INSTITUTO NACIONAL DE PESQUISAS DA AMAZÔNIA - INPA

PROGRAMA DE PÓS-GRADUAÇÃO EM ECOLOGIA

EFEITO DO PULSO DE INUNDAÇÃO NA ASSEMBLEIA DE FORMIGAS EM ILHAS
FLUVIAIS DA AMAZÔNIA

Carolina Veronese Corrêa da Silva

Manaus

Agosto, 2022

Carolina Veronese Corrêa da Silva

EFEITO DO PULSO DE INUNDAÇÃO NA ASSEMBLEIA DE FORMIGAS EM ILHAS
FLUVIAIS DA AMAZÔNIA

Orientador: Fabricio Beggiato Baccaro

Coorientador: Sérgio Henrique Borges

Dissertação apresentada ao Instituto Nacional de Pesquisas da Amazônia como parte dos requisitos para obtenção do título de Mestre em Biologia (Ecologia).

Manaus, 2022

PG·ECO·INPA
PÓS-GRADUAÇÃO EM ECOLOGIA

INPA
INSTITUTO NACIONAL DE
PESQUISAS DA AMAZÔNIA
UNIDADE DE PESQUISA DO MCTIC

MINISTÉRIO DA
CIÊNCIA, TECNOLOGIA
E INOVAÇÕES

PÁTRIA AMADA BRASIL
GOVERNO FEDERAL

PROGRAMA DE PÓS-GRADUAÇÃO EM ECOLOGIA

ATA DA DEFESA PÚBLICA DA DISSERTAÇÃO DE MESTRADO DO PROGRAMA DE PÓS-GRADUAÇÃO EM ECOLOGIA DO INSTITUTO NACIONAL DE PESQUISAS DA AMAZÔNIA.

Aos 02 dias do mês de Agosto do ano de 2022, às 09h00min, por videoconferência. Reuniu-se a Comissão Examinadora de Defesa Pública, composta pelos seguintes membros: a Dra. **Cintia Cornelius Frische**, da Universidade Federal do Amazonas – UFAM, a Dra. **Juliana Hipólito de Sousa**, da Universidade Federal da Bahia – UFBA e o Dr. **Thiago Junqueira Izzo**, da Universidade Federal de Mato Grosso – UFMT, tendo como suplentes o Dr. Igor Luís Kaefer, da Universidade Federal do Amazonas – UFAM e Dr. Jorge Luiz P. de Souza, do Instituto Nacional da Mata Atlântica – INMA, sob a presidência do orientador, a fim de proceder a arguição pública do trabalho de **DISSERTAÇÃO DE MESTRADO** de **CAROLINA VERONESE CORRÊA DA SILVA**, intitulado: **"EFEITO DO PULSO DE INUNDAÇÃO NA ASSEMBLEIA DE FORMIGAS EM ILHAS FLUVIAIS DA AMAZÔNIA"**, orientada pelo Dr. Fabricio Beggiato Baccaro, do Instituto Nacional de Pesquisas da Amazônia – INPA e co-orientada pelo Dr. Sergio Henrique Borges, da Universidade Federal do Amazonas – UFAM.

Após a exposição, o discente foi arguido oralmente pelos membros da Comissão Examinadora, tendo recebido o conceito final:

[X] APROVADO (A)   [ ] REPROVADO (A)

[X] POR UNANIMIDADE   [ ] POR MAIORIA

Nada mais havendo, foi lavrada a presente ata, que, após lida e aprovada, foi assinada pelos membros da Comissão Examinadora.

DRA. CINTIA CORNELIUS FRISCHE

DR. THIAGO JUNQUEIRA IZZO

DR. IGOR LUÍS KAEFER

DR. JORGE LUIZ P. DE SOUZA

DRA. JULIANA HIPÓLITO DE SOUSA

(Coordenação PPG-ECO/INPA)

Ficha catalográfica

Sinopse

Estudou-se como o alagamento e o isolamento das ilhas fluviais atuaram como filtro ambiental, estruturando a diversidade taxonômica das assembleias de formigas.

Palavras-chave: Distúrbio; inundação; filtro ambiental; guildas; aninhamento.

Às mulheres cientistas que vieram antes &
abriram caminho para outras iguais a mim.

Agradecimentos

Este trabalho foi fruto de vários esforços. A eles agradeço imensamente todo o apoio. De início, agradeço à coordenação do programa de pós-graduação em Ecologia do INPA pelos assessoramentos e aos professores por toda a formação, ensinamentos dentro e fora de sala de aula, orientações e acolhimento. Ao CNPQ pela bolsa concedida e à FAPEAM pelo financiamento do projeto. Agradeço imensamente meu orientador Fabricio Baccaro pelo acolhimento, suporte, orientação e inspiração. Além das conversas e ideias sobre o projeto, lá em 2019, agradeço pelas conversas que acalmaram e motivaram que tivemos durante os períodos mais críticos da pandemia. Agradeço ao Serginho, meu coorientador, pelas orientações, pelas risadas, e por me ensinar tudo que sei sobre logística de campo na Amazônia. Ao pessoal do laboratório de ecologia de comunidades da UFAM, por serem inspiração e minha fortaleza. Agradeço em especial Amanda, Talitha e Isa por serem tão parceiras durante todo esse período. Pela ajuda que tivemos umas com as outras. Pelos cafés, risadas, conselhos, choros e alegrias. Vocês foram e continuam essenciais na minha vida.

Agradeço às pessoas que me ajudaram em campo: Tiago, Jorge, Maurício, Jéssica e Eduardo, e meus mateiros: Cleber e Gerley. Sem vocês nada disso teria acontecido. Lembrarei com muito carinho todos os momentos em campo e no alojamento. Jamais ouvirei Calypso sem lembrar de vocês. Aproveito para agradecer todo o pessoal do Parque Nacional de Anavilhanas, em nome da Chefe, Priscila, por toda a disponibilidade, ajuda e apoio em todas as expedições. Agradeço especialmente aos vigilantes da base 2 e 3 pela segurança, companhia, comilanças e risadas.

Ao pessoal da turma de mestrado em ecologia 2019 por toda a parceria e companhia. Passar por esse processo desgastante foi mais fácil pelo carinho de vocês. Agradeço especialmente à Marina, Jessica e João. Que bom que conseguimos levar essa amizade para a vida. Vocês foram minha segunda família em Manaus. Lembro com muito carinho de todas as conversas, rolês, risadas e choradeiras que compartilhamos (inclusive muitas saudades de tudo isso). Agradeço também à minha psicóloga Karol, por me manter sã no período mais caótico da minha vida.

Agradeço por fim, minha família, que me apoiou tanto na ida à Manaus quanto na volta a Porto Alegre. Obrigada por me deixarem sonhar e me apoiarem incondicionalmente. Vocês são tudo para mim. Sou muito privilegiada em ter uma família que me incentiva e apoia sempre. Agradeço também àquelas pessoas que cruzaram meu caminho e me ouviram, me motivaram ou simplesmente me ajudaram a seguir em frente. Guardo com carinho todos esses gestos.

"Minha mãe sacrificou seus sonhos para que eu sonhasse"

(Rupi Kaur)

Resumo

Distúrbios estão entre os principais fatores que afetam a dinâmica e a estrutura das assembleias de espécies. O pulso de inundação, comum aos grandes rios da Amazônia, é uma perturbação natural e sazonal que alaga grandes extensões de terra anualmente. O nível dá água da maioria dos rios varia de 10 a 15 metros entre os picos secos e inundados e modificam o funcionamento desses ecossistemas. As ilhas fluviais naturais da Amazônia também são fortemente afetadas, sendo completamente inundadas durante a fase de enchente, transformando temporariamente ambientes terrestres em aquáticos. Espera-se que o efeito da perturbação seja mais forte para organismos sésseis e terrestres, como formigas, que apresentam poucas adaptações para o período de inundação. Dessa forma, nós avaliamos como o alagamento e o isolamento das ilhas fluviais atuam como filtro ambiental, estruturando a diversidade taxonômica e de guildas de formigas. Para isso, nós amostramos 36 transectos, 12 em cada ambiente: terra-firme (floresta não-inundável), igapó (floresta inundada conectada com a terra-firme) e ilha fluvial (floresta inundada isolada da terra-firme). Nós coletamos formigas terrícolas, utilizando pitfall de solo, e formigas arborícolas, combinando pitfall arbóreo e bateção, nesses locais durante a estação seca no Parque Nacional de Anavilhanas, Amazonas. Nós registramos 210 espécies e morfoespécies, representando 52 gêneros e sete subfamílias. A riqueza de espécies de formigas do estrato arborícola foi similar entre os ambientes, mas no estrato terrícola, maior riqueza foi amostrada na terra-firme. A composição de espécies diferiu entre os ambientes tanto no estrato arborícola quanto no terrícola. A assembleia de formigas no estrato terrícola teve um padrão aninhado de acordo com a distância da terra-firme. Já no estrato arborícola o aninhamento não foi evidente. Também observamos que a proporção de espécies das guildas mais associadas ao solo (cortadeiras, atines criptobióticas, predadoras caçadoras e onívoras de solo) tiveram a proporção muito reduzida ou inexistente nas ilhas. Nossos resultados sugerem que o pulso de inundação modifica a estrutura das assembleias de formigas que vivem em florestas sazonalmente inundadas, reduzindo o número e alterando a identidade das espécies nesses ambientes. O filtro ambiental agiu mais fortemente nas formigas terrícolas, pois com a supressão do solo durante a fase alagada, há redução de locais de nidificação e da disponibilidade de recursos alimentares. Assim, as espécies e guildas de formiga que vivem no solo possivelmente só conseguem sobreviver em locais onde a influência das inundações é menor e acabam desaparecendo nas ilhas fluviais. Já as formigas arborícolas mantiveram a riqueza entre os ambientes provavelmente devido à alta similaridade alimentar das espécies e o aumento da dominância, independentemente do tipo de ambiente. O distúrbio e isolamento parecem favorecer a presença de espécies dominantes e oportunistas pois há um aumento destas guildas de espécies nas ilhas fluviais. Ilhas fluviais sujeitas a inundações e isoladas da floresta de terra-firme abrigam em geral uma diversidade empobrecida, o que pode alterar as funções desempenhadas pelas formigas nesses ambientes. A perturbação e o isolamento podem, portanto, representar fatores importantes para as assembleias de espécies de formigas e estar operando como filtros para dispersão e competição.

Palavras-chave: Distúrbio; inundação; filtro ambiental; guildas; aninhamento.

Abstract

Disturbances are one the main factors affecting species assemblages' dynamics and structure. The flood pulse, observed in rivers in the Amazon, is a natural and seasonal disturbance that floods large tracts of land annually. The water level of most rivers varies from 10-15 meters between dry and flooded peaks and modifies the functioning of these ecosystems. The natural fluvial islands of the Amazon are also heavily affected, being wholly flooded during the flooding phase, temporarily transforming terrestrial environments into aquatic ones. The disturbance effect is expected to be stronger for sessile and terrestrial organisms, such as ants, which have few adaptations to the flood period. In this way, we evaluated how flooding and isolation of river islands act as an environmental filter, structuring taxonomic and guild diversity of ant assemblage. For this, we sampled 36 transects, 12 in each type of environment: terra-firme forest (non-flooded forest), igapó (flooded forest connected with terra-firme), and fluvial island (flooded forest isolated from terra-firme). We collected terrestrial ants, using soil pitfall, and arboreal ants combining arboreal pitfall and beating, at these sites during the dry season in Anavilhanas National Park, Amazonas. We recorded 210 species and morphospecies, representing 52 genera and seven subfamilies. The ant richness of the arboreal stratum was similar between the environments, but in the terrestrial stratum, greater richness was sampled in the terra-firme. Ant composition differed between environments in arboreal and terrestrial strata. The ant assemblage in the terrestrial stratum had a nested pattern according to the distance from the terra firme. Nested pattern was not evident in the arboreal stratum. We also observed that the proportion of species' guild most associated with the soil (leaf cutters, cryptobiotic atines, raid hunter predators, and ground-dwelling omnivores) had a very low or non-existent proportion on the islands. Our results suggest that the flood pulse modifies the structure of ant assemblages that live in seasonally flooded forests, reducing the number and changing the identity of species in these environments. The environmental filter acted more strongly on terrestrial ants because, with the suppression of the soil during the flooded phase, there is a reduction in nesting sites and the availability of food resources. Thus, the ant species and guilds that live on the ground are possibly only able to survive in places where the influence of floods is less and end up disappearing on the river islands. On the other hand, arboreal ants-maintained richness between environments, probably due to the high food similarity of the species and the increase in dominance, regardless of the type of environment. Disturbance and isolation seem to favor the presence of dominant and opportunistic species as there is an increase in these species' guilds on river islands. Fluvial islands subject to flooding and isolated from the terra-firme forest generally harbor an impoverished diversity, which can alter the functions performed by ants in these environments. Disturbance and isolation may, therefore, represent important factors for ant assemblages and may be operating as filters for dispersal and competition.

Keywords: Disturbance; inundation; environmental filter; guilds; nestedness.

Sumário

Introdução geral

Distúrbio é um dos principais fatores que estruturam e modificam o funcionamento das comunidades (White & Jentsch 2004, Matthews et al. 2013). Os distúrbios são eventos naturais ou antropogênicos que modificam abruptamente o ambiente físico e influenciam na disponibilidade de recursos (Picket & White 1985, Mouillot et al. 2013). Dependendo da intensidade, os distúrbios podem reduzir localmente a diversidade (Levin 2000, Gerisch et al. 2011) ou aumentar, facilitando a coocorrência das espécies por modificar as relações competitivas (Tilman et al. 2012, Abreu et al. 2017). Em muitos casos, os efeitos do distúrbio sobre a estrutura das comunidades podem ser entendidos como um filtro ambiental, que exclui espécies sem características que conferem resistência e resiliência ao distúrbio, e favorece (ou "filtra") espécies com características que conferem alguma vantagem ecológica frente ao distúrbio (Southwood 1977). O filtro ambiental tende a reduzir as estratégias de sucesso entre as espécies que coexistem (Weiher et al. 1996, Li et al. 2018) fazendo com que as características dessas espécies sejam convergentes.

O pulso de inundação, observado nos grandes rios da Amazônia, é um distúrbio natural, sazonal e previsível para organismos terrestres que ocorre há pelo menos um milhão de anos (Irion & Adis, 1979). É caracterizado por um período de enchente (cheia) e vazante (seca), com amplitude média anual de 10-15 metros (Adis 1984, Piedade et al. 2010) e ocorre nas florestas alagáveis localizadas nas margens dos rios, e nas ilhas fluviais. As florestas alagáveis cobrem aproximadamente 17% da bacia amazônica (Hess et al. 2015) e são anualmente recobertas por águas quando os níveis dos rios sobem, devido ao acúmulo das chuvas em toda a área da bacia (Piedade et al. 2015). O tipo de floresta alagável utilizada nesse trabalho foi o igapó, que são florestas banhadas por rios de água preta e possuem solos pobres em nutrientes (Prance 1985). No período de cheia, pequenas árvores dessas florestas podem ficar totalmente submersas por até seis meses (Parolin et al. 2004; Wittmann et al. 2010).

Segundo Junk (1989), o pulso de inundação é a principal força reguladora da biota nesses ambientes, e afeta atributos taxonômicos e funcionais das assembleias de espécies nesses locais (Lambeets et al. 2008). Por ser um distúrbio previsível, ou seja, ter uma regularidade de ocorrência; adaptações e estratégias para a utilização desse hábitat e seus recursos estão presentes em diversos organismos (Junk, 1989). Por exemplo, a presença de aerênquimas nas raízes das plantas para facilitar o transporte de oxigênio (Junk, 1989b, Drew et al. 2000, de Simone et al. 2002).

Evidências de adaptações de animais, principalmente invertebrados, ao pulso de inundação, são menos frequentes (Ballinger et al. 2007). Parte porque foi relativamente menos estudado, mas também porque os animais terrestres podem se deslocar para locais mais adequados durante a cheia. Nas florestas de igapó, os animais capazes de voar migram para a floresta de terra-firme vizinha, na qual não é inundável ou se deslocam verticalmente para setores da floresta não alcançados pela água (Adis 1997, Adis & Junk 2002, Roweder et al. 2021). Dessa forma, adaptações para lidar com o pulso de inundação seriam mais frequentes em organismos relativamente sésseis e estritamente terrestres, como as formigas.

De fato, algumas espécies de formigas possuem estratégias de adaptação para o período de inundação, como a migração vertical para a copa das árvores (Adis 1982, Adis 1997, Adis et al. 2001), construção de diques que colapsam fechando a entrada dos ninhos (Nielsen 1997), ou ingestão e regurgitação da água para fora dos ninhos (Klein et al. 1993, Maschwitz & Moog 2000). No entanto, o número de espécies de formigas que apresentam tais adaptações é pequeno e sabe-se que a maioria dos ninhos subterrâneos ou no folhiço são destruídos durante a inundação da floresta (Adis 1982, Mertl et al. 2009). Ou seja, apesar de previsível, o pulso de inundação modifica fortemente a diversidade e estrutura das assembleias de formigas que vivem nas florestas sazonalmente alagáveis (Majer & Delabie 1994, Ballinger et al. 2007).

Além disso, nem todas as formigas conseguem migrar verticalmente, evento mais comum e documentado nas espécies da Amazônia (Adis, 1982), já que as condições ambientais na copa das árvores são bem diferentes do solo e folhiço (Yanoviak & Kaspari 2000). Formigas arborícolas são bem adaptadas a altos índices de radiação solar e risco de dessecação (Yanoviak & Kaspari 2000; Kaspari & Weiser 2006). Já as formigas de solo, que vivem sob um ambiente de maior umidade, são menos resistentes à irradiação solar (Spicer et al. 2017). Por conta disso, existe uma forte estratificação vertical das comunidades de formigas (Wilson 1987, Yanoviak & Kaspari 2000), que confere diferentes assembleias de formigas em diferentes estratos da floresta (Arruda et al. 2021, Torres et al. 2021).

O efeito do distúrbio por pulso de inundação provavelmente é ainda mais forte nas ilhas fluviais amazônicas. Por serem isoladas da floresta de terra-firme e por ficarem totalmente submersas ao longo do ciclo hidrológico, o único hábitat disponível nas ilhas fluviais durante a cheia para animais terrestres está na copa das árvores (Piedade et al. 2005). Dessa forma, espécies de formiga que não conseguem alcançar a copa das árvores,

ou que não se desloquem horizontalmente para a floresta de terra-firme, provavelmente terão sua densidade drasticamente reduzida, ou até mesmo eliminada. Já no período de seca, o hábitat terrestre volta a ficar disponível, permitindo que haja um novo ciclo de colonização (Piedade et al. 2005). Dessa forma, durante o início da estação seca as ilhas são como substratos abertos à colonização, mas para que isso aconteça, as formigas necessitam migrar até esses locais, fazendo com que ilhas mais distantes da terra-firme (consideradas aqui como mais isoladas) sejam locais mais difíceis de chegar.

O distúrbio causado pela inundação em conjunto com o isolamento pode amplificar um padrão aninhado da composição de espécies nas ilhas (Darlington 1975, Meyer 2017). O aninhamento das assembleias das espécies ocorre quando as biotas de locais com menor número de espécies são subconjuntos das biotas de locais mais ricos (Wright & Reeves 1992, Ulrich e Gotelli 2007, mas veja também Baselga 2010). Isso ocorre porque ilhas distantes só podem ser alcançadas por organismos com boa capacidade de dispersão, fazendo com que a fauna desses locais seja menor e seja um subconjunto dos locais mais próximos do continente (Meyer 2017), nesse caso, as florestas de terra-firme.

Porém, a influência do distúrbio e isolamento não afeta todas as formigas de forma similar. Diferentes ambientes (floresta de terra-firme, floresta de igapó e ilha fluvial) possuem condições ambientais diferentes, que podem ser entendidas como diferenças na disponibilidade de hábitat e de recurso alimentar. Com isso, espécies mais associadas ao solo, por exemplo, como as formigas cortadeiras, devem ser mais afetadas nos ambientes onde o solo, seu hábitat de nidificação, passa por perturbações, como as ilhas e a floresta de igapó. Em áreas de distúrbio é comum que haja uma redução de espécies especialistas e um aumento de espécies oportunistas (Hoffmann & Andersen 2003). Por outro lado, o distúrbio do alagamento pode facilitar a predação, dado um possível aumento da densidade de insetos na copa das árvores (Rowedder et al. 2021), e, portanto, pode favorecer a presença de espécies de formiga predadoras nesse estrato. Esses grupos de espécies podem ser entendidos como guildas, uma ferramenta importante para descrever padrões em comunidades (Simberloff & Dayan 1991) e em estudos comparativos de comunidades em diferentes ambientes (Hawkins & MacMahon 1989; Wilson 1999).

Guilda é definida aqui como um grupo de espécies que explora de forma similar uma classe de recursos ambientais (Root 1967) e agrupa organismos que têm uma sobreposição significativa nos requerimentos de nicho (Root 1967; Pianka 1980) (i. e.

relações ecológicas, disponibilidade de recursos e condições para um indivíduo ou uma espécie; Hutchinson 1944; Begon 2009). A utilização de guildas em estudos ecológicos é útil porque guildas refletem não só o que as formigas estão fazendo, mas também possíveis funções ecossistêmicas que elas desempenham (Macedo et al. 2011; Groc et al. 2013). Além disso, guildas podem predizer a estrutura da comunidade de formigas em resposta à perturbação quando o distúrbio causa uma mudança na estrutura da vegetação (Hoffmann & Andersen 2003). Ou seja, de acordo com as condições e disponibilidade de hábitat e recurso, é possível que determinadas guildas ocorram em alguns locais, em outros não, ou ocorram em diferentes proporções.

Objetivos

Objeto geral

Avaliar como o alagamento e o isolamento das ilhas fluviais atuam como filtro ambiental, estruturando a diversidade taxonômica das assembleias de formigas.

Objetivos específicos

1. Avaliar se a assembleia de espécies de formigas das ilhas fluviais diferirá dos outros ambientes e com uma riqueza menor de espécies.
2. Avaliar se a composição de espécies de formigas nas ilhas é um subconjunto da composição da terra-firme e igapó, e se esse aninhamento está ordenado pela distância da floresta de terra-firme
3. Avaliar se a proporção de espécies de guildas mais associadas ao solo (e.g. cortadeiras) será muito reduzida nas ilhas fluviais; e a de espécies de guildas predadoras mais associadas a vegetação (e.g. predadoras arborícolas) será maior nas ilhas fluviais.

Silva, C.V.C., Santos, T. F., Gonçalves, A. L. S., Borges, S. H., Baccaro, F. B. **Effect of the flood pulse on ant assemblages on fluvial islands in the Amazon.** Manuscrito submetido ao Journal of Animal Ecology.

Effect of the flood pulse on ant assemblages on fluvial islands in the Amazon

Carolina Veronese Corrêa da Silva[1, *], Talitha Ferreira dos Santos[2,3], André Luis Sousa Gonçalves[1], Sergio Henrique Borges[2,3], Fabricio Beggiato Baccaro[2,3]

[1]Programa de Pós-Graduação em Ecologia, Instituto Nacional de Pesquisas da Amazônia – INPA, Av. André Araújo 2936, Petrópolis, Manaus, 69067-375 Brazil

[2]Programa de Pós-Graduação em Zoologia, Instituto de Ciências Biológicas, Universidade Federal do Amazonas, Brazil, Av. General Rodrigo Otávio, 3000, Manaus, AM 69077-000, Brazil

[3]Universidade Federal do Amazonas, Departamento de Biologia, Av. General Rodrigo Otávio, 3000, Manaus, AM 69077-000, Brazil

*Corresponding author: caroltaita@gmail.com

Abstract

1. Disturbances can shape assemblage structure locally, while processes that limit species dispersal can modify assemblage structure at regional scales. The flood pulse in most Amazon rivers is a natural and seasonal disturbance for riverbank forests (floodplains) and fluvial islands. Areas can remain flooded for up to six months, so the disturbance effect is expected to be stronger for sessile organisms, such as ants.

2. Here, we evaluated how flooding and isolation of islands act as an environmental filter, structuring taxonomic and functional group diversity of ant assemblage.

3. We collected epigaeic and arboreal ants during the dry season in 12 transects in each environment: terra-firme forest (non-flooded forest), igapó (flooded forest connected with terra-firme), and fluvial island (flooded forest isolated from terra-firme), in Anavilhanas National Park, Amazonas, Brazil.

4. We recorded 210 species and morphospecies. The arboreal ant richness was similar between the environments, but terra-firme harbored higher richness in the epigaeic strata. Ant composition differed between environments in both strata. The ant assemblage in the epigaeic stratum showed a nested pattern at the regional scale, but this pattern was not evident for the arboreal assemblages. The proportion of species' functional groups linked with the soil decreases from terra-firme to islands.

5. With the soil suppression during the flood, there is a reduction in nesting sites and availability of food resources. Thus, the ant species that exclusively live on the ground can only survive where the influence of flood is minimal. Disturbance and isolation seem to favor the presence of arboreal predators and generalist omnivores species because of the increase in these groups on islands. Our results suggest that disturbance modifies the structure of ant assemblages in flooded forests fostering species turnover. At the same time, the isolation is related to species loss, mainly in the epigaeic stratum. Fluvial islands harbor an impoverished functional diversity, which can alter the functions performed by

ants. However, the species turnover suggests that islands have potential conservation value for ants.

Introduction

Disturbances are a main factor affecting the communities' structure worldwide (White & Jentsch 2004, Matthews et al. 2013). Disturbances are natural or anthropogenic events that abruptly modify the physical environment and influence resource availability (Picket & White 1985, Mouillot et al. 2013). Depending on their intensity, disturbances can reduce or increase the diversity (Levin 2000, Gerisch et al. 2011), facilitating the co-occurrence of species by modifying competitive relationships (Tilman et al. 2012, Abreu et al. 2017). In many cases, the effects of a disturbance on the community structure are understood as an environmental filter, which excludes species that lack specific traits that confer resistance and resilience and favors species with characteristics that confer some ecological advantage in the face of the disturbance (Southwood 1977). Such environmental filter tends to reduce successful strategies among coexisting species (Weiher et al. 1996, Li et al. 2018), causing the characteristics of these species to converge.

The flood pulse, observed in rivers in the Amazon, is a natural, seasonal, and predictable disturbance for terrestrial organisms that has occurred for at least one million years (Irion & Adis, 1979). It is characterized by a period of flood and dry season, with an average annual amplitude of 10-15 meters (Adis 1984, Piedade et al. 2010) and occurs in floodplain forests located on riverbanks and fluvial islands. Floodplain forests cover approximately 17% of the Amazon basin (Hess et al. 2015), being annually covered by water when river levels rise due to the accumulation of rainfall throughout the basin (Piedade et al. 2015). The forest periodically flooded by black water, which is nutrient poor, is known as igapó forest (Prance 1985). During the rainy season, small trees in these forests can remain completely submerged for up to six months (Parolin et al. 2004; Wittmann et al. 2010).

The flood pulse is the main regulatory force of the biota in these environments (Junk 1989), affecting the taxonomic and functional attributes of species assemblages (Lambeets et al. 2008). Several organisms evolve adaptations and strategies to thrive in these forests (Junk 1989). For example, the presence of aerenchyma in plant roots facilitates oxygen transportation during long flooding periods (Junk 1989b, Drew et al. 2000, de Simone et al. 2002). Also, many plant species synchronize phenological patterning of leaf and fruit production with the annual flooding cycle (Montero et al. 2014), responsible for seasonal lateral movements of vertebrates between flooded and non-flooded environments (Haugaasen and Peres 2007; Costa et al. 2018).

Evidence of animal adaptations to flooding, especially among invertebrates, is less frequent (Ballinger et al. 2007). This is partly because it has been relatively less studied and because terrestrial animals may move to more suitable locations during the flood. Animals capable of flight in igapó forests can migrate to the neighboring terra-firme forest, which is non-floodable, or move vertically to sectors of the forest not reached by water (Adis 1997, Adis & Junk 2002, Roweder et al. 2021). Thus, adaptations to deal with the flood pulse would be more frequent in relatively sessile organisms, such as ants.

Some ant species have adaptation strategies for the flooding period, such as vertical migration to the canopy (Adis 1982, Adis 1997, Adis et al. 2001), construction of dikes that collapse, closing to the nest entrance (Nielsen 1997), or ingestion and regurgitation of water out of the nests (Klein et al. 1993, Maschwitz & Moog 2000). However, the number of ant species that exhibit such adaptations is small, suggesting that most subterranean or leaf litter nests are flooded during high water periods (Adis 1982, Mertl et al. 2009). Furthermore, not all ants can migrate vertically to higher forest strata since the environmental conditions in the understory and canopy are markedly different from those of the soil and leaf litter (Yanoviak & Kaspari 2000). Arboreal ants are well

adapted to high solar radiation and desiccation risk (Yanoviak & Kaspari 2000; Kaspari & Weiser 2006). On the other hand, ground-dwelling ants, which live in a higher humidity environment, are less resistant to solar irradiation (Spicer et al. 2017). Therefore, there is a substantial vertical stratification of ant communities (Wilson 1987, Yanoviak & Kaspari 2000), forming various ant assemblages throughout different forest strata (Arruda et al. 2021, Torres et al. 2021). Therefore, despite being predictable, the flood pulse strongly modifies the diversity and structure of ant assemblages that live in seasonally flooded forests (Majer & Delabie 1994, Ballinger et al. 2007, Pringle et al. 2019).

The effect of the flood pulse is likely to be even stronger on the Amazonian fluvial islands. Because they are isolated from the terra-firme forest and are entirely submerged throughout the hydrological cycle. The canopy is the only habitat on fluvial islands during the flooded season for terrestrial animals (Piedade et al. 2005). Thus, ant species that cannot reach the canopy or that do not move to the adjacent terra-firme forest will likely have their density drastically reduced or even eliminated. The terrestrial habitat becomes available again in the dry season, allowing for a new colonization cycle (Piedade et al. 2005). Thus, the islands are substrates open to colonization during the beginning of the dry season. Still, the ants need to migrate to these sites, making isolated fluvial islands harder to recolonize.

The disturbance caused by flooding and isolation can strengthen a nested pattern of species composition on fluvial islands (Darlington 1975, Meyer 2017). The nestedness of species assemblages occurs when biotas from sites with fewer species are subgroups of biotas from richer sites (Wright & Reeves 1992, Ulrich & Gotelli 2007, but see Baselga 2010). This happens because isolated islands can only be reached by organisms with good dispersal abilities, causing the fauna of these sites to be smaller and turning it into a subgroup of the sites closer to the mainland (terra-firme forests; Meyer 2017).

Nevertheless, disturbance and isolation do not affect all ants in the same way. A reduction of specialist species and an increase of opportunistic species is frequent (Hoffmann & Andersen 2003) in disturbed areas. On the other hand, given a possible increase in the density of insects in the canopy (Rowedder et al. 2021), the flooding may facilitate predation e favor the presence of predatory ant species in this stratum. Furthermore, grouping ants into "functional groups" may promote further insights into how disturbance and isolation shape the ant assemblage structure and ecosystem functions (Macedo et al. 2011; Groc et al. 2013; Hoffmann & Andersen 2003).

Here, we evaluated how flooding and isolation of fluvial islands interact in structuring the diversity of ant assemblages. We hypothesized that disturbance would promote drastically compositional changes, while isolation will be more related to species loss, mainly in epigaeic strata. Precisely, we predict that (1) the epigaeic ant assemblage composition is different between environments, while the arboreal assemblage composition is not; (2) the ant composition on the fluvial islands is a subset of the terra-firme and igapó forest, and this nestedness pattern is ordered by the distance from the terra-firme forest; (3) the proportion of ground-dwelling or specialist species will be lower, whereas predatory and arboreal species will be higher on fluvial islands.

Material and methods

Study area

This study was carried out in the Anavilhanas National Park (2°23'41" S 60°55'14" W), located on the Negro River, between the municipalities of Manaus and Novo Airão, Amazonas state, Brazil. The Park covers an area of more than 3,500 km², and the fluvial ecosystems represent 60% of the park's area. The remaining 40% represents terra-firme forest. The fluvial archipelago is formed by more than 400 islands

and lakes (ICMBio 2017). Fluvial islands are flooded for up to seven months of the year, reaching a depth of up 15 meters during peak water levels (Irion et al. 1997). The highest and lowest levels occur from June to July and October to November, respectively (Montero & Latrubesse 2013).

Sampling design

Sampling took place in three environments: terra-firme forests (never flooded), igapó forest (periodic flooded), and fluvial islands (periodic flooded and isolated from the terra-firme) during the dry period (November/2019 to January/2020), when the islands emerge. In each environment, 12 transects (sample unit) of 250 meters were positioned. The transects in the terra-firme forest areas were arranged along the trails already present in the park; in the areas of igapó forest, they were placed parallel to the river's course; and, on fluvial islands, along their length. The minimal distance between transects was 500 meters. Overall, 36 transects were distributed throughout the three environments.
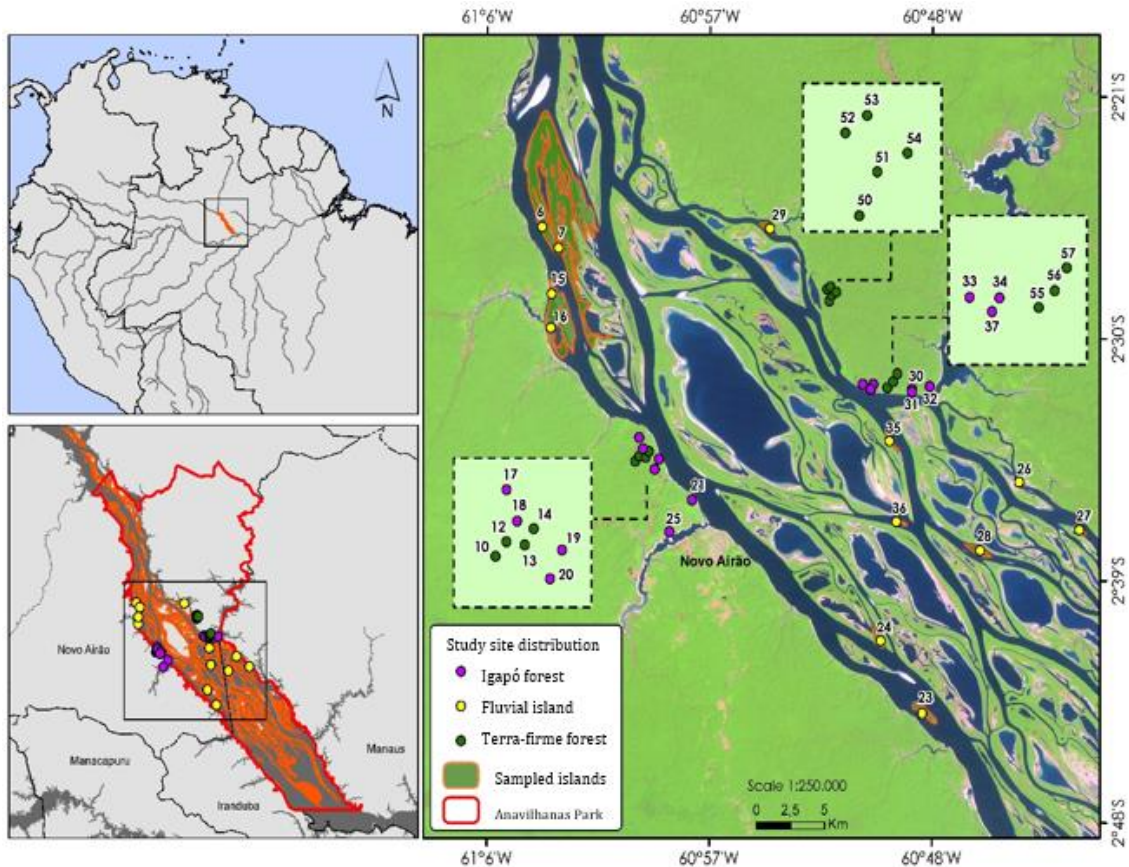
Figure 1: Study area and sampling points in Anavilhanas National Park – Amazonas, Brazil. Green dots represent terra-firme forest, purple dots the igapó forest, and yellow dots represent fluvial islands.

We selected 12 small islands (average size ± SD = 39 km² ± 761.24; the smallest = 4.23 km²; the largest = 2657.12 km²; Table S1) positioned along the archipelago. We chose small islands because they have less topographic variation and are completely submerged during the flood. Our objective was to control the effect of flooding on ant assemblages as best as possible.

We considered the distance of each floodable area concerning the ecotone between the igapó forest and the terra-firme forest (Table S1) as a measure of isolation. The ecotone was defined as the transition line between igapó forest and terra firme forest and was estimated based on the classification of satellite images. These values were

obtained based on three types of information: the background image of the quickbird satellite (the one used in Google Earth), an SRTM radar image (altitude and slope), and the raster of floodable areas (Hess et al. 2003). The different elevation quotas of the land, marked at every 10 m, were created using the SRTM image. These three variables were combined to classify the area's vegetation. Thus, we calculated: the Euclidean distance from the midpoint of each transect to the transition between the igapó forest and the nearest terra-firme forest. The igapó and island distances to the nearest igapó/forest transition were coded as positive values. In contrast, the Euclidean distances between the ecotone and the terra-firme transects were coded as negative values to create an extended gradient that combines isolation and disturbance by flooding. Therefore, the smaller the distance (large negative values), the deeper in the terra-firme forest the transect is located. Likewise, the greater the distance (positive values), the further the igapó or island transect was from the transition between terra-firme and the flooded area.

Ant sampling

We carried out three expeditions for data collection: two between November and December 2019 and another in January 2020. We collected ants in the three environments from both epigaeic and arboreal strata. We sampled the epigaeic ants (considered here those foraging on the ground and leaf litter) at 10 points (every 25 m) in each transect. A pitfall trap was installed at each point, consisting of a 500 ml plastic cup buried in the ground containing alcohol 70%.

We sampled arboreal ants (those that nest and forage on the understory vegetation) at 10 points of the transect using two methods: vegetation-beating trap and arboreal pitfall trap (fig. 3b). At each sampling point of the pitfall trap, three trees were selected (diameter at breast height – DBH ≤ 10 cm), in which an entomological umbrella

(a white tissue supported by two wooden rods, 1 m²) was positioned below their canopy. Thus, the understory trees were shaken five times on average, and the ants that fell on the tissue were collected and fixed in alcohol 70%. We also installed arboreal pitfall traps at 10 points along the transect every 25 m. We selected the trees closest to the pitfall trap. The arboreal pitfall trap consisted of a 500 ml solution of urine, detergent, and water, positioned approximately 150 cm from the ground. Urine has been used as the most efficient bait in arboreal ant collection, collecting comparatively more species than other baits (Powell et al. 2011; Vasconcelos et al. 2017). Both pitfall traps and arboreal pitfall traps remained in operation for 48 h in each transect. The specimens were transferred to flasks with alcohol 70% after being collected.

The collected material was taken to the Community Ecology Lab at the Federal University of Amazonas (UFAM) for sample processing. The samples were sorted, the ants separated in each of them, and then each morphospecies of each point was assembled. We identified the ants to their lowest possible taxonomic level using identification keys (e.g., Baccaro et al. 2015), comparison with specimens on image bank websites (e.g., AntWeb), and reference collection from the Community Ecology Laboratory. We also consulted ant taxonomists, such as Dr. Itanna Fernandes, from the INPA entomology collection and Dr. Rodrigo Feitosa from the Federal University of Paraná (UFPR).

Functional group classification

We classified the ant species into nine functional groups proposed by Groc et al. (2013) that considered diet, foraging and nesting habits (Table S2). The functional groups were: two fungus-growing (i.e., leaf cutters and cryptobiotic attines), three omnivores (i.e., ground-dwelling omnivores, generalist omnivores, and arboreal omnivores), and four predators (i.e., ground-dwelling generalist predators, ground-dwelling specialist

predators, arboreal predators, and raid hunting predators). For most species, the categorization into guilds occurred at the genus level. For the morphospecies in which the genus occupied two guilds (i.e., arboreal predators and ground-dwelling predators), we used the predominant capture stratum in our samples to classify. In the species not resented in Groc et al. (2013) (e.g., *Myrcidris epicharis*), we searched in the taxonomical literature information about the diet and foraging of the species.

Data analyses

We separately analyzed the occurrence patterns along the gradient of epigaeic ants (pitfall trap) and arboreal ants (combination of vegetation-beating and arboreal pitfall trap). In all analyzes, our sample unit was the transect (n = 36). We used an analysis of variance (ANOVA) to assess whether the pattern of species richness varied among environments. The number of ant species per transect was our dependent variable, and the environments (terra-firme forest, igapó forest, and fluvial islands) were the independent variables. We used the post hoc Tukey test (Tukey HSD) to discriminate possible differences in species richness between pairwise combinations.

We built a presence and absence matrix, with the transects in the rows and the ant species in the columns. The composition of ant species between the strata and environments was ordered using non-metric multidimensional scaling (NMDS), based on the Bray-Curtis dissimilarity. We generated a two-dimension NMDS solution, which captured 63% of the variation in the epigaeic and 52% of the arboreal stratum. We then used the two-dimension axis as the dependent variable in a permutational multivariate analysis of variance (PERMANOVA) to verify whether the ant composition changed between environments. We calculated p values based on 999 permutations. We also carried out PERMANOVA pairwise comparisons between environments. For these

analyses, we applied Holm's correction for multiple testing. The PERMANOVA (*adonis* function) and the NMDS (*metaMDS* function) were performed using the package *vegan* (Oksanen et al. 2013).

We used NODF to test for nestedness patterns in epigaeic and arboreal ant assemblages. NODF calculates the nestedness among all pairs of rows and columns independently, considering the differences in filling and degree of overlapping (Almeida-Neto *et al.* 2008). We chose NODF because it is a consistent metric, does not depend on the shape and size of the matrix, and reduces detection biases present in other metrics (Almeida-Neto et al. 2008; Ulrich & Almeida-Neto 2012). The NODF ranges from 0 – 100, with 0 being no nestedness and 100 being perfect nestedness. According to our hypothesis, we calculated the NODF based on the ordered matrix (i.e., transects ordered in relation to the distance of the transition between terra firme forest and igapó). The observed NODF was compared with the null distribution generated by the randomization of the data matrix. The NODF null distribution was based on 999 permutations, using the "swap" algorithm, which keeps the total of rows and columns constant in all iterations. The NODF was determined using the function *nestednodf*, and the permutations were calculated using the function *oecosimu,* both from the package *vegan* (Oksanen *et al.* 2013).

To provide further insights into ant assemblages' structure, we partitioned the beta diversity into two separate components of species turnover and nestedness-resultant dissimilarities (Baselga 2010). We used the Sørensen dissimilarity index family as a measure of overall β diversity (β_{SOR}) for each ant assemblage stratum and environment. The β_{SOR} was then decomposed into two additive components: the spatial turnover component (without the effect of species richness variation), obtained by applying the Simpson dissimilarity index (i.e., β_{SIM}), and a nestedness component (i.e., β_{SNE}),

calculated by the difference between β_{SOR} and β_{SIM} (Baselga 2012). We used multiple-site compositional comparisons to quantify the overall heterogeneity (Baselga 2013). The ratio between β_{SIM} and β_{SOR} indicates the relative contribution of the turnover component in each stratum and environment. Multiple-site dissimilarity partitioning was performed in R using the *betapart* package (Baselga et al. 2021).

We built Beta Regression models for ratios and proportions (species occurrence per transect in each functional group) to assess whether the distance from terra-firme affects the proportion of species per guild. The occurrence of species per transect can be interpreted as the density of colonies in that area, as the distance among samples within the transects was 25 m (Baccaro et al. 2013). We used the proportion of ant species per functional group per transect as the dependent variable and the distance from igapó/terra-firme ecotone as the independent variable. As the beta distribution does not accept values equal to zero and one, we used the *transform_perc* function that transforms the values within the range (0,1) following the Cribari-Neto & Zeileis (2010) recommendation. This transformation maintains the relations among the proportions without altering the investigated patterns. We checked the distribution of residuals and the adjustment to the model in each of the regressions. The beta regressions we calculated using the package *betareg* (Cribari-Neto & Zeileis 2010). We performed all analyzes in the software R (version 4.1.2; R Core Development Team 2021).

Results

We recorded 210 ant species and morphospecies, representing 52 genera and seven subfamilies. The families with the greater number of species were Myrmicinae (102 spp), followed by Formicinae (28 spp), and the genera with the greater number of species were *Pheidole* (26 spp), *Camponotus* (18 spp), and *Crematogaster* (16 spp). In the terra-

firme forest we recorded 160 spp (80 in the arboreal and 111 in the epigaeic strata); 95 spp in the igapó forest (63 - arboreal and 65 - epigaeic strata); and 94 spp in the fluvial islands (60 - arboreal and 67 - epigaeic strata). Overall, 81 spp (39%) were collected exclusively in the terra-firme forest, 16 (8%) in the igapó forest, and 22 (10%) in the fluvial islands. Around 35% of species occurred in both stratum in fluvial islands and igapó forests, but this ratio drops to ~19% in terra-firme forests.

The number of ant species varied among the environments in the epigaeic stratum (ANOVA; $F_{2,31}$ = 10,18; p = 0,0036). The terra-firme forest had the greater number of species, differing from the number of species in the igapó forest (p < 0.001) and fluvial islands (p < 0.001), but the number of species in the igapó forest and fluvial islands is quite similar (p = 0.92). In the arboreal stratum, there was no difference in species richness among environments (ANOVA; $F_{2,31}$ = 0,17; p = 0,84).

The ant composition differed among the three types of environments in epigaeic (PERMANOVA, p = 0.001) and in the arboreal stratum (PERMANOVA, p = 0.001). Figure 2 shows that the overlap of epigaeic ants between fluvial islands and igapó forest was strongly influenced by one island that harbor an ant species composition close to terra-firme forests.
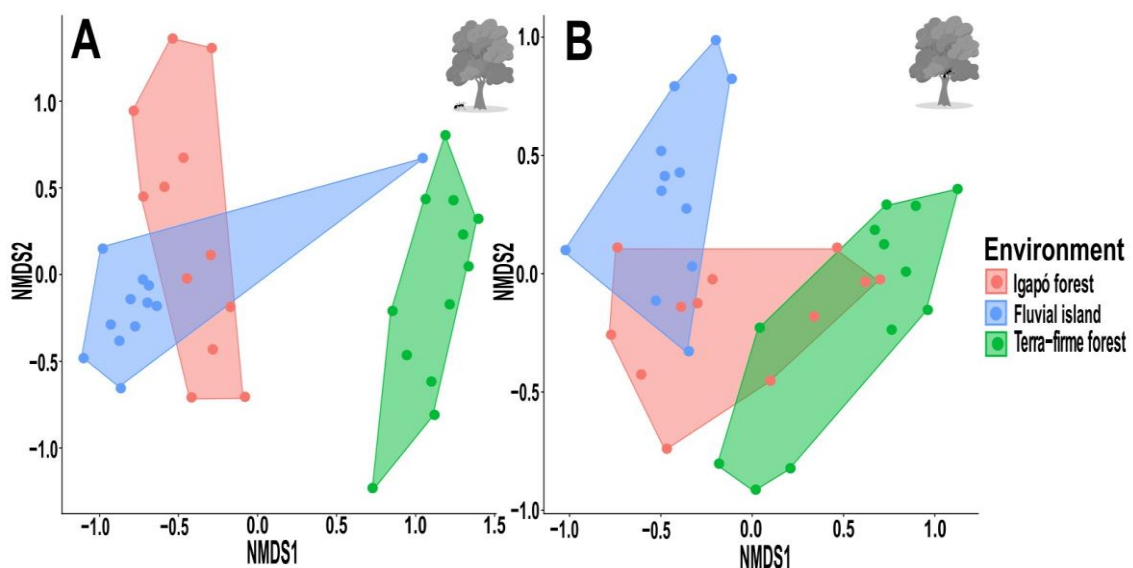
Figure 2: Two dimensions NMDS solution for epigaeic (A) and arboreal (B) ant assemblage composition along the three environments.

We observed a matrix filling of 10% for epigaeic ants and 13% for arboreal ants for the nestedness analysis. We observed a nested pattern related to the distance of the transition between terra-firme and igapó of epigaeic ant assemblages (NODF = 17.41; p = 0.001), which suggests that the assemblage of ants from the fluvial islands is a subgroup of the assemblage of ants from the igapó and terra-firme forests (Figure 3). In the arboreal stratum, this pattern was not detected (NODF = 12.39; p = 0.5), contrary to our predictions.
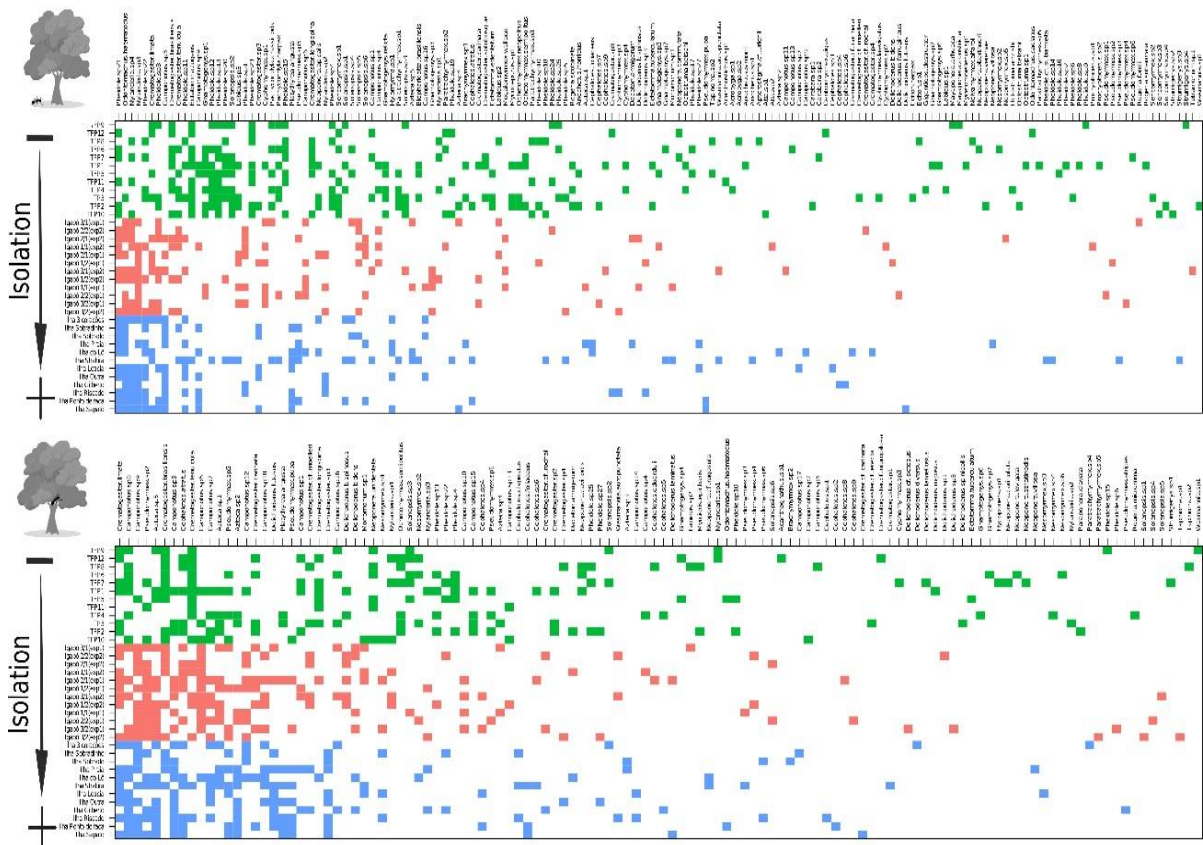

Figure 3: Ant assemblages ordered by the transition distance between igapó and terra-firme forest in the epigaeic (top) and arboreal (bottom) strata. Fluvial islands are represented in blue, igapó forest in green and terra-firme forest in magenta dots. The ant

species are in the columns, and the transects ordered by the distance from the terra-firme forest in the lines.

The turnover (βSIM) component of β diversity dominated the multiple-site overall β diversity in both environments and stratum (Figure 4). Despite the nestedness component contributing slightly more to island multiple-site overall β diversity, the βratio was higher than 0.90 in all cases.
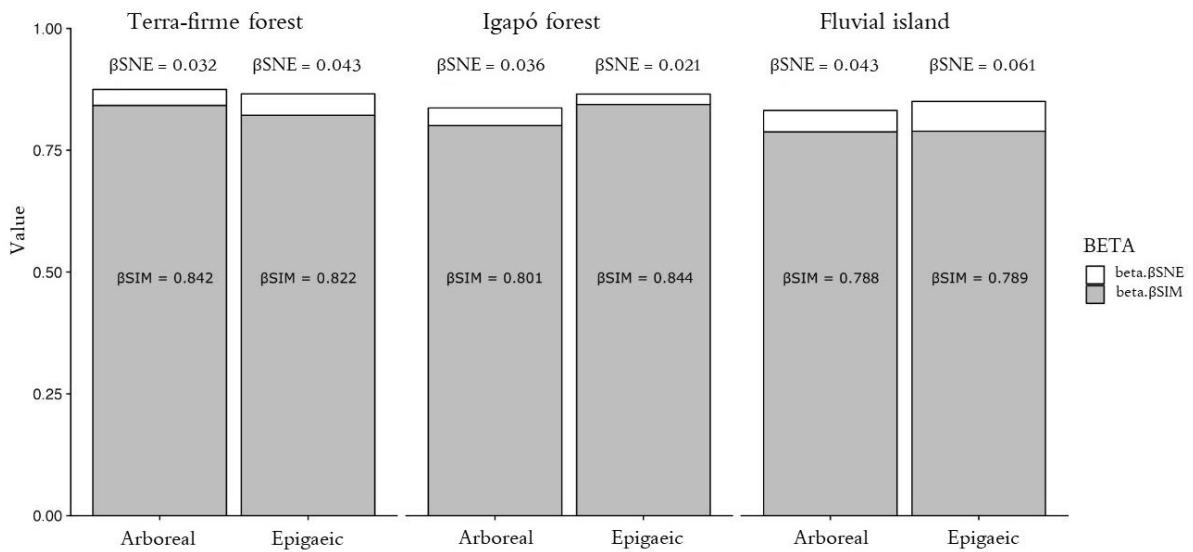

Figure 4: The relative contributions of spatial turnover (βSIM) and nestedness (βSNE) components of multiple-site overall β diversity between environments and stratum in the Anavilhanas archipelago. The βratio was the ratio between the value of turnover (βSIM) and the value of overall multiple site β diversity (βSOR).

Most ant species were classified as arboreal omnivores (62 spp), followed by generalist omnivores (49 spp), ground-dwelling generalist predators (32 spp), ground-dwelling omnivores (20 spp), arboreal predators (11 spp; *Daceton*, *Gnamptogenys*, *Platythyrea,* and *Pseudomyrmex*) and cryptobiotic attines (11 spp; *Apterostigma*, *Cyphomyrmex*, *Mycopepurus,* and *Sericomyrmex*). Ground-dwelling specialist predators, leaf cutters and raid hunting predators had less than 10 species each (Supplemental material). Among the nine functional groups, six were related to the distance from the

transition between igapó and terra-firme forests (Figure 5). Proportionally more arboreal predators (p < 0.001) and generalist omnivorous (p = 0.04) were sampled further from the igapó/terra-firme ecotone. On the other hand, the proportion of cryptobiotic attines (p = 0.008), ground-dwelling omnivores (p = 0.02), leaf cutters (p = 0.018) and raid hunting predators (p = 0.02) decreased as the distance from terra-firme increased. Cryptobiotic attines and raid hunting predators were not present on fluvial islands.
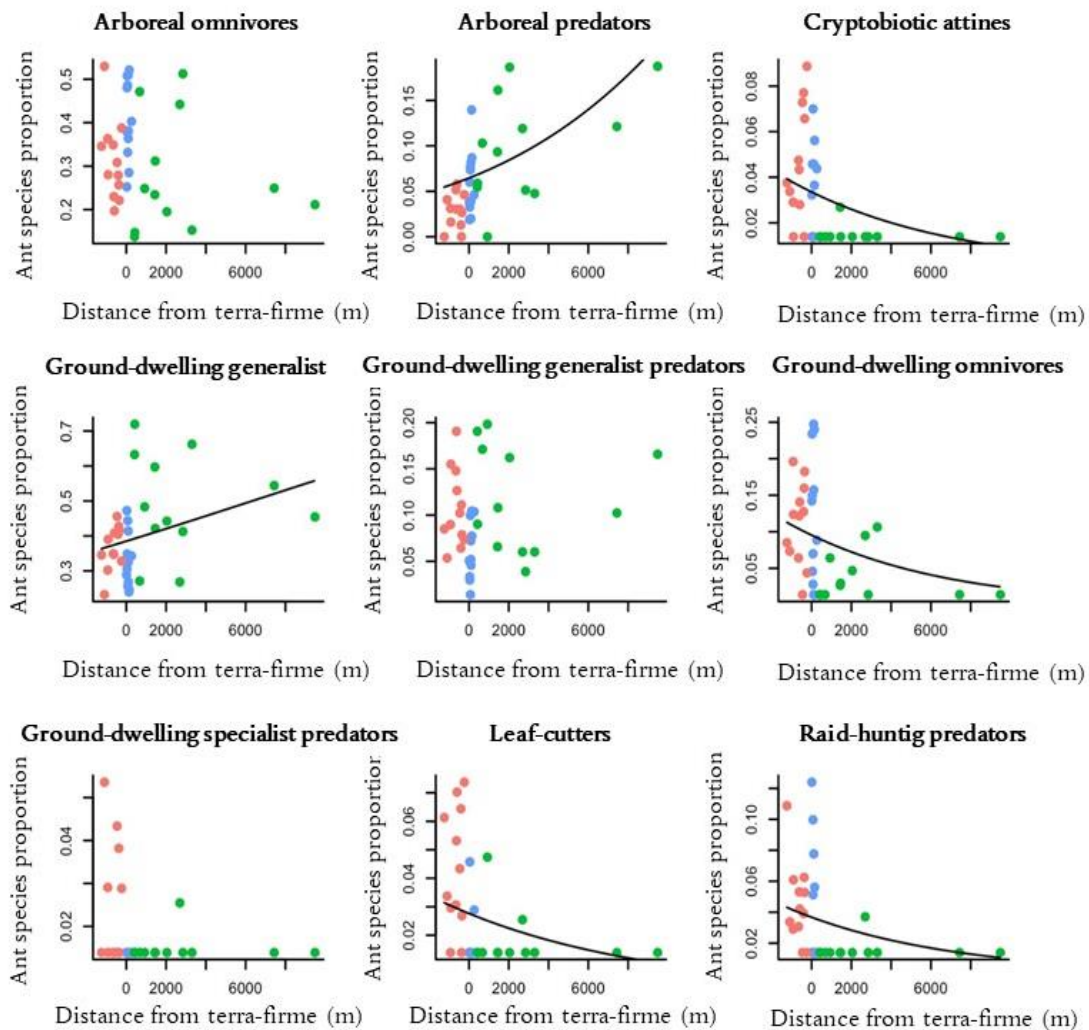

Figure 5: Relation between distance from terra-firme and the ant species proportion per functional group. Magenta: terra-firme forest; green: igapó forest; blue: fluvial islands.

Discussion

This study demonstrated how disturbance and isolation structure the epigaeic and arboreal ant assemblages, affecting the arboreal and epigaeic diversity differently. Our results suggest that the flood pulse modifies the structure of ant assemblages in seasonally flooded forests, increasing the species turnover. On a larger scale, islands more distant from the terra-firme harbor a subset of epigaeic species of closer and less isolated islands. Disturbance and isolation seem to favor the presence of arboreal predators and generalist omnivores species as there is an increase in these species' functional groups on river islands. Overall, fluvial islands generally harbor an impoverished functional diversity compared with undisturbed forests, which can alter the functions performed by ants in these environments. However, the species turnover component dominates in both environments and strata, suggesting that fluvial islands have potential conservation value for ants.

We showed that fluvial islands and igapó forests have a lower ant species richness than terra-firme forests. This is a predicted and recurrent pattern reported in previous studies (e.g., Majer & Delabie 1994; Mertl et al. 2009; Pringle et al. 2019; Oliveira et al. 2021). The igapó forest and fluvial islands can be flooded for up to six months, limiting the use of the ground layer during this period. Therefore, the occurrence and abundance of ground-nesting species are limited since suitable nesting locations (Mertl et al. 2009; Vasconcelos et al. 2010) and food resources are scarce during the flood (Fernandes et al. 2019). In the igapó forest, colonies can migrate horizontally to the terra-firme forest while rising river levels, returning in the retreat of the waters (Adis, 1997). However, the habitat limitation during the high-water period is especially severe for the ant species in the fluvial islands. Thus, even if some epigaeic species can migrate

vertically from the ground to the canopy and co-exist with arboreal species (Adis 1997; Adis & Junk 2002), many other species cannot by a lack of traits or by competition with arboreal species already established (Blüthgen & Stork 2007), decreasing the local species richness (Ward 1999). The horizontal migration between terra-firme and igapó may explain the presence of some strict ground-dwelling species in igapó forests during the dry season, resulting in intermediate species richness between terra-firme and islands.

If vertical and horizontal migration is largely reduced in islands, ground-dwelling species will probably go extinct locally during the flood period, though being able to recolonize the area in the dry season from other areas such as the terra-firme forest through flight (Hölldobler & Wilson 1990). Furthermore, smaller islands (sampled in this study) tend to have fewer species because of their smaller area (e.g., MacArthur & Wilson 1967) and being more affected than larger islands by the edge effect and resource limitation (Ewers & Didham, 2006). However, we did not detect differences in the number of epigaeic ant species between fluvial islands and the igapó connected to the terra-firme forest, suggesting that the disturbance caused by flooding is the predominant process in this system.

In contrast to the epigaeic stratum, the number of ant species in the arboreal stratum did not differ between environments. The food resource used by arboreal species is more like epigaeic species (Blüthgen & Fiedler, 2002; Camarota et al. 2006). Arboreal species tend to be predators and consumers of liquid sugar resources, such as using extrafloral nectaries and exudates from sap-sucking insects (Blüthgen et al. 2000). This similarity increases the role of competition, increasing the dominance (Cerdá et al. 2013). Consequently, dominant species prevent other dominant species from occurring on the same plant, reducing the number of species locally (Blüthgen & Feldhaar 2010). Camarota et al. 2016 suggest that competition is the most significant mechanism affecting

the distribution of arboreal ant species. Furthermore, the arboreal stratum in fluvial islands and igapó forest may be partially exposed during the flood, keeping a portion of the habitat always available. The higher stability of nesting sites in the arboreal stratum on islands and igapós may maintain a species richness like the terra-firme forest.

We observed different ant assemblages' compositions in the three environments in both strata. In floodplain forests, the epigaeic stratum is suppressed during the flood period, and the availability of food resources and nesting sites reduces severely. This event explains the presence of genera that nest only on the ground, in the leaf litter or rotten trunks (*Acanthognathus, Acanthostichus, Gigantiops, Mycocepurus, Octostruma, and Sericomyrmex*) exclusively in the areas of terra-firme forest. The same occurs for some species that forage in the vegetation but nest on the ground, such as *Paraponera clavata* and *Ectatomma tuberculatum* (Dejean 2007). The absence of these species on the fluvial islands and in the igapó forest may indicate how flooding may directly affect the arboreal ant stratum. However, the indirect effects of disturbance caused by flooding may be more pervasive for the arboreal ant stratum. Due to the flood pulse, the diversity, richness, and biomass of plant species in Amazonian floodplain forests are lower than in the adjacent terra-firme forests (Gentry 1982; Parolin et al. 2004; Piedade et al. 2005). Vegetation structure is closely related to resources and nesting sites for arboreal ants (Blüthgen & Feldhaar, 2010, Powell et al. 2011), as well as the competitive interactions among species (Perfecto & Snelling 1995; Ribas et al. 2003, Camarota et al. 2016).

We observed a nested pattern of epigaeic ants, demonstrating that their assemblage on fluvial islands (locations farther from terra firme) is a subgroup of the epigaeic species assemblage on igapó and terra firme. Isolated communities generally form nested subgroups. Only species with good dispersal abilities can colonize remote islands (Moore et al. 2008). In addition, the environmental conditions on islands are

considered more stressful for most taxa since food resources and habitat diversity are scarcer (Gravel et al. 2011). For this reason, the ant species able to disperse to these sites also need to find a suitable habitat for colony foundation (Hakala et al. 2019). However, the magnitude of nestedness was low (NODF = 17.4), which suggests that much of the difference in ant composition cannot be explained by the nested loss of species on fluvial islands. Our β diversity decomposition reinforces this pattern. We found that the species replacement component dominated all environments in both strata.

Our results also suggest a consistent restructuring of ant assemblages. Some ant functional groups were not detected on fluvial islands (i.e., cryptobiotic attines, ground-dwelling omnivores, leaf cutters, and raid hunting predators), while others increased their proportion. The guild of leaf cutters (comprising the genera *Atta*, *Mycetomoellerius*, and *Paratrachymyrmex*) and cryptobiotic attines (*Apterostigma*, *Cyphomyrmex*, *Mycocepurus*, and *Sericomyrmex*) is part of the fungus-growing ants' group (Groc et al. 2013). These genera nest mainly on the ground, amid leaf litter, or on trunks (Baccaro et al. 2015), an ephemeral habitat on islands and in the igapó forest, where most ground nests are destroyed during forest flooding (Adis 1982). Thus, ground-dwelling ant species can usually only survive in places where the influence of flooding is minimal (Majer & Delabie 1994). This may explain why these genera exist only in the terra-firme and igapó forest. Furthermore, even if some fungus-growing ant species can migrate vertically to the trees (Adis et al. 2001; Adis 1982), cryptobiotic attine ants, may be affected by the increased solar irradiance that occurs in higher vegetation stratum, a condition to which they are not adapted (Jacquemin et al. 2016; Yanoviak & Kaspari 2000).

In other cases, the proportion of arboreal predators and generalist omnivores increased with the distance from the transition between igapó and terra-firme forests (genera *Daceton*, *Gnamptogenys*, *Platythyrea*, *Pseudomyrmex, Blepharidatta,*

Brachymyrmex Camponotus, Crematogaster, Ectatomma, Monomorium, Nylanderia, Pheidole). Predatory ants typically feed on other invertebrates (Blüthgen & Feldhaar 2010), which may increase their density in floodplain forests (Rowedder et al. 2021). Hence, arboreal predator ants, such as *Daceton armigerum* (Dejean et al. 2012) and *Pseudomyrmex* species (Hölldobler & Wilson 1990), may stand as better competitors and be able to dominate the food resource. On the other hand, generalist omnivorous ants have a more flexible diet, feeding on invertebrates and different types of resources, such as extrafloral nectary and hemipteran exudate (Blüthgen & Feldhaar 2010). In most cases, areas experiencing disturbance are dominated by opportunistic or generalist species, such as *Pheidole, Brachymyrmex*, and *Nylanderia*, assumably because these species can take advantage of changes in resource availability (Hoffmann and Andersen 2003). Genera consisting of specialist predators seem to have less tolerance to flooding (Mertl 2009). Thus, specialists tend to disappear after disturbance (Adis & Junk 2002), while generalist species tend to increase (Baccaro et al. 2013).

Ants comprise a crucial group for forest structure and dynamics, being a relevant component of the biota in flooded and non-flooded ecosystems in the Amazon (Adis & Junk 2002; Pringle et al. 2019). Our findings suggest that the flood pulse modifies the structure of ant assemblages that live in seasonally flooded forests. These changes are more profound on fluvial islands. Fluvial islands generally harbor an impoverished functional diversity fauna, which can alter the functions performed by ants in these environments. However, the high species turnover suggests that fluvial islands have potential conservation value for ants at larger scales. This is especially relevant given the fluvial islands and flooded forests are vulnerable to threats such as hydroelectric dam construction (Marinho et al. 2020) and sand mining activities (ICMBio 2017). Therefore, improving our understanding of the spatial distribution of ant assemblages in such a

dynamic ecosystem could help predict the resilience face other tropical disturbed ecosystems.

References

Abreu, R. C. R., Hoffmann, W. A., Vasconcelos, H. L., Pilon, N. A., Rossatto, D. R., & Durigan, G. (2017). The biodiversity cost of carbon sequestration in tropical savanna. *Sci. Adv*. 3, e1701284. http://dx.doi.org/10.1126/sciadv.1701284

Adis, J. (1982). Eco-entomogical observations from the Amazon III. How do leaf cutting ants of inundation-forests survive flooding? *Acta amazonica* 12: 839-840. https://doi.org/10.1590/1809-43921982124839

Adis, J. (1984). 'Seasonal igapó'-forests of Central Amazonian black-water rivers and their terrestrial arthropod fauna. In: Sioli H. (Ed*.*) *The Amazon. Limnology and landscape ecology of a mighty tropical river and its basin*. Monographiae Biologicae, Junk Pubi. Dordrecht. 245-268.

Adis, J. (1997). Estratégias de sobrevivência de invertebrados terrestres em florestas inundáveis da Amazônia Central: uma resposta à inundação de longo período. *Acta Amazonica* 27(1): 43-54. https://doi.org/10.1590/1809-43921997271054

Adis, J., Marques, M. I., & Wantzen, K. M. (2001). First observations on the survival strategies of terricolous arthropods in the northern Pantanal wetland of Brazil. *Andrias* 15: 127-128.

Adis, J., & Junk, W. J. (2002). Terrestrial invertebrates inhabiting lowland river floodplains of Central Amazonia and Central Europe: a review. *Freshwater Biol*. 47: 711–731. https://doi.org/10.1046/j.1365-2427.2002.00892.x

Adis, J., Erwin T. L., Battirola, L. D., & Ketelhut S. M. (2010). The Importance of Amazonian Floodplain Forests for Animal Biodiversity: Beetles in Canopies of Floodplain and Upland Forests. In: Junk, Piedade, Wittmann, Shöngart, Parolin (Eds). *Amazonian floodplain forest*. Springer.

Agosti, D., & Alonso, L. E., (2000). The ALL protocol – a standard protocol for the collection of ground-dwelling ants. In: Agosti, D., Majer, J. D., Alonso, L. E., & Schultz, T. R. (Eds.), *Ants – Standard Methods for Measuring and Monitoring Biodiversity, Biological Diversity Handbook Series* (pp. 204–206). Smithsonian Institution Press, Washington, DC.

Alexander, D. E. (1990). Drag Coefficients of Swimming Animals: Effects of Using Different Reference Areas. *Biol Bull*. 179: 186–190. https://doi.org/10.2307/1541768

Almeida-Neto, M., Guimaraes, P., Guimaraes, 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

Andersen, A. N. (1992). Regulation of 'momentary' diversity by dominant species in exceptionally rich ant communities of the australian seasonal tropics. *Am. Nat.* 140, 401–20. https://doi.org/10.1086/285419

Baccaro, F. B., Ketelhut, S. M. & De Morais, J. W. (2010). Resource distribution and soil moisture content can regulate bait control in an ant assemblage in Central Amazonian Forest. *Austral Ecology* 35: 274-281. https://doi.org/10.1111/j.1442-9993.2009.02033.x

Baccaro, F. B., Rocha, I. R., Aguila, B. E. G., Schietti, J. Emilio, T., Pinto, J. L. P. V., Lima, A. P. & Magnusson, W. E. (2013). Changes in ground-dwelling ant functional diversity are correlated with water-table level in an amazonian terra firme forest. *Biotropica*, 45(6): 755–763. https://doi.org/10.1111/btp.12055

Baccaro, F., Feitosa, R., Fernández, F., Fernandes, I., Izzo, T., Souza, J., & Solar, R. (2015). *Guia para os gêneros de formigas do Brasil*. INPA, Manaus.

Ballinger, A., Lake, P. S., & Nally, R. M. (2007). Do terrestrial invertebrates experience floodplains as landscape mosaics? Immediate and longer-term effects of flooding on ant assemblages in a floodplain forest. *Oecologia*, 152: 227-238. https:/10.1007/s00442-006-0648-0

Baselga, A. (2010). Partitioning the turnover and nestedness components of beta diversity. – Global Ecol. *Biogeogr.* 19: 134–143. https://doi.org/10.1111/j.1466-8238.2009.00490.x

Begon, M., Townsend, C.R., & Harper, J. L. (2007). *Ecologia: de indivíduos a ecossistemas*. 4 ed. Artmed, Porto Alegre.

Blüthgen, N., & Fiedler, K. (2002). Interactions between weaver ants (*Oecophylla smaragdina*), homopterans, trees and lianas in an Australian rainforest canopy. *Journal of Animal Ecology* 71:793–801. http://www.jstor.org/stable/1555793.

Blüthgen, N., & Feldhaar, H. (2010). Food and shelter: how resources influence ant ecology. In: Lach L, Parr C, Abbott K (Eds). *Ant ecology* (pp. 115-156). Oxford University Press, Oxford.

Borges, S. H., Baccaro, F., Moreira, M., & Choueri, E. L. (2019). Bird assemblages on Amazonian River islands: Patterns of species diversity and composition. *Biotropica*, 51: 903– 912. https://doi.org/10.1111/btp.12716

Camarota F., Powell S., Melo A. S., Priest G., Marquis R. J., & Vasconcelos H. L. (2016). Co-occurrence patterns in a diverse arboreal ant community are explained more by competition than habitat requirements. *Ecol Evol.,* 6(24):8907– 8918. https://doi.org/10.1002/ece3.2606

Chung, N. C., Miasojedow, B., & Gambin, A. (2019). Jaccard/Tanimoto similarity test and estimation methods for biological presence-absence data. *BMC Bioinformatics*, 20, 644. https://doi.org/10.1186/s12859-019-3118-5

Cribari-Neto, F., & Zeileis, A. (2010). Beta Regression in R. *Journal of Statistical Software*, 34(2) 1–24. https://doi.org/10.18637/jss.v034.i02

Cutler, A. (1991). Nested Faunas and Extinction in Fragmented Habitats. *Conservation Biology*, 5: 496-504. http://www.jstor.org/stable/2386072

Darlington, P. J. (1957). *Zoogeography: the geographical distribution of animals* (675 pp.). John Wiley, New York.

de Arruda, F. V., Camarota, F., Ramalho, W. P., Izzo, T. J., & Almeida, R. P. S. (2021). Seasonal variation of ground and arboreal ants in forest fragments in the highly threatened Cerrado-Amazon transition. *J Insect Conserv* 25, 897–904. https://doi.org/10.1007/s10841-021-00356-1

de Simone, O., Müller, E., Junk, W. J., & Schmidt W. (2002). Adaptations of Central Amazon tree species to prolonged flooding: Root morphology and leaf longevity. *Functional Plant Biology* 29: 1025-1035. https://doi.org/10.1055/s-2002-34127

Dejean, A., Delabie, J. H. C., Corbara, B., Azémar, F., Groc, S., Orivel, J., & Leponce, M. (2012). The Ecology and Feeding Habits of the Arboreal Trap-Jawed Ant *Daceton armigerum. PLOS ONE* 7(5): e37683. https://doi.org/10.1371/journal.pone.0037683

Drew, M. C., He, C. J., & Morgan, P. W. (2000). Programmed cell death and aerenchyma formation in roots. *Trends Plant Sci* 5: 123-127. https://doi.org/10.1016/s1360-1385(00)01570-3

Dunn, R. R., Parker, C. R., Geraghty, M., & Sanders, N. J. (2007). Reproductive phenologies in a diverse temperate ant fauna. *Ecol. Entomol*. 32: 135-142. https://doi.org/10.1111/j.1365-2311.2006.00839.x

Ewers, R. M., & Didham, R. K. (2006). Confounding factors in the detection of species responses to habitat fragmentation. *Biol Rev* 81:117–142. https://doi.org/10.1017/S1464793105006949

Fernandes, T. T., Dáttilo, W., Silva, R. R., Luna, P., Oliveira, C. M., & Morini, M. S. C. (2019). Ant occupation of twigs in the leaf litter of the Atlantic Forest: influence of the environment and external twig structure. *Trop Conserv Sci* 12:1–9. https://doi.org/10.1177/1940082919852943

Frick, W. F., Hayes, J. P. & Heady, III, P. A. (2009). Nestedness of desert bat assemblages: species composition patterns in insular and terrestrial landscapes. *Oecologia* 158, 687. https://www.jstor.org/stable/40309787

Gauer, U. (1997). The Collembola. In: Junk, W. J. (Ed). *The Central Amazon Floodplain* (pp. 351-359). Vol. 126. Springer Berlin Heidelberg, Berlin, Germany. https://www.jstor.org/stable/40309787

Gerisch, M., Agostinelli, V., Henle, K., Dziock, F., (2012). More species, but all do the same: contrasting effects of flood disturbance on ground beetle functional and species diversity. *Oikos* 121:508-515. https://www.jstor.org/stable/41429319

Gravel, D., Massol, F., Canard, E., Mouillot, D., & Mouquet, N. (2011). Trophic theory of island biogeography. *Ecology Letters*, 14, 1010– 1016. https://doi.org/10.1111/j.1461-0248.2011.01667.x

Greenleaf, S. S., Williams, N. M., Winfree, R. & Kremen, C. (2007). Bee foraging ranges and their relationship to body size. *Oecologia* 153: 589-596. https://doi.org/10.1007/s00442-007-0752-9

Groc, S., Delabie, J. H. C., Fernández, F., Leponce, M., Orivel, J., Silvestre, R., Vasconcelos, H. L., & Dejean, A. (2014). Leaf-litter ant communities (Hymenoptera: Formicidae) in a pristine Guianese rainforest: stable functional structure versus high species turnover. *Myrmecological News* 19: 43-51.

Guilherme, D. R., Pequeno, P. A. C. L., Baccaro, F. B., Franklin, E., Neto, C. R. S, & Souza, J. L. P. (2022). Direct and indirect effects of geographic and environmental factors on ant beta diversity across Amazon basin. *Oecologia* 198, 193–203. https://doi.org/10.1007/s00442-021-05083-7

Hakala, S. M., Seppä P., Helanterä, H. (2019). Evolution of dispersal in ants (Hymenoptera: Formicidae): a review on the dispersal strategies of sessile superorganisms. *Myrmecological News* 29: 35-55.

Hawkins, C. P., & MacMahon, J. A. (1989). Guilds: the multiple meanings of a concept. *Ann. Rev. Entomol*, 34, 423–451. https://doi.org/10.1146/annurev.en.34.010189.002231

Hess, L. L., Melack, J. M., Affonso, A. G., Barbosa, C., Gastil-Buhl, M., & Novo, E. M. L. M. (2015). Wetlands of the Lowland Amazon Basin: Extent, Vegetative Cover, and Dual-season Inundated Area as Mapped with JERS-1 Synthetic Aperture Radar. *Wetlands* 35, 745–756. https://doi.org/10.1007/s13157-015-0666-y

Hoffmann, B. D. & Andersen, A. N. (2003). Responses of ants to disturbance in Australia, with particular reference to functional groups. *Austral Ecology*, 28: 444-464. https://doi.org/10.1046/j.1442-9993.2003.01301.x

Hölldobler, B., Wilson E. O. (1990). *The Ants* (732 pp.). Cambridge: Belknap Press of Harvard University Press.

Hooper, D. U., Chapin, F. S., III, Ewel, J. J., Hector, A., Inchausti, P., Lavorel, S., Lawton, J. H., Lodge, D.M., Loreau, M., Naeem, S., Schmid, B., Setälä, H., Symstad, A. J., Vandermeer, J. & Wardle, D. A. (2005). Effects of biodiversity on ecosystem functioning: a consensus of current knowledge. *Ecological Monographs*, 75: 3-35. https://doi.org/10.1890/04-0922

Hotelling, H. (1993). Analysis of a complex of statistical variables into principal components. *J. Educ. Psychol.* 24:417-441. http://dx.doi.org/10.1037/h0071325

Hutchinson., E. (1944). Limnological studies in Connecticut. VII. A critical examination of the supposed relationship between phytoplankton periodicity and chemical changes in lake waters. *Ecology* 25, 3-26. https://doi.org/10.2307/1930759

ICMBio (2017). Plano de Manejo do Parque Nacional de Anavilhanas. Instituto Brasileiro do Meio Ambiente e dos Recursos Naturais Renováveis. Ministério do Meio Ambiente, ICMBio/MMA, Brasília.

Irion, G. & Adis, J. (1979). Evolução de florestas amazônicas inundadas, de igapó – um exemplo do rio Tarumã Mirim. *Acta Amazônica*, 9: 299-303. https://doi.org/10.1590/1809-43921979092299

Irion, G., Junk W. J., & Mello, J. A. S. N. (1997). The large central Amazonian River floodplains near and geomorphological aspects. In: Junk W. J. (Ed) The Central Amazon Floodplain: Ecology of a Pulsing System (pp. 23–46). Springer-Verlag, Berlin.

Jacquemin, J., Roisin, Y., & Leponce, M. (2016). Spatio-temporal variation in ant (Hymenoptera: Formicidae) communities in leaf-litter and soil layers in a premontane tropical forest. *Myrmecol News* 22:129–139.

Jolliffe, I. T. (2002). *Principal Component Analysis*. Springer, 2nd edition, New York.

Junk, W. J., Bayley, P. B., Sparks, R. E. (1989a). The Flood Pulse Concept in River-Floodplain-Systems. *Canadian Special Publications for Fisheries and Aquatic Sciences* 106: 110-127. https://publications.gc.ca/site/eng/9.816457/publication.html

Junk, W. J. (1989b). Flood tolerance and tree distribution in Central Amazonian floodplains. *In: Tropical forests: Botanical dynamics, speciation, and diversity.*

Academic Press London, New York. 47-64. http://dx.doi.org/10.1016/b978-0-12-353550-4.50012-5

Junk, W. J., & Welcomme, R. L. (1990). Floodplains. In: Patten, B. C. Wetlands and shallow continental waters bodies (pp. 524). 1nd. Academic Publishing: The Netherlands.

Kaspari, M., & Weiser, M. D. (2000). Ant activity along moisture gradients in a neotropical forest. *Biotropica* 32:703–711. https://doi.org/10.1111/j.1744-7429.2000.tb00518.x

Kaspari, M., Pickering, J., & Windsor, D. (2001). The reproductive flight phenology of a neotropical ant assemblage. *Ecol. Entomol.* 26: 245-257. https://doi.org/10.1046/j.1365-2311.2001.00320.x

Klein, R. W., Maschwitz, U., & Kovac, D. (1993). Flood control by ants: a Southeast Asian bamboo dwelling *Tetraponera* (Formicidae, *Pseudomyrmecinae*) bails water from its internode nests. *Insectes sociaux*, 40(1): 115-118. https://doi.org/10.1007/BF01338838

Lambeets, K., Vandegehuchte, M. L., Maelfait J., & Bonte, D. (2008). Understanding the impact of flooding on trait-displacements and shifts in assemblage structure of predatory arthropods on riverbanks. *Journal of Animal Ecology* 77:1162-1174.

Latombe, G., Roura-Pascual, N., & Hui, C. (2019). Similar compositional turnover but distinct insular environmental and geographical drivers of native and exotic ants in two oceans. *J Biogeogr*. 46: 2299– 2310. https://doi.org/10.1111/jbi.13671

Levin, S. A. (2000). Multiple scales and the maintenance of biodiversity. *Ecosystems*, 3(6): 498-506. https://doi.org/10.1007/s100210000044

Li, Y., Shipley B., Price J. N. et al., (2018). Habitat filtering determines the functional niche occupancy of plant communities worldwide. *J Ecol*.106: 1001-1009. https://doi.org/10.1111/1365-2745.12802

MacArthur, R. H., & Wilson, E. O. (1967). *The theory of island biogeography*. Princeton, NJ: Princeton University Press.

Macedo, L. P. M., Berti, Filho E., & Delabie J. H. C. (2011). Epigean ant communities in Atlantic Forest remnants of Sao Paulo: a comparative study using the guild concept. *Revista Brasileira de Entomologia*; 55(1): 75-78. https://doi.org/10.1590/ S0085-56262011000100012

Majer, J. D. (1990). The Abundance and Diversity of Arboreal Ants in Northern Australia. *Biotropica* 22(2), 191–199. https://doi.org/10.2307/2388412

Majer, J. D. & Delabie, J. H. C. (1994). Comparison of the ant communities of annually inundated and terra-firme forests at Trombetas in the Brazilian Amazon. *Insectes Sociaux*, 41(4): 343-359. https://doi.org/10.1007/BF01240639

Marden, J. H. (2000). Variability in the size, composition, and function of insect flight muscles. *Annu. Rev. Physiol*. 62: 157-178. https://doi.org/10.1146/annurev.physiol.62.1.15

Marinho, R. R., Filizola Junior, N. P., & Cremon, É.H. (2020). Analysis of Suspended Sediment in the Anavilhanas Archipelago, Rio Negro, Amazon Basin. *Water 12,* 1073. https://doi.org/10.3390/w12041073

Maschwitz, U., & Moog, J. (2000). Communal peeing: a new mode of flood control in ants. *Naturwissenschaften* 87: 563-565. https://doi.org/10.1007/s001140050780

Matthews, W. J., Marsh-Matthews, E., Cashner, R. C., & Gelwick, F. (2013). Disturbance and trajectory of change in a stream fish community over four decades. *Oecologia*, 17*3*(3): 955-969. https://doi.org/10.1007/s00442-013-2646-3

Matthews, T. J., Cottee-Jones, H. E. W. & Whittaker, R. J. (2015). Quantifying and interpreting nestedness in habitat islands: a synthetic analysis of multiple datasets. *Diversity Distrib*., 21: 392-404. https://doi.org/10.1111/ddi.12298

Matthews, T. J., Guilhaumon, F., Triantis, K. A., Borregaard, M. K., & Whittaker, R. J. (2016). Island species–area relationships and species accumulation curves are not equivalent: an analysis of habitat island datasets. *Global Ecology and Biogeography*, 25: 847-858. https://doi.org/0.1111/geb.12439

McGill, B. J., Enquist, B. J., Weither, E., & Westoby, M. (2006). Rebuilding community ecology from functional traits. *Trends in Ecology and Evolution*, 21:178-185. https://doi.org/10.1016/j.tree.2006.02.002

Mertl, A. L., Wilkie, K. T. R., & Traniello, J. F. A. (2009). Impact of flooding on the species richness, density and composition of amazonian litter-nesting ants. *Biotropica*, 41(5): 633-641. https://doi.org/10.1111/j.1744-7429.2009.00520.x

Meyer, K. S. (2017). Islands in a Sea of Mud: Insights from Terrestrial Island Theory for Community Assembly on Insular Marine Substrata. *Advances in Marine Biology* 76:1-40. https://doi.org/10.1016/bs.amb.2016.09.002

Montero J. C, & Latrubesse E. M. (2013). The igapo of the Rio Negro in central Amazonia: linking late-successional inundation forest with fluvial geomorphology. *J S Am Earth Sci* 46:137–149. http://dx.doi.org/10.1016/j.jsames.2013.05.009

Moore, R. P., Robinson, W. D., Lovette, I. J., & Robinson, T. R. (2008). Experimental evidence for extreme dispersal limitation in tropical forest birds. *Ecology Letters*, 11, 960–968. https://doi.org/10.1111/j.1461-0248.2008.01196.x

Mouillot, D. Graham, A. J., Villéger, S., Mason, N. W. H., Bellwood, D. R. (2013). A functional approach reveals community responses to disturbances. *Trends Ecol. Evol.*, 28: 167-177. https://doi.org/10.1016/j.tree.2012.10.004

Nekola, J. C. & White, P. S. (1999). The distance decay of similarity in biogeography and

ecology. *Journal of Biogeography*, 26, 867–878. https://doi.org/10.1046/j.1365-2699.1999.00305.x

Nielsen, M. G. (1997). Nesting biology of the mangrove mud-nesting ant *Polyrhachis sokolova* Forel (Hymenoptera, Formicidae) in northern Australia. *Insectes Sociaux*, 44(1), 15-21. https://doi.org/10.1007/s000400050026

Oksanen, J., Blanchet, F. G., Kindt, R., Legendre, P., Minchin, P. R., O'Hara, R., et al., 2013. Package 'Vegan'. *Community Ecology Package*, Version 2. Available at: http://CRAN.R-project.org/package=vegan.

Parolin, P., de Simone, O., Haase, K. et al. (2004). Central Amazonian floodplain forests: Tree adaptations in a pulsing system. *Bot. Rev* 70, 357–380. https://doi.org/10.1663/0006-8101(2004)070[0357:CAFFTA]2.0.CO;2

Pianka, E.R. (1980). Guild struture in desert lizards. *Oikos* 35:194-201. https://doi.org/10.2307/3544427

Picket, S. T. A., & White, P. S. (1985) The Ecology of Natural Disturbance and Patch Dynamics (472 pp.). Academic Press, London. https://doi.org/10.1016/C2009-0-02952-3

Piedade, M. T. F., Junk, W. J., D'Angelo, S. A., Wittmann, F., Schöngart, J., Barbosa, K. M. N., & Lopes, A. (2010). Aquatic herbaceous plants of the Amazon floodplains: state

of the art and research needed. *Acta Limnologica Brasiliensia* 22:165-178. https://doi.org/10.4322/actalb.02202006

Piedade, M. T. F., Junk, W. J., Adis, J., & Parolin, P. (2005). Ecologia, zonação e colonização da vegetação arbórea das ilhas de Anavilhanas. Pesquisas, Botânica 56: 117-144. http://hdl.handle.net/11858/00-001M-0000-000F-DA1B-5

Prance, G.T., & Pires, J. M. (1985). The vegetation types of the Brazilian Amazon. In: Prance, G.T. & Lovejoy, T. E. (Eds.). *Key Environments: Amazonia* (pp. 109-145). Pergamon Press, Oxford.

Powell, S., Costa A. N., Lopes, C. T, Vasconcelos, H. L (2011). Canopy connectivity and the availability of diverse nesting resources affect species coexistence in arboreal ants. *J Anim Ecol* 80:352–360.

Pringle, E. G., Santos, T. F., dos Gonçalves, M. S., Hawes, J. E., Peres, C. A., & Baccaro, F. B. (2019). Arboreal ant abundance tracks primary productivity in an Amazonian whitewater river system. *Ecosphere* 10, 10. https://doi.org/10.1002/ecs2.2902

R Core Team (2021). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL https://www.R-project.org/.

Ribas, C. R., Schoereder, J. H., Pic, M., Soares, S. M. (2003). Tree heterogeneity, resource availability, and larger scale process regulating arboreal ant species richness. *Austral Ecol*. 28, 305–314. https://doi.org/10.1046/j.1442-9993.2003.01290.x

Rico-Gray V., Oliveira P. S. 2007. The ecology and evolution of ant– plant interactions. University of Chicago Press. https://doi.org/10.7208/chicago/9780226713540.001.0001

Rizali, A., Lohman, D. J., Buchori, D., Prasetyo, L. B., Triwidodo, H., Bos, M. M., Yamane, S., & Schulze, C. H. (2010). Ant communities on small tropical islands: effects of island size and isolation are obscured by habitat disturbance and 'tramp' ant species. *Journal of Biogeography*, 37: 229-236. https://doi.org/10.1111/j.1365-2699.2009.02194.x

Roces, F., & Klaipeda, C. (2000). Humidity preference for fungus culturing by workers of the leaf-cutting ant *Atta sexdens rubropilosa*. *Insectes soc*. 47, 348–350. https://doi.org/10.007/PL00001728

Root, R. B. (1967). The niche exploitation pattern of the blue-gray gnatcatcher. *Ecol. Monogr*. 37, 317e350. https://doi.org/10.2307/1942327

Rowedder, A. R. P., Laranjeiras, T. O., Haugaasen, T., Gilmore, B., & Cohn-Haft, M. (2021). Response of Understory Avifauna to Annual Flooding of Amazonian Floodplain Forests. *Forests* 12, 1004. https://doi.org/10.3390/f12081004

Russell, F. L., & Roy, A. (2008). Spatial variation in seed limitation of plant species richness and population sizes in floodplain tallgrass prairie. *Oecologia* 158, 569–578. https://doi.org/10.1007/s00442-008-1159-y

Simberloff, D. & Dayan, T. (1991). The guild concept and the structure of ecological communities. *Annu. Rev. Ecol. Syst.* 22: 115-143. https://doi.org/10.1146/annurev.es.22.110191.000555

Southwood, T. R. E. (1977). Habitat, the templet for ecological strategies? *J. Anim. Ecol*. 46: 337-365. https://doi.org/10.2307/3817

Spicer, M. E., Stark, A. Y., Adams, B. J., Kneale, R., Kaspari, M., & Yanoviak, S. (2017). Thermal constraints on foraging of tropical canopy ants. *Oecologia* 183, 1007–1017. https://doi.org/10.1007/s00442-017-3825-4

Tilman, D., Reich, P. B. & Isbell, F. (2012). Biodiversity impacts ecosystem productivity as much as resources, disturbance, or herbivory. *Proc. Natl Acad. Sci. USA* 109:10394-10397. https://doi.org/10.1073/pnas.120824010

Torres, M. T., Souza, J. L. P., & Baccaro, F. B. (2020). Distribution of epigeic and hypogeic ants (Hymenoptera: Formicidae) in ombrophilous forests in the Brazilian Amazon. *Sociobiology*, 67(2), 186-200.
https://doi.org/10.13102/sociobiology.v67i2.4851

Ulrich, W., & N. J. Gotelli. (2007). Disentangling community patterns of nestedness and species co-occurrence. *Oikos* 116: 2053-2061. http://www.jstor.org/stable/40235043.

Vicente, R. E., Prado, L. P., & Izzo, T. J. (2016). Amazon Rainforest Ant-Fauna of Parque Estadual do Cristalino: Understory and Ground-Dwelling Ants. *Sociobiology*, 63(3), 894–908. https://doi.org/10.13102/sociobiology.v63i3.1043

Villéger, S., Mason, Norman W. H., & Mouillot, D., (2008). New multidimensional functional diversity indices for a multifaceted framework in functional ecology. *Ecology* 89:2290-2301. https://doi.org/10.1890/07-1206.1

Wang, Y., Wang, X., Ding, P. (2012). Nestedness of snake assemblages on islands of an inundated lake. *Current Zoology*, 58(6):828–836. https://doi.org/10.1093/czoolo/58.6.828

Ward, J. V., Malard, F., Tockner, K. & Uehlinger, U. (1999). Influence of ground water on surface water conditions in a glacial flood plain of the Swiss Alps. *Hydrological Processes*,13(3):277-293. https://doi.org/10.1002/(SICI)10991085(19990228)13:3<277::AID-HYP738>3.0.CO;2-N

Weiher, E., Clarke, G. D. P., & Keddy, P. A. (1998). Community assembly rules, morphological dispersion, and the coexistence of plant species. *Oikos* 81: 309-322.

Wilson, E. O. (1987). The arboreal ant fauna of Peruvian Amazon forests - a first assessment. *Biotropica* 19:245–251. https://doi.org/10.2307/2388342

Wilson, J.B. (1999). Guilds, functional types and ecological groups. *Oikos* 86, 507–522. https://doi.org/10.2307/3546655

Wittmann, F., Schöngart, J., & Junk, W. J. (2010). Phytogeography, species diversity, community structure and dynamics of central Amazonian floodplain forests. In: Junk, W. J., et al. (Eds). *Central Amazonian floodplain forests: ecophysiology, biodiversity, and sustainable management* (pp. 61-102). Dordrecht-Heidelberg-London-New York. Springer Verlag. https://doi.org/10.1007/978-90-481-8725-6_4

White, P. S. & Jentsch, A. (2004). Disturbance, succession, and community assembly in terrestrial plant communities. In: *Assembly Rules and Restoration Ecology*: Bridging the Gap Between Theory and Practice. Island Press.

Wright, D. H. & Reeves, J. H. (1992). On the meaning and measurement of nestedness of species assemblages. *Oecologia* 92: 416-42. https://doi.org/10.1007/BF00317469

Wright, D. H., Patterson, B. D., Mikkelson, G. M., Cutler, A., & Atmar, W. (1998). A comparative analysis of nested subset patterns of species composition. *Oecologia* 113:1-20. https://doi.org/10.1007/s004420050348

Yanoviak S. P., & Kaspari M. (2000). Community structure and the habitat templet: ants in the tropical forest canopy and litter. *Oikos* 89(2):259–266. https://doi.org/10.1034/j.1600-0706.2000.890206.x

Zhao, Y., Dunn, R. R., Zhou, H., Si, X., & Ding, P. (2020). Island area, not isolation, drives taxonomic, phylogenetic, and functional diversity of ants on land-bridge islands. *J Biogeogr*. 47: 1627– 1. https://doi.org/10.1111/jbi.13860

Conclusão

Esse foi o primeiro estudo que mostrou como a assembleia de formigas está estruturada nas ilhas fluviais da Amazônia. O pulso de inundação e o isolamento das ilhas afetaram a diversidade taxonômica das assembleias, mas de modos distintos entre os estratos terrícola e arborícola. A riqueza de espécies arborícolas não mudou entre ilhas, floresta de igapó e floresta de terra-firme, enquanto a riqueza de espécies terrícolas foi menor nas ilhas e florestas de igapó. A composição de espécies diferiu entre os ambientes, tanto no estrato terrícola quanto arborícola; porém, o padrão aninhado da assembleia foi apenas observado no estrato terrícola. Já as guildas que tiveram maior proporção nas ilhas foram aquelas predadoras (com um certo grau de agressividade) e onívoras generalistas (oportunistas e com uma dieta ampla), enquanto guildas mais associadas ao solo como atines criptobióticas e cortadeiras não ocorreram nas ilhas fluviais.

Essas diferenças que ocorreram, não só do aninhamento, mas da composição de espécies entre os ambientes e os estratos, podem refletir também em diferenças nas funções desempenhadas pelas espécies em cada ambiente. Distúrbios tipicamente aumentam o número de espécies oportunistas e redução de espécies especialistas (Andersen 1990), e isso modifica, por exemplo, a forma de utilização dos recursos alimentares da assembleia de ambientes perturbados e não perturbados. Filtros ambientais, como limitação de dispersão e o hábitat, processos presentes nas ilhas, podem formar assembleias cujo conjunto de espécies possua respostas similares às condições ambientais (Hooper et al. 2005). Isso é importante pois mostra a singularidade da assembleia de formigas de cada ambiente, sobretudo das ilhas fluviais, ambiente sensível que sofre ameaças como construção de hidrelétricas (Marinho et al. 2020) e atividades minerárias de extração de areia (ICMBio 2017).

Portanto, através desse estudo compreendemos como o alagamento e o isolamento estruturam a assembleia de formigas nas ilhas fluviais. Para um melhor entendimento da dinâmica de dispersão e estabelecimento das espécies nesses ambientes, é importante realizarmos trabalhos que busquem amostrar não só na estação seca, mas também na estação cheia, para que nosso entendimento sobre espécies migrantes e residentes durante o pulso de inundação seja ampliado. Um estudo da assembleia de formigas, incluindo ilhas maiores e adjacentes, também é interessante para entendermos melhor a origem da dispersão das espécies que chegam nas ilhas menores. Além disso, os padrões de diversidade das ilhas fluviais também podem ser melhor entendidos através de estudos utilizando traços morfológicos relacionados à capacidade de dispersão que

permitem uma maior compreensão de como fatores como o isolamento da ilha está afetando a dispersão das assembleias de formigas.

Apêndice

SUPPLEMENTARY MATERIAL

Silva, C.V.C., Santos, T. F., Gonçalves, A. L, S., Borges, S. H., Baccaro, F. B. **Effect of the flood pulse on ant assemblages on fluvial islands in the Amazon.** Manuscrito submetido ao Journal of Animal Ecology.

Figure S1: Environment types sampled in Anavilhanas National Park. A-B: terra-firme forest; C-D: igapó forest; E-F: fluvial island.
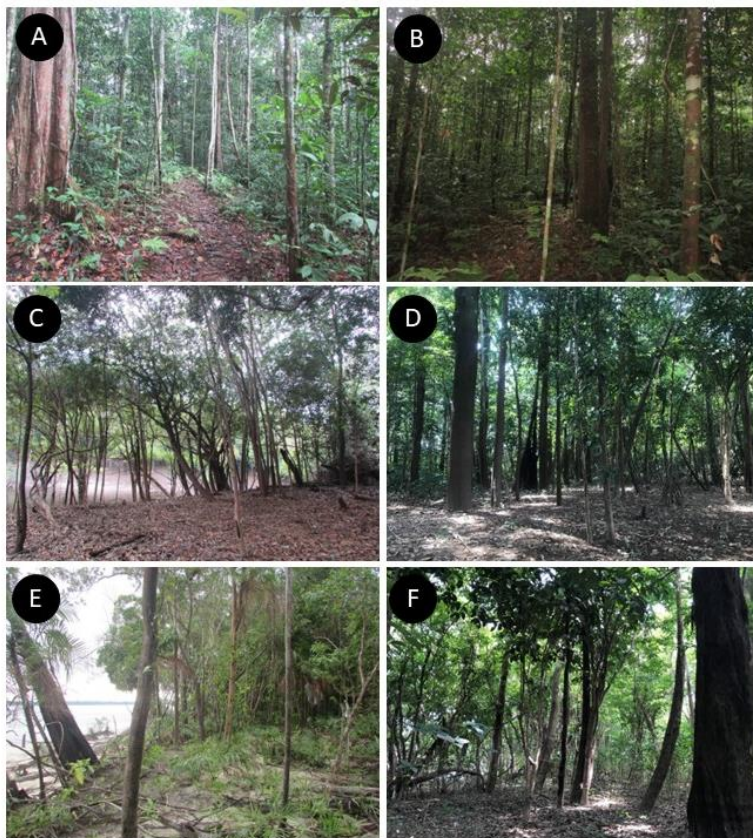
Table S1: Area and distance from terra-firme forest of the sampled fluvial island

Fluvial island	Area (km²)	Distance from terra-firme (m)
Praia	85.65	924.27
Gilberto	43.81	2844.7
Sobradinho	612.85	429.56
Sobrado	612.85	673.97
Três corações	34.26	417.61
Letícia	4.23	2042.57
Shakira	5.22	1456.23
Lô	2657.12	1434.5
Sapato	24.07	9487.98
Outra	8.83	2692.56
Ponta de faca	68.07	7437.17
Riscado	19.02	3301.51

Table S2: Ant species sampled in each functional group followed Groc et al. (2013). Species that were not included in the classification by Groc et al. (2013), we looked for the description of the species, or articles with information about the feeding and foraging habits of the species. Morphospecies in which the genus occupied two functional groups (i.e., arboreal predators and soil predators), we fit into the predominant capture stratum in our samples.

Ant species	Functional group
Daceton armigerum (LATREILLE, 1802)	
Gnamptogenys sp4	
Platythyrea angusta FOREL, 1901	
Pseudomyrmex atripes (SMITH, 1860)	
Pseudomyrmex pupa FOREL, 1911	
Pseudomyrmex sp1	Arboreal predators
Pseudomyrmex sp2	
Pseudomyrmex sp3	
Pseudomyrmex sp4	
Pseudomyrmex sp5	
Pseudomyrmex sp6	
Eciton rapax SMITH, 1855	
Eciton sp1	
Labidus sp1	
Labidus sp2	Raid hunting predators
Labidus sp3	
Neivamyrmex alfaroi (EMERY, 1890)	
Neoponera commutata (ROGER, 1860)	

Pachycondyla crassinoda (LATREILLE, 1802)

Acanthognathus sp1 *Acanthostichus* sp1 *Centromyrmex gigas* FOREL, 1911 *Strumigenys* sp1 *Strumigenys* sp2 *Strumigenys* sp3 *Strumigenys* sp4	Ground-dwelling specialist predators
Anochetus horridus KEMPF, 1964 *Anochetus simoni* EMERY, 1890 *Anochetus* sp1 *Gigantiops destructor* (FABRICIUS, 1804) *Gnamptogenys relicta* (MANN, 1916) *Gnamptogenys* sp1 *Gnamptogenys* sp2 *Gnamptogenys* sp3 *Gnamptogenys* sp5 *Gnamptogenys* sp6 *Gnamptogenys* sp7 *Hylomyrma* sp1 *Hypoponera* sp1 *Mayaponera arhuaca* (FOREL, 1901) *Mayaponera constricta* (MAYR, 1884) *Neoponera apicalis* (LATREILLE, 1802) *Neoponera carinulata* (ROGER, 1891) *Neoponera cavinodis* MANN, 1916 *Neoponera laevigata* (SMITH, 1858) *Neoponera oberthueri* (EMERY, 1890) *Neoponera* prox. *Rugosula* (EMERY, 1902) *Neoponera striatinodis* (EMERY, 1890) *Neoponera unidentata* (MAYR, 1862) *Neoponera verenae* FOREL, 1922 *Neoponera villosa* (FABRICIUS, 1804) *Octostruma amrishi* (MAKHAN, 2007) *Octostruma balzani* (EMERY, 1894) *Octostruma betschi* PERRAULT, 1988 *Octostruma* sp1 *Odontomachus caelatus* BROWN, 1976 *Odontomachus haematodus* (LINNAEUS, 1758) *Pachycondyla harpax* (FABRICIUS, 1804)	Ground-dwelling generalist predators
Azteca sp1 *Azteca* sp2 *Azteca* sp3 *Azteca* sp4 *Azteca* sp5 *Camponotus* sp1 *Camponotus* sp5	Arboreal omnivores

Camponotus sp10
Camponotus sp12
Camponotus sp14
Camponotus sp15
Camponotus sp17
Camponotus sp18
Camponotus sp2
Cephalotes atratus (LINNAEUS, 1758)
Cephalotes clypeatus (FABRICIUS, 1804)
Cephalotes eduarduli (FOREL, 1921)
Cephalotes foliaceus (EMERY, 1906)
Cephalotes sp1
Cephalotes sp2
Cephalotes sp3
Cephalotes sp4
Cephalotes sp5
Cephalotes sp6
Cephalotes sp7
Cephalotes sp8
Crematogaster brasiliensis MAYR, 1878
Crematogaster carinata MAYR, 1862
Crematogaster cf. *carinata* MAYR, 1862
Crematogaster cf. *erecta* MAYR, 1866
Crematogaster cf. *moelleri* FOREL, 1912
Crematogaster cf. *nigropilosa* MAYR, 1870
Crematogaster cf. *rochai* FOREL, 1903
Crematogaster limata SMITH, 1858
Crematogaster longispina EMERY, 1890
Crematogaster sp1
Crematogaster sp2
Crematogaster sp4
Crematogaster tenuicula FOREL, 1904
Dolichoderus bidens (LINNAEUS, 1758)
Dolichoderus bispinosus (OLIVIER, 1792)
Dolichoderus cf. *setosus* (KEMPF, 1959)
Dolichoderus diversus EMERY, 1894
Dolichoderus ferrugineus FOREL, 1903
Dolichoderus lamellosus (MAYR, 1870)
Dolichoderus laminatus (MAYR, 1870)
Dolichoderus lutosus (SMITH, 1858)
Dolichoderus rugosus (SMITH, 1858)
Dolichoderus sp1
Dolichoderus sp3
Dolichoderus spinicollis (LATREILLE, 1817)
Myrcidris epicharis WARD, 1990
Nesomyrmex sp1
Nesomyrmex sp2

Nesomyrmex sp3
Nesomyrmex sp4
Nesomyrmex sp5
Nesomyrmex sp6
Paraponera clavata (FABRICIUS, 1775)
Procryptocerus sp1
Procryptocerus sp2

Blepharidatta brasiliensis WHEELER, 1915
Brachymyrmex sp1
Brachymyrmex sp2
Camponotus sp11
Camponotus sp13
Camponotus sp6
Camponotus sp3
Camponotus sp4
Camponotus sp6
Camponotus sp7
Camponotus sp8
Camponotus sp9
Crematogaster sotobosque LONGINO, 2003
Crematogaster sp3
Crematogaster sp5
Ectatomma edentatum ROGER, 1863
Ectatomma lugens EMERY, 1894
Ectatomma tuberculatum (OLIVIER, 1792)
Monomorium sp1
Nylanderia sp1   Ground-dwelling
Nylanderia sp2   generalist
Nylanderia sp3
*Nylanderia s*p4
Pheidole aff. s*ubarmata* MAYR, 1884
Pheidole sp1
Pheidole sp10
Pheidole sp11
Pheidole sp12
Pheidole sp13
Pheidole sp14
Pheidole sp15
Pheidole sp16
Pheidole sp17
Pheidole sp18
Pheidole sp19
Pheidole sp2
Pheidole sp20
Pheidole sp21
Pheidole sp22
Pheidole sp23

Pheidole sp24
Pheidole sp25
Pheidole sp27
Pheidole sp3
Pheidole sp4
Pheidole sp5
Pheidole sp6
Pheidole sp8
Pheidole sp9

Carebara sp1	
Carebara sp2	
Megalomyrmex wallacei MANN, 1916	
Ochetomyrmex neopolitus FERNÁNDEZ, 2003	
Ochetomyrmex semipolitus MAYR, 1878	
Rogeria foreli EMERY, 1894	
Rogeria micromma KEMPF, 1961	
Rogeria scobinata KUGLER, 1994	
Rogeria subarmata (KEMPF, 1961)	
Solenopsis sp1	Ground-dwelling
Solenopsis sp2	omnivores
Solenopsis sp3	
Solenopsis sp4	
Solenopsis sp5	
Solenopsis sp6	
Tapinoma sp1	
Tapinoma sp2	
Tetramorium sp1	
Wasmannia auropunctata (ROGER, 1863)	
Wasmannia sp1	

Apterostigma cf. *urichii* FOREL, 1893	
Cyphomyrmex laevigatus WEBER, 1938	
Cyphomyrmex sp1	
Cyphomyrmex sp2	
Cyphomyrmex sp3	
Cyphomyrmex sp4	Cryptobiotic attines
Mycocepurus sp1	
Sericomyrmex sp1	
Sericomyrmex sp2	
Sericomyrmex sp3	
Sericomyrmex sp4	

Atta sp1	
Atta sp2	
Mycetomoellerius sp1	
Paratrachymyrmex sp1	Leaf-cutters
Paratrachymyrmex sp2	
Paratrachymyrmex sp3	
Paratrachymyrmex sp4	