central Amazonia. *Biodivers. Conserv.* 10, 1349–1364. <https://doi.org/10.1023/A:1008899900654>

Ferreira, LV, Almeida, SS, Parolin, P, 2010. Amazonian white and black water floodplain forests in Brazil: Large differences on a small scale. *Ecotropica* 16, 31–41.

Fragoso, JMV, 1997. Tapir-generated seed shadows: scale dependent patchiness in the Amazon rain forest. *Journal of Ecology*, 85, 519–529. <https://doi.org/10.2307/2960574>

Galetti, M, Donatti, CI, Pizo, MA, Giacomini, HC, 2008. Big fish are the best: seed dispersal of *Bactris glaucescens* by the Pacu fish (*Piaractus mesopotamicus*) in the Pantanal, Brazil. *Biotropica* 40, 386–389. <https://doi.org/10.1111/j.1744-7429.2007.00378.x>

Goulding, M, 1980. The fishes and the forest: explorations in Amazonian natural history. University of California Press, Berkeley, California.

Goulding, M, 1983. The role of fish in seed dispersal and plant distribution in Amazonian floodplains ecosystems. In: Kubitzki, K (Ed.), *Dispersal and distribution*. Verlag Paul Parey, Hamburg, pp. 271–284.

Horn, MH, 1997. Evidence for dispersal of fig seeds by the fruit-eating characid fish *Brycon guatemalensis* Regan in a Costa Rican tropical rain forest. *Oecologia* 109, 259–264. <https://doi.org/10.1007/s004420050081>

Horn, M, Correa, SB, Parolin, P, Pollux, BJA, Anderson, JT, Lucas, C, Widmann, P, Tjiu, A, Galetti, M, Goulding, M, 2011. Seed dispersal by fishes in tropical and temperate fresh waters: the growing evidence. *Acta Oecol.* 37, 561–577. <https://doi.org/10.1016/j.actao.2011.06.004>

Howe, HF, Smallwood, J, 1982. Ecology of seed dispersal. *Ann. Rev. Ecol. Syst.* 13, 201–228. <https://doi.org/10.1146/annurev.es.13.110182.001221>

- Howe, HF, 1993. Specialized and generalized dispersal systems: where does ‘the paradigm’ stand? *Vegetatio* 107, 3–13. <https://doi.org/10.1007/BF00052208>
- Hulme, PE, Benkman, CW, 2002. Granivory. In: Herrera, CM, Pellmyr, O (Eds), *Plant-Animal Interactions: An Evolutionary Approach*. Blackwell Science, Oxford, pp. 132–154.
- Hyslop, J, Trowsdale, S, 2012. A review of hydrochory (seed dispersal by water) with implications for riparian rehabilitation. *J. Hydrol.* 51, 137–152.
- Irion, G, Mello, J, Morais, J, Piedade, MTF, Junk, WJ, Garming, L, 2010. Development of the Amazon valley during the middle to late quaternary: sedimentological and climatological observations. In: Junk, WJ, Piedade, MTF, Wittmann, F, Schöngart, J, Parolin, P (Eds.), *Amazonian floodplain forest: ecophysiology, biodiversity and sustainable management*. Springer, Berlin, pp. 27–42.
- Jordano, P, 2000. Fruits and frugivory. In: Fenner, M (Ed.), *Seeds: the ecology of regeneration in plant communities*. CABI Publ., Wallingford, pp. 125–166
- Jordano, P, Schupp, EW, 2000. Seed Disperser Effectiveness: The Quantity Component and Patterns of Seed Rain for *Prunus mahaleb*. *Ecol. Monogr.* 70, 591–615. [https://doi.org/10.1890/0012-9615\(2000\)070\[0591:SDETQC\]2.0.CO;2](https://doi.org/10.1890/0012-9615(2000)070[0591:SDETQC]2.0.CO;2)
- Junk, WJ, 1989. Flood tolerance and tree distribution in central Amazonian floodplains. In: Holm-Nielsen, LB, Nielsen, IC, Balslev, H (Eds.), *Tropical forest: botanical dynamics, speciation and diversity*. Academic Press, New York, 47–64.
- Junk, WJ, Bayley, PB, Sparks, RE, 1989. The flood pulse concept in river floodplain systems. In: Dodge, DP (Ed.), *Proceedings of the International Large River Symposium*. Canadian Special Publication in Fisheries and Aquatic Sciences, Ontario, pp. 110–127.
- Junk, WJ, Ohly, JJ, Piedade, MTF, Soares, MGM, 2000. *The Central Amazon Floodplain: Actual use and options for sustainable management*. Backhuys Publishers, Leiden.
- Junk, WJ, Piedade, MTF, Schöngart, J, Cohn-Haft, M, Adeney, JM, Wittmann, F, 2011. A classification of major naturally-occurring Amazonian lowland wetlands. *Wetlands* 31, 623–640. <https://doi.org/10.1007/s13157-011-0190-7>
- Junk, WJ, Piedade, MTF, Schöngart, J, Wittmann, F, 2020. Áreas alagáveis: Definições e

- características ecológicas gerais. In: Junk, WJ, Piedade, MTF, Wittmann, F, Schöngart, J (Eds.), *Várzeas amazônicas: desafios para um Manejo Sustentável*. Editora do INPA, Manaus, pp. 18–35.
- Kaye, TN, Liston, A, Love, RM, Louma, DL, Meinke, RJ, Wilson, MV, 1997. Conservation and management of native plants and fungi. Native Plant Society of Oregon, Corvallis.
- Kubitzki, K, Ziburski, A, 1994. Seed dispersal in floodplain forests of Amazonia. *Biotropica* 26, 30–43. <https://doi.org/10.2307/2389108>
- Lehouck, V, Spanhove, T, Lens, L, 2011. Avian fruit ingestion differentially facilitates seed germination of four fleshy-fruited plant species of an Afrotropical forest. *Plant Ecol. Evol.* 144, 96–100. <https://doi.org/10.5091/plecevo.2011.503>
- Lozano-Isla, F, Benites-Alfaro, OE, Pompelli, MF, 2019. GerminaR: An R package for germination analysis with the interactive web application “GerminaQuant for R”. *Ecol. Res.* 34, 339–346. <https://doi.org/10.1111/1440-1703.1275>
- Maia, LA, Santos, LM, Parolin, P, 2007. Germinação de sementes de *Bothriospora corymbosa* (Rubiaceae) recuperadas do trato digestório de *Triportheus angulatus* (sardinha) no Lago Camaleão, Amazônia Central. *Acta Amaz.* 37, 321–326. <https://doi.org/10.1590/S0044-59672007000300002>
- Malanson, GP, 1993. *Riparian Landscapes*. Cambridge University Press, Cambridge.
- Mannheimer, S, Bevilacqua, G, Caramaschi, EP, Scarano, FR, 2003. Evidence for seed dispersal by the catfish *Auchenipterichthys longimanus* in an Amazonian lake. *J. Trop. Ecol.* 19, 215–218. <https://doi.org/10.1017/S0266467403003249>
- Melack, JM, Hess, LL, 2010. Remote Sensing of the Distribution and Extent of Wetlands in the Amazon Basin. In: Junk, WJ, Piedade, MTF, Wittmann, F, Schöngart, J, Parolin, P (Eds.), *Central Amazonian Floodplain Forests: Ecophysiology, Biodiversity and Sustainable Management*. Springer, Berlin/Heidelberg/New York, pp. 43–59.
- Neuschulz, EL, Mueller, T, Schleuning, M, Böhning-Gaese, K, 2016. Pollination and seed dispersal are the most threatened processes of plant regeneration. *Sci. Rep.* 6, 29839. <https://doi.org/10.1038/srep29839>

Nikolaeva, MG, 1977. Factors controlling the seed dormancy pattern. In: Khan, AA (Ed.), *The Physiology and Biochemistry of Seed Dormancy and Germination*. North Holland Publ. Co., Amsterdam, pp. 51–74.

Nilsson, C, Gardfjell, M, Grelsson, G, 1991. Importance of hydrochory in structuring plant communities along rivers. *Can. J. Bot.* 69, 2631–2633. <https://doi.org/10.1139/b91-328>

Oliveira-Wittmann, A, Lopes, A, Conserva, ADS, Wittmann, F, Piedade, MTF, 2010. Seed Germination and Seedling Establishment of Amazonian Floodplain Trees. In: Junk, WJ, Piedade, MTF, Wittmann, F, Schöngart, J, Parolin, P (Eds.), *Central Amazonian Floodplain Forests: Ecophysiology, Biodiversity and Sustainable Management*. Springer, Berlin/Heidelberg/New York, pp. 260–279.

Parolin, P, 1997. Auswirkungen periodischer Vernässung und Überflutung auf Phänologie, Photosynthese und Blattphysiologie von Baumarten unterschiedlicher Wachstumsstrategie in zentralamazonischen Überschwemmungsgebieten. Herbert Utz, Wissenschaft, München. 166 p.

Parolin, P, 2000. Phenology and CO²-assimilation of trees in Central Amazonian floodplains. *J. Trop. Ecol.* 16, 465–473. <https://doi.org/10.1017/S0266467400001516>

Parolin, P, 2002. Life history and environment of *Cecropia latiloba* in Amazonian floodplains. *Revis. Biol. Trop.* 50 (2), 531–545.

Parolin, P, De Simone, O, Haase, K, Waldhoff, D, Rottenberger, S, Kuhn, U, Kesselmeier, J, Schmidt, W, Piedade, MTF, Junk, WJ, 2004. Central Amazon floodplain forests: tree survival in a pulsing system. *Bot. Rev.* 70, 357–380.

Parolin, P, Waldhoff, D, Piedade, MTF, 2010. Fruit and seed chemistry, biomass and dispersal. In: Junk, WJ, Piedade, MTF, Wittmann, F, Schöngart, J, Parolin, P (Eds.), *Central Amazonian Floodplain Forests: Ecophysiology, Biodiversity and Sustainable Management*. Springer, Berlin/Heidelberg/New York, pp. 243–258.

Parolin, P, Wittmann, F, Ferreira, LV, 2013. Fruit and seed dispersal in Amazonian floodplain trees – a review. *Ecotropica*, 19, 15–32.

Piedade, MTF, Parolin, PJ, Junk, W, 2003. Estratégias de dispersão, produção de frutos e

extrativismo da palmeira *Astrocaryum jauari* Mart. nos igapós do rio negro: implicações para a ictiofauna. *Ecol. Apl.* 2, 31–40. <https://doi.org/10.21704/rea.v2i1-2.244>

Piedade, MTF, Parolin, P, Junk, WJ, 2006. Phenology, fruit production and seed dispersal of *Astrocaryum jauari* (Arecaceae) in Amazonian blackwater foodplains. *Rev. Biol. Trop.* 54, 1171–1178. <https://doi.org/10.15517/rbt.v54i4.3094>

Pollux, BJA, de Jong, M, Steegh, A, Ouborg, NJ, van Groenendael, JM, Klaassen, M, 2006. The effect of seed morphology on the potential dispersal of aquatic macrophytes by the common carp (*Cyprinus carpio*). *Freshwater Biol.* 51, 2063–2071. <https://doi.org/10.1111/j.1365-2427.2006.01637.x>

Pollux, BJA, Verbruggen, E, Ouborg, NJ, van Groenendael, JM, 2009. Intraspecific variation of seed floating ability in *Sparganium emersum* suggests a bimodal dispersal strategy. *Aquat. Bot.* 90, 199–203. <https://doi.org/10.1016/j.aquabot.2008.07.002>

Pollux, BJA, 2011. The experimental study of seed dispersal by fish (ichthyochory). *Freshwater Biol.* 56, 197–212. <https://doi.org/10.1111/j.1365-2427.2010.02493.x>

Prudente, BS, Carneiro-Marinho, P, Valente, RM, Montag, LFA, 2016. Feeding ecology of *Serrasalmus gouldingi* (Characiformes: Serrasalminidae) in the lower Anapu River region, Eastern Amazon, Brazil. *Acta Amaz.* 46, 259–270. <https://doi.org/10.1590/1809-4392201600123>

Reid, S, Armesto, JJ, 2011. Avian gut-passage effects on seed germination of shrubland species in Mediterranean central Chile. *Plant Ecol.* 212, 1–10. <https://doi.org/10.1007/s11258-010-9796-8>

Renó, V, Novo, E, Escada, M, 2016. Forest fragmentation in the Lower Amazon Floodplain: implications for biodiversity and ecosystem service provision to riverine populations. *Remote Sens.* 8, 886. <https://doi.org/10.3390/rs8110886>

Renó, V, Novo, E, 2019. Forest depletion gradient along the Amazon floodplain. *Ecological Indicators*, 98, 409–419. <https://doi.org/10.1016/j.ecolind.2018.11.019>

Rocha, BS, García-Berthou, E, Novaes, JLC, Bini, LM, Cianciaruso, MV, 2021. Interspecific synchrony is related to body-length similarity in a fish community under prolonged drought

conditions. *Sci. Total Environ.* 781, 146721. <https://doi.org/10.1016/j.scitotenv.2021.146721>

Santos, J, Correa, SB, Boudreau, MR, Carvalho, LN, 2020. Differential ontogenetic effects of gut passage through fish on seed germination. *Acta Oecol.* 108, 103628. <https://doi.org/10.1016/j.actao.2020.103628>

Sousa, JIM, Oliveira, JCD, Oliveira, JF, Rebouças, LGF, Novaes, JLC, Costa, RS, Peretti, D, 2017. Variação temporal e espacial na dieta de *Trachelyopterus galeatus* (Siluriformes, Auchenipteridae) em dois reservatórios no semiárido Neotropical. *Iheringia, Série Zoologia*, 107, e2017040. <https://doi.org/10.1590/1678-4766e2017040>

Schöngart, J, 2003. Dendrochronologische Untersuchungen in Überschwemmungswäldern der várzea Zentralamazoniens. göttinger beiträge zur land- und Forstwirtschaft in den Tropen und Subtropen 149, Erich Goltze Verlag, Göttingen, Alemanha.

Schupp, EW, 1993. Quantity, quality and the effectiveness of seed dispersal by animals. *Vegetatio* 108, 15–29.

Smits, AJM, Van Ruremonde, R, Van der Velde, G, 1989. Seed dispersal of three nymphaeid macrophytes. *Aquat. Bot.* 35, 167–180. [https://doi.org/10.1016/0304-3770\(89\)90103-4](https://doi.org/10.1016/0304-3770(89)90103-4)

Therneau, TM, 2023. A Package for Survival Analysis in R. <https://cran.r-project.org/web/packages/survival/vignettes/survival.pdf>

Traveset, A, 1998. Effect of seed passage through vertebrate frugivores' guts on germination: a review. *Perspect. Plant Ecol.* 1, 151–190. <https://doi.org/10.1078/1433-8319-00057>

Traveset, A, Verdú, M, 2002. A meta-analysis of the effect of gut treatment on seed germination. In Levey, DJ, Silva, WR, Galetti, M (Eds.), *Seed Dispersal and Frugivory: Ecology, Evolution and Conservation*. CABI Publishing, Wallingford, pp. 339–350.

Traveset, A, Robertson, AW, Rodríguez-Pérez, J, 2007. A review on the role of endozoochory in seed germination. In: Dennis, AJ, Schupp, EW, Green, RJ, Westcott, DW (Eds.), *Seed dispersal: theory and its application in a changing world*. CABI Publishing, Wallingford, pp. 78–101.

Tregidgo, DJ, Barlow, J, Pompeu, PS, Almeida Rocha, M, Parry, L, 2017. Rainforest metropolis casts 1,000-km defaunation shadow. *P. Natl. Acad. Sci. Usa.* 114, 8655–8659.

<https://doi.org/10.1073/pnas.1614499114>

Van der Pijl, L, 1982. Principles of Dispersal in Higher Plants. Springer-Verlag, Berlin.

Van der Sleen, P, Albert, JS, 2018. Field guide to the fishes in the Amazon, Orinoco and Guianas. Princeton University Press, Princeton.

Vasconcelos, JM, Rodrigues, MA, Filho, VSC, Sales, JF, Silva, FG, Santana, JG, 2011. Dormancy break in seeds of "quina" (*Strychnos pseudoquina* A. St.-Hil.). *Rev. Bras. Pl. Med.* 13, 507–511. <https://doi.org/10.1590/S1516-05722011000400017>

Verdú, M, Traveset, A, 2005. Early emergence enhances plant fitness: a phylogenetically controlled meta-analysis. *Ecology* 86, 1385–1394. <https://doi.org/10.1890/04-1647>

Weiss, B, Zuanon, JAS, Piedade, MTF, 2016. Viability of seeds consumed by fishes in a lowland forest in the Brazilian Central Amazon. *Trop. Conserv. Sci.* 9, 1–10. <https://doi.org/10.1177/1940082916676129>

Weiss, B, Costa, G, Correa, SB, Zuanon, J, Piedade, MTF, 2022. Does the consumption of pioneer-tree seeds from flooded forests by freshwater sardines affect seed germination? *Acta Oecol.* 117, 103850. <https://doi.org/10.1016/j.actao.2022.103850>

Weiss, B, D. Santana, F, Petene, Calvi, G, Costa, G, Zuanon, J. & Piedade, MTF, 2023. Effectiveness of fish assemblage as seed dispersers in Amazon oligotrophic flooded forests. *Austral Ecology*, 00, 1–18. <https://doi.org/10.1111/aec.13330>

Williamson, GB, Costa, F, 2000. Dispersal of Amazonian trees: Hydrochory in *Pentaclethra macroloba*. *Biotropica* 32, 548–552. <https://doi.org/10.1111/j.1744-7429.2000.tb00501.x>

Wittmann, F, Anhufo, D, Junk, WJ, 2002. Tree species distribution and community structure of central Amazonian várzea forests by remote-sensing techniques. *J. Trop. Ecol.* 8, 805–820. <https://doi.org/10.1017/S0266467402002523>

Wittmann, F, Schöngart, J, Montero, JC, Motzer, M, Junk, WJ, Piedade, MTF, Queiroz, HL, Worbes, M, 2006. Tree species composition and diversity gradients in white water forests across the Amazon Basin. *J. Biogeog.* 33, 1334–1347. <https://doi.org/10.1111/j.1365-2699.2006.01495.x>

Wittmann, F, Schöngart, J, Junk, WJ, 2010. Phytogeography, species diversity, community structure and dynamics of central Amazonian floodplain forests. In: Junk, WJ, Piedade, MTF, Wittmann, F, Schöngart, J, Parolin, P (Eds.), Central Amazonian Floodplain Forests: Ecophysiology, Biodiversity and Sustainable Management. Springer, Berlin/Heidelberg/New York, pp. 61–102.

Worbes, M, 2002. One hundred years of tree research in the tropics – a brief history and an outlook to future challenges. *Dendrochronologia*, 20 (1-2): 217–231.

Worbes, M, 1997. The forest ecosystem of the floodplains. In: Junk, WJ (Ed.), The central Amazon floodplain: ecology of a pulsating system. Ecological Studies Springer, Berlin, pp. 223–265.

Yule, TS, Severo-Neto, F, Tinti-Pereira, AP, Costa, LBLC, 2015. Freshwater sardines of the Pantanal delay seed germination in a floodplain tree species. *Wetlands* 36, 195–199. <https://doi.org/10.1007/s13157-015-0723-6>

Zamorano, D, Labra, FA, Vila, I, Meier, CI, 2022. Rivers as a potential dispersing agent of the invasive tree *Acacia dealbata*. *Rev. Chil. Hist. Nat.* 95, 6. <http://dx.doi.org/10.1186/s40693-022-00109-7>

Capítulo 2

Structure and vulnerability of the ichthyochory network in wetland forests of Central Amazonia

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Structure and vulnerability of the ichthyochory network in wetland forests of Central Amazonia

Abstract

The interaction between fish and plants is vital for the dynamics of ecosystems since it influences plant distribution and regeneration patterns. In the floodable areas of the Amazon, these interactions are mainly structured by the flood pulse, which enables seed dispersal via water (hydrochory) and fish (ichthyochory), and which contributes to the formation of complex mutualistic networks. Our study evaluated the structure (modularity, nestedness, specialization, and robustness) of the network of dispersal of seeds by frugivorous fish in a floodplain forest in Central Amazonia. We expect the binary network to have a nested pattern, while the weighted network is expected to have a non-nested structure; that generalist frugivorous species should constitute the core of the network, while specialist frugivorous species will be peripheral; that the size of fish and seeds is related to specialization, and that the robustness of the network weakens as generalist frugivorous fish are removed. We found 5,012 intact seeds from 49 plant species in the digestive tracts of 11 species of frugivorous fish. A nested and modular pattern was found for the binary and weighted networks, albeit with a low degree of nestedness. Our network proved relatively robust when the frugivores were removed. No relationship was found between the size of the fish and the seeds and the degree of specialization. Considering the anthropogenic impacts that can cause modifications in seed dispersal networks, knowing the structure of mutualistic networks is fundamental in order to be able infer the vulnerability of the interactions as a result of changes in the ecosystem.

Keywords: floodplain forests, frugivorous fish, modularity, nestedness, specialization

Introduction

Seed dispersal by animals (zoochory) is an important form of dissemination of propagules for many plant species (Wunderle Jr., 1997). The interaction between animals and plants is vital for the dynamics of ecosystems (Traveset, 1998; Costa et al., 2023) and the complexity of the interactions has important implications for species coexistence and stability (Bascompte and Jordano, 2007). In addition, dispersal influences plant distribution and regeneration patterns (Jordano, 2000).

The Neotropical region is the richest in the world in terms of freshwater fish and plant species (Helfman, 2013; Corlett, 2016; Brummitt et al., 2020); at least 150 species of fish are frugivores (Horn et al., 2011) and are directly related to the dispersal of about 600 plant species (Correa et al., 2015a). In the floodable areas of the Amazon, these interactions are mainly influenced by the flood pulse (Junk et al., 1989; Parolin et al., 2013), which triggers biotic and abiotic processes, and structures food chains (Goulding, 1980; Junk et al., 2011). In these environments, there are more than 1,600 plant species (Wittmann et al., 2006, 2010), with flowering and fruiting periods that coincide with the increase in the level of the river (Parolin et al., 2004; Parolin et al., 2013). This allows seed dispersal via water (hydrochory) and fish (ichthyochory) (Parolin et al., 2013; Correa et al., 2015A; Costa et al., 2023) and the formation of complex mutualistic networks (Correa et al., 2016; Araujo et al., 2021; Mateus et al., 2022; Pereyra et al., 2023).

These networks can be measured through interaction occurrences (in binary networks) or frequency of interactions (in weighted networks) (Guimarães Jr., 2020), and can present modularity, nestedness, specialization, and robustness (Memmott et al., 2004; Blüthgen et al., 2006; Burgos et al., 2007; Silva et al., 2022). Modular networks are formed by closely connected subgroups of species (modules), and can be linked to other groups through species that interact beyond their modules (Mello et al., 2011; Olesen et al., 2007). While nested

networks form a pattern of interaction in which specialists (the less connected) interact with species that form perfect subsets of the species with which generalists (the highly connected) interact (Bascompte and Jordano, 2007). Specialization or generalization of interactions are commonly characterized as the number of partners and, in general, there are two levels of specialization measures: first, the characterization of focal species (d') and, second, the degree of specialization of an entire interaction network (H_2') (Blüthgen et al., 2006). In flooded forests, specialist or generalist habits can influence the effectiveness of frugivorous fish in seed dispersal (Weiss et al., 2023). While generalist species tend to interact with a greater number of plants than specialist species (Correa et al., 2016), specialist species are fundamental in the organization and connection of modules within the network (Olesen et al., 2007). Thus, the diversity of species, both frugivores and plants in the community influences the nestedness and modularity of seed dispersal networks (Mello et al., 2011a) and, consequently, its vulnerability.

Freshwater environments are especially vulnerable to species loss (Dudgeon, 2019; WWF, 2022), which is a growing problem in tropical ecosystems and has far-reaching consequences for biotic interactions (Dirzo and Miranda, 1990; Costa-Pereira et al., 2018). In the Amazon floodplains, several human impacts (mainly overfishing and deforestation) can result in population decline or even species loss of frugivorous fish and plants (Tregidgo et al. 2017; Costa-Pereira et al. 2018; Renó et al. 2016; Renó and Novo 2019). The consequences of the disappearance of large and generalist seed dispersers due to overexploitation or habitat loss, could cause large secondary extinctions of plant species, with negative consequences for seed dispersal (Wright, 2003; Correa et al., 2016; Costa-Pereira et al., 2018) and network robustness (Albert et al., 2000). Robustness is the resistance of the network to species loss (Bascompte and Jordano, 2007), where a robust system has a low risk of secondary extinctions (Dunne et al., 2002). Robustness and modularity can be positively correlated, as a modular structure confers greater robustness to the network by avoiding a cascade of extinctions (Ramos-Robles et al.,

2018; Sheikhalı et al., 2020). Thus, a modular structure can provide resilience to environmental disturbances.

The study of mutualistic networks has focused mainly on the structure of the networks of mammals and frugivorous birds (Mello et al., 2011a,b; Sarmiento et al., 2014; Silva et al., 2023), and only recently has it focused on networks with frugivorous fish (Correa et al., 2016; Araujo et al., 2021; Mateus et al., 2022; Pereyra et al., 2023) due to the potential harm that the loss of frugivorous fish could cause to the diversity of floodable forests (Correa et al., 2007; Correa et al., 2015a,b; Costa-Pereira and Galetti, 2015; Costa-Pereira et al., 2017, 2018; Costa et al., 2023). These studies can provide a baseline of how environmental changes influence the stability and functioning of communities (Bascompte and Olesen, 2015). Thus, knowing the structure of mutualistic networks is fundamental in order to be able to infer the robustness of interactions as a result of changes in the ecosystem (Jordano et al., 2003).

Here, we evaluate the structure (modularity, nestedness, specialization, and robustness) of the network of seed dispersal by frugivorous fish in an Amazonian floodable forest. We expect that: a) the binary network has a nested pattern, while the weighted network has a non-nested structure due to heterogeneity in the frequencies of interaction between species; b) generalist frugivorous species should constitute the core of the network by dispersing the seeds of the majority of plant species in the community, while specialist frugivorous species will be peripheral, dispersing a subset of the species of plants; c) the size of the fish and the seeds is related to specialization, where larger fish are more generalist, and larger seeds interact with fewer fish species, and d) that the robustness of the network weakens as the generalist frugivorous fish are removed.

Materials and Methods

Study area

This study was conducted in a stretch of flooded forest of the Solimões River known as Ilha da Paciência (03° 18' 12" S; 60° 13' 51" W), which is located in Central Amazonia. The Solimões River is a typical “várzea” floodplain river, and has white waters, with a pH close to neutral, and is rich in suspended matter that carries clay minerals and releases nutrients to the alluvial soils (Irion et al., 2010). The annual rainfall in the region is approximately 2,100 mm/year, with a marked difference between the dry (June/October) and rainy (December/May) seasons (Parolin, 2000).

Sampling design and collection of fish and seeds

A total of twelve biweekly collections were carried out between the months of 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 (Parolin et al., 2013). The fish were collected using a set of nine gillnets (with meshes from 24 to 110 mm, 10 m long and between 1.5 to 3.0 m high), which were joined together. Each collection lasted 60 hours, with day and night sampling and inspections every four hours. For each collection, the nine fishing nets were placed at a subsequent point (N=12) that was separated by a distance of about 400 meters. The captured fish were immersed in an anesthetic (eugenol) dissolved in water, and kept in the solution for up to 10 minutes until the opercular movements ceased. While in the field, the standard weight and length of the subjects were determined and the digestive tracts (stomach and intestine) were removed for further analysis in the laboratory. A representative of each species was labeled and stored in a Styrofoam box and sent to the National Institute for Amazonian Research (INPA) for confirmation of the identity of the species via the help of specialists. The analysis of the digestive tract was performed with the aid of a magnifying glass (10x) in the laboratory. The seeds that were found intact in the digestive tract were quantified

and identified in the herbarium of the National Institute for Amazonian Research (INPA). The licenses for fish collection were obtained through the Biodiversity Authorization and Information System (SISBio; under protocol No. 81822-1/2022) of the Chico Mendes Institute for Biodiversity Conservation (ICMBio). The research was approved by the Ethics Committee on the Use of Animals of INPA (CEUA; under number 67/2022).

Morphometry of fish and seeds

The standard length (SL) of the fish was obtained from the tip of the nose to the end of the caudal peduncle with the aid of a millimeter ruler (0.1 cm precision) and the fish was also weighed on a precision digital scale (0.01 g precision). The size of the seeds was obtained at the points of greater width or length of the seeds with the aid of a digital caliper (0.01 mm precision). For each seed species found in large quantities in the digestive tract, ten seeds were randomly quantified to obtain an average size.

Network construction and analysis

To construct the networks, we used a binary (presence and absence) and a weighted (frequency of interactions) adjacency matrix, with 11 fish species as rows and 49 plant species as columns, in a bipartite network. Based on this data, we calculated the metrics of modularity (W and Q), nestedness (NODF and WNODF), specialization (d' and H_2'), and robustness (R). For specialization and robustness metrics, only weighted data were used.

To access the degree of specialization for fish and plant species, we calculated the d' index (standardized Kullback-Leibler distance) for population and the H_2' index (standardized two-dimensional Shannon entropy) for the community using the *specieslevel* and *networklevel* functions of the *bipartite* package of R. These indices range from 0 (lack of specialization) to 1 (high specialization) (Blüthgen et al., 2006). To estimate the degree of nestedness, we used the metrics NODF for the binary network and WNODF for the weighted network (Weighted

Nestedness based on Overlap and Decreasing Fill), with values ranging from 0 (not nested) to 100 (perfectly nested) (Almeida-Neto et al., 2008; Almeida-Neto and Ulrich, 2011). The modularity for the binary network was measured with the metric M using the annealing algorithm via the *netcarto* function of the *rnetcarto* package of R (Stouffer et al., 2023) and, for the weighted network, we used the Q metric to determine which species are more densely connected (Newman, 2006) via the QuanBiMO algorithm (Quantitative Bipartite Modularity algorithm) using the *computeModules* function of the *bipartite* package (Dorman and Strauss, 2014, 2022). The level of modularity ranges from 0 (not modular) to 1 (highly modular). To determine the importance of fish and plant species for modularity, we evaluated the connectivity (participation coefficient) between modules (c) and the degrees within the module (z) using the *czvalues* function of the *bipartite* package (Guimerà and Amaral, 2005; Olesen et al., 2007), with critical values ranging from $c \leq 0.62$ to $z > 2.5$). Species that exceed c and z values are called “hubs” because they link different modules together, combining high connectivity between modules and high connectivity within the module (Dormann and Strauss, 2014). Species can be separated into four subcategories according to c and z values: peripheral ($c \leq 0.62$ and $z \leq 2.5$); connectors ($c > 0.62$ and $z \leq 2.5$); module hubs ($c \leq 0.62$ and $z \geq 2.5$); network hubs ($c > 0.62$ and $z > 2.5$) (Guimerà and Amaral, 2005; Olesen et al., 2007).

The metrics of H_2' , NODF, WNODF, W and Q were compared with a randomized null model 1,000 times, via the *r2dtable* function of the *bipartite* package, which uses the Patefield algorithm to generate random tables (Dormann et al., 2022). The significance of each metric was obtained via the *null t.test* function, and compared the real value of each metric with the values from randomized networks 1,000 times (Dormann et al., 2022). Nestedness, modularity, and specialization (H_2') 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 see whether the length and weight of the fish, and the size of the seeds, influence the structure of the network, we

performed a regression analysis using the *lm* function, with the fish and the seeds as the predictor variable and specialization (d') as the response variable. We performed the Shapiro-Wilk test to assess the normality of residuals and the Breusch-Pagan test to evaluate the homogeneity of variance, using the *nortest* and *lmttest* packages, respectively. Regression analysis and calculations of network metrics were performed using the software R.

Robustness of the network to the extinction of frugivores

To calculate the robustness of the network to extinctions (R), we performed removal simulations for the six fish species that interacted with more plant species (*Trachelyopterus galeatus*, *Pterodoras granulosus*, *Triportheus albus*, *Brycon amazonicus*, *Mylosoma albiscopum*, *Colossoma macropomum*), following the method of Memmott et al. (2004), which calculates the slope of the extinction curve (β), and the method of Burgos et al. (2007), which calculates the area under the extinction curve (R). In this type of procedure, one of the sides of the bipartite network is chosen and one vertex is removed at a time (Melo et al., 2011a). First, we simulated the removal of each of the six fish species, followed by the cumulative removal of *T. galeatus* and *P. granulosus* and, finally, the cumulative removal of *T. galeatus*, *P. granulosus* and *T. albus*. R values range from 0 to 1, where $R \rightarrow 1$ corresponds to a very robust system in which most plant species survive even if a large part of the fish species is eliminated, while $R \rightarrow 0$ corresponds to a fragile system in which even if a very small fraction of fish species is eliminated, most plants lose all their interactions and become extinct (Burgos et al., 2007). The robustness of the network against extinctions was obtained through 100 repetitions with the *second.extinct* function of the *bipartite* package in R software (R version 4.3.1-2023).

Results

A total of 5,012 intact seeds distributed among 49 species and 33 families were found in the digestive tracts of 420 specimens of 11 species of frugivorous fish (Figure 1). The most

abundant fish species were *Mylossoma albiscopum* (N = 106), *Pterodoras granulosus* (N = 99), and *Trachelyopterus galeatus* (N = 86). The three fish species that consumed the most seed species were *T. galeatus* (N = 23), *P. granulosus* (N = 18), and *Triportheus albus* (N = 12) (Table 1). The three most abundant plant species consumed by fish were *Cecropia latiloba* (N = 2,503), *Bothriospora corymbosa* (N = 1,277) and *Ficus amazonica* (N = 792).

Table 1: Species of frugivorous fish that consumed fruits. Number of fish, mean of standard length ($\pm$ SL mm) and weight ($\pm$ W g) of fish and species of seeds consumed.

Family	Fish species	Total Fish	$\pm$ SL (mm)	$\pm$ W (g)	Plant species
Anostomidae	<i>Leporinus fasciatus</i> (Bloch, 1794)	1	270	386	1
	<i>Rhytiodus microlepis</i> Kner, 1858	14	275	300.7	1
	<i>Schizodon fasciatus</i> Spix & Agassiz, 1829	21	217	209	2
Auchenipteridae	<i>Trachelyopterus galeatus</i> (Linnaeus, 1766)	86	154	113.2	23
Bryconidae	<i>Brycon amazonicus</i> (Spix & Agassiz, 1829)	18	184	168.3	9
Chalceidae	<i>Chalceus erythrurus</i> (Cope, 1870)	18	192	149.6	2
Doradidae	<i>Pterodoras granulosus</i> (Valenciennes, 1821)	99	178	253.2	18
Serrasalminidae	<i>Colossoma macropomum</i> (Cuvier, 1816)	8	210	210.1	6
	<i>Myloplus asterias</i> (Müller & Troschel, 1844)	2	157	179	3
	<i>Mylossoma albiscopum</i> (Cuvier, 1818)	106	144	129	8
Triportheidae	<i>Triportheus albus</i> Cope, 1872	47	170	75.3	12

The fish species with the highest rates of specialization (d') were *Myloplus asterias* ($d' = 0.826$), *Leporinus fasciatus* ($d' = 0.626$), and *Colossoma macropomum* ($d' = 0.590$). Specialization was significant for the network at community level ($H_2' = 0.406$; $p < 0.001$), indicating a narrow niche breadth and more specialized seed dispersal.

The network presented significantly nested structure (NODF = 29.56; $p < 0.001$; WNODF = 11.31; $p < 0.001$), and no random network showed NODF and WNODF values higher than those observed in our networks. Modularity was significant for the binary network

($M = 0.26$; $p < 0.001$), though not significant for the weighted network ($Q = 0.50$; $p > 0.05$) (Figure 2).

All plant species were peripheral ($c \leq 0.62$ and $z \leq 2.5$): *Myrciaria dubia* was a connector ($c = 0.66$, $z = -0.18$), *Quiina rhytidopus* ($c = 0.52$, $z = 3.16$) and *Bactris riparia* ($c = 0.49$, $z = 2.55$) were module hubs, but no species was network hub. All fish species were peripheral ($c \leq 0.62$ and $z \leq 2.5$) and none of the fish species were considered connectors, module hubs or network hubs.

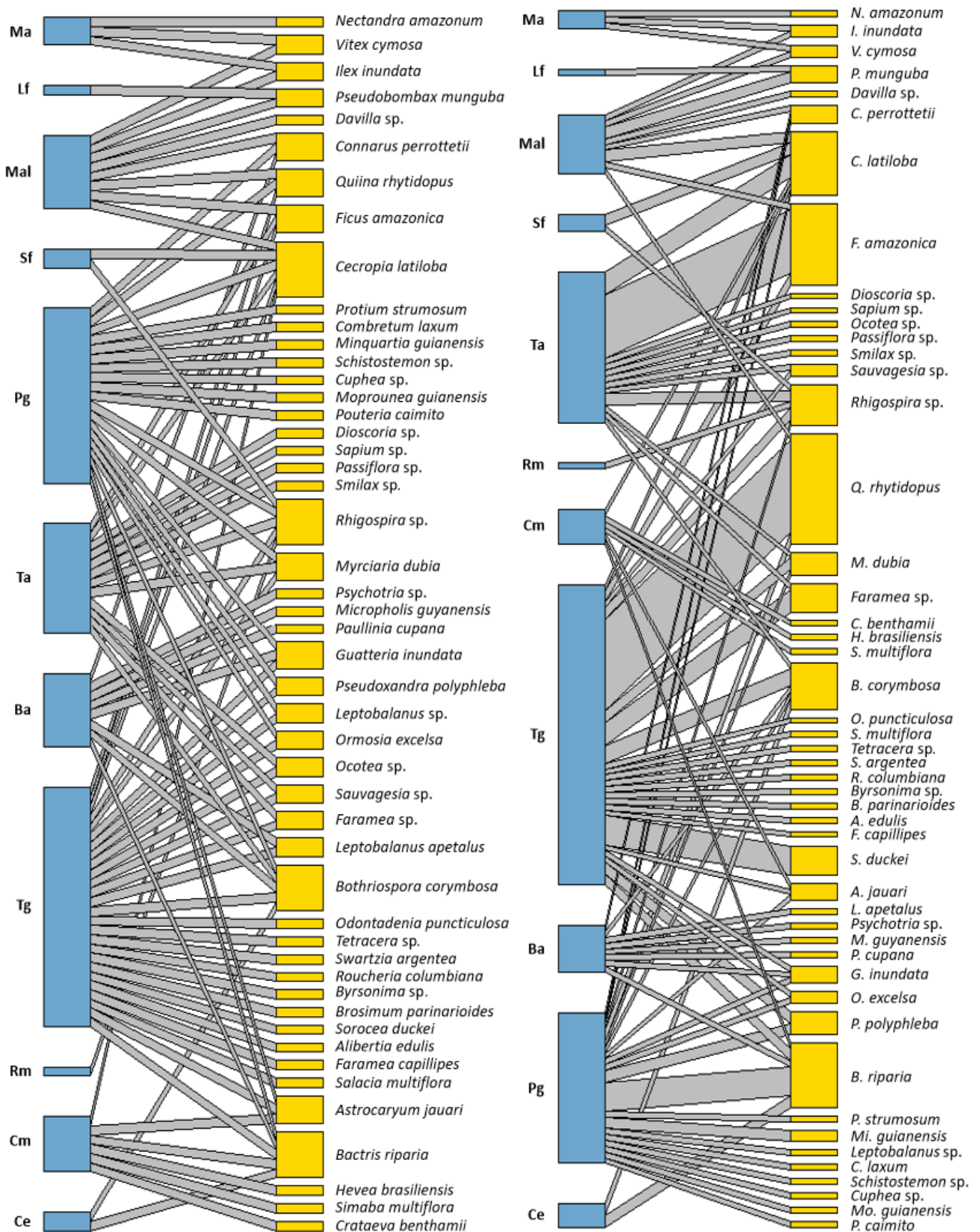


Figure 1. Binary (left) and weighted (right) bipartite network among frugivorous fish species and consumed seeds. Fish code: Ba – *B. amazonicus*, Ce – *C. erythrus*, Cm – *C. macropomum*, Lf – *L. fasciatus*, Ma – *M. asterias*, Mal – *M. albiscopum*, Pg – *P. granulosus*, Rm – *R. microlepis*, Sf – *S. fasciatus*, Ta – *T. albus*, Tg – *T. galeatus*.

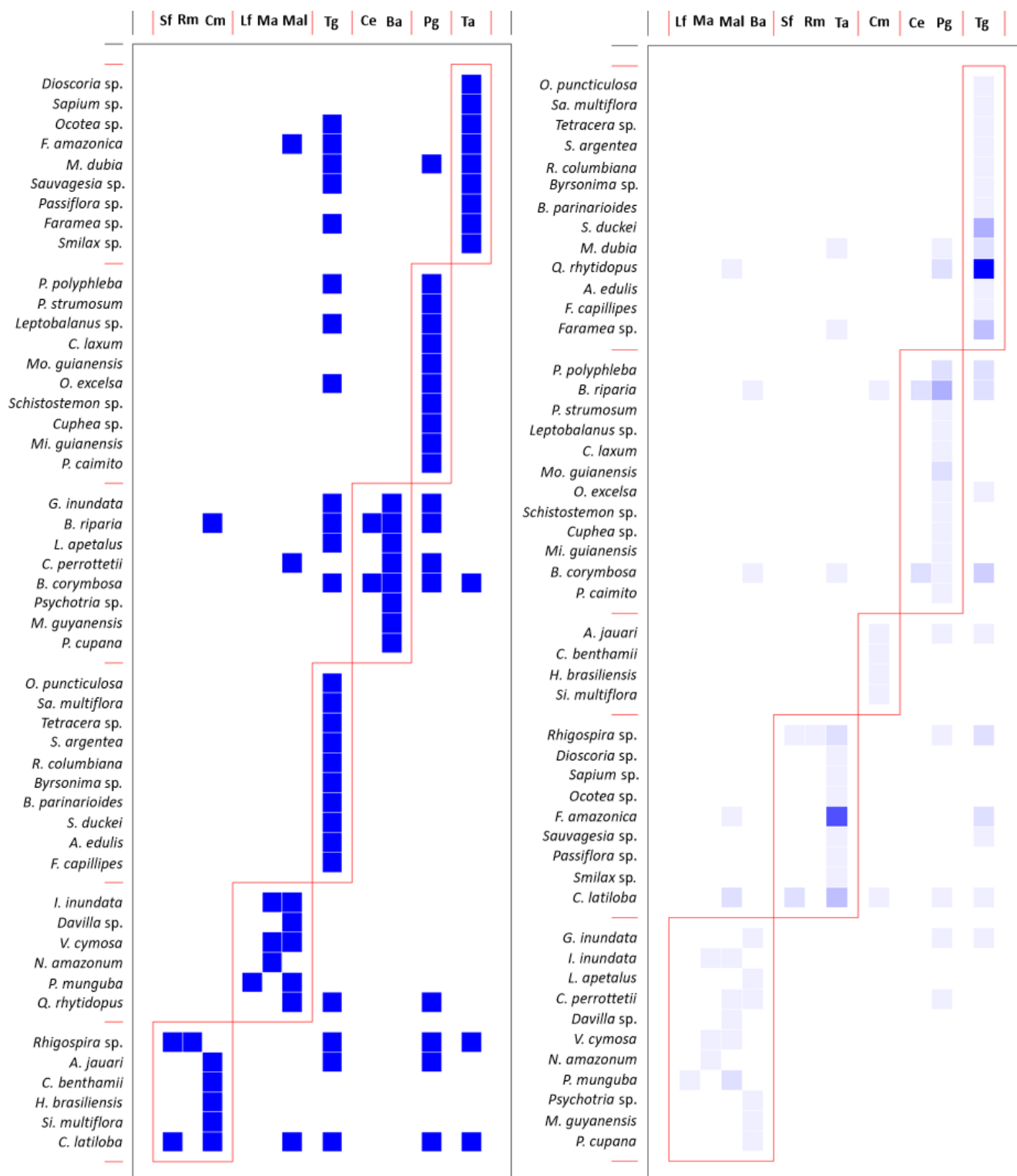


Figure 2. Binary (left) and weighted modular (right) network structure among frugivorous fish species and consumed seeds. Fish code: Ba – *B. amazonicus*, Ce - *C. erytrutus*, Cm- *C. macropomum*, Lf – *L. fasciatus*, Ma - *M. asterias*, Mal – *M. albiscopum*, Pg - *P. granulatus*, Rm – *R. microlepis*, Sf – *S. fasciatus*, Ta – *T. albus*, Tg – *T. galeatus*.

The length ($F = 0.1404$, $df = 9$, $p > 0.716$) and weight ($F = 0.009$, $df = 9$, $p > 0.924$) of the fish and the size of the seeds ($F = 0.004$, $df = 47$, $p > 0.947$) did not show significant differences in relation to the specialization indices (d') (Figure 3). These results indicated that larger fish do not interact with plant species more than the smaller fish do, and that small seeds do not interact with fish species more than large seeds do.

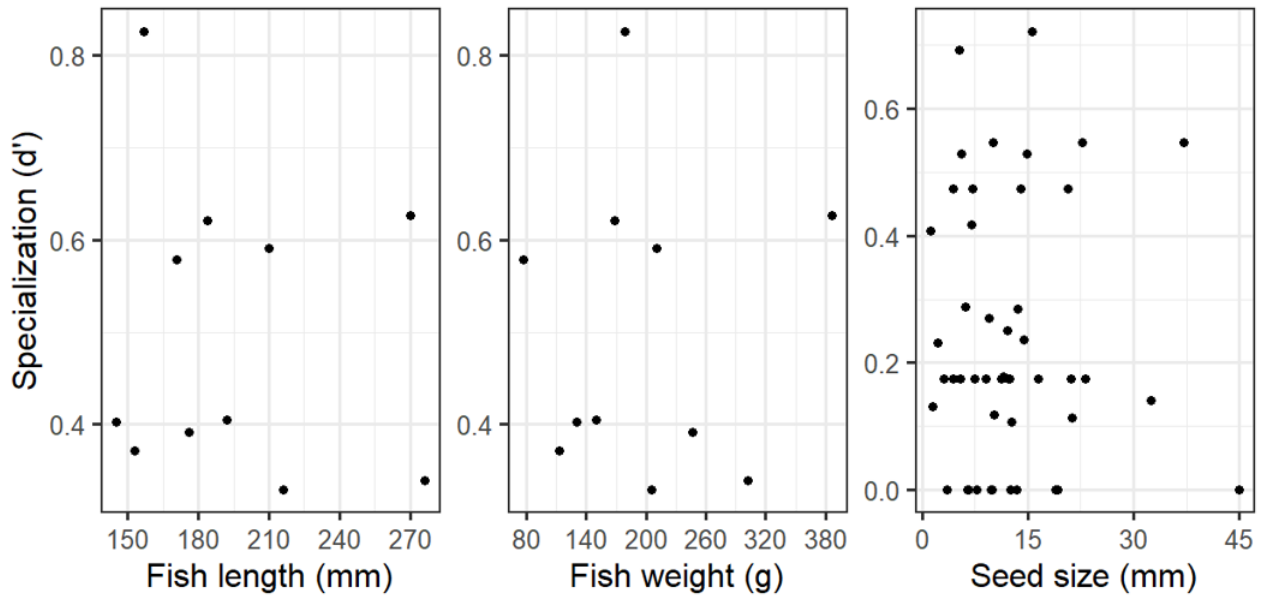


Figure 3. Relationship between length and weight of fish species and size of seeds as a function of specialization (d').

Robustness of the network against the extinction of frugivores

The frugivory network was relatively robust against extinctions when one species was removed at a time: *T. galeatus* ($R = 0.59$), *P. granulosus* ($R = 0.62$), *T. albus* ($R = 0.67$), *B. amazonicus* ($R = 0.69$), *M. albiscopum* ($R = 0.72$), and *C. macropomum* ($R = 0.71$) (Figure 4 a-f), when considering the robustness of the network with the eleven species of fish present ($R = 0.76$; Figure 4 g). However, the cumulative extinction of only two fish species (*T. galeatus* and *P. granulosus*) makes the network fragile ($R = 0.43$). With the removal of the three fish species that interacted with more plant species (*T. galeatus*, *P. granulosus*, and *T. albus*), the network tends to collapse ($R = 0.29$; Figure 4 h-i).

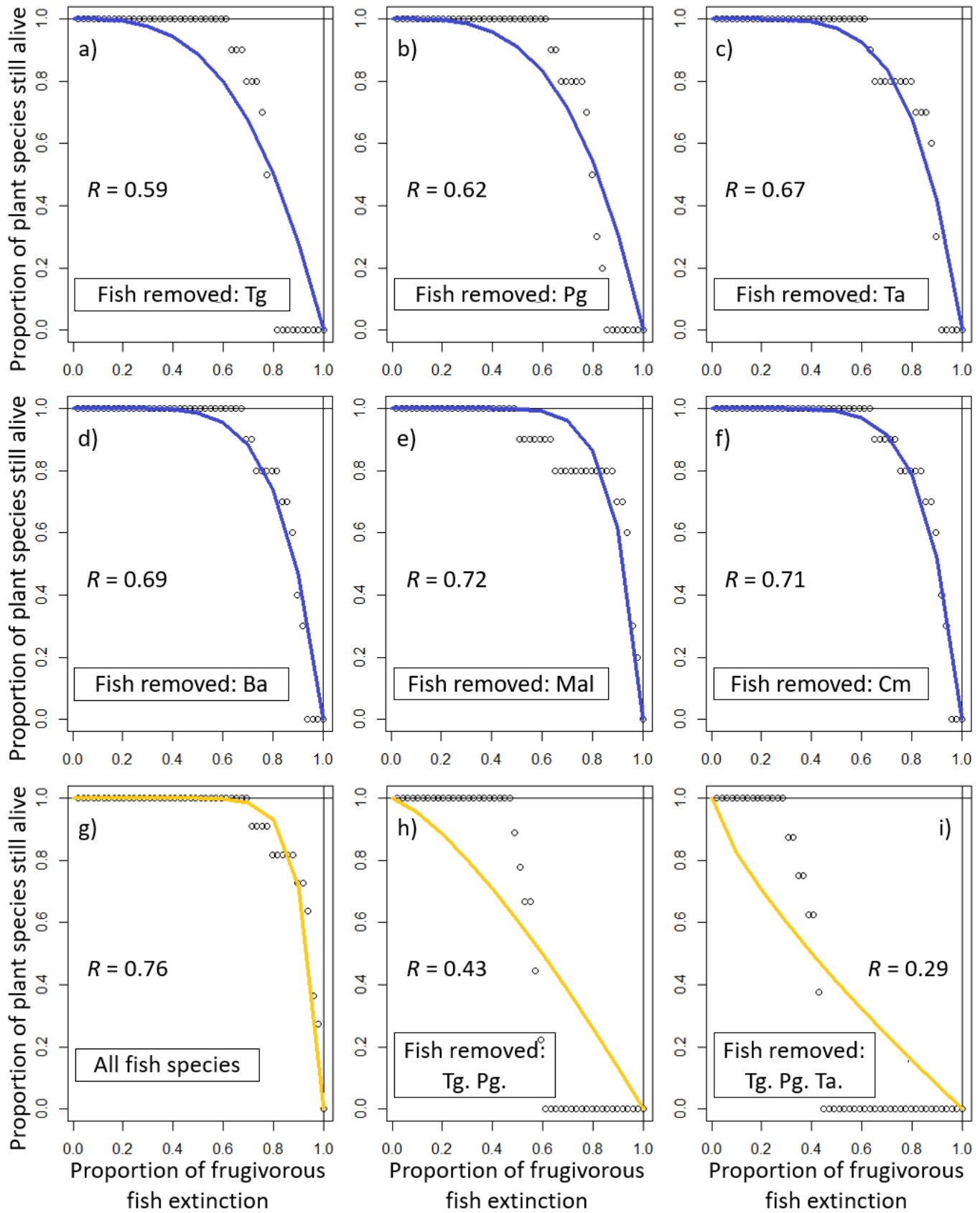


Figure 4. Robustness of the network against extinctions: by fish species removed (a–f), with all species (g), and cumulative removal of frugivorous fish (h–i). Fish code: Tg – *T. galeatus*, Pg – *P. granulosus*, Ta – *T. albus*, Ba – *B. amazonicus*, Mal – *M. albiscopum*, Cm – *C. macropomum*.

Discussion

Seasonal flooding in floodable areas of the Amazon triggers complex interactions between fish and plants (Goulding, 1980). Our results showed that three species of fish (*Trachelyopterus galeatus*, *Pterodoras granulosus*, and *Triportheus albus*) presented a higher frequency of interactions with plant species and had a greater contribution to network nestedness. These species, with the highest number of connections and frequencies of interactions, are fundamental for maintaining ecosystems functioning and should be the main focus of conservation efforts (Correa et al., 2016). In our study, the binary network presented a higher nestedness index than the weighted network, both with a significantly nested structure, showing that the fish-seed interactions in floodable areas of the Amazon may be resistant to environmental disturbances (Memmott et al., 2004; Tylianakis et al., 2010). Similar pattern has found for ichthyochory networks in regions of the Pantanal (Brazil) and the Amazon (Correa et al., 2016; Araujo et al., 2021; Pereyra et al., 2023). Our network also showed significant specialization at the community level (H_2'), due to many species of fish and plants with few connections. Some studies have shown that larger individuals tend to be less specialized, in other words, they are able to interact with more plant species than smaller fish (Galetti et al., 2008; Correa et al., 2015a; Araujo et al., 2021). However, our results did not show this pattern, as both the size of the fish and the size of the seeds found in the digestive tracts were not related to specialization (d'). This can be explained by the tendency for smaller fish to consume smaller-sized seeds, while larger fish consume larger-sized seeds (Costa et al., 2023, 2024), thus making the number of interactions between fish of different sizes more similar.

In our study, all the fish and plant species were peripheral. There are different reasons for why species may be classified as peripherals, including a high degree of specialization and low abundance (Ramos-Robles et al., 2018). The plant species *Myrciaria dubia* was a connector, *Quiina rhytidopus* and *Bactris riparia* were module hubs. These species were

important in maintaining the robustness of the whole network. In conservationist terms, the removal of these hubs and connectors within the network leads to the loss and fragmentation of many compartments and, therefore, a mass extinction of species (Olesen et al., 2007). In this sense, network size is a characteristic that can influence modularity and nestedness (Bascompte et al., 2003; Dormann and Strauss, 2013). In seed dispersal networks, the balance between modularity and nestedness may largely depend on the diversity of available frugivores (Mello et al., 2011) and the occurrence of fruits and seeds. However, co-occurrence does not mean occurrence of ecological interactions (Blanchet et al., 2020) since the spatio-temporal distribution may impose restrictions on interactions (Vázquez et al., 2009), thus affecting the likelihood of potential interactions (Dáttilo et al., 2014). Species that do not overlap either spatially or temporally cannot interact, even if they are abundant at a certain point in the fruiting season (Vázquez et al., 2009). In floodable areas of the Amazon, topographic gradients, to which different levels of flooding correspond, can impose temporal restrictions on interactions between fish and fruits. For example, trees located at higher elevations of the plain, where the flooding arrives later, begin to bear fruit several months later than trees at lower elevations (Parolin et al., 2010), which reduces niche overlap between frugivorous fish species.

Communities can form distinct modules based on the functional complementarity of their characteristics (Thompson, 2005). Therefore, the phenotype of the species can affect the structure of the community, as it influences the outcome of interactions between the species (Vázquez et al., 2009). For example, morphological characteristics of fish, such as size (Galetti et al., 2008; Costa-Pereira and Galetti, 2015; Costa et al., 2023) and type of teeth (multicuspid, molariform and villiform) (Goulding, 1980; Lucas, 2008), can influence the size, quantity and type of fruit and seed consumed. Plant-frugivore interactions are considered mutualisms because fruit consumption by frugivores primarily results in seed dispersal (Schupp et al., 2010;

Snell et al., 2019). Notwithstanding, frugivores can also act as predators of seeds when seeds do not survive (Correa et al., 2015a), thus resulting in an antagonistic interaction.

The rewards tend to favor interactions (Gilman et al., 2012). In our study, fleshy fruits accounted for 69.3% of plant species consumed. Fish can be attracted by the chemical signals that are released by fruit when it falls into the water, which is an adaptation of fish and fruits for efficient seed dispersal from the flooded forest (Goulding, 1980), thus the presence of fleshy fruit can increase the frequency of interactions between the seeds and the fish. The frequency of interactions between fish and plants also depends on the abundance of fish and fruit produced in the environment. In our study, three plant species (*Cecropia latiloba*, *Bothriospora corymbosa*, and *Ficus amazonica*) represented 90% of the abundance of seeds found in the digestive tracts of fish. These tree species are abundant in floodable areas of the Amazon (Parolin, 1997; Costa et al., 2023). Interactions involving rare species are less likely to be observed in the field than those involving abundant species (Dupont et al., 2003). However, even abundant species occupying the core of a nested network can change geographically since local communities vary in species composition in relation to regional species assemblages, which results in different local assemblies of mutualists (Bascompte and Jordano, 2007).

Our network proved itself to be robust against extinctions of fish species when assessed one species at a time. Considering the removal of *T. galeatus*, which interacted with 46% of the plant species, the network remained relatively robust, which can be explained by the existence of other fish species that interacted with the same plant species in other modules, thereby reducing secondary plant extinctions. Modular networks guarantee robustness and allow greater stability against disturbances, since impacts can be retained in a single module, which cushions its spread to the others (Thébault and Fontaine, 2010). However, with the cumulative removal of fish species (*T. galeatus*, *P. granulatus*, and *T. albus*) that interact with more plant species, the robustness of the network decreases and tends to collapse. The removal of these three fish

species would prevent the dispersal of the seeds of 42% of the tree species in this environment. Considering that the seeds of many of these species (e.g. *Astrocaryum jauari*, *Bactris riparia*, *Nectandra amazonum*, and *Pouteria caimito*) do not have adaptations for dispersal via hydrochory, the decrease in the abundance in some species of frugivorous fish due to overexploitation could have serious consequences for the dispersion of many tree species in Amazonian floodable forests. For example, adult *Colossoma macropomum* are now rare in fisheries in this region due to decades of overexploitation of both mature and immature fish (Isaac and Ruffino, 1996; Tregidgo et al., 2017; Prestes et al., 2022). Nonetheless, this effect can be mitigated by the vast geographical area of the floodplains of the region (Melack and Hess, 2010), where the variation in the distribution and composition of tree species and fish (Wittmann et al., 2010, 2022; Van der Sleen and Albert, 2018; Dagosta and De Pinna, 2019) could form distinct modules that do not spatially overlap with other modules, thus making this region more resilient to environmental disturbances.

Finally, our study contributes to a better understanding of the role of frugivorous fish in ichthyochory networks in floodable areas of the Amazon. We show a significant nestedness of the binary and weighted networks and with a modular pattern. However, contrary to expectations, all the fish and plant species were peripheral, indicating that even though there are fish species (generalists) that have interacted with many plant species, these plants can interact with other fish species in the environment, making our network relatively robust when the frugivores are removed. Considering these aspects, in terms of conservation, seed dispersal networks can be modified by anthropogenic activities. Among them, the overexploitation of frugivorous fish stands out (Correa et al., 2015b; Costa-Pereira and Galetti, 2015; Costa-Pereira et al., 2018), which could have significant effects for the interactions and dispersal of seeds (Costa-Pereira et al., 2017; Costa et al., 2023); as well as the deforestation of floodable forests (Renó et al., 2016; Renó and Novo, 2019), which can reduce the supply of fruits and seeds to

fish, and the construction of hydroelectric dams that prevent the movement and migration of frugivorous fish and other species (Castello et al., 2013; Duponchelle et al., 2021), and reduces the likelihood of interactions between fish and plant species and, consequently, modifies the structure of dispersal networks in the floodable areas of the Amazon.

References

- Albert, R., Jeong, H., Barabasi, A. L. (2000). Error and attack tolerance of complex networks. *Nature*, 406, 378–382. <https://doi.org/10.1038/35019019>
- Almeida-Neto, M., Guimarães, P., Guimarães, P. R., Loyola, R. D., Ulrich, W. (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., Ulrich, W. (2011). A straightforward computational approach for measuring nestedness using quantitative matrices. *Environmental Modelling & Software*, 26, 173–178. <https://doi.org/doi:10.1016/j.envsoft.2010.08.003>
- Araujo, J. M., Correa, S. B., Penha J., Anderson J., Traveset, A. (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>
- Barrat, A., Barthélemy, M., Pastor-Satorras, R., Vespignani, A. (2004). The architecture of complex weighted networks. *Proceedings of the National Academy of Sciences*, 101, 3747–3752. <https://doi.org/10.1073/pnas.0400087101>
- Bascompte, J., Jordano, P., Melián, C. J., Olesen, J. M. (2003). The nested assembly of plant–animal mutualistic networks. *Proceedings of the National Academy of Sciences*, 100, 9383–9387. <https://doi.org/10.1073/pnas.1633576100>
- Bascompte, J., Jordano, P. (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>

- Bascompte, J., Olesen, J. M. (2015). Mutualistic networks. In: Bronstein, J. L. (Ed.), *Mutualism*. Oxford University Press, United Kingdom, pp. 203–210. <https://doi.org/10.1093/acprof:oso/9780199675654.003.0011>
- Blanchet, F. G., Cazelles, K., Gravel, D. (2020). Co-occurrence is not evidence of ecological interactions. *Ecology Letters*, 23, 1050–1063. <https://doi.org/10.1111/ele.13525>
- Blüthgen, N., Menzel, F., Blüthgen, N. (2006). Measuring specialization in species interaction networks. *BMC Ecology*, 6, 9. <https://doi.org/10.1186/1472-6785-6-9>
- Brummitt, N., Araújo, A. C., Harris, T. (2020). Areas of plant diversity—What do we know? *Plants, People, Planet*, 3, 33–44. <https://doi.org/10.1002/ppp3.10110>
- Burgos, E., Ceva, H., Perazzo, R. P. J., Devoto, M., Medan, D., Zimmermann, M., Maria Delbue, A. (2007). Why nestedness in mutualistic networks? *Journal of Theoretical Biology*, 249, 307–313. <https://doi.org/10.1016/j.jtbi.2007.07.030>
- Castello, L., Mcgrath, D. G., Hess, L. L., Coe, M. T., Lefebvre, P. A., Petry, P., Macedo M. N., Reno, V. F., Arantes, C. C. (2013). The vulnerability of Amazon freshwater ecosystems. *Conservation Letters*, 6, 217–229. <https://doi.org/10.1111/conl.12008>
- Corlett, R. T. (2016). Plant Diversity in a Changing World: Status, Trends, and Conservation Needs. *Plant Diversity*, 38, 10–16. <https://doi.org/10.1016/j.pld.2016.01.001>
- Correa, S. B., Winemiller, K. O., López-Fernández, H., Galetti, M. (2007). Evolutionary perspectives on seed consumption and dispersal by fishes. *BioScience*, 57, 748–756. <https://doi.org/10.1641/B570907>
- Correa, S. B., Costa-Pereira, R., Fleming, T., Goulding, M., Anderson, J. T. (2015a). Neotropical fish–fruit interactions: eco-evolutionary dynamics and conservation. *Biological Reviews*, 90, 1263–1278. <https://doi.org/10.1111/brv.12153>
- Correa, S. B., Araújo, J. K., Penha, J. M. F., Cunha, C. N., Stevenson, P. R., Anderson, J. T. (2015b). Overfishing disrupts an ancient mutualism between frugivorous fishes and plants in Neotropical wetlands. *Biological Conservation*, 191, 159–167. <https://doi.org/10.1016/j.biocon.2015.06.019>

- Correa, S. B., Araujo, J. K., Penha, J., Nunes da Cunha, C., Bobier, K. E., Anderson, J. T. (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>
- Costa, G., Piedade, M. T. F., Ferreira, E. J., Maltchik, L. (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., Weiss, B., Piedade, M. T. F. (2024). Larger fish disperse larger seeds in oligotrophic wetlands of the central Amazon. *Wetlands*, 44, 18. <https://doi.org/10.1007/s13157-024-01779-7>
- Costa-Pereira, R., Galetti, M. (2015). Frugivore downsizing and the collapse of seed dispersal by fish. *Biological Conservation*, 191, 809–811. <https://doi.org/10.1016/J.BIOCON.2015.07.011>
- Costa-Pereira, R., Correa, S. B., Galetti, M. (2017). Fishing-down within populations harms seed dispersal mutualism. *Biotropica*, 50, 319–325. <https://doi.org/10.1111/btp.12516>
- Costa-Pereira, R., Lucas, C., Crossa, M., Anderson, J. T., Weiss, B. A., Dary, E. P., Piedade, M. T. F., Demarchi, L. O., Rebouças, E. R., Costa, G. S., Galetti, M., Correa, S. B. (2018). Defaunation shadow on mutualistic interactions. *Proceedings of the National Academy of Sciences*, 115, E2673–E2675. <https://doi.org/10.1073/pnas.1801106115>
- Dagosta, F. C. P., De Pinna, M. (2019). The Fishes of the Amazon: Distribution and Biogeographical Patterns, with a Comprehensive List of Species. *American Museum of Natural History*. 431, 163 p. <https://doi.org/10.1206/0003-0090.431.1.1>
- Dáttilo, W., Fagundes, R., Gurka, C. A. Q., Silva, M. S. A., Vieira, M. C. L., Izzo, T. J., Díaz-Castelazo, C., Del-Claro, K., Rico-Gray, V. (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>
- Dirzo, R., Miranda, A. (1990). Contemporary neotropical defaunation and forest structure, function, and diversity. *Conservation Biology*, 4, 444–447.

- Dormann, C. F., Strauss, R. (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>
- Dormann, C. F., Fruend, J., Gruber, B., Beckett S., Devoto, M., Gabriel, M. F. F., Iriondo, J. M., Opsahl, T., Pinheiro, R. B. P., Strauss, R., Vázquez, D. P. (2022). Package ‘bipartite’ - Visualising Bipartite Networks and Calculating Some (Ecological) Indices. 181 p. <https://cran.r-project.org/web/packages/bipartite/bipartite.pdf>
- Dudgeon, D. (2019). Multiple threats imperil freshwater biodiversity in the Anthropocene. *Curr Biol*, 29(19), R942–R995. <https://doi.org/10.1016/j.cub.2019.08.002>
- Dunne, J. A., Williams, R. J., Martinez, N. D. (2002). Network structure and biodiversity loss in food webs: robustness increases with connectance. *Ecology Letters*, 5, 558–567. <https://doi.org/10.1046/j.1461-0248.2002.00354.x>
- Duponchelle, F., Isaac, V. J., Da Costa Doria, C. R., Van Damme, P. A., Herrera-R, G. A., Anderson, E. P., Cruz, R. E. A., Hauser, M., Hermann, T. W., Agudelo, E., Bonilla-Castillo C., Barthem, R., Freitas, C. E. C., García-Dávila, A., Renno, J., Castello, L. (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>
- Dupont, Y. L., Hansen, D. M., Olesen, J. M. (2003). Structure of a plant–flower–visitor network in the high-altitude sub-alpine desert of Tenerife, Canary Islands. *Ecography*, 26, 301–310. <https://doi.org/10.1034/j.1600-0587.2003.03443.x>
- Galetti, M., Donatti, C. I., Pizo, M. A., Giacomini, H. C. (2008). Big fish are the best: seed dispersal of *Bactris glaucescens* by the Pacu fish (*Piaractus mesopotamicus*) in the Pantanal, Brazil. *Biotropica*, 40, 386–389. <https://doi.org/10.1111/j.1744-7429.2007.00378.x>
- Gilman, R. T., Nuismer, S. L., Jhwueng, D. C. (2012). Coevolution in multidimensional trait space favours escape from parasites and pathogens. *Nature*, 483, 328–330. <https://doi.org/10.1038/nature10853>
- Goulding, M. (1980). The fishes and the forest: explorations in Amazonian natural history. University of California Press, Berkeley, California.

Guimarães Jr, P. R. (2020). The Structure of Ecological Networks Across Levels of Organization. *Annual Review of Ecology, Evolution, and Systematics*, 51, 433–460. <https://doi.org/10.1146/annurev-ecolsys-012220-120819>

Guimerà, R., Amaral, L. A. N. (2005). Functional cartography of complex metabolic networks. *Nature*, 433, 895–900. <https://doi.org/10.1038/nature03288>

Helfman, G. S. (2013). Fishes, Biodiversity of. *Encyclopedia of Biodiversity*, 3, 456–476. <https://doi.org/10.1016/B978-0-12-384719-5.00054-X>

Horn, M., Correa, S. B., Parolin, P., Pollux, B. J. A., Anderson, J. T., Lucas, C., Widmann, P., Tjiu, A., Galetti, M., Goulding, M. (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>

Irion, G., Mello, J., Morais, J., Piedade, M. T. F., Junk, W. J., Garming, L. (2010). Development of the Amazon valley during the middle to late quaternary: sedimentological and climatological observations. In: Junk, W. J., Piedade, M. T. F., Wittmann, F., Schöngart, J., Parolin, P. (Eds.), *Amazonian Floodplain Forest: Ecophysiology, Biodiversity and Sustainable Management*. Springer, Berlin, pp. 27–42.

Isaac, V. J., Ruffino, M. L. (1996). Population dynamics of tambaqui, *Colossoma macropomum* Cuvier, in the Lower Amazon, Brazil. *Fisheries Management and Ecology*, 3(4), 315–333. <https://doi.org/10.1046/j.1365-2400.1996.d01-154.x>

Jordano, P. (2000). Fruits and frugivory. In: Fenner, M. (Ed.), *Seeds: the ecology of regeneration in plant communities*. CABI Publ., Wallingford, pp. 125–166. <https://doi.org/10.1079/9780851994321.0125>

Jordano, P., Bascompte, J., Olesen, J. M. (2003). Invariant properties in coevolutionary networks of plant–animal interactions. *Ecology Letters*, 6, 69–81. <https://doi.org/10.1046/j.1461-0248.2003.00403.x>

Junk, W. J., Bayley, P. B., Sparks, R. E. (1989). The flood pulse concept in river floodplain systems. In: Dodge, D. P. (Ed.), *Proceedings of the International Large River Symposium*. Canadian Special Publication in Fisheries and Aquatic Sciences, Ontario, pp. 110–127.

Junk, W. J., Piedade, M. T. F., Schöngart, J., Cohn-Haft, M., Adeney, J. M., Wittmann, F., (2011). A classification of major naturally-occurring Amazonian lowland wetlands. *Wetlands*, 31, 623–640. <https://doi.org/10.1007/s13157-011-0190-7>

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.1744-7429.2008.00415.x>

Mateus, L., Rodrigues Costa, R. M., Penha, J. (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., Hess, L. L. (2010). Remote Sensing of the Distribution and Extent of Wetlands in the Amazon Basin. In: Junk, W. J., Piedade, M. T. F., Wittmann, F., Schöngart, J., Parolin, P. (Eds.), *Central Amazonian Floodplain Forests: Ecophysiology, Biodiversity and Sustainable Management*. Springer, Berlin/Heidelberg/New York, pp. 43–59.

Mello, M. A. R., Marquitti, F. M. D., Guimarães Jr., P. R., Kalko, E. K. V., Jordano, P., De Aguiar, M. A. M. (2011a). 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>

Mello, M. A. R., Marquitti, F. M. D., Guimarães Jr., P. R., Kalko, E. K. V., Jordano, P., Aguiar, M. A. M. (2011b). 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>

Memmott, J., Waser, N. M., Price, M. V. (2004). Tolerance of pollination networks to species extinctions. *Proceedings of the Royal Society B*, 271, 2605–2611. <https://doi.org/10.1098/rspb.2004.2909>

Olesen, J. M., Bascompte, J., Dupont, Y. L., Jordano, P. 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. (1997). Auswirkungen periodischer Vernässung und Überflutung auf Phänologie, Photosynthese und Blattphysiologie von Baumarten unterschiedlicher Wachstumsstrategie in

zentralamazonischen Überschwemmungsgebieten. Herbert Utz, Wissenschaft, München. 166 p.

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., De Simone, O., Haase, K., Waldhoff, D., Rottenberger, S., Kuhn, U., Kesselmeier, J., Schmidt, W., Piedade, M. T. F., Junk, W. J. (2004). Central Amazon floodplain forests: tree survival in a pulsing system. *Botanical Review*, 70, 357–380.

Parolin, P., Waldhoff, D., Piedade, M. T. F. (2010). Fruit and seed chemistry, biomass and dispersal. In: Junk, W. J., Piedade, M. T. F., Wittmann, F., Schöngart, J., Parolin, P. (Eds.). Central Amazonian Floodplain Forests: Ecophysiology, Biodiversity and Sustainable Management. Springer, Berlin/Heidelberg/New York, pp. 243–258.

Parolin, P., Wittmann, F., Ferreira, L. V. (2013). Fruit and seed dispersal in Amazonian floodplain trees – a review. *Ecotropica*, 19, 15–32.

Pereyra, P. E. R., Hallwass, G., Begossi, A., Giacomini, L. L., Silvano, R. A. M. (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>

Prestes, L., Barthelm, R., Mello-Filho, A., Anderson, E., Correa, S. B., Couto, T. B. D., Venticinque, E., Forsberg, B., Cañas C., Bentes, B., Goulding, M. (2022). Proactively averting the collapse of Amazon fisheries based on three migratory flagship species. *PLoS ONE*, 17(3), e0264490. <https://doi.org/10.1371/journal.pone.0264490>

Ramos-Robles, M., Andresen, E., Daz-Castelazo, C. (2018). Modularity and robustness of a plant-frugivore interaction network in a disturbed tropical forest. *Écoscience*, 25, 209–222. <https://doi.org/10.1080/11956860.2018.1446284>

Renó, V., Novo, E., Escada, M. (2016). Forest fragmentation in the Lower Amazon Floodplain: implications for biodiversity and ecosystem service provision to riverine populations. *Remote Sensing*, 8(11), 886. <https://doi.org/10.3390/rs8110886>

Renó, V., Novo, E. (2019). Forest depletion gradient along the Amazon floodplain. *Ecological Indicators*, 98, 409–419. <https://doi.org/10.1016/j.ecolind.2018.11.019>

- Sarmiento, R., Alves-Costa, C. P., Ayub, A., Mello, M. A. R. (2014). Partitioning of seed dispersal services between birds and bats in a fragment of the Brazilian Atlantic Forest. *Zoologia*, 31, 245–255. <http://doi.org/10.1590/S1984-46702014000300006>
- Silva, G. G., Pizo, M. A., Green, A. J., Sebastián-González, E., Bugoni, L., Maltchik, L. (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>
- Sheykhal, S., Fernández-Gracia, J., Traveset, A., Ziegler, M., Voolstra, C. R., Duarte, C. M., Eguíluz, V. M. (2020). Robustness to extinction and plasticity derived from mutualistic bipartite ecological networks. *Scientific Reports*, 10, 9783. <https://doi.org/10.1038/s41598-020-66131-5>
- Snell, R. S., Beckman, N. G., Fricke, E., Loiselle, B. A., Carvalho, C. S., Jones, L. R., Lichti, N. I., Lustenhouwer, N., Schreiber, S. J., Strickland, C., Sullivan, L. L., Cavazos, B. R., Giladi, I., Hastings, A., Holbrook, K. M., Jongejans, E., Kogan, O., Montaña-Centellas, F., Rudolph, J., Rogers, H. S., Zwolak, R., Schupp, E. W. (2019). Consequences of intraspecific variation in seed dispersal for plant demography, communities, evolution and global change. *AoB Plants*, 11, plz016. <https://doi.org/10.1093/aobpla/plz016>
- Thébault, E., Fontaine, C. (2010). Stability of ecological communities and the architecture of mutualistic and trophic networks. *Science*, 329, 853–856. <https://doi.org/10.1126/science.1188321>
- Thompson, J. N. (2005). *The Geographic Mosaic of Coevolution*. University of Chicago Press, Chicago.
- 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>
- Tregidgo, D. J., Barlow, J., Pompeu, P. S., De Almeida Rocha, M., Parry, L. (2017). Rainforest metropolis casts 1,000-km defaunation shadow. *Proceedings of the National Academy of Sciences*, 114(32), 8655–8659. <https://doi.org/10.1073/pnas.1614499114>

- Tylianakis, J. M., Laliberté, E., Nielsen, A., Bascompte, J. (2010). Conservation of species interaction networks. *Biological Conservation*, 143, 2270–2279. <https://doi.org/10.1016/j.biocon.2009.12.004>
- Van der Sleen, P., Albert, J. S. (2018). Field guide to the fishes in the Amazon, Orinoco and Guianas. Princeton University Press, Princeton.
- Vázquez, D. P., Blüthgen, N., Cagnolo, L., Chacoff, N. P. (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>
- Weiss, B., Santana, F. D., Petene Calvi, G., Costa, G., Zuanon, J., Piedade, M. T. F. (2023). Effectiveness of fish assemblage as seed dispersers in Amazon oligotrophic flooded forests. *Austral Ecology*, 00, 1–18. <https://doi.org/10.1111/aec.13330>
- Wittmann, F., Schöngart, J., Montero, J. C., Motzer, M., Junk, W. J., Piedade, M. T. F., Queiroz, H. L., Worbes, M. (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., Schöngart, J., Junk, W. J. (2010). Phytogeography, species diversity, community structure and dynamics of central Amazonian floodplain forests. In: Junk, W. J., Piedade, M. T. F., Wittmann, F., Schöngart, J., Parolin, P. (Eds.), *Central Amazonian Floodplain Forests: Ecophysiology, Biodiversity and Sustainable Management*. Springer, Berlin/Heidelberg/New York, pp. 61–102.
- Wittmann, F., Householder, J. E., Piedade, M. T. F., Schöngart, J., Demarchi, L. O., Quaresma, A. C., Junk, W. J. (2022). A Review of the Ecological and Biogeographic Differences of Amazonian Floodplain Forests. *Water*, 14, 3360. <https://doi.org/10.3390/w14213360>
- Wright, S. J. (2003). The myriad consequences of hunting for vertebrates and plants in tropical forests. *Perspectives in Plant Ecology, Evolution and Systematics*, 6, 73–86. <https://doi.org/10.1078/1433-8319-00043>
- Wunderle, Jr., J. M. (1997). The role of animal seed dispersal in accelerating native forest regeneration on degraded tropical lands. *Forestry Ecology and Management*, 99, 223–235. [https://doi.org/10.1016/S0378-1127\(97\)00208-9](https://doi.org/10.1016/S0378-1127(97)00208-9)

WWF Living Planet Report (2022). <https://livingplanet.panda.org/en-US/>. Accessed February 6, 2023.

Capítulo 3

The flooding gradient affects seed dispersal by fruit-eating fishes in Amazonian whitewater floodplain forests

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The flooding gradient affects seed dispersal by fruit-eating fishes in Amazonian whitewater floodplain forests

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 per year, 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.

Keywords: Frugivory, frugivorous fish, high várzea, ichthyochory, low várzea, modularity, nestedness, seed dispersal networks

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 & 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 & 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 2021; 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 1,000 tree species are found, making it the most species-rich floodplain forest in the world (Wittmann et al. 2006, 2010a; Householder et al. 2024). These forests associated with whitewater rivers occupy an extensive area of approximately 450,000 km² (Wittmann and Junk 2016), and have experienced increases in the intensity of extreme flood and drought events (Fleischmann et al. 2023; Espinosa 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 6-9 m in the western Amazon (Solimões-Marañon), and between 12-15 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 leads 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 to 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 being endemic species (Wittmann et al. 2010a), 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 et al. 2010a). Moreover, the central Amazonian LV and HV forests share only $\approx 17.5\%$ of their tree species and differ in floristic and structural characteristics induced by the hydroperiod (Wittmann et al. 2010a). 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 2,716 known fish species (Dagosta and De Pinna 2019) and at least 103 consume fruits and seeds from flooded forests (Rodriguez et al. *in press*). 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 et al. 2024a), 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 (Serrasalminidae 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 likely 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 et al. 2024b), 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 & 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 & Jordano 2007). Modular and nested structures increase the network stability and robustness against species loss (Memmott et al. 2004; Costa et al. 2024b). 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 et al. 2024b).

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.

Material and Methods

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, with a marked difference between the dry (June/October) and rainy (December/May) seasons (Parolin 2000). The average ($\pm$ 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 2020-2024 was 11.3 m (Figure 1b).

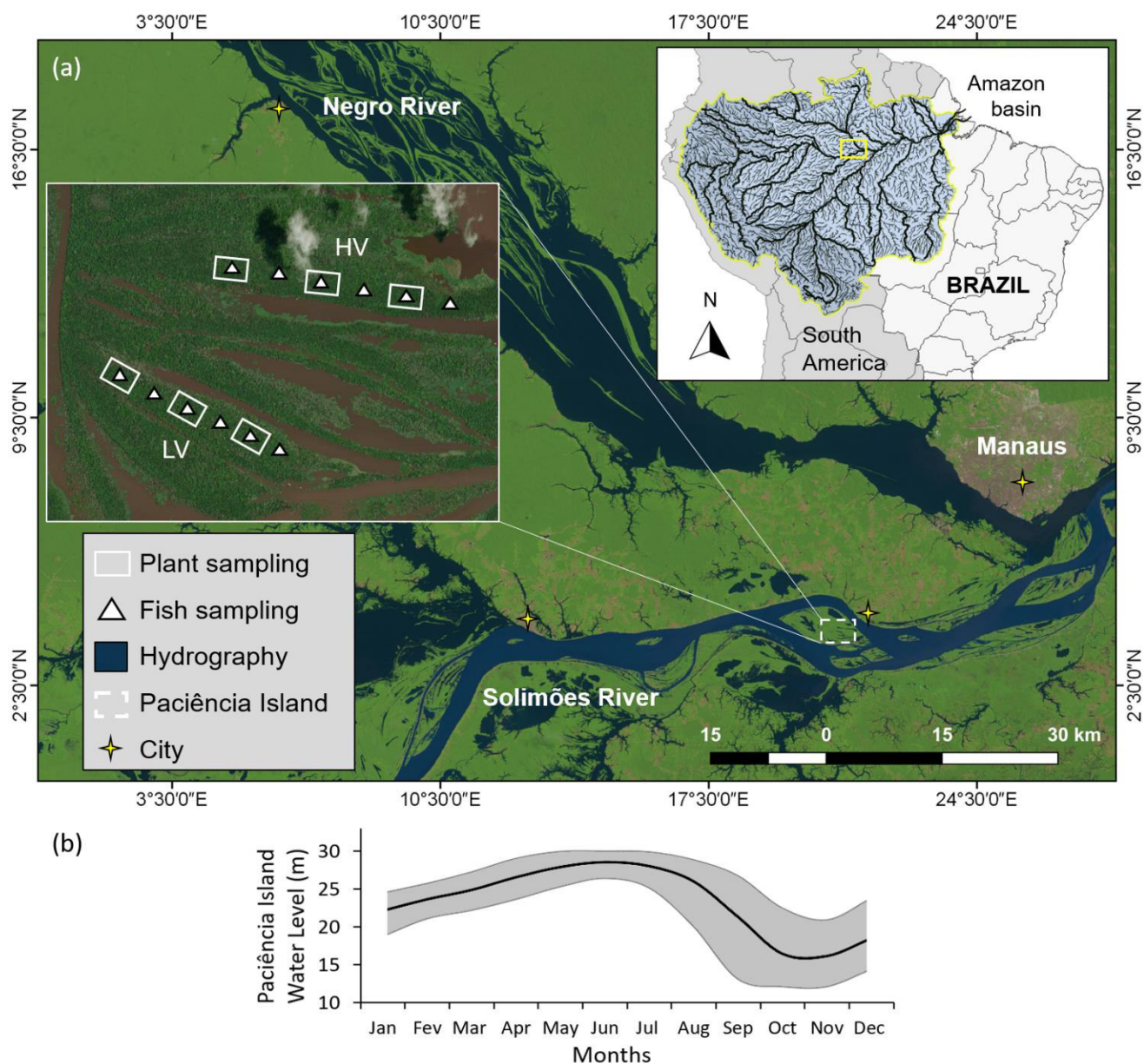


Figure 1. Study area (a) located on Paciência Island in the Solimões River, showing the Low várzea (LV) and high várzea (HV). Flooding pattern on Paciência Island (b), data: Hidroweb/Brazilian National Water and Sanitation Agency – ANA; fluviometric station code 14990000 (Negro-Amazon confluence).

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 1,000 meters. 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 to 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 minutes 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 $\times$) 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).

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 x 100 m (0.5 ha) were set up, separated by a distance of 200 meters. 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 to the INPA's Herbarium for taxonomic identification with the help of a specialist.

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.

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; Wittmann et al. 2004; Wittmann et al. 2006; Wittmann et al. 2009; Wittmann et al. 2010b; Wittmann et al. 2012). 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.

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. 2011; Costa et al. 2024) and for quantifying and comparing network patterns statistically (Bascompte & 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 $\pm$ Sd. To test significance, we compared observed modularity against two complementary null

models, each run 1,000 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 & 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).

Results

Our field collections yielded a total of 5,012 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 1). 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 brachipomus* (N = 36 species, 18%) and *Mylossoma albiscopeum* (N = 20 species, 10%), all belonging to the Serrasalminidae 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 ($t = -1.039$, $df = 72$, $p = 0.322$; Fig. 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 ($t = -2.170$, $df = 47$, $p = 0.015$; Fig. 2b). Although the network is not significantly modular (mean observed $Q = 0.44 \pm 0.03$, $z \text{ score}_{PAT} = 0.25$, null $CI_{PAT} 2.5$ and $97.5\% = 0.43 - 0.47$; $z \text{ score}_{VAZ} = 3.95$, null $CI_{VAZ} 2.5$ and $97.5\% = 0.41 - 0.44$; Fig. 3a), it presents a nested structure (mean observed $NODF = 36.38$, null $CI_{PAT} 2.5$ and $97.5\% = 20.49 - 21.03$; Fig. 3b). No random network showed nestedness values higher than those observed in our networks.

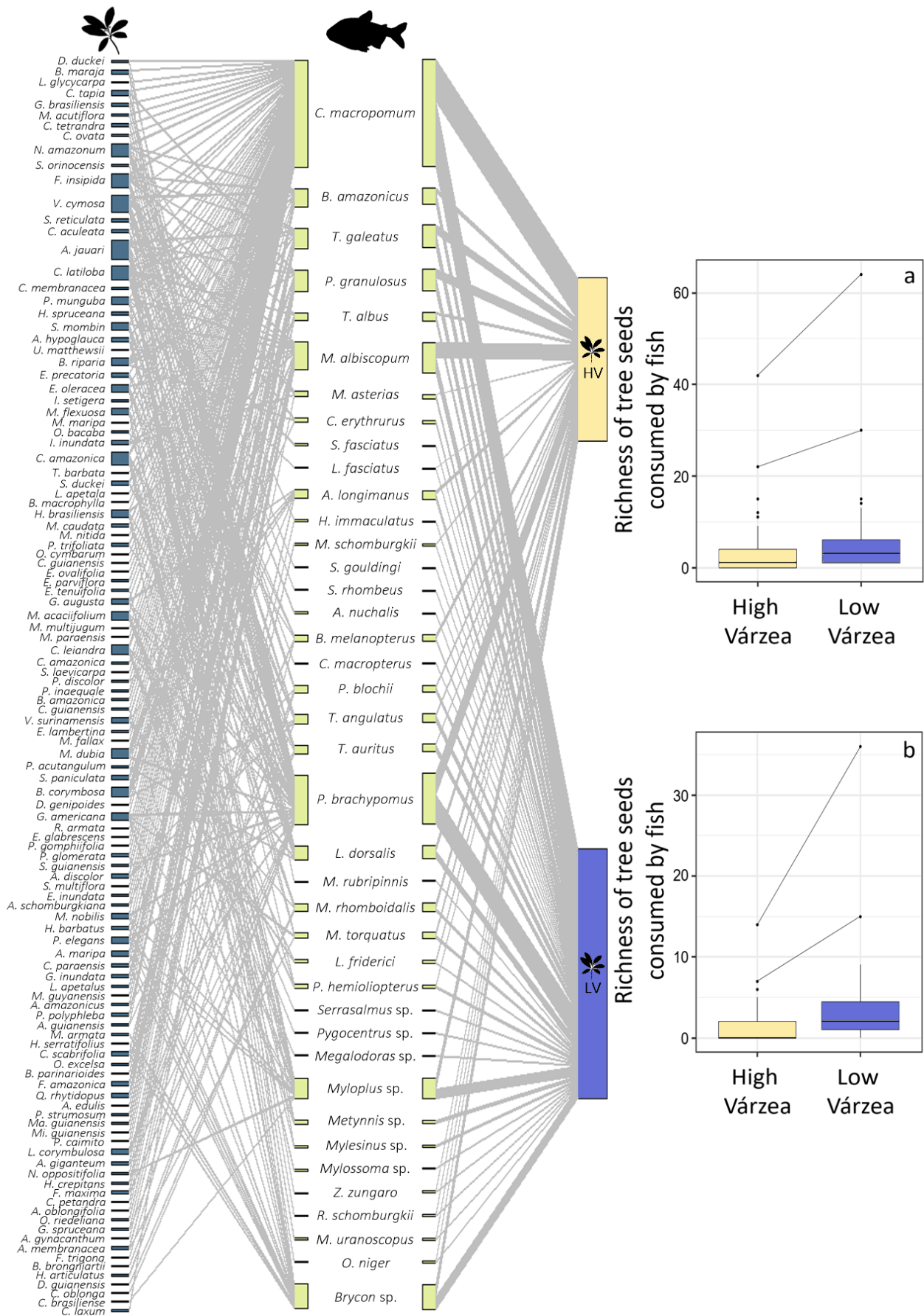


Figure 2: Network (binary) on the left showing the tree fruits and seeds consumed by each fish species, and on the right (weighted), showing the origin along the flood gradient of tree fruits and seeds consumed by fish in Amazonian floodplain forests: (a) all tree species recorded per flooded habitat,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

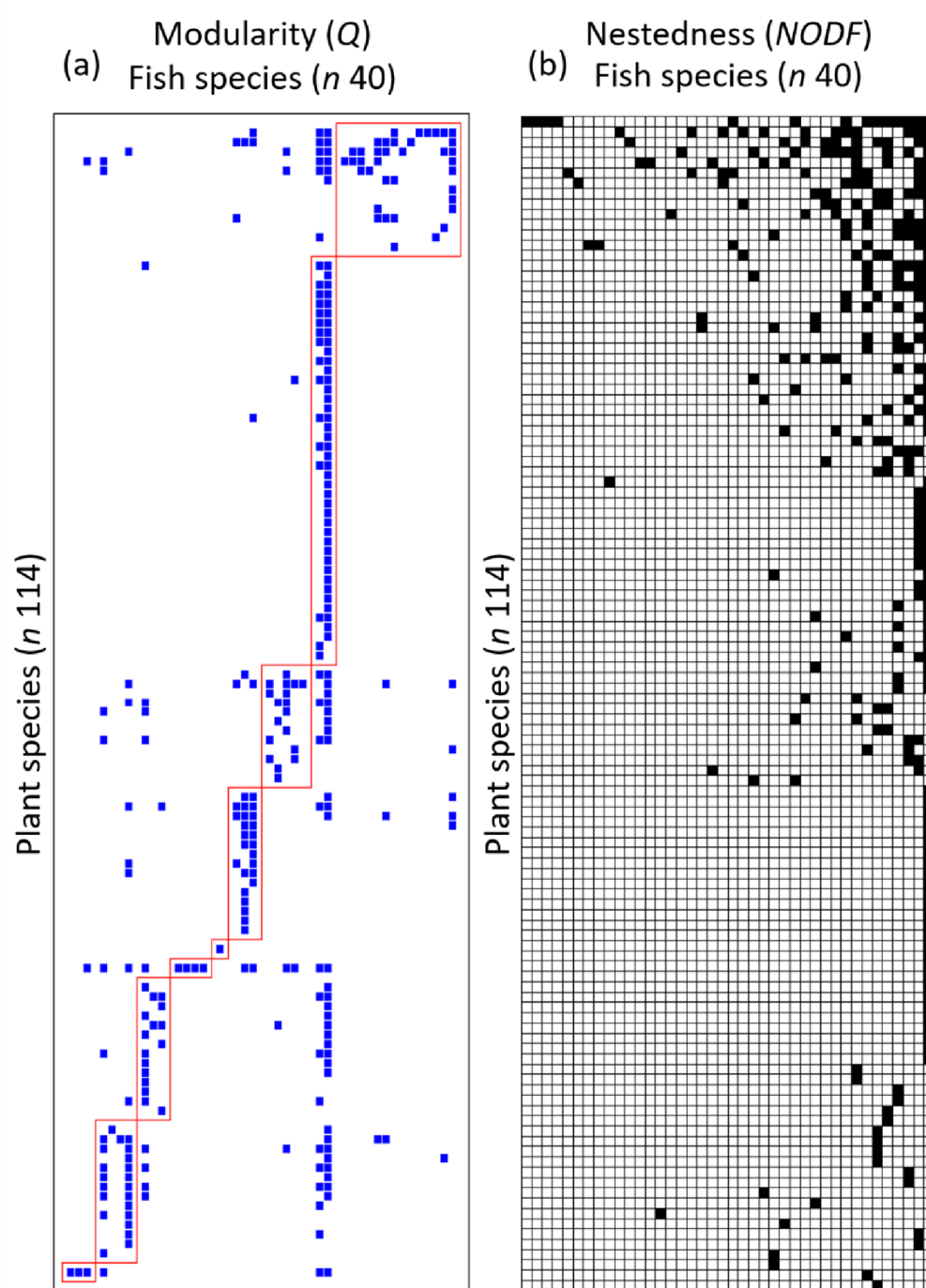


Figure 3: Structure of the ichthyochory network.

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 trees 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. Spatio-temporal 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 to 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).

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 1997). 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

et al. 2010a; 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 interactions 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 (Rodriguez et al. *in press*), 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 Serrasalminae, 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; Figueredo 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 1997), 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; Espinosa 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 et al. 2024b). 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 & Novo 2019), can lead to local extinction or severe reductions in the abundance of species along the flood gradient (Costello et al. 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.

References

- Abelha, M. C. F., Agostinho, A. A., Goulart, E. (2001). Plasticidade trófica em peixes de água doce. *Acta Scientiarum*, 23(2), 425–434. <https://doi.org/10.4025/actasciobiolsci.v23i0.2696>
- Albernaz, A. L., Pressey, R. L., Costa, L. R. F., Moreira, M. P., Ramos, J. F., Assunção, P. A., Franciscan, C. H. (2012). Tree species compositional change and conservation implications in the whitewater flooded forests of the Brazilian Amazon. *Journal of Biogeography*, 39(5), 869–883. <https://doi.org/10.1111/j.1365-2699.2011.02640.x>
- Almeida-Neto, M., Guimarães, P., Guimarães, P. R., Loyola, R. D., & Ulrich, W. (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., & Ulrich, W. (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, J. T., Saldaña Rojas, J., Flecker, A. S. (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>
- Anderson, E. P., Jenkins, C. N., Heilpern, S., Maldonado-Ocampo, J. A., Carvajal-Vallejos, F. M., Encalada, A. C., Rivadeneira, J. F., Hidalgo, M., Cañas, C. M., Ortega, H., Salcedo, N., Maldonado, M., Tedesco, P. A. (2018). Fragmentation of Andes-to-Amazon connectivity by hydropower dams. *Science Advances*, 4(1), eaao1642. <https://doi.org/10.1126/sciadv.aao1642>
- Arantes, C. C., Winemiller, K. O., Petrere, M., Castello, L., Hess, L. L., Freitas, C. E. C. (2018). Relationships between forest cover and fish diversity in the Amazon River floodplain. *J Appl Ecol.*, 55(1), 386–395. <https://doi.org/10.1111/1365-2664.12967>
- Arantes, C. C., Winemiller, K. O., Asher, A., Castello, L., Hess, L. L., Petrere, M., Freitas, C. E. C. (2019). Floodplain land cover affects biomass distribution of fish functional diversity in the Amazon River. *Sci Rep.*, 9(1), 16684. <https://doi.org/10.1038/s41598-019-52243-0>
- Araujo, J. M., Correa, S. B., Penha, J., Anderson, J., & Traveset, A. (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, Resende, A. F., Trumbore, S. E., Wittmann, F., Cintra, B. B. L., Batista, E. S. (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., Wittmann, F. (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. MCT-CNPq-Programa do Trópico Úmido, Sociedade Civil de Mamirauá, 3º ed., Belém.

- Bailly, D., Agostinho, A. A., Suzuki, H. I. (2008). Influence of the flood regime on the reproduction of fish species with different reproductive strategies in the Cuiabá River, Upper Pantanal, Brazil. *River Res Appl.*, 24(9), 1218–1229. <https://doi.org/10.1002/rra.1147>
- Barichivich, J., Gloor, E., Peylin, P., Brien, R. J. W., Schöngart, J., Espinoza, J. C., Pattnayak, K. C. (2018). Recent intensification of Amazon flooding extremes driven by strengthened Walker circulation. *Science Advances*, 4, eaat8785. <https://doi.org/10.1126/sciadv.aat8785>
- Barbosa, T. A. P., Montag, L. F. A. (2017). The role of *Lithodoras dorsalis* (Siluriformes: Doradidae) as seed disperser in Eastern Amazon. *Neotropical Ichthyology*, 15(2), e160061. <https://doi.org/10.1590/1982-0224-20160061>
- Barbosa, T. A. P., Rosa, D. C. O., Soares, B. E., Costa, C. H. A., Esposito, M. C., Montag, L. F. A. (2018). Effect of flood pulses on the trophic ecology of four piscivorous fishes from the eastern Amazon. *J Fish Biol.*, 93(1), 30–39. <https://doi.org/10.1111/jfb.13669>
- Bartel, S. L., Orrock, J. L. (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., & Jordano, P. (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>
- Boujard, T., Sabatier, D., Rojas-Beltrán, R., Prevost, M. F., Renno, J. F. (1990). The food habits of three allochthonous feeding characoids in French Guiana. *Rev. Ecol. (Terre Vie)*, 45, 247e258.
- Burgos, E., Ceva, H., Perazzo, R. P. J., Devoto, M., Medan, D., Zimmermann, M., & María Delbue, A. (2007). Why nestedness in mutualistic networks? *Journal of Theoretical Biology*, 249, 307–313. <https://doi.org/10.1016/j.jtbi.2007.07.030>
- Blondel, V. D., Guillaume, J. L., Lambiotte, R., Lefebvre, E. (2008). Fast un-folding of communities in large networks. *Journal of Statistical Mechanics: Theory and Experiment*, 2008, 10008. <https://doi.org/10.1088/1742-5468/2008/10/P10008>

Cardoso, D., Särkinen, T., Alexander, S., Amorim, A. M., Bittrich, V., Celis, M., Daly, D. C., Fiaschi, P., Funk, V. A., Giacomini, L. L., et al. (2017). Amazon plant diversity revealed by a taxonomically verified species list. *Proc. Natl. Acad. Sci. USA*, 114, 10695–10700. <https://doi.org/10.1073/pnas.1706756114>

Cattaneo, J. H., Anderson, A. B., Carvalho, M. S. (2002). Floristic composition and topographic variation in a tidal floodplain forest in the Amazon Estuary. *Revista Brasil. Bot.*, 25(4), 419–430.

Claro-Jr, L., Ferreira, E., Zuanon, J., Araujo-Lima, C. (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(1), 133–137. <https://doi.org/10.1590/s0044-59672004000100018>

Correa, S. B., Winemiller, K. O., Lopez-Fernandez, H., Galetti, M. (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). Texas A&M University, 167 p.

Correa, S. B., Costa-Pereira, R., Fleming, T., Goulding, M., Anderson, J. T. (2015). Neotropical fish–fruit interactions: eco-evolutionary dynamics and conservation. *Biological Reviews*, 90(4), 1263–1278. <https://doi.org/10.1111/brv.12153>

Correa, S. B., Araujo, J. K., Penha, J., Nunes da Cunha, C., Bobier, K. E., Anderson, J. T. (2016). Stability and generalization in seed dispersal networks: a case study of frugivorous fish in Neotropical wetlands. *Proceedings of the Royal Society B*, 283, 20161267. <http://doi.org/10.1098/rspb.2016.1267>

Correa, S. B., de Oliveira, P. C., Nunes da Cunha, C., Penha, J., Anderson, J. T. (2018). Water and fish select for fleshy fruits in tropical wetland forests. *Biotropica*, 50(2), 312–318. <https://doi.org/10.1111/btp.12524>

Correa, S. B., Van Der Sleen, P., Siddiqui, S. F., Bogotá-Gregory, J. D., Arantes, C. C., Barnett, A. A., Couto, T. B. A., Goulding, M., Anderson, E. P. (2022). Biotic Indicators for Ecological State Change in Amazonian Floodplains. *BioScience*, 72(8), 753–768. <https://doi.org/10.1093/biosci/biac038>

- Correa, S. B., Coronado-Franco, K. V., Jézéquel, C., Rodrigues, A. C. et al. (2025). Floodplain forests drive fruit-eating fish diversity at the Amazon Basin-scale. *Proceedings of the National Academy of Sciences*, 122(3), e2414416122. <https://doi.org/10.1073/pnas.2414416122>
- Costa, G., Piedade, M. T. F., Ferreira, E. J., Maltchik, L. (2023). The effectiveness of ichthyochoric dispersal in forested wetlands of the Amazon depends on the species of fish and its size. *For Ecol Manag.*, 549, 121481. <https://doi.org/10.1016/j.foreco.2023.121481>
- Costa, G., Weiss, B., Piedade, M. T. F. (2024a). Larger fish disperse larger seeds in oligotrophic wetlands of the central Amazon. *Wetlands*, 44, 18. <https://doi.org/10.1007/s13157-024-01779-7>.
- Costa, G., Weiss, B., Piedade, M. T. F., Ferreira, E. J., & Maltchik, L. (2024b). Structure and vulnerability of the ichthyochory network in wetland forests of Central Amazonia. *Ecology of Freshwater Fish*, 00, e12780. <https://doi.org/10.1111/eff.12780>
- Dagosta, F. C. P., De Pinna, M. (2019). The fishes of the Amazon: distribution and Biogeographical patterns, with a comprehensive list of species. *American Museum of Natural History*, New York. <https://doi.org/10.1206/0003-0090.431.1.1>
- Dáttilo, W., Fagundes, R., Gurka, C. A. Q., Silva, M. S. A., Vieira, M. C. L., Izzo, T. J., Díaz Castelazo, C., Del-Claro, K., Rico-Gray, V. (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., Strauss, R. (2014). A method for detecting modules in quantitative bipartite networks. *Methods in Ecology and Evolution*, 5, 90–98. <https://doi.org/10.1111/2041-210X.12139>
- Dormann, C. F., Fruend, J., Gruber, B., Beckett, S., Devoto, M., Gabriel, M. F. F., Iriondo, J. M., Opsahl, T., Pinheiro, R. B. P., Strauss, R., & Vázquez, D. P. (2022). Package ‘bipartite’ – Visualising Bipartite Networks and Calculating Some (Ecological) Indices. 181 p. <https://cran.r-project.org/web/packages/bipartite/bipartite.pdf>
- Duponchelle, F., Isaac, V. J., Da Costa Doria, C. R., Van Damme, P. A., Herrera-R, G. A., Anderson, E. P. 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., Jimenez, J. C., Marengo, J. A. 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., Fleischmann, A. S., Papa, F., Paiva, R. C. D., Wongchuig, S., Melack, J. M. et al. (2021). Amazon Hydrology From Space: Scientific Advances and Future Challenges. *Reviews of Geophysics*, 59 (4), e2020RG000728.
<https://doi.org/10.1029/2020RG000728>

Feeley, K. J. (2015). Are we filling the data void? An assessment of the amount and extent of plant collection records and census data available for tropical South America. *PLoS ONE*, 10, e0125629.

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., Parolin, P. (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.

Ferreira, L. V. (1998). Intraspecific variation in phenology in relation to flooding duration in *Eschweilera parviflora* (Lecythidaceae) in central Amazonian floodplain forest. *An. Acad. Bras. Ci.*, 70, 1–4.

Figueiredo, J., Hoorn, C., van der Ven, P., Soares, E. (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>

Fleischmann, A. S., Papa, F., Hamilton, S. K., Fassoni-Andrade, A., Wongchuig, S., Espinoza, J. et al. (2023). Increased floodplain inundation in the Amazon since 1980. *Environmental Research Letters*, 18(3), 34024. <https://doi.org/10.1088/1748-9326/acb9a7>

- Flecker, A. S., Shi, Q., Almeida, R. M., Angarita, H., Gomes-Selman, J. M., García-Villacorta, R. et al. (2022). Reducing adverse impacts of Amazon hydropower expansion. *Science*, 375(6582), 753–760. <https://doi.org/10.1126/science.abj4017>
- Fleming, T. H., Breitwisch, R., Whitesides, G. H. (1987). Patterns of tropical vertebrate frugivore diversity. *Annu. Rev. Ecol. Syst.*, 18, 91–109.
- Freitas, T. M. S., Almeida, V. H. C., Montag, L. F. A. (2018). Evidence of seed dispersal of *Virola surinamensis* (Myristicaceae) by a catfish in Eastern Amazonia, Brazil. *Bol. Mus. Para. Emílio Goeldi. Cienc. Nat.*, 13(2), 213–219.
- Goulding, M. (1980). The fishes and the forest: explorations in Amazonian natural history. University of California Press, Berkeley, California.
- Goulding, M. (1983). The role of fish in seed dispersal and plant distribution in Amazonian floodplains ecosystems. In: Kubitzki, K. (Ed.). Dispersal and Distribution (pp. 271–284). Hamburg: Verlag Paul Parey.
- Gottsberger, G. (1978). Seed dispersal by fish in the inundated regions of Humaitá, Amazonia. *Biotropica*, 10, 170–183.
- Haugaasen, T., Peres C. A. (2005a). Tree phenology in adjacent Amazonian flooded and unflooded forests. *Biotropica*, 37, 620–630.
- Hawes, J. E., Peres, C. A. (2016). Patterns of plant phenology in Amazonian seasonally flooded and unflooded forests. *Biotropica*, 48, 465–475.
- Herrera-R, G. A., Heilpern, S. A., Couto, T. B., Victoria-Lacy, L., Duponchelle, F., Correa, S. B., Farah-Pérez, A., López-Casas, S., Cañas-Alva, C. M., Doria, C. R., Anderson, E. P. 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>
- Hoorn, C., Guerrero, J., Sarmiento, G. A., Lorente, M. A. (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](https://doi.org/10.1130/0091-7613(1995)023<0237:ATAACF>2.3.CO;2)
- Honda, E. M. S. (1974). Contribuição ao conhecimento da biologia de peixes do Amazonas: II. Alimentação do tambaqui, *Colossoma bidens*. *Acta Amazonica*, 4, 47e53.

- Hopkins, M. J. G. (2007). Modelling the known and unknown plant biodiversity of the Amazon Basin. *J. Biogeogr.*, 34, 1400–1411. <https://doi.org/10.1111/j.1365-2699.2007.01737.x>
- Horn, M., Correa, S. B., Parolin, P., Pollux, B. J. A., Anderson, J. T., Lucas, C., Widmann, P., Tjiu, A., Galetti, M., Goulding, M. (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., Schöngart, J., Piedade, M. T. F., Junk, W. J. et al. (2021). Modeling the Ecological Responses of Tree Species to the Flood Pulse of the Amazon Negro River Floodplains. *Front. Ecol. Evol.*, 9, 628606. <https://doi.org/10.3389/fevo.2021.628606>
- Householder, J. E., Wittmann, F., Schöngart, J. et al. (2024). One sixth of Amazonian tree diversity is dependent on river floodplains. *Nat. Ecol. Evol.*, 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(3), 261–281. [https://doi.org/10.1016/0006-3207\(84\)90087-9](https://doi.org/10.1016/0006-3207(84)90087-9)
- Howe, H. F., Smallwood, J. (1982). Ecology of seed dispersal. *Ann. Rev. Ecol. Syst.*, 13, 201–228. <https://doi.org/10.1146/annurev.es.13.110182.001221>
- 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(1), 103–113. <https://doi.org/doi:10.1111/j.1095-8312.1983.tb01592.x>
- Jordano, P. (2000). Fruits and frugivory. In: Fenner, M. (Ed.). *Seeds: the Ecology of Regeneration in Plant Communities* (pp. 125–166). Wallingford: CABI Publ.
- Junk, W. J. (1980). Áreas inundáveis: um desafio para a limnologia. *Acta Amazonica*, 10(4), 775–796.
- Junk, W. J. (1989). Flood tolerance and tree distribution in central Amazonian floodplains. In: Holm-Nielsen, L. B., Nielsen, I. C., Balslev, H. (Eds.). *Tropical Forest: Botanical Dynamics, Speciation and Diversity* (pp. 47–64). New York: Academic Press.

Junk, W. J., Bayley, P. B., Sparks, R. E. (1989). The flood pulse concept in river floodplain systems. In: Dodge, D.P. (Ed.). Proceedings of the International Large River Symposium (pp. 110–127). Canadian Special Publication in Fisheries and Aquatic Sciences.

Junk, W. J., Piedade, M. T. F. (2010). An Introduction to South American Wetland Forests: Distribution, Definitions and General Characterization. In: Junk, W. J., Piedade, M. T. F., Wittmann, F., Schöngart, J., Parolin, P. (Eds.). Amazon floodplain forests: Ecophysiology, biodiversity and sustainable management (pp. 3–25). Ecological Studies 210, Berlin Heidelberg-New York: Springer Verlag.

Junk, W. J., Piedade, M. T. F., Schöngart, J., Cohn-Haft, M., Adeney, J. M., Wittmann, F., (2011). A classification of major naturally-occurring Amazonian lowland wetlands. *Wetlands*, 31, 623–640. <https://doi.org/10.1007/s13157-011-0190-7>

Kolmann, M. A., Hughes, L. C., Hernandez, L. P., Arcila, D., Betancur-R, R., Sabaj, M. H., López-Fernández, H., Ortí, G. (2021). Phylogenomics of piranhas and pacus (Serrasalminidae) uncovers how dietary convergence and parallelism obfuscate traditional morphological taxonomy. *Systematic Biology*, 70, 576–592. <https://doi.org/10.1093/sysbio/syaa065>

Kubitzki, K., Ziburski, A. (1994). Seed dispersal in floodplain forests of Amazonia. *Biotropica*, 26, 30–43. <https://doi.org/10.2307/2389108>

Kubitzki, K. (1985). The dispersal of forest plants. In: Prance, G. T., Lovejoy, T. E. (Eds.). Amazonia-Key Environments (pp. 129–163). Pergamon.

Knab-Vispo, C., Daza, F., Vispo, C. R., González, N. (2003). The diet of Morocoto (*Piaractus brachipomus*) in the lower Rio Caura in relation to its ecological role and its conservation. *Scientia Guianae*, 12, 367–391.

Latrubesse, E. M., Arima, E. Y., Dunne, T., Park, E., Baker, V. R., d’Horta, F. M., Wight, C., Wittmann, F., Zuanon, J., Baker, P. A., Ribas, C. C., Norgaard, R. B., Filizola, N., Ansar, A., Flyvbjerg, B., Stevaux, J. C. (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. Manaus, 77p.

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. Dissertação. Instituto Nacional de Pesquisas da Amazônia – INPA. Manaus, 82p.

Lobón-Cerviá, J., Hess, L. L., Melack, J. M., Araujo-Lima, C. A. R. M. (2015). The importance of forest cover for fish richness and abundance on the Amazon floodplain. *Hydrobiologia*, 750(1), 245–255. <https://doi.org/10.1007/s10750-014-2040-0>

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

Luize, B. G., Magalhães, J. L. L., Queiroz, H., Lopes, M. A., Venticinque, E. M., de Moraes Novo, E. M. L., Silva, T. S. F. (2018). The tree species pool of Amazonian wetland forests: Which species can assemble in periodically waterlogged habitats? *PLoS ONE*, 13, e0198130.

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.1744-7429.2008.00415.x>

Luque, F. J., Pinilla, G. A. (2019). Juveniles of the overexploited Amazonian fish *Colossoma macropomum* (Characiformes: Serrasalminae) as potential seed dispersers of *Cecropia* spp. *Revista de Biología Tropical*, 67, 654–666. <https://doi.org/10.15517/rbt.v67i3.34925>

Lundberg, J. G., Sabaj Pérez, M. H., Dahdul, W. M., Aguilera, O. A. (2010). The Amazonian Neogene fish fauna. In: Hoorn, C., Wesselingh, F. P. (Eds). *Amazonia: Landscape and Species Evolution: A look into the past* (pp. 281–301). Blackwell Publishing.

Lytle, D. A., Poff, N. L. (2004). Adaptation to natural flow regimes. *Trends in Ecology and Evolution*, 19, 94–100.

Maia, L. A., Chalco, F. P. (2002). Produção de frutos de espécies da floresta de Várzea da Amazônia Central importantes na alimentação de Peixes. *Acta Amazonica*, 32(1), 45–53. <https://doi.org/10.1590/1809-43922002321054>

Maia, L. A., Santos, L. M., Parolin, P. (2007). Germinação de sementes de *Bothriospora corymbosa* (Rubiaceae) recuperadas do trato digestório de *Triportheus angulatus* (sardinha) no

Lago Camaleão, Amazônia Central. *Acta Amazonica*, 37(3), 321–326.
<https://doi.org/10.1590/S0044-59672007000300002>

Mannheimer, S., Bevilacqua, G., Caramaschi, E. P., Scarano, F. R. (2003). Evidence for seed dispersal by the catfish *Auchenipterichthys longimanus* in an Amazonian lake. *J. Trop. Ecol.*, 19, 215–218. <https://doi.org/10.1017/S0266467403003249>

Mateus, L., Rodrigues Costa, R. M., & Penha, J. (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., Hess, L. L. (2010). Remote sensing of the distribution and extent of wetlands in the Amazon Basin. In: Junk, W. J., Piedade, M. T. F., Wittmann, F., Schöngart, J., Parolin, P. (Eds). Central amazonian floodplain forests: Ecophysiology, Biodiversity and Sustainable Management (pp. 43–59). London: Springer.

Mello, M. A. R., Marquitti, F. M. D., Guimarães, P. R., Jr., Kalko, E. K. V., Jordano, P., & Aguiar, M. A. M. (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., Marquitti, F. M. D., Guimarães, P. R., Jr., Kalko, E. K. V., Jordano, P., & De Aguiar, M. A. M. (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., Waser, N. M., & Price, M. V. (2004). Tolerance of pollination networks to species extinctions. *Proceedings of the Royal Society B*, 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. Manaus, 71p.

Parolin, P., Armbrüster, N., Wittmann, F., Ferreira, L. V., Piedade, M. T. F., Junk, W. J. (2002). A review of tree phenology in central Amazonian floodplains. *Botanica*, 52, 195–222.

- Parolin, P., Wittmann, F., Schöngart, J. (2010). Tree Phenology in Amazonian Floodplain Forests. In: Junk, W. J., Piedade, M. T. F., Wittmann, F., Schöngart, J., Parolin, P. (Eds.). Central Amazonian Floodplain Forests: Ecophysiology, Biodiversity and Sustainable Management (pp. 61–102). Berlin/Heidelberg/New York: Springer. https://doi.org/10.1007/978-90-481-8725-6_5
- Parolin, P., Wittmann, F., Ferreira, L.V. (2013). Fruit and seed dispersal in Amazonian floodplain trees – a review. *Ecotropica*, 19, 15–32.
- 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(1), 91–97.
- Pereira, D. P., Arantes, C. C., Sousa, K. N. S., Freitas, C. E. C. (2022). Relationships between fishery catch rates and land cover along a longitudinal gradient in floodplains of the Amazon River. *Fish Res.*, 258, 106521. <https://doi.org/10.1016/j.fishres.2022.106521>
- Pereyra, P. E. R., Hallwass, G., Begossi, A., Giacomini, L. L., Silvano, R. A. M. (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., Parolin, P., Junk, W. J. (2006). Phenology, fruit production and seed dispersal of *Astrocaryum jauari* (Arecaceae) in Amazonian blackwater floodplains. *Rev. Biol. Trop.*, 54, 1171–1178. <https://doi.org/10.15517/rbt.v54i4.3094>
- Pocock, M. J. O., Evans, D. M., Memmott, J. (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. *Philos. Trans. R. Soc. B Biol. Sci.*, 345, 89–99.
- Resende, A. F., Schöngart, J., Streher, A. S., Ferreira-Ferreira, J., Piedade, M. T. F., Silva, T. S. F. (2019). Massive tree mortality from flood pulse disturbances in Amazonian floodplain forests: The collateral effects of hydropower production. *Sci Total Environ.*, 659, 587–598. <https://doi.org/10.1016/j.scitotenv.2018.12.208>

- Rocha, M., Feitosa, Y. O., Wittmann, F., Piedade, M. T. F., Resende, A. F., Assis, R. L. (2020). River damming affects seedling communities of a floodplain forest in the Central Amazon. *Acta Bot Bras.*, 34(1), 192–203. <https://doi.org/10.1590/0102-33062019abb0263>
- Silva, J. A. M., Pereira-Filho, M., Oliveria-Pereira, M. I. (2003a). Frutos e sementes consumidos pelo Tambaqui, *Colossoma macropomum* (Cuvier, 1818) incorporados em rações. Digestibilidade e velocidade de trânsito pelo trato gastrointestinal. *R. Bras. Zootec.*, 32(6), 1815–1824. <https://doi.org/10.1590/S1516-35982003000800003>
- Silva, J. A. M., Pereira-Filho, M., Oliveria-Pereira, M. I. (2003b). Valor nutricional e energético de espécies vegetais importantes na alimentação do Tambaqui. *Acta Amazonica*, 33(4), 687–700. <https://doi.org/10.1590/S0044-59672003000400014>
- Silva, G. G., Pizo, M. A., Green, A. J., Sebastián-González, E., Bugoni, L., & Maltchik, L. (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>
- 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. Manaus, 84p.
- Schöngart, J., Piedade, M. T. F., Ludwigshausen, S., Horna, V., Worbes, M. (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., Junk, W. J. (2007). Forecasting the floodpulse in Central Amazonia by ENSO indices. *Journal of Hydrology*, 335, 124–132.
- Schöngart, J., Wittmann, F., Resende, A. F., Assahira, C., Lobo, G. S., Neves, J. R. D. et al. (2021). The shadow of the Balbina dam: A synthesis of over 35 years of downstream impacts on floodplain forests in Central Amazonia. *Aquat Conserv.*, 31(5), 1117–1135. <https://doi.org/10.1002/aqc.3526>
- Schleuning, M., Ingmann, L., Strauss, R., Fritz, S. A., Dalsgaard, B. O., Matthias Dehling, D., Plein, M., Saavedra, F., Sandel, B., Svenning, J., Böhning-Gaese, K., Dormann, C. F. (2014). Ecological, historical and evolutionary determinants of modularity in weighted seed-dispersal networks. *Ecology Letters*, 17(4), 454-463.

Timpe, K., Kaplan, D. (2017). The changing hydrology of a dammed Amazon. *Science Advances*, 3, e1700611. <https://doi.org/10.1126/sciadv.1700611>

Thompson, A. W., Betancur-R, R., López-Fernández, H., Ortí, G. (2014). A time-calibrated, multi-locus phylogeny of piranhas, pacus, and allies (Characiformes: Serrasalminidae) and a comparison of species tree methods. *Mol. Phylogenet. Evol.*, 81, 242–257. <https://doi.org/10.1016/j.ympev.2014.06.018>

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., Melián, C. J., Williams, N. M., Blüthgen, N., Krasnov, B. R., Poulin, R. (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>

Vázquez, D. P., Blüthgen, N., Cagnolo, L., Chacoff, N. P. (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>

Weiss, B., Zuanon, J. A. S., Piedade, M. T. F. (2016). Viability of seeds consumed by fishes in a lowland forest in the Brazilian Central Amazon. *Trop. Conserv. Sci.*, 9, 1–10. <https://doi.org/10.1177/1940082916676129>

Winemiller, K. O., McIntyre, P. B., Castello, L., Fluet-Chouinard, E., Giarrizzo, T., Nam, S. et al. (2016). Balancing hydropower and biodiversity in the Amazon, Congo, and Mekong. *Science*, 351(6269), 128–129. <https://doi.org/10.1126/science.aac7082>

Wittmann, F., Anhuaf, D., Junk, W. J. (2002). Tree species distribution and community structure of central Amazonian várzea forests by remote-sensing techniques. *J. Trop. Ecol.*, 8, 805–820. <https://doi.org/10.1017/S0266467402002523>

Wittmann, F., Junk, W. J., Piedade, M. T. F. (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., Schöngart, J., Montero, J. C., Motzer, M., Junk, W. J., Piedade, M. T. F., Queiroz, H. L., Worbes, M. (2006). Tree species composition and diversity gradients in white water forests across the Amazon Basin. *J. Biogeog.*, 33, 1334–1347. <https://doi.org/10.1111/j.1365-2699.2006.01495.x>

Wittmann, F., Schöngart, J., Queiroz, H. L., Wittmann, A. O., Conserva, A. S., Piedade, M. T. F., Kesselmeier, J., Junk, W. J. (2009). The Amazon floodplain Demonstration Site: Sustainable timber production and management of Central Amazonian white-water floodplains. *Ecohydrology & Hydrobiology*, 9(1), 41–54. <https://doi.org/doi:10.2478/v10104-009-0038-4>

Wittmann, F., Schöngart, J., Junk, W. J. (2010a). Phytogeography, species diversity, community structure and dynamics of central Amazonian floodplain forests. In: Junk, W. J., Piedade, M. T. F., Wittmann, F., Schöngart, J., Parolin, P. (Eds.). Central Amazonian Floodplain Forests: Ecophysiology, Biodiversity and Sustainable Management (pp. 61–102). Berlin/Heidelberg/New York: Springer.

Wittmann, A. de O., Parolin, P., Piedade, M. T. F., Junk, W. J., Guillaumet, J. L. (2010b). Manual of trees from Central Amazonian várzea floodplains: taxonomy, ecology and use / Manual de árvores de várzea da Amazônia Central: taxonomia, ecologia e uso. (F. Wittmann, J. Schöngart, J. M. de Brito, Eds.), Instituto Nacional de Pesquisas da Amazônia - INPA. Manaus, 286 p.

Wittmann, F., Householder, E., Piedade, M. T. F., de Assis, R. L., Schöngart, J., Parolin, P., Junk, W. J. (2012). Habitat specificity, endemism and the neotropical distribution of Amazonian white-water floodplain trees. *Ecography*, 36(6), 690–707. <https://doi.org/10.1111/j.1600-0587.2012.07723.x>

Wittmann, F., Householder, E., de Oliveira Wittmann, A., Lopes, A., Junk, W. J., Piedade, M. T. (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., Junk, W. J. (2016). The Amazon River basin. In: Finlayson, C. M., Milton, G. R., Prentice, R. C., Davidson, N. C. (Eds.). The Wetland Book II: Distribution, Description and Conservation (pp. 1–20). Berlin/Heidelberg, Germany; Springer.

Worbes, M. (1997). The forest ecosystem of the floodplains. In: Junk, W. J. (Ed). The central Amazon floodplain: ecology of a Pulsating system (pp. 223–266). Berlin: 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: Rauh, W. (Ed.). Tropische und subtropische Pflanzenwelt. Akademie der Wissenschaften und der Literatur (pp. 1–9).

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 et al. 2010b (12); Wittmann et al. 2012 (13); Our field collections (14).

Fish species*	Plant species*	LV**	HV**	*References	**References
<i>Colossoma macropomum</i>	<i>Duroia duckei</i>	X		Anderson et al. 2009	2, 12, 13
	<i>Bactris maraja</i>	X	X	Anderson et al. 2009	13
	<i>Leonia glycyarpa</i>	X	X	Anderson et al. 2009	13
	<i>Crateva tapia</i>	X		Our field collections	9, 10, 14
	<i>Garcinia brasiliensis</i>	X	X	Lucas 2008	2, 13, 14
	<i>Mouriri acutiflora</i>	X	X	Lucas 2008	2, 13
	<i>Cordia tetrandra</i>	X	X	Lucas 2008	13
	<i>Coccoloba ovata</i>	X		Lucas 2008	4, 13
	<i>Nectandra amazonum</i>	X		Lucas 2008	2, 8, 9, 10, 12, 13, 14
	<i>Simaba orinocensis</i>	X		Lucas 2008	5
	<i>Ficus insipida</i>	X		Lucas 2008	11
	<i>Vitex cymosa</i>	X		Lucas 2008	8, 9, 10, 13, 14
	<i>Senna reticulata</i>		X	Lucas 2008	6, 13, 14
	<i>Casearia aculeata</i>	X	X	Lucas 2008	1, 12, 13
	<i>Astrocaryum jauari</i>	X	X	Our field collections	12, 13, 14
	<i>Cecropia latiloba</i>	X		Our field collections	2, 8, 12, 13, 14
	<i>Cecropia membranacea</i>	X	X	Luque and Pinilla 2019	12, 13
	<i>Pseudobombax munguba</i>	X	X	Silva et al. 2003a	2, 8, 9, 10, 12, 13, 14
	<i>Hevea spruceana</i>	X	X	Silva et al. 2003a	2, 8, 10, 13, 14
	<i>Spondias mombin</i>		X	Silva et al. 2003b	13
	<i>Annona hypoglauca</i>	X	X	Silva et al. 2003b	2, 9, 12, 13

<i>Unonopsis matthewsii</i>	X	X	Silva et al. 2003b	13
<i>Bactris riparia</i>	X		Our field collections	12, 13, 14
<i>Euterpe precatoria</i>		X	Silva et al. 2003b	12
<i>Euterpe oleracea</i>	X	X	Silva et al. 2003b	10, 13
<i>Iriartella setigera</i>	X	X	Silva et al. 2003b	13
<i>Mauritia flexuosa</i>		X	Silva et al. 2003b	12, 13
<i>Maximiliana maripa</i>		X	Silva et al. 2003b	13
<i>Oenocarpus bacaba</i>		X	Silva et al. 2003b	13
<i>Ilex inundata</i>	X		Silva et al. 2003b	12, 13, 14
<i>Crescentia amazonica</i>	X		Silva et al. 2003b	8, 12, 13, 14
<i>Tabebuia barbata</i>	X		Silva et al. 2003b	2, 8, 9, 10, 12, 13, 14
<i>Sorocea duckei</i>	X		Silva et al. 2003b	2, 6, 12, 13, 14
<i>Licania apetala</i>	X	X	Silva et al. 2003b	12, 13
<i>Buchenavia macrophylla</i>	X		Silva et al. 2003b	13
<i>Hevea brasiliensis</i>		X	Our field collections	12, 13, 14
<i>Mabea caudata</i>	X	X	Silva et al. 2003b	1, 13
<i>Mabea nitida</i>	X	X	Silva et al. 2003b	2, 8, 9, 10, 12, 13
<i>Piranhea trifoliata</i>	X		Silva et al. 2003b	10, 12, 13, 14
<i>Ocotea cymbarum</i>		X	Silva et al. 2003b	2, 10, 12, 13
<i>Couroupita guianensis</i>		X	Silva et al. 2003b	13
<i>Eschweilera ovalifolia</i>	X		Silva et al. 2003b	6, 12, 13, 14
<i>Eschweilera parviflora</i>	X	X	Silva et al. 2003b	1
<i>Eschweilera tenuifolia</i>	X		Silva et al. 2003b	6
<i>Gustavia augusta</i>	X	X	Silva et al. 2003b	2, 6, 8, 9, 10, 12, 13, 14
<i>Macrolobium acaciifolium</i>	X		Silva et al. 2003b	6, 12, 13, 14
<i>Macrolobium multijugum</i>	X	X	Silva et al. 2003b	6, 13
<i>Mora paraensis</i>	X	X	Silva et al. 2003b	6, 13
<i>Cassia leiandra</i>	X		Silva et al. 2003b	12, 13
<i>Crudia amazonica</i>	X		Silva et al. 2003b	12, 13
<i>Swartzia laevicarpa</i>	X		Silva et al. 2003b	6
<i>Parkia discolor</i>	X		Silva et al. 2003b	6, 6
<i>Pithecellobium inaequale</i>	X		Silva et al. 2003b	6

	<i>Byrsonima amazonica</i>	X		Silva et al. 2003b	13
	<i>Carapa guianensis</i>	X	X	Silva et al. 2003b	13
	<i>Virola surinamensis</i>		X	Silva et al. 2003b	2, 12, 13
	<i>Eugenia lambertina</i>	X		Silva et al. 2003b	5, 7
	<i>Myrcia fallax</i>		X	Silva et al. 2003b	2
	<i>Myrciaria dubia</i>	X	X	Silva et al. 2003b	2, 12, 13, 14
	<i>Psidium acutangulum</i>	X		Silva et al. 2003b	2, 6, 8, 12, 13
	<i>Symmeria paniculata</i>	X		Silva et al. 2003b	4, 10, 12, 13, 14
	<i>Bothriospora corymbosa</i>	X		Silva et al. 2003b	12, 13
	<i>Duroia genipoides</i>	X		Silva et al. 2003b	2
	<i>Genipa americana</i>	X	X	Silva et al. 2003b	2, 4, 10, 12, 13, 14
	<i>Randia armata</i>		X	Silva et al. 2003b	13
	<i>Elaeoluma glabrescens</i>	X		Silva et al. 2003b	2, 13
	<i>Pouteria gomphiifolia</i>	X		Silva et al. 2003b	2, 13
	<i>Pouteria glomerata</i>	X		Silva et al. 2003b	6, 12, 13, 14
	<i>Simaba guianensis</i>	X	X	Silva et al. 2003b	13
	<i>Alchornea discolor</i>	X	X	Weiss et al. 2016	2, 12, 13, 14
	<i>Simaba multiflora</i>	X	X	Our field collections	12, 13
	<i>Eugenia inundata</i>	X		Lopes de Souza 2005	4, 6, 12
	<i>Alchornea schomburgkiana</i>	X		Goulding 1980	6
	<i>Margaritaria nobilis</i>		X	Pereyra et al. 2023	13
	<i>Handroanthus barbatus</i>	X		Pereyra et al. 2023	5
	<i>Pouteria elegans</i>	X	X	Pereyra et al. 2023	2, 9, 10, 12
	<i>Attalea maripa</i>		X	Pereyra et al. 2023	5
	<i>Couepia paraensis</i>	X		Pereyra et al. 2023	1, 2, 12, 13
<i>Brycon amazonicus</i>	<i>Nectandra amazonum</i>	X		Costa et al. 2024	2, 8, 9, 10, 12, 13, 14
	<i>Guatteria inundata</i>	X	X	Our field collections	2, 9, 12, 13
	<i>Bactris riparia</i>	X		Our field collections	12, 13, 14
	<i>Leptobalanus apetalus</i>	X	X	Our field collections	7
	<i>Bothriospora corymbosa</i>	X		Our field collections	12, 13
	<i>Micropholis guyanensis</i>		X	Our field collections	13
	<i>Cecropia latiloba</i>	X		Our field collections	2, 8, 12, 13, 14

	<i>Ficus insipida</i>	X		Weiss et al. 2016	11
	<i>Allophylus amazonicus</i>	X	X	Weiss et al. 2016	13
	<i>Vitex cymosa</i>	X		Weiss et al. 2016	8, 9, 10, 13, 14
	<i>Amaioua guianensis</i>		X	Correa et al. 2015	5
	<i>Cassia leiandra</i>	X		Maia and Chalco 2002	12, 13
	<i>Crescentia amazonica</i>	X		Maia and Chalco 2002	8, 12, 13, 14
<i>Trachelyopterus galeatus</i>	<i>Guatteria inundata</i>	X	X	Our field collections	2, 9, 12, 13
	<i>Pseudoxandra polyphleba</i>	X	X	Our field collections	8, 13, 14
	<i>Astrocaryum jauari</i>	X	X	Our field collections	12, 13, 14
	<i>Bactris riparia</i>	X		Our field collections	12, 13, 14
	<i>Ormosia excelsa</i>	X		Our field collections	6
	<i>Brosimum parinarioides</i>		X	Our field collections	13
	<i>Ficus amazonica</i>	X	X	Our field collections	12, 13, 14
	<i>Sorocea duckei</i>	X		Our field collections	2, 6, 12, 13, 14
	<i>Myrciaria dubia</i>	X	X	Our field collections	2, 12, 13, 14
	<i>Quiina rhytidopus</i>	X	X	Our field collections	2, 12, 13, 14
	<i>Alibertia edulis</i>	X	X	Our field collections	2, 12, 13
	<i>Bothriospora corymbosa</i>	X		Our field collections	12, 13
	<i>Cecropia latiloba</i>	X		Our field collections	2, 8, 12, 13, 14
	<i>Ficus insipida</i>	X		Weiss et al. 2016	11
	<i>Nectandra amazonum</i>	X		Weiss et al. 2016	2, 8, 9, 10, 12, 13, 14
<i>Pterodoras granulosus</i>	<i>Guatteria inundata</i>	X	X	Our field collections	2, 9, 12, 13
	<i>Pseudoxandra polyphleba</i>	X	X	Our field collections	8, 13, 14
	<i>Astrocaryum jauari</i>	X	X	Our field collections	12, 13, 14
	<i>Bactris riparia</i>	X		Our field collections	12, 13, 14
	<i>Protium strumosum</i>		X	Our field collections	12, 14
	<i>Combretum laxum</i>	X		Our field collections	3
	<i>Maprounea guianensis</i>	X	X	Our field collections	5, 6
	<i>Ormosia excelsa</i>	X		Our field collections	6
	<i>Myrciaria dubia</i>	X	X	Our field collections	2, 12, 13, 14
	<i>Minquartia guianensis</i>		X	Our field collections	1, 12, 13, 14
	<i>Quiina rhytidopus</i>	X	X	Our field collections	2, 12, 13, 14

	<i>Bothriospora corymbosa</i>	X		Our field collections	12, 13
	<i>Pouteria caimito</i>	X	X	Our field collections	12, 13
	<i>Crateva tapia</i>	X		Weiss et al. 2016	9, 10, 14
	<i>Ficus insipida</i>	X		Weiss et al. 2016	11
<i>Triportheus albus</i>	<i>Ficus amazonica</i>	X	X	Our field collections	12, 13, 14
	<i>Myrciaria dubia</i>	X	X	Our field collections	2, 12, 13, 14
	<i>Bothriospora corymbosa</i>	X		Our field collections	12, 13
	<i>Cecropia latiloba</i>	X		Our field collections	2, 8, 12, 13, 14
	<i>Ficus insipida</i>	X		Weiss et al. 2016	11
	<i>Laetia corymbulosa</i>	X		Weiss et al. 2016	2, 8, 9, 10, 12, 13, 14
<i>Mylossoma albiscopum</i>	<i>Ilex inundata</i>	X		Our field collections	12, 13, 14
	<i>Vitex cymosa</i>	X		Our field collections	8, 9, 10, 13, 14
	<i>Pseudobombax munguba</i>	X	X	Our field collections	2, 8, 9, 10, 12, 13, 14
	<i>Ficus amazonica</i>	X	X	Our field collections	12, 13, 14
	<i>Quiina rhytidopus</i>	X	X	Our field collections	2, 12, 13, 14
	<i>Cecropia latiloba</i>	X		Our field collections	2, 8, 12, 13, 14
	<i>Hevea brasiliensis</i>		X	Pereyra et al. 2023	12, 13, 14
	<i>Euterpe oleracea</i>	X	X	Pereyra et al. 2023	10, 13
	<i>Spondias mombin</i>		X	Pereyra et al. 2023	13
	<i>Anacardium giganteum</i>	X	X	Pereyra et al. 2023	13
	<i>Neea oppositifolia</i>	X	X	Pereyra et al. 2023	13
	<i>Pouteria elegans</i>	X	X	Pereyra et al. 2023	2, 9, 10, 12
	<i>Attalea maripa</i>		X	Pereyra et al. 2023	5
	<i>Astrocaryum jauari</i>	X	X	Pereyra et al. 2023	12, 13, 14
	<i>Hura crepitans</i>	X	X	Pereyra et al. 2023	1, 2, 12, 13
	<i>Symmeria paniculata</i>	X		Pereyra et al. 2023	4, 10, 12, 13, 14
	<i>Ficus maxima</i>		X	Pereyra et al. 2023	10, 13
	<i>Cordia scabrifolia</i>	X		Pereyra et al. 2023	13
	<i>Ceiba petandra</i>		X	Pereyra et al. 2023	4, 6
	<i>Myrciaria dubia</i>	X	X	Pereyra et al. 2023	2, 12, 13, 14
<i>Myloplus asterias</i>	<i>Ilex inundata</i>	X		Our field collections	12, 13, 14
	<i>Vitex cymosa</i>	X		Our field collections	8, 9, 10, 13, 14

	<i>Nectandra amazonum</i>	X		Our field collections	2, 8, 9, 10, 12, 13, 14
	<i>Amanoa oblongifolia</i>	X	X	Costa et al. 2024	13
<i>Chalceus erythrus</i>	<i>Bactris riparia</i>	X		Our field collections	12, 13, 14
	<i>Bothriospora corymbosa</i>	X		Our field collections	12, 13
	<i>Vitex cymosa</i>	X		Weiss et al. 2016	8, 9, 10, 13, 14
<i>Schizodon fasciatus</i>	<i>Cecropia latiloba</i>	X		Our field collections	2, 8, 12, 13, 14
<i>Leporinus fasciatus</i>	<i>Pseudobombax munguba</i>	X	X	Our field collections	2, 8, 9, 10, 12, 13, 14
<i>Auchenipterichthys longimanus</i>	<i>Virola surinamensis</i>		X	Freitas et al. 2018	2, 12, 13
	<i>Alchornea schomburgkiana</i>	X		Mannheimer et al. 2003	6
	<i>Myrciaria dubia</i>	X	X	Lima 2023	2, 12, 13, 14
	<i>Parkia discolor</i>	X		Lima 2023	5, 5
	<i>Gustavia augusta</i>	X	X	Lima 2023	2, 6, 8, 9, 10, 12, 13, 14
	<i>Oxandra riedeliana</i>	X		Noronha 2018	2, 8, 10, 12, 13
<i>Hemiodus immaculatus</i>	<i>Genipa spruceana</i>	X		Lopes de Souza 2005	6
	<i>Nectandra amazonum</i>	X		Lopes de Souza 2005	2, 8, 9, 10, 12, 13, 14
<i>Myloplus schomburgkii</i>	<i>Astrocaryum gynacanthum</i>	X	X	Costa et al. 2024	13
<i>Serrasalmus gouldingi</i>	<i>Nectandra amazonum</i>	X		Costa et al. 2024	2, 8, 9, 10, 12, 13, 14
<i>Serrasalmus rhombeus</i>	<i>Nectandra amazonum</i>	X		Costa et al. 2024	2, 8, 9, 10, 12, 13, 14
<i>Auchenipterus nuchalis</i>	<i>Ficus insipida</i>	X		Weiss et al. 2016	11
<i>Brycon melanopterus</i>	<i>Euterpe precatoria</i>		X	Correa et al. 2015	12
	<i>Apeiba membranacea</i>		X	Correa et al. 2015	9, 13
	<i>Amaioua guianensis</i>		X	Correa et al. 2015	5
	<i>Cecropia latiloba</i>	X		Correa et al. 2015	2, 8, 12, 13, 14
	<i>Astrocaryum jauari</i>	X	X	Piedade et al. 2006	12, 13, 14
<i>Calophysus macropterus</i>	<i>Vitex cymosa</i>	X		Weiss et al. 2016	8, 9, 10, 13, 14
<i>Pimelodus blochii</i>	<i>Alchornea discolor</i>	X	X	Weiss et al. 2016	2, 12, 13, 14
	<i>Ficus insipida</i>	X		Weiss et al. 2016	11
	<i>Ficus trigona</i>	X	X	Weiss et al. 2016	13
	<i>Laetia corymbulosa</i>	X		Weiss et al. 2016	2, 8, 9, 10, 12, 13, 14
	<i>Nectandra amazonum</i>	X		Weiss et al. 2016	2, 8, 9, 10, 12, 13, 14
<i>Triportheus angulatus</i>	<i>Alchornea discolor</i>	X	X	Weiss et al. 2016	2, 12, 13, 14
	<i>Ficus insipida</i>	X		Weiss et al. 2016	11

	<i>Laetia corymbulosa</i>	X		Weiss et al. 2016	2, 8, 9, 10, 12, 13, 14
	<i>Bothriospora corymbosa</i>	X		Maia et al. 2007	12, 13
	<i>Vitex cymosa</i>	X		Maia et al. 2007	8, 9, 10, 13, 14
	<i>Cecropia latiloba</i>	X		Maia et al. 2007	2, 8, 12, 13, 14
	<i>Pseudobombax munguba</i>	X	X	Maia et al. 2007	2, 8, 9, 10, 12, 13, 14
<i>Triportheus auritus</i>	<i>Allophylus amazonicus</i>	X		Weiss et al. 2016	13
	<i>Ficus insipida</i>	X		Weiss et al. 2016	11
	<i>Laetia corymbulosa</i>	X		Weiss et al. 2016	2, 8, 9, 10, 12, 13, 14
	<i>Pseudobombax munguba</i>	X	X	Claro-Jr. et al. 2004	2, 8, 9, 10, 12, 13, 14
	<i>Vitex cymosa</i>	X		Maia and Chalco 2002	8, 9, 10, 13, 14
	<i>Crescentia amazonica</i>	X		Maia and Chalco 2002	8, 12, 13, 14
<i>Piaractus brachypomus</i>	<i>Genipa spruceana</i>	X		Anderson et al. 2009	6
	<i>Crateva tapia</i>	X		Anderson et al. 2009	9, 10, 14
	<i>Garcinia brasiliensis</i>	X	X	Lucas 2008	2, 13, 14
	<i>Mouriri acutiflora</i>	X	X	Lucas 2008	2, 13
	<i>Cordia tetrandra</i>	X	X	Lucas 2008	13
	<i>Coccoloba ovata</i>	X		Lucas 2008	4, 13
	<i>Nectandra amazonum</i>	X		Lucas 2008	2, 8, 9, 10, 12, 13, 14
	<i>Simaba orinocensis</i>		X	Lucas 2008	6
	<i>Senna reticulata</i>		X	Lucas 2008	6, 13, 14
	<i>Casearia aculeata</i>	X	X	Lucas 2008	1, 12, 13
	<i>Astrocaryum jauari</i>	X	X	Lucas 2008	12, 13, 14
	<i>Ficus insipida</i>	X		Weiss et al. 2016	11
	<i>Myrciaria dubia</i>	X	X	Knab-Vispo et al. 2003	2, 12, 13, 14
	<i>Crescentia amazonica</i>	X		Knab-Vispo et al. 2003	8, 12, 13, 14
	<i>Spondias mombin</i>		X	Knab-Vispo et al. 2003	13
	<i>Bactris brongniartii</i>	X		Knab-Vispo et al. 2003	12, 13
	<i>Euterpe precatoria</i>		X	Knab-Vispo et al. 2003	12
	<i>Sorocea duckei</i>	X		Honda 1974	2, 6, 12, 13, 14
	<i>Simaba guianensis</i>	X	X	Honda 1974	13
	<i>Gustavia augusta</i>	X	X	Honda 1974	2, 6, 8, 9, 10, 12, 13, 14
	<i>Hevea brasiliensis</i>		X	Honda 1974	12, 13, 14

	<i>Hevea spruceana</i>	X	X	Honda 1974	2, 8, 10, 13, 14
	<i>Mabea caudata</i>	X	X	Honda 1974	1, 13
	<i>Vitex cymosa</i>	X		Honda 1974	8, 9, 10, 13, 14
	<i>Piranhea trifoliata</i>	X		Goulding 1980	10, 12, 13, 14
	<i>Cassia leiandra</i>	X		Maia and Chalco 2002	12, 13
	<i>Macrolobium acaciifolium</i>	X		Maia and Chalco 2002	6, 12, 13, 14
	<i>Margaritaria nobilis</i>		X	Pereyra et al. 2023	13
	<i>Euterpe oleracea</i>	X	X	Pereyra et al. 2023	10, 13
	<i>Anacardium giganteum</i>	X	X	Pereyra et al. 2023	13
	<i>Ficus maxima</i>		X	Pereyra et al. 2023	10, 13
	<i>Pouteria elegans</i>	X	X	Pereyra et al. 2023	2, 9, 10, 13
	<i>Genipa americana</i>	X	X	Pereyra et al. 2023	2, 4, 10, 12, 13, 14
	<i>Bactris maraja</i>	X	X	Pereyra et al. 2023	13
	<i>Cordia scabrifolia</i>	X		Pereyra et al. 2023	13
	<i>Himatanthus articulatus</i>	X		Pereyra et al. 2023	5
<i>Lithodoras dorsalis</i>	<i>Cecropia latiloba</i>	X		Kubitzki and Ziburski 1994	2, 8, 12, 13, 14
	<i>Psidium acutangulum</i>	X		Kubitzki and Ziburski 1994	2, 6, 8, 12, 13
	<i>Astrocaryum jauari</i>	X	X	Kubitzki and Ziburski 1994	12, 13, 14
	<i>Crateva tapia</i>	X		Kubitzki and Ziburski 1994	9, 10, 14
	<i>Annona hypoglauca</i>	X	X	Kubitzki and Ziburski 1994	2, 9, 12, 13
	<i>Vitex cymosa</i>	X		Kubitzki and Ziburski 1994	8, 9, 10, 13, 14
	<i>Euterpe oleracea</i>	X	X	Barbosa and Montag 2017	10, 13
	<i>Mauritia flexuosa</i>		X	Barbosa and Montag 2017	12, 13
	<i>Spondias mombin</i>		X	Barbosa and Montag 2017	13
	<i>Cassia leiandra</i>	X		Maia and Chalco 2002	12, 13
<i>Myloplus rubripinnis</i>	<i>Duroia duckei</i>	X		Lopes de Souza 2005	2, 12, 13
<i>Myloplus rhomboidalis</i>	<i>Euterpe oleracea</i>	X	X	Boujard et al. 1990	10, 13
	<i>Diospyros guianensis</i>	X	X	Boujard et al. 1990	2, 13
	<i>Oenocarpus bacaba</i>		X	Boujard et al. 1990	13
	<i>Crudia oblonga</i>	X	X	Boujard et al. 1990	13
	<i>Virola surinamensis</i>		X	Boujard et al. 1990	2, 12, 13
<i>Myloplus torquatus</i>	<i>Annona hypoglauca</i>	X	X	Correa et al. 2015	2, 9, 12, 13

	<i>Apeiba membranacea</i>		X	Correa et al. 2015	9, 13
	<i>Cecropia latiloba</i>	X		Correa et al. 2015	2, 8, 12, 13, 14
	<i>Genipa americana</i>	X	X	Correa et al. 2015	2, 4, 10, 12, 13, 14
<i>Leporinus friderici</i>	<i>Gustavia augusta</i>	X	X	Boujard et al. 1990	2, 6, 8, 9, 10, 12, 13, 14
	<i>Virola surinamensis</i>		X	Boujard et al. 1990	2, 12, 13
<i>Phractocephalus hemioliopus</i>	<i>Macrobium acaciifolium</i>	X		Maia and Chalco 2002	6, 12, 13
	<i>Crescentia amazonica</i>	X		Maia and Chalco 2002	8, 12, 13, 14
	<i>Astrocaryum jauari</i>	X	X	Piedade et al. 2006	12, 13, 14
<i>Serrasalmus</i> sp.	<i>Macrobium acaciifolium</i>	X		Maia and Chalco 2002	6, 12, 13, 14
<i>Pygocentrus</i> sp.	<i>Macrobium acaciifolium</i>	X		Maia and Chalco 2002	6, 12, 13, 14
<i>Megalodoras</i> sp.	<i>Cassia leiandra</i>	X		Maia and Chalco 2002	12, 13
<i>Myloplus</i> sp.	<i>Cassia leiandra</i>	X		Maia and Chalco 2002	12, 13
	<i>Crescentia amazonica</i>	X		Maia and Chalco 2002	8, 12, 13, 14
	<i>Macrobium acaciifolium</i>	X		Pereyra et al. 2023	6, 12, 13
	<i>Mauritia flexuosa</i>		X	Pereyra et al. 2023	12, 13
	<i>Spondias mombin</i>		X	Pereyra et al. 2023	13
	<i>Symmeria paniculata</i>	X		Pereyra et al. 2023	4, 10, 12, 13, 14
	<i>Margaritaria nobilis</i>		X	Pereyra et al. 2023	13
	<i>Neea oppositifolia</i>	X	X	Pereyra et al. 2023	13
	<i>Pouteria elegans</i>	X	X	Pereyra et al. 2023	2, 9, 10, 13
	<i>Attalea maripa</i>		X	Pereyra et al. 2023	5
	<i>Calophyllum brasiliense</i>	X	X	Pereyra et al. 2023	2, 6, 10, 12, 13
	<i>Astrocaryum jauari</i>	X	X	Pereyra et al. 2023	12, 13, 14
	<i>Genipa americana</i>	X	X	Pereyra et al. 2023	2, 4, 10, 12, 13, 14
	<i>Pseudobombax munguba</i>	X	X	Pereyra et al. 2023	2, 8, 9, 10, 12, 13, 14
	<i>Hevea brasiliensis</i>		X	Pereyra et al. 2023	12, 13, 14
<i>Metynnis</i> sp.	<i>Cassia leiandra</i>	X		Maia and Chalco 2002	12, 13
	<i>Vitex cymosa</i>	X		Maia and Chalco 2002	8, 9, 10, 13, 14
	<i>Crescentia amazonica</i>	X		Maia and Chalco 2002	8, 12, 13, 14
<i>Mylesinus</i> sp.	<i>Vitex cymosa</i>	X		Maia and Chalco 2002	8, 9, 10, 13, 14
	<i>Crescentia amazonica</i>	X		Maia and Chalco 2002	8, 12, 13, 14
<i>Mylossoma</i> sp.	<i>Crescentia amazonica</i>	X		Maia and Chalco 2002	8, 12, 13, 14

Zungaro zungaro	<i>Astrocaryum jauari</i>	X	X	Piedade et al. 2006	12, 13, 14
Rhamdia schomburgkii	<i>Astrocaryum jauari</i>	X	X	Piedade et al. 2006	12, 13, 14
Megalodoras uranoscopus	<i>Astrocaryum jauari</i>	X	X	Piedade et al. 2006	12, 13, 14
Oxydoras niger	<i>Astrocaryum jauari</i>	X	X	Piedade et al. 2006	12, 13, 14
Brycon sp.	<i>Pouteria glomerata</i>	X		Pereyra et al. 2023	6, 12, 13, 14
	<i>Euterpe oleracea</i>	X	X	Pereyra et al. 2023	10, 13
	<i>Carapa guianensis</i>	X	X	Pereyra et al. 2023	13
	<i>Mauritia flexuosa</i>		X	Pereyra et al. 2023	12, 13
	<i>Spondias mombin</i>		X	Pereyra et al. 2023	13
	<i>Handroanthus barbatus</i>	X		Pereyra et al. 2023	5
	<i>Mauritiella armata</i>		X	Pereyra et al. 2023	7
	<i>Margaritaria nobilis</i>		X	Pereyra et al. 2023	13
	<i>Eschweilera tenuifolia</i>	X		Pereyra et al. 2023	6
	<i>Pouteria elegans</i>	X	X	Pereyra et al. 2023	2, 9, 10, 13
	<i>Attalea maripa</i>		X	Pereyra et al. 2023	5
	<i>Astrocaryum jauari</i>	X	X	Pereyra et al. 2023	12, 13, 14
	<i>Genipa americana</i>	X	X	Pereyra et al. 2023	2, 4, 10, 12, 13, 14
	<i>Bactris maraja</i>	X	X	Pereyra et al. 2023	13
	<i>Handroanthus serratifolius</i>	X		Pereyra et al. 2023	5
	<i>Couepia paraensis</i>	X		Pereyra et al. 2023	2, 13
	<i>Hevea brasiliensis</i>		X	Pereyra et al. 2023	12, 13, 14
	<i>Cordia scabrifolia</i>	X		Pereyra et al. 2023	13

CONSIDERAÇÕES FINAIS E PERSPECTIVAS

Nesta Tese, investigamos alguns fatores que podem influenciar a dispersão de sementes pelos peixes (ictiochoria) em florestas de várzea da Amazônia Central, incluindo a viabilidade e velocidade de germinação das sementes após passagem pelo trato digestório dos peixes e a relação entre o tamanho dos peixes e o tamanho das sementes encontradas nos seus tratos digestórios (capítulo 1); a estrutura e vulnerabilidade (modularidade, aninhamento, especialização e robustez) da rede de dispersão de sementes (capítulo 2); e a influência do gradiente de inundação (várzea baixa e várzea alta) na dispersão de sementes pelos peixes e na estrutura da rede de dispersão (capítulo 3). Para alcançar esses objetivos, realizamos coletas de peixes e plantas (inventário florístico) em campo e complementamos essas informações com dados obtidos da literatura científica, tanto para peixes consumidores de sementes, quanto para espécies arbóreas de florestas de várzea da Amazônia.

Finalizamos esta Tese com algumas perspectivas para futuros estudos relacionados às interações entre peixes e plantas em áreas alagáveis da Amazônia:

No primeiro capítulo, investigamos a efetividade da dispersão de sementes pelos peixes, onde encontramos que o comprimento e o peso dos peixes frugívoros estavam positivamente relacionados ao tamanho das sementes no trato digestório, ou seja, peixes maiores possuem uma maior efetividade em dispersar sementes de maior tamanho. Esse é um importante resultado, porque indica que a remoção de peixes de maior porte dos ecossistemas poderá ter consequências para a dispersão das sementes de algumas espécies de árvores das várzeas amazônicas, e podem servir de base para estratégias de manejo e planos de conservação dessas espécies. Quanto à passagem das sementes das diferentes espécies de plantas pelo trato digestório dos peixes, não observamos aumento significativo na velocidade de germinação. Contudo, destacamos a importância dos estudos de viabilidade e germinação para se avaliar a efetividade da dispersão, principalmente quando associados a outros métodos para se determinar a viabilidade, como os testes com tetrazólio (WEISS *et al.*, 2023), fornecendo informações mais precisas sobre a efetividade da dispersão.

No segundo capítulo, avaliamos a estrutura e vulnerabilidade (modularidade, aninhamento, especialização e robustez) da rede de dispersão de sementes, onde observamos um padrão aninhado e modular. Estudos sobre redes ecológicas são especialmente suscetíveis a efeitos de amostragem (NIELSEN & BASCOMPTE, 2007), onde tanto o número e o tamanho dos módulos quanto o aninhamento aumentam com o número de espécies (BASCOMPTE *et*

al., 2003; OLESEN *et al.*, 2007). Considerando que o padrão de distribuição de riqueza e abundância de peixes frugívoros pode variar consideravelmente entre as diferentes sub-bacias amazônicas (CORREA *et al.*, 2025), estimativas robustas do número real de interações em redes ecológicas diversificadas exigem um esforço de amostragem adequado (JORDANO, 2016). Por isso, futuros estudos devem considerar a influência do esforço amostral e a possibilidade de amostragem em florestas alagáveis de rios com diferentes tipologias de água (águas brancas, pretas e claras) e em diferentes anos, pois no caso das florestas alagáveis, existem espécies que não produzem frutos anualmente (AYRES, 1993; GRIBEL *et al.*, 1999; PAROLIN *et al.*, 2010), sendo necessários estudos de longo prazo para se compreender de forma mais realista a dimensão das redes de ictiocoria em áreas alagáveis. Embora o inventário completo de interações seja provavelmente impossível, uma caracterização robusta de seus principais padrões e métricas é provavelmente realista (JORDANO, 2016).

No terceiro capítulo, avaliamos o consumo de frutos por peixes e o potencial de dispersão de sementes ao longo do gradiente de inundação (várzea baixa e várzea alta), e verificamos que a riqueza de espécies de frutos e sementes consumidos pelos peixes foi significativamente maior na floresta várzea baixa, quando consideradas apenas as espécies de árvores com distribuição restrita a cada gradiente. Ao considerarmos a grande quantidade de usinas hidrelétricas em operação ou em planejamento na região amazônica (FLECKER *et al.*, 2022), que tem o potencial de afetar os regimes de inundação a jusante e, consequentemente as florestas alagáveis ao longo dos gradientes (ASSAHIRA *et al.*, 2017; RESENDE *et al.*, 2019; ROCHA *et al.*, 2020), recomendamos que futuros estudos sobre dispersão de sementes sejam realizados antes e após a implantação desses empreendimentos, levando em consideração seus potenciais efeitos na estrutura das redes de dispersão de sementes por peixes. De forma semelhante, entender como as mudanças climáticas, que têm causado eventos de secas e cheias extremas na bacia amazônica (SCHÖNGART *et al.*, 2024), afetam as florestas alagáveis ao longo do gradiente de inundação será de grande relevância para se compreender seus efeitos sobre a ictiocoria.

Referências

ASSAHIRA, C.; RESENDE, A. F.; TRUMBORE, S. E.; WITTMANN, F.; CINTRA, B. B. L.; BATISTA, E. S. Tree mortality of a flood-adapted species in response of hydrographic changes caused by na Amazonian river dam. **Forest Ecology and Management**, v. 396, p. 113–123, 2017.

AYRES J. M. As matas de várzea do Mamirauá. In: Sociedade civil Mamirauá (Ed) Estudos de Mamirauá. Sociedade civil Mamirauá, Mamirauá, v. 1, pp. 1–123, 1993.

BASCOMPTE, J.; JORDANO, P.; MELIAN, C. J.; OLESEN, J. M. The nested assembly of plant animal mutualistic networks. **Proceedings of the National Academy of Sciences of the United States of America**, v. 100, p. 9383–9387, 2003.

CORREA, S. B.; CORONADO-FRANCO, K. V.; JÉZÉQUEL, C.; RODRIGUES, A. C. et al. Floodplain forests drive fruit-eating fish diversity at the Amazon Basin-scale. **Proceedings of the National Academy of Sciences**, v. 122, n. 3, p. e2414416122, 2025.

FLECKER, A. S.; SHI, Q.; ALMEIDA, R. M.; ANGARITA, H.; GOMES-SELMAN, J. M.; GARCÍA-VILLACORTA, R. *et al.* Reducing adverse impacts of Amazon hydropower expansion. **Science**, v. 375, n. 6582, p. 753–60, 2022.

GRIBEL, R; GIBBS, P. E., QUEIRÓZ, A. L. Flowering phenology and pollination biology of *Ceiba pentandra* in Central Amazonia. **Journal of Tropical Ecology**, v. 15, n. 3, p. 247–263, 1999.

JORDANO, P. Sampling networks of ecological interactions. **Functional Ecology**, v. 30, n. 12, p. 1883–1893, 2016.

NIELSEN, A.; BASCOMPTE, J. Ecological networks, nestedness and sampling effort. **Journal of Ecology**, v. 95, p. 1134–1141, 2007.

OLESEN, J. M.; BASCOMPTE, J.; DUPONT, Y. L.; JORDANO, P. The modularity of pollination networks. **Proceedings of the National Academy of Sciences**, v. 104, p. 19891–19896, 2007.

PAROLIN, P.; WITTMANN, F.; SCHÖNGART, J. Tree Phenology in Amazonian Floodplain Forests. In: JUNK, W. J.; PIEDADE, M. T. F.; WITTMANN, F.; SCHÖNGART, J.; PAROLIN, P. (Eds.). Central Amazonian Floodplain Forests: Ecophysiology, Biodiversity and Sustainable Management. Berlin/Heidelberg/New York: Springer, pp. 61–102, 2010.

RESENDE, A. F.; SCHÖNGART, J.; STREHER, A. S.; FERREIRA-FERREIRA, J.; PIEDADE, M. T. F.; SILVA, T. S. F. Massive tree mortality from flood pulse disturbances in

Amazonian floodplain forests: The collateral effects of hydropower production. **Science of the Total Environment**, v. 659, p. 587–598, 2019.

ROCHA, M.; FEITOSA, Y. O.; WITTMANN, F.; PIEDADE, M. T. F.; RESENDE, A. F.; ASSIS, R. L. River damming affects seedling communities of a floodplain forest in the Central Amazon. **Acta Botanica Brasilica**, v. 34, n. 1, p. 192–203, 2020.

SCHÖNGART, J.; WITTMANN, F.; JUNK, W. J.; LOPES, A.; DEMARCHI, L. O.; MORI, G. B., RESENDE, A. F. *et al.* Fate of Floodplain Forests in a Changing Amazon. In: DE SOUZA, S. S.; BRAZ-MOTA, S.; VAL, A. L. (Eds). *The Future of Amazonian Aquatic Biota*. Cham: Springer, pp. 163–222, 2024.

WEISS, B.; SANTANA, F. D.; PETENE, C. G.; COSTA, G.; ZUANON, J.; PIEDADE, M. T. F. Effectiveness of fish assemblage as seed dispersers in Amazon oligotrophic flooded forests. **Austral Ecology**, v. 00, p. 1–18, 2023.

ANEXOS

Anexo 1. Outras publicações realizadas durante o doutorado (2021–2025).

Artigos

Schöngart, J., Wittmann, F., Faria de Resende, A., Assahira, C., Lobo, G. S., Neves, J. R. D., **Costa, G. S.**, 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 Conserv: Mar Freshw Ecosyst.*, 1–19. <https://doi.org/10.1002/aqc.3526>

Weiss, B. A., **Costa, G. S.**, Correa, S. B., Zuanon, J. A. S. & Piedade, M. T. F. 2022. Does the consumption of pioneer-tree seeds from flooded forests by freshwater sardines affect seed germination? *Acta Oecologica*, 117(11), 103850. <https://doi.org/10.1016/j.actao.2022.103850>

Weiss, B., Santana, F. D., Petene, C. G., **Costa, G.**, Zuanon, J., Piedade, M. T. F. 2023. Effectiveness of fish assemblage as seed dispersers in Amazon oligotrophic flooded forests. *Austral Ecology*, 00, 1–18. <https://doi.org/10.1111/aec.13330>

Costa, G., Weiss, B., & Piedade, M. T. F. 2024. Larger fish disperse larger seeds in oligotrophic wetlands of the central Amazon. *Wetlands*, 44, 18. <https://doi.org/10.1007/s13157-024-01779-7>

Costa, G., Weiss, B., Piedade, M. T. F. 2024. Responses of trophic fish guilds upstream and downstream of the Balbina dam, Central Amazon, Northern Brazil. *Neotropical Ichthyology*, 22(2), e230009. <https://doi.org/10.1590/1982-0224-2023-0009>

Veiga, J. B., Piedade, M. T. F., Franco, A. C., **Costa, G. S.**, Ferreira, C. S. 2024. Prolonged seed submersion influences germination and early seedling growth of Amazonian floodplain trees. *Seed Science Research*, 1–8. <https://doi.org/10.1017/S0960258524000138>

Weiss, B., Costa, F., Santana, F., Klein, V. P., Lopes, A., **Costa, G.**, Schöngart, J., Wittmann, F., Durgante, F., Zuanon, J., Piedade, M. T. F. 2025. Fish Assemblage Characteristics and Allochthonous Food Resources Shape the Topology of Trophic Networks in Blackwater Floodplain Forests. *Wetlands*, 45, 1–14. <https://doi.org/10.1007/s13157-025-01937-5>

Capítulo

Schöngart, J., Wittmann, F., Junk, W. J., Lopes, A., Demarchi, L. O., Mori, G. B., Resende, A. F., Durgante, F. M., Quaresma, A. C., Householder, J. E., **Costa, G.** et al. 2024. Fate of Floodplain Forests in a Changing Amazon. In: Souza, S. S., Braz-Mota, S., Val, A. L. (Eds.), The Future of Amazonian Aquatic Biota. *Springer*, pp. 590. <https://doi.org/10.1007/978-3-031-66822-7>

Anexo 2. Autorização para coletas.

12/07/2022 10:59

SEI/MCTI - 10157078 - Parecer Técnico



MINISTÉRIO DA
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INSTITUTO NACIONAL DE PESQUISAS DA AMAZÔNIA PARECER TÉCNICO Nº 67/2022/SEI-INPA

PARECER CONSUBSTANCIADO E CERTIFICADO SOBRE PROTOCOLOS DE PESQUISAS NO USO DE ANIMAIS

CERTIFICADO DE APROVAÇÃO

Certificamos que a proposta intitulada "Influência do gradiente de inundação na dispersão de sementes e nicho trófico de peixes

frugívoros em áreas de várzea, Amazônia Central", registrada com o SEI 01280.000828/2022-45, sob a responsabilidade de Gilvan da Silva Costa - que envolve a produção, manutenção ou utilização de animais pertencentes ao *filo Chordata*, *subfilo Vertebrata* (exceto humanos), para fins de pesquisa científica (ou ensino) - encontra-se de acordo com os preceitos da Lei Nº 11.794, de 8 de outubro de 2008, do Decreto nº 6.899, de 15 de julho de 2009, e com as normas editadas pelo Conselho Nacional de Controle de Experimentação Animal (CONCEA), e foi APROVADA pela COMISSÃO DE ÉTICA NO USO DE ANIMAIS (CEUA) do INSTITUTO NACIONAL DE PESQUISAS DA AMAZÔNIA - INPA, em reunião de 30/06/2022.

Finalidade	() Ensino (X) Pesquisa Científica
Vigência da autorização:	Início: 05/09/2022 a Final: 28/07/2023
Espécie/linhagem/raça:	Leporinus sp. Brycon sp. Myloplus sp. Triportheus sp
Número de animais:	25 de cada espécie/ total 100 animais
Peso/Idade:	
Sexo:	
Origem:	Ilha da Paciência, rio Solimões, Estado do Amazonas

Raimunda Liege Souza de Abreu -Presidente CEUA-INPA - PO 115/2022



Documento assinado eletronicamente por Raimunda Liege Souza de Abreu, Pesquisador(a) em Ciência e Tecnologia, em 11/07/2022, às 18:56 (horário oficial de Brasília), com fundamento no § 3º do art. 4º do [Decreto nº 10.543, de 13 de novembro de 2020](#).



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