



UNIVERSIDADE FEDERAL DO AMAZONAS
INSTITUTO NACIONAL DE PESQUISAS DA AMAZÔNIA
PROGRAMA DE PÓS-GRADUAÇÃO EM ZOOLOGIA

**Padrões ecológicos e funcionais em diferentes tipos de interações mutualistas
formiga-planta na Amazônia Brasileira**

TALITHA FERREIRA DOS SANTOS

Manaus, Amazonas

Março - 2026



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formiga-planta na Amazônia Brasileira**

Tese apresentada ao Programa de Pós-graduação em Zoologia, da Universidade Federal do Amazonas em parceria com o Instituto Nacional de Pesquisas da Amazônia para obtenção do título de Doutora em Zoologia.

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“It is interesting to contemplate an entangled bank...”
Charles Darwin, 1859

SUMÁRIO

LISTA DE TABELAS	iii
LISTA DE FIGURAS	iv
RESUMO GERAL	11
ABSTRACT	12
INTRODUÇÃO GERAL	13
REFERÊNCIAS	17
CAPÍTULO 1: Environmental Filtering and Network Structure in Ant-plant Mutualisms across Flooded and Unflooded Amazonian Forests	22
ABSTRACT	23
RESUMO	24
INTRODUCTION	25
MATERIAL AND METHODS.....	27
Field observations and species sampling.....	28
Mutualistic and opportunistic ants.....	29
Data Analyses	29
RESULTS	31
Species diversity	31
Network structure	31
DISCUSSION.....	36
CONCLUSION	39
REFERENCES	40
SUPPLEMENTARY MATERIAL	46
CAPÍTULO 2: Morphological convergence is stronger in myrmecophyte-associated ants than in facultative EFN-foragers in the Brazilian Amazon.....	49
ABSTRACT	51
INTRODUCTION	52
MATERIAL AND METHODS.....	54
Ant occurrence and interaction datasets	54
Morphological trait database	55
Analysis	56
RESULTS	58

Taxonomic diversity	58
Mobility-related traits	59
Feeding-related traits	60
DISCUSSION.....	62
Taxonomic overview	62
Mobility-related traits in symbiotic ants.....	64
Feeding-related traits in symbiotic ants.....	65
CONCLUSION	66
REFERENCES	67
SUPPLEMENTARY MATERIAL	75
CONSIDERAÇÕES GERAIS.....	87
DIVULGAÇÃO CIENTÍFICA	90

LISTA DE TABELAS

Capítulo 1

Table 1 - Structural metrics of ant-plant mutualistic networks in *terra-firme* and *igapó* forests by interaction type (facultative = EFN-bearing plants; obligate = myrmecophytes). Metrics include the number of ant and plant species, total number of ant-plant interactions, weighted nestedness (WNODF_{Obs}) and modularity (Q). *P*-values indicate significance based on comparisons with null models. Statistically significant values are in bold.....28

Table S1 - Summary of plot-level nestedness metrics (weighted NODF) for EFN-ant networks in *terra-firme* and *igapó* forests.....42

Table S2. Ant species associated with myrmecophytic plants in plots of *terra-firme* and *igapó* forests. The table presents the host plant and interacting ant species by forest type (TF = *terra-firme*, I = *igapó*), type of interaction (M = mutualist, O = opportunist), and observed interaction frequency.....43

Capítulo 2

Table 1. Morphological traits with functional categories and ecological roles associated with ant morphology used in the present study. Adapted from Silva & Brandão (2010)...52

Table S1. List of ant species associated with extrafloral nectaries across the Brazilian Amazon Basin, including nesting stratum classification and number of species per genus.....69

Table S2. List of arboreal ant species associated with myrmecophyte plants across the Brazilian Amazon Basin.....78

LISTA DE FIGURAS

Capítulo 1

Figure 1. Location of the study area and sampling points at Tarumã-Mirim, state of Amazonas, Brazil. Red dots = *terra-firme* forest (TF) and blue dots = *igapó* forest (IG)..25

Figure 2. Facultative ant-plant networks at Tarumã-Mirim. Links represent interactions between ants and plants mediated by extrafloral nectaries. Green bars indicate plant species, while red bars indicate ant species, in *igapó* (upper network) and *terra-firme* forests (lower network).....29

Figure 3. Obligatory ant-plant networks at Tarumã-Mirim. Links represent interactions between ants and plants mediated by domatias. Green bars indicate plant species, while red bars indicate ant species, in *igapó* (upper network) and *terra-firme* forests (lower network).....30

Figure 4. NMDS ordination represents the assemblage of facultative and obligatory interactions given the ant-plant distances (Bray-Curtis) at the network, for *terra-firme* (green dots) and *igapó* (blue dots) forests at Tarumã-Mirim.....31

Figure 5. Comparison between the density of myrmecophytic plants and opportunistic ant species in *terra-firme* (green dots) and *igapó* (blue dots) forests at Tarumã-Mirim...32

Figure S1. Observed weighted NODF values (bars) with null model means (dots) and standard deviations (error bars) for EFN-ant networks in each plot across *Terra-firme* and *Igapó* forests.....42

Capítulo 2.

Figure 1. Ant-mediated interactions with EFN-bearing and myrmecophytic plants. (A, B) *Pheidole biconstricta* and *Solenopsis* sp. visiting extrafloral nectaries of Bignoniaceae. (C) *Crematogaster brasiliensis* foraging on an extrafloral nectary located on the stem of *Inga* sp. (D, E) *Allomerus octoarticulatus* patrolling the domatia of *Miconia tococoronata* and *Hirtella myrmecophila*, respectively. (F) *Pseudomyrmex concolor* at the entrance of a domatium on *Tachigali plumbea*. Photo credit: F. Farroñay; T. Santos.....51

Figure 2. Morphospace of mobility-related traits for EFN-associated ants (blue) compared to the general arboreal ant assemblage (gray). Kernel density contours represent trait distributions across principal component axes.....55

Figure 3. Morphospace of mobility traits for myrmecophyte-associated ants (red) compared to the general arboreal ant assemblage (gray). Kernel density contours represent trait distributions across principal component axes.....56

Figure 4. Morphospace of feeding-related traits for EFN-associated ants (blue; **216 spp.**) compared to the general arboreal ant assemblage (gray; **475 spp.**). Kernel density contours represent trait distributions across principal component axes.....57

Figure 5. Morphospace of feeding-related traits for myrmecophyte-associated ants (red) compared to the general arboreal ant assemblage (gray). Kernel density contours represent trait distributions across principal component axes.....58

RESUMO GERAL

Interações mutualistas entre formigas e plantas são componentes centrais da estrutura e do funcionamento de comunidades tropicais. Essas associações variam em grau de especialização, abrangendo desde interações mais generalizadas mediadas por recursos alimentares (por exemplo, nectários extraflorais) até mutualismos altamente especializados, como a interação entre formigas e plantas mirmecófitas. No entanto, os fatores ecológicos e funcionais que estruturam essas interações em diferentes contextos ambientais ainda são pouco compreendidos. Nesse contexto, a presente tese busca compreender como filtros ambientais e funcionais influenciam a estrutura de interações facultativas e obrigatórias na Amazônia Brasileira. No **primeiro capítulo**, avaliamos como a variação nas condições de hábitat em florestas de igapó e florestas de terra-firme afeta a estrutura de redes de interações formiga-planta. Testamos a hipótese de que a instabilidade das florestas periodicamente inundáveis atua como filtro ambiental sobre as assembleias de formigas, resultando em mudanças na composição de espécies e na arquitetura das redes de interação. As redes em florestas de terra-firme apresentaram maior diversidade de interações, enquanto nas florestas de igapó houve maior especialização das interações. No **segundo capítulo**, utilizamos um conjunto abrangente de dados de formigas arbóreas da Amazônia brasileira para testar se espécies associadas a plantas mirmecófitas e a plantas com nectários extraflorais apresentam convergência funcional em traços morfológicos relacionados à locomoção e à alimentação. Utilizando análises multivariadas e funcionais, testamos a hipótese de que mutualismos mais especializados (formigas-mirmecófitas) estão associados a um conjunto mais restrito de traços. Os resultados indicaram forte convergência funcional, particularmente em traços de locomoção, em formigas associadas a mirmecófitas, enquanto associações com nectários extraflorais envolveram maior diversidade funcional. Em conjunto, os resultados demonstram que filtros ambientais e a especialização mutualista atuam de forma complementar na organização de interações formiga-planta na Amazônia. Esta tese contribui para a compreensão integrada de como processos ecológicos e funcionais moldam mutualismos tropicais, com implicações para a ecologia de comunidades e para a previsão de respostas a mudanças ambientais em florestas amazônicas.

Palavras-chave: Amazônia; formigas arbóreas; mutualismo; mirmecófitas; nectários extraflorais; redes ecológicas; traços funcionais; filtro ambiental.

ABSTRACT

Ant-plant mutualistic interactions are central components of the structure and functioning of tropical communities. These associations vary in specialization and frequency, ranging from generalized interactions mediated by food rewards (e.g., extrafloral nectaries) to highly specialized mutualisms, involving ant nesting in myrmecophytic plants. However, the ecological and functional drivers structuring these interactions across environmental contexts remain poorly understood. In this thesis, we investigated how environmental filtering in seasonally flooded forests and ant functional traits shape ant-plant interaction patterns in the Brazilian Amazon using ecological network and functional traits approaches. In **Chapter 1**, we evaluated how variation in habitat conditions between *igapó* forests and *terra-firme* forests affects the structure of ant-plant interaction networks. We tested the hypothesis that the instability of seasonally flooded forests acts as an environmental filter on ant assemblages, resulting in changes in species composition and in the architecture of interaction networks. Networks in *terra-firme* forests exhibited higher interaction diversity, whereas *igapó* forests showed higher interaction specialization. In **Chapter 2**, we used a comprehensive dataset of arboreal ant species from the Brazilian Amazon to test whether species associated with myrmecophytic plants and plants with extrafloral nectaries exhibit functional convergence in morphological traits related to locomotion and feeding. We use multivariate analyses and functional hypervolumes and hypothesize that more specialized mutualisms (ant-myrmecophyte associations) are linked to a narrower trait set. Results revealed strong functional convergence, particularly in locomotion traits, among ants associated with myrmecophytes, whereas extrafloral-nectary associations involved greater functional diversity. Together, these findings show that environmental filtering and mutualist specialization act complementarily in organizing ant-plant interactions in the Amazon. This thesis provides an integrated understanding of how ecological and functional processes shape tropical mutualisms, with implications for community ecology and for predicting responses to environmental change in Amazonian forests.

Keywords: Amazon; arboreal ants; mutualism; myrmecophytes; extrafloral nectaries; ecological networks; functional traits; environmental filtering.

INTRODUÇÃO GERAL

Interações mutualistas entre formigas e plantas são destacadas como sistemas-modelo para a compreensão de mecanismos ecológicos e comportamentais que moldam a biodiversidade (Beattie, 1985; Heil & McKey, 2003; Rico-Gray & Oliveira, 2007). Historicamente, evidências indicam que essas interações evoluíram por meio da exploração de recursos derivados de plantas por formigas terrícolas, inicialmente para substrato de forrageio e posteriormente para oportunidades de nidificação (Moreau et al., 2006; Nelsen et al., 2019), um processo reforçado pela coevolução e adaptações morfológicas (Brouat et al., 2001; Guimarães et al., 2017).

Associações mutualistas formiga-plantas variam amplamente em grau, especificidade e dependência, abrangendo desde associações facultativas e não especializadas até mutualismos altamente especializados e obrigatórios (Guimarães et al. 2006; Heil, 2010; Bronstein et al. 2006; Del-Claro et al., 2018). As recompensas às formigas incluem néctar extrafloral, corpos alimentares, domácias e substratos para jardins de formigas, promovendo diferentes gradientes de especialização entre parceiros (Guimarães et al. 2017; Rico-Gray & Oliveira, 2007; Mayer et al., 2014). Interações entre formigas e plantas com nectários extraflorais (NEFs), por exemplo, são compostas por espécies de formigas que forrageiam e se alimentam de néctar extrafloral localizado em estruturas não-reprodutivas das plantas. Além disso, a planta é utilizada pelas formigas como substrato para a interação com outros insetos, como hemípteros, em troca de proteção indireta contra herbívoros e outros potenciais inimigos (Rico-Gray & Oliveira 2007; Byk & Del-Claro 2011; Del-Claro et al. 2016). Esses sistemas são amplos e difusos, nos quais a proteção pelas formigas impacta não somente a planta hospedeira, mas também plantas vizinhas, destacando o papel das formigas como agentes de defesa indireta (Calixto et al., 2021; Nogueira, 2025).

Por outro lado, sistemas formigas-mirmecófitas envolvem forte dependência e fidelidade entre parceiros, sendo consideradas interações especializadas e obrigatórias, nas quais as plantas desenvolvem estruturas pré-formadas (domácias) em diferentes partes da planta, como caules ocos (ex.: *Cecropia*), espinhos (*Acácia*) ou bolsas foliares (*Hirtella*, *Maieta*) fornecendo às formigas sítios de nidificação em troca de proteção duradoura (Benson, 1985; Heil & McKey, 2003; Guimarães et al., 2006; Rico-Gray & Oliveira 2007). Em tais interações pelo menos um dos parceiros depende criticamente do outro para a sobrevivência ou reprodução. Vale ressaltar, que nesse caso, as linhagens de

formigas e plantas não tem relação filogenética. Contudo, análises comparativas indicam que a interação é fruto de coevolução entre a planta e sua formiga parceira, envolvendo a coadaptação de traços morfológicos e comportamentais entre as espécies (Fonseca & Ganade 1996; Ayala et al. 1996; Nelsen et al., 2019). Em contraste à natureza simbiótica do sistema formiga-mirmecófita, espécies de oportunistas podem nidificar e se estabelecer nas domácias, especialmente em ambientes que passam por distúrbio (Emer et al. 2013). Essas espécies não apresentam comportamento territorial, no entanto, podem deter herbívoros e atuar como conectores em rede de interações (Vasconcelos & Davidson 2000; Giusto et al. 2001; Emer et al. 2013).

Atualmente existem diversos métodos para estudos de interações ecológicas, que nos possibilitam investigar fenômenos cada vez mais complexos (Del-Claro et al. 2009). Uma abordagem relativamente recente em ecologia de interações são as redes de interações, com métricas que vem sendo utilizadas como ferramenta para compreender como pares de espécies que interagem estão estruturados em um determinado tempo ou espaço (Bascompte & Jordano, 2007; Dáttilo et al., 2014). Métricas de estrutura de rede (ou topologia) como aninhamento (nestedness) e modularidade revelam padrões de organização que refletem estabilidade, redundância e especialização dentro dos sistemas ecológicos (Olesen et al., 2007; Dáttilo et al., 2013a). Em redes aninhadas, espécies especialistas tendem a interagir com subconjuntos das espécies que interagem com espécies mais generalistas (Bascompte et al., 2006; Guimarães et al., 2006). Já as redes modulares são formadas por subgrupos de espécies fortemente interligados entre si, mas poucas interações com outras espécies da mesma rede.

Os filtros ambientais exercem papel crucial na configuração desses sistemas (Poff, 1997; Keddy & Laughlin, 2021). Na Amazônia Central, florestas de *terra-firme* e de *igapó* representam dois extremos de um gradiente ambiental moldado pelo regime de inundações sazonais (Junk et al., 1989; Junk et al., 2011; Wittmann et al., 2010). Enquanto as florestas de *Terra-firme* permanecem relativamente estáveis, as florestas de *Igapó* enfrentam longos períodos de submersão, com baixa disponibilidade de nutrientes e alta acidez recorrente das águas pretas (Melack & Hess, 2010; Hess et al., 2015). Esse distúrbio crônico e previsível atua como filtro ecológico sobre a composição das comunidades, selecionando espécies capazes de tolerar variações hidrológicas temporariamente extremas e excluindo localmente espécies não adaptadas à sobrevivência sob tais condições (Adis & Junk 2002; Veronese et al. 2025). Assim, os

regimes de inundação tendem a modificar tanto a composição de espécies de formigas quanto a arquitetura das interações ecológicas (Izzo et al., 2018; Pringle et al., 2019). Em sistemas formiga-mirmecófitas, por exemplo, as rainhas simbióticas geralmente localizam suas plantas hospedeiras por meio de sinais químicos (Heil et al. 2010), e em um estudo com *Tococa coronata* foi observado que a mirmecófito investe em crescimento rápido enquanto retarda a produção de domácias, garantindo o estabelecimento da formiga parceira em zonas ripárias amazônicas (Izzo et al., 2018). Dessa forma, torna-se fundamental compreender os efeitos indiretos dos filtros ambientais impostos pelas inundações sazonais sobre a estrutura das redes mutualistas entre formigas e plantas, a fim de elucidar como tais processos influenciam a distribuição da biodiversidade em ecossistemas amazônicos sujeitos a inundações cíclicas cada vez mais intensas.

Para além dos aspectos descritivos das redes, a persistência das interações ecológicas a longo prazo pode ser impulsionada pelo grau de correspondência entre as características dos parceiros (Bachmann & Drosel, 2025). Na ecologia funcional, traços morfológicos, fisiológicos ou comportamentais influenciam o desempenho ecológico das espécies e seu papel nos ecossistemas, refletindo como os organismos adquirem energia, interagem com o ambiente e se adaptam a restrições ecológicas e evolutivas (Violle et al., 2007; Schmitz et al., 2015). Quando considerados em conjunto dentro de um espaço morfológico multivariado, esses traços podem revelar os mecanismos ecológicos e evolutivos que moldam a ocupação e a dominância de recursos.

No caso das formigas, que são insetos primitivamente terrícolas, a capacidade de acessar e explorar recursos vegetais pode estar associada a adaptações morfológicas. Traços relacionados à alimentação (ex.: comprimento da mandíbula e do clípeo) estão associadas à capacidade das formigas de explorar fontes de alimento líquido (Davidson et al., 2004; Weiser & Kaspari, 2006). Além disso, traços relacionados à mobilidade, como tamanho corporal maior e pernas mais longas, podem facilitar o movimento sobre a superfície das plantas, mas dificultar o acesso a cavidades vegetais, como domácias (Davidson, 1989; Kaspari & Weiser, 1999). Características morfológicas associadas a tipos específicos de interação podem ser interpretadas dentro de uma estrutura de filtragem ecológica, na qual as plantas hospedeiras atuam como filtros ambientais que favorecem (ou excluem) determinadas combinações de traços das formigas, promovendo padrões de convergência funcional (Keddy & Laughlin, 2021). No entanto, a maior parte das evidências até o momento provém de estudos focados em traços e sistemas

específicos, e ainda não está claro se esses padrões de filtragem ecológica são consistentes em múltiplos tipos de interação em escalas regionais mais amplas.

Portanto, o uso integrado de abordagens baseadas em redes de interação e ecologia funcional (traços morfológicos) permite investigar como fatores ecológicos e evolutivos moldam a diversidade e a estrutura de mutualismos entre formigas e plantas. Nesse contexto, a presente tese busca compreender como filtros ambientais e funcionais influenciam a estrutura de interações facultativas e obrigatórias na Amazônia Brasileira. Para avaliar esse objetivo central, dividimos a tese em dois capítulos:

No **primeiro capítulo** (1) investigamos como a variação nas condições de hábitat em florestas de *igapó* sazonalmente inundadas e florestas adjacentes de *terra-firme* influencia a estrutura modular e aninhada de redes de interações facultativas (formigas e plantas com nectários extraflorais) e obrigatórias (formigas e plantas mirmecófitas) na Amazônia Central; (2) analisamos como a composição das interações facultativas e obrigatórias entre formigas e plantas varia entre os tipos de floresta; e (3) avaliamos se a presença de espécies de formigas oportunistas está correlacionada com a densidade de mirmecófitas e como essa associação afeta os padrões de interação em ambos os tipos de floresta. No **segundo capítulo** utilizamos um conjunto de dados abrangente baseado em traços de formigas arborícolas da Amazônia brasileira para: (1) investigar se a amplitude do espaço morfológico ocupado por assembleias de formigas está associada ao grau de especialização das interações com plantas, especificamente em associações com plantas com nectários extraflorais e mirmecófitas; (2) testar se traços relacionados à locomoção tem maior convergência funcional em interações obrigatórias; (3) analisar a similaridade entre traços morfológicos relacionados à alimentação em formigas que exploram plantas com nectários extraflorais.

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CAPÍTULO 1: Environmental Filtering and Network Structure in Ant-plant Mutualisms across Flooded and Unflooded Amazonian Forests

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Environmental filtering and network structure in ant-plant mutualisms across flooded and unflooded Amazonian forests

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ABSTRACT

Environmental filtering associated with contrasting hydrological regimes may influence species persistence and the organization of network interactions in Amazonian forests. We evaluated how facultative (ant-extrafloral nectary) and obligate (ant-myrmecophyte) mutualisms differ between seasonally flooded *igapó* and unflooded *terra-firme* forests in Central Amazon. Across 14 plots, we recorded 446 interactions (273 facultative; 173 obligate) involving 72 plant and 72 ant species. Facultative interactions were richer and more frequent in *terra-firme* forests, forming significantly nested and modular networks, whereas *igapó* networks exhibited lower richness and no statistically significant network structure. In contrast, obligate interactions remained nested and modular in both forest types, despite substantial reductions in species richness in seasonally flooded *igapó* forests. The composition of ant-plant interaction pairs differed strongly between environments, mainly for obligate networks. Opportunistic ants nesting in myrmecophytes occurred almost exclusively in *terra-firme* and increased with myrmecophyte density. Overall, our results show that the structure and composition of ant-plant interactions differ markedly across flooded and unflooded Amazonian forests, with contrasting responses between facultative and obligate mutualisms. These findings

reinforce the role of environmental heterogeneity in conserving ecological interactions in Amazonian forests.

Keywords: ecological networks, extrafloral nectar, myrmecophyte plants, modularity, nestedness, opportunistic species.

Filtragem ambiental e estrutura de redes mutualistas formiga-planta em florestas Amazônicas inundáveis e não inundáveis

RESUMO

A filtragem ambiental associada a regimes hidrológicos contrastantes pode influenciar a persistência das espécies e a organização das redes de interações ecológicas em florestas amazônicas. Avaliamos como redes mutualistas facultativas (formigas e nectários extraflorais) e obrigatórias (formigas e mirmecófitas) diferem entre florestas de *igapó* sazonalmente alagadas e florestas de *terra-firme* adjacentes. Registramos 446 interações (273 facultativas; 173 obrigatórias) envolvendo 72 espécies de plantas e 72 espécies de formigas. As interações facultativas foram mais frequentes em florestas de *terra-firme*, formando redes significativamente aninhadas e modulares, enquanto as redes de *igapó* apresentaram menor riqueza e não exibiram estrutura de rede estatisticamente significativa. Em contraste, as interações obrigatórias permaneceram aninhadas e modulares em ambos os tipos de floresta, apesar de reduções substanciais na riqueza de espécies em florestas de *igapó* sazonalmente alagadas. A composição das interações formiga-planta diferiu fortemente entre os ambientes, particularmente nas redes obrigatórias. Formigas oportunistas que nidificam em mirmecófitas ocorreram quase exclusivamente em florestas de *terra-firme*. De modo geral, nossos resultados mostram que a estrutura e a composição das interações formiga-planta diferem marcadamente entre florestas amazônicas alagáveis e não alagáveis, com respostas contrastantes entre mutualismos facultativos e obrigatórios. Os padrões encontrados reforçam a importância da heterogeneidade ambiental para a conservação das interações ecológicas em florestas amazônicas.

Palavras-chave: redes ecológicas; nectário extrafloral; plantas mirmecófitas; modularidade; aninhamento; espécies oportunistas.

INTRODUCTION

Ecological network approaches provide a complex framework for understanding how species interactions are organized within communities, revealing patterns of specialization, asymmetric dependencies, and the distribution of ecological roles (Jordano et al. 2003; Bascompte 2010). In mutualistic systems, network structure is often characterized by non-random patterns such as nestedness and modularity. Nestedness describes how interactions are distributed among generalist and specialist species, whereas modularity reflects the organization of interaction compartments within assemblages (Dáttilo and Rico-Gray 2018).

Environmental disturbances can influence both species composition and the organization of ecological networks by constraining species persistence and patterns of interaction. In tropical ecosystems, natural disturbances such as forest fires, severe droughts, and seasonal flooding play a key role in shaping species composition and ecological interactions (Laurance and Williamson 2001; Viljur et al. 2022; Rodrigues-Filho et al. 2024). Depending on their intensity and predictability, such disturbances may reduce or enhance diversity by modifying competitive dynamics and resource availability (Miller et al. 2011; Sévêque et al. 2020). However, while the effects of disturbances on species composition are well documented, their consequences for the structure of ecological interaction networks in Amazonian forests remain comparatively understudied (Emer et al. 2013; Miranda et al. 2025). Mutualistic interactions, in particular, may respond strongly to environmental filtering, as they depend on coordinated interactions between partner species whose persistence is shaped by habitat conditions.

Ant-plant interactions are a classic model for studying mutualisms, in which plants offer rewards such as extrafloral nectar, food bodies, domatia, or substrates for ant gardens in exchange for protection against herbivores (Heil and McKey 2003; Rico-Gray and Oliveira 2007; Mayer et al. 2014). These associations span a continuum from facultative and generalized associations to highly specialized and obligate partnerships, and ant-plant systems are particularly suitable for evaluating how environmental context shapes mutualistic network structure (Guimarães et al. 2006).

Plants bearing extrafloral nectaries (EFNs) engage in facultative interactions with a wide range of ant species attracted by accessible nectar rewards (Rosumek et al. 2009; Calixto et al. 2018). Such interactions often exhibit networks with nested patterns, in which specialist species interact with subsets of the partners used by generalists (Almeida-Neto et al. 2008; Bascompte 2010). In contrast, ant-myrmecophyte systems

involve obligate interactions in which plants provide domatia as nesting sites for myrmecophilous ants, and, in turn, they defend host plants from herbivory (Benson 1985; Davidson and McKey 1993). These particular interactions are typically more specialized and frequently organized into modular networks, reflecting stronger partner fidelity and evolutionary history (Guimerà and Amaral 2005; Dáttilo et al. 2013; Cagnolo and Tavella 2015). However, in some cases myrmecophytes may also be occupied by opportunistic, non-specialized ants, which can alter interaction patterns and potentially affect network modularity (Giusto et al. 2001; Yu 2001; Emer et al. 2013).

The Amazon forest is shaped by distinct hydrological, topographical, and ecological factors that influence the distribution and composition of associated flora and fauna (Junk et al. 1989; Junk et al. 2011). *Terra-firme* forests represent approximately 80% of Amazonian forests, occupying elevated terrains that are unaffected by seasonal flooding. On the other hand, floodplain forests such as *igapó* account for approximately 17% of the basin and are characterized by seasonal black-water flooding during the rainy season, when low vegetation may remain completely submerged for up to six months (Melack and Hess 2010; Hess et al. 2015; Junk et al. 2015). The seasonal flood regime exerts a strong influence on forest structure and resource distribution, thereby acting as a long-term environmental filter for floodplain forests and their associated species. These hydrological differences are likely to influence ant species composition and interaction patterns, potentially leading to distinct network structures across forest types.

Here, we examine how habitat variation between seasonally flooded *igapó* forests and adjacent unflooded *terra-firme* forests affects the modularity, nestedness, and composition of ant-EFN and ant-myrmecophyte interactions in Central Amazonia, and whether the presence of opportunistic ants correlates with myrmecophyte density. We hypothesize that ant-EFN networks in *terra-firme* exhibit higher interaction frequency and nestedness due to the absence of seasonal flooding and differences in vegetation structure, which may increase spatial overlap among generalist ants and EFN-bearing plants. In contrast, we expect ant-myrmecophyte networks in *igapó* forests to be more modular and less nested, reflecting more specialized and compartmentalized associations. Accordingly, we predict stronger differences in the composition of obligate interactions between forest types, with opportunistic ants being more frequent in *terra-firme* forests, whereas *igapó* forests are dominated by specialist species adapted to seasonally flooded environments.

MATERIAL AND METHODS

Study area and sampling design

The study was conducted in the Tarumã-Mirim region, within the Negro River basin, Amazonas State, Brazil (60° 02' 18.3" S, 20° 47' 43.7" W) (Figure 1). The area experiences a flood season from November to May and a dry season from June to October (Ferreira and Parolin 2011). Currently, the area comprises a mosaic of forests seasonally flooded by black-waters (*igapó*), unflooded upland forests (*terra-firme*) and white-sand forests (*campinaranas*) (Rossetti et al. 2012; Figure 1). *Terra-firme* forests are situated on higher ground, represented by plateaus with well-drained clay soils, a canopy reaching 30 m, and high floristic diversity (Ribeiro et al. 1999). *Igapó* forests occur in low-elevation areas subject to seasonal river overflow and are characterized by prolonged inundation of the forest floor and lower vegetation strata. The flood phase typically lasts from December to early July, with receding water from late July to November (Ferreira and Parolin 2011).

We established 14 plots along the *Tarumã-Mirim* stream, with seven plots in *igapó* forests and seven in *terra-firme* forests. Each plot measured 180 x 30 m (0.54 ha), with a minimum distance of 1 km between them, resulting in a total sampling area of 75,600 m² (7.56 ha). Plots were established during the dry season, with *igapó* plots located at least 100 m away from the stream margin and *terra-firme* plots placed in plateau areas. Sampling was conducted in February, August, and September 2020 and in October 2021, due to restrictions imposed by the pandemic period.

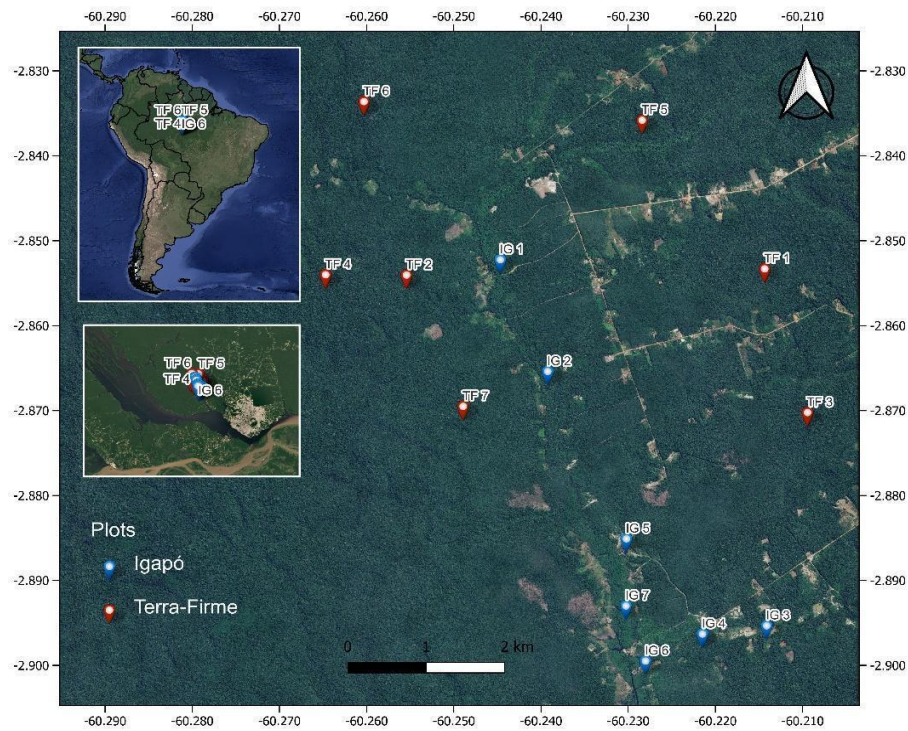


Figure 1. Location of the study area and sampling points at *Tarumã-Mirim*, state of Amazonas, Brazil. Red dots = *Terra-firme* forest (TF) and blue dots = *Igapó* forest (IG).

Field observations and species sampling

Field observations were conducted during daytime in each plot, when extrafloral nectary activity is commonly higher (Anjos et al. 2017; Nogueira et al. 2020). All understory plants up to 5 m tall bearing active EFNs or colonized myrmecophytes were marked across both forest types. We recorded all active EFN-bearing plants, monitoring each individual for at least 5 minutes. The presence of foraging ants was investigated in stems, leaves and petioles, following standard morphological criteria (Díaz-Castelazo et al. 2004; Heil 2010). We primarily monitored young branches, a developmental stage at which plants tend to experience higher herbivory and, consequently, increased extrafloral nectar secretion (Chamberlain and Holland 2009; Heil 2010). When young branches were absent, we monitored mature branches bearing active extrafloral nectaries and recorded ant visitors associated.

For myrmecophyte plants, we monitored all colonized myrmecophytes, identified by the presence of ants patrolling domatia or stem cavities. Posteriorly, we collected approximately seven domatias that were dissected to confirm the presence of ant colonies.

When possible, individuals from different castes (e.g., queens, major workers) were also collected, to ensure accurate species identification and to confirm which species were actively nesting and reproducing inside the domatia. In plants with more than ten domatia, at least three were sampled from the upper, middle, and lower portions of the plant, following the methodology applied by Bruna et al. (2005). After sampling and identification by authors, ant and plant vouchers were deposited in the Invertebrates Collection of *Universidade Federal do Amazonas* and Herbarium of the *Instituto Nacional de Pesquisas da Amazônia* (INPA), respectively.

Mutualistic and opportunistic ants

Ant species nesting in domatia-bearing plants were classified as mutualists or opportunists based on direct field observations and a review of behavioral myrmecology literature. Mutualists were defined as species that exhibited territorial behavior and actively defended the host plant, whereas opportunists were those occupying domatia without clear evidence of territoriality or host defense (Beattie 1985; Yu 2001). Opportunistic species typically encounter the plant incidentally, rather than through chemical cues involved in true myrmecophyte associations (Yu 2001; Blatrix and Mayer 2010). To distinguish these categories in the field, we recorded specific defensive and territorial behaviors. Mutualistic ants were identified when workers consistently patrolled the plant surface, responded rapidly to disturbances, recruited nestmates, or displayed aggressive interactions toward herbivores or intruders. Opportunistic ants, in contrast, showed no territorial patrolling, displayed slow or absent recruitment, and rarely defended the host plant, generally foraging individually and using the plant merely as a nesting substrate (Yu 2001; Giusto et al. 2001). For ant morphospecies (e.g., *Azteca* sp. 1), classification was based on a combination of observed behaviors and the ecological history of the genus associated with the respective host plant. For example, *Azteca* sp. 6 was classified as a specialist because it actively defended its host plants during fieldwork.

Data Analyses

We represented ant-plant networks as quantitative $m \times n$ matrices, with m and n denoting plant and ant species, respectively. Cell values were weighted by interaction frequency, defined as the number of independent interaction events recorded for each ant-plant pair (Vázquez et al. 2009). Four networks were constructed: two for *terra-firme* and two for *igapó* forests, each representing one type of mutualism (facultative or obligate

interactions). We opted to aggregate data at the forest-type level rather than constructing networks per plot, as our goal was to capture patterns in interaction structure across forest types. Additionally, plot-level analyses using the weighted NODF index yielded results highly consistent with those from the aggregated matrices, supporting our decision to focus on forest-level networks in the main analysis (see Table S1 and Figure S1). As expected, the number of interactions per plot was low - particularly in obligate ant-myrmecophyte networks, limiting the potential for finer-scale analyses.

To assess nestedness, we used the Weighted Nestedness based on the Overlap and Decreasing Fill (WNODF) metric, which accounts for both interaction frequency and partner overlap, and performs consistently across networks of varying size and shape (Almeida-Neto and Ulrich 2011). This index reflects how consistently less-connected species interact with subsets of partners used by more generalist species, revealing structural patterns associated with redundancy, hierarchy, and ecological stability (Almeida-Neto et al. 2008; Thebault and Fontaine 2010). WNODF was calculated using the network level function (**bipartite** R package), and each observed network was compared against 999 randomized matrices generated using the Patefield algorithm (`r2dtable` method), which preserves row and column totals (i.e., species richness and total interaction frequency).

We evaluated modular structure using QuanBiMo, a quantitative modularity index ranging from 0 (non-modular) to 1 (highly modular) (Dormann and Strauss 2014). This algorithm detects whether species form cohesive subgroups that interact more frequently among themselves than with other species in the network. To assess significance, we generated null models by randomly reallocating interactions across the matrix in 999 iterations. High modularity values (Q) indicate the formation of discrete compartments within the network (Olesen et al. 2007). Observed modularity was then compared to the distribution of simulated values.

We used Permutational Multivariate Analysis of Variance (PERMANOVA; Anderson 2017), based on the Bray-Curtis dissimilarity calculated from interaction matrices weighted by interaction frequency (i.e., relative abundance), to assess differences in the composition of ant-plant interactions between forest types. Matrices were constructed separately for facultative and obligate interactions, with sampling units defined at the plot level. The PERMANOVA was performed with 999 permutations. To visualize compositional patterns, we used a two-dimensional non-metric

multidimensional scaling (NMDS) ordination, also based on the Bray-Curtis dissimilarity matrices.

We used analysis of covariance (ANCOVA) to test the hypothesis that the frequency of opportunistic ant species is lower in myrmecophyte plants of *igapó* forests, compared to *terra-firme* forests. Species diversity and abundance were dependent variables, the density of myrmecophytic plants and forest types were the covariates. All analyses were done in R (R Core Team 2025), using **vegan**, **bipartite** and **ggplot2** packages.

RESULTS

Species diversity

We recorded a total of 72 plant species/morphospecies (not individuals) from 13 botanical families across 14 sampling plots. We documented 446 ant-plant interactions, of which 273 were facultative (61.2%) and 173 were obligate (38.8%). We identified 72 ant species or morphospecies nesting or foraging on plants, belonging to 20 genera and six subfamilies, totaling 10,645 specimens. Species richness was consistently higher in *terra-firme* forests for both plants and ants, regardless of interaction type (Table 1).

Table 1. Structural metrics of ant-plant mutualistic networks in *terra-firme* and *igapó* forests by interaction type (facultative = EFN-bearing plants; obligate = myrmecophytes). Metrics include the number of ant and plant species, total number of ant-plant interactions, weighted nestedness (WNODE_{Obs}) and modularity (Q). *P*-values indicate significance based on comparisons with null models. Statistically significant values are in bold.

Forest Type	Interaction type	No. ant species	No. plant species	No. ant-plant interactions	WNODE _{Obs}	P-value WNODE	Modularity (Q)	P-value Modularity
<i>Terra-firme</i>	Facultative	36	50	196	22.42	<0.001	0.30	<0.001
<i>Igapó</i>	Facultative	30	14	77	12.36	0.060	0.42	0.165
<i>Terra-firme</i>	Obligate	20	8	139	4.82	<0.001	0.19	<0.001
<i>Igapó</i>	Obligate	4	3	39	33.33	0.002	0.03	<0.001

Network structure

Facultative interactions were more frequent in *terra-firme* forests (Table 1, Figure 2), with 36 ant species (vs. 30 in *igapó*) foraging in 50 EFN-bearing plant species (vs. 14

in *igapó*), involving an overall frequency of 196 associations (vs. 77 in *igapó*). *Inga* represented 56% of EFN-bearing plant species in *terra-firme* forests, with the most frequent interaction occurring between *Inga glomeriflora* and *Crematogaster brasiliensis* (28 interactions). *Zygia latifolia* showed the highest abundance and interaction frequency, being associated mainly with *C. brasiliensis* and *C. tenuicula* (7 interactions each). At the network level, associations between ants and EFN-bearing plants were highly nested in *terra-firme* forests ($WNODF_{obs} = 22.42$; null mean = 26.57 ± 2.26 ; $p < 0.001$), whereas in *igapó* forests nestedness was low and only marginally non-significant ($WNODF_{obs} = 12.36$; null mean = 16.12 ± 2.48 ; $p = 0.060$). The general topology showed a well-defined modular structure in *terra-firme* forests ($Q = 0.30$, Table 1), which was higher than expected under the null model (null mean = 0.20 ± 0.02 ; $p < 0.001$). Although modularity in *igapó* was relatively high ($Q = 0.42$), it did not differ from null expectations (null mean = 0.36 ± 0.06 ; $p = 0.165$).

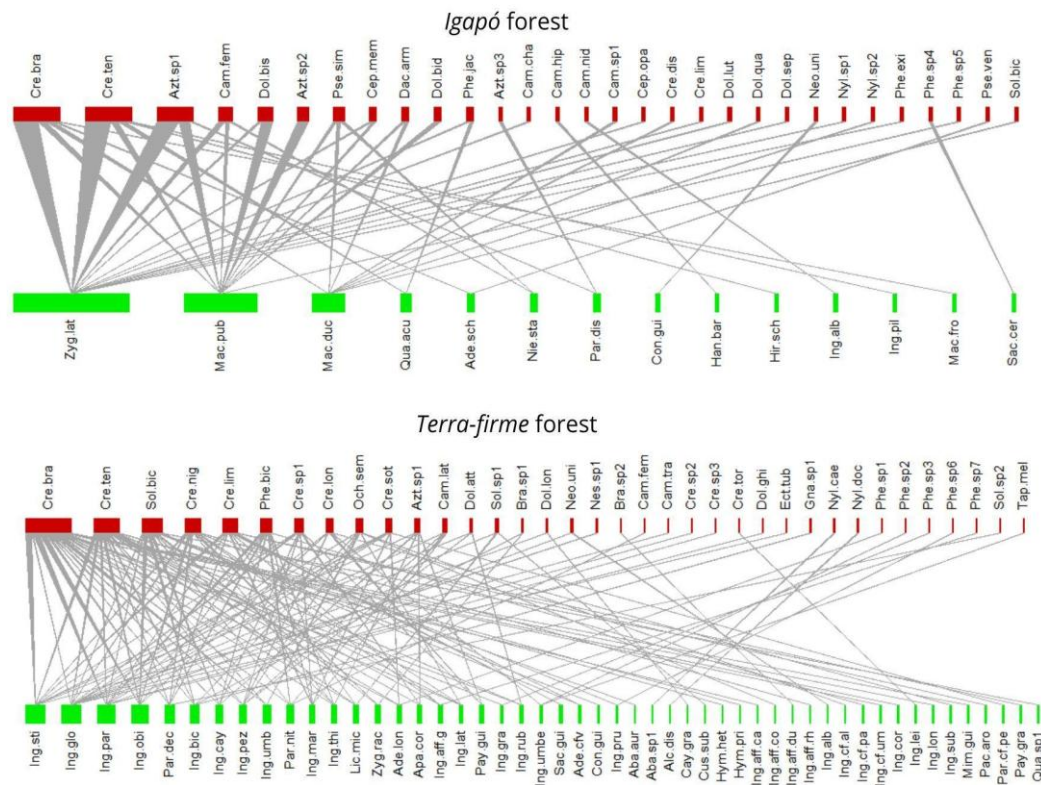


Figure 2. Facultative ant-plant networks at Tarumã-Mirim. Links represent interactions between ants and plants mediated by extrafloral nectaries. Green bars indicate plant species, while red bars indicate ant species, in *igapó* (upper network) and *terra-firme* forests (lower network).

Obligate interactions were more frequent in *terra-firme* forests, where eight myrmecophyte species hosted 20 ant species, resulting in 139 quantitative interactions. The most frequent associations were between *Allomerus octoarticulatus* and *Hirtella myrmecophila* (55 occurrences), followed by *Allomerus decemarticulatus* on *Pourouma myrmecophila* (13) and *Pseudomyrmex concolor* on *Tachigali plumbea* (9). In *Igapó* forests, obligate interactions were less diverse, involving only three plant species and four associated ant species, totaling 39 quantitative interactions (Figure 3, Table S2). *Azteca* sp. 6 was exclusively recorded on *Miconia tocoronata* (new taxonomic combination for *Tococa coronata*), with 31 occurrences, and was considered a specialist species. Additionally, we found two occurrences of the specialized interaction between *Hirtella myrmecophila* and *Allomerus octoarticulatus*, and one between *Miconia alternidomatia*

(new taxonomic combination for *Maieta poeppigii*) with its specialist ant, *Pheidole minutula* (Table S2).

Obligate networks showed significantly non-random nestedness in both forest types (*terra-firme*: WNODFobs = 4.82; null mean = 35.31 ± 4.44 ; $p < 0.001$; *igapó*: WNODFobs = 33.33; null mean = 64.25 ± 16.91 ; $p = 0.002$; Table 1). Both networks were also significantly modular, with observed values exceeding null expectations in *terra-firme* ($Q = 0.19$; null mean = 0.18 ± 0.02 ; $p < 0.001$) and *igapó* ($Q = 0.03$; null mean = 0.05 ± 0.02 ; $p < 0.001$).

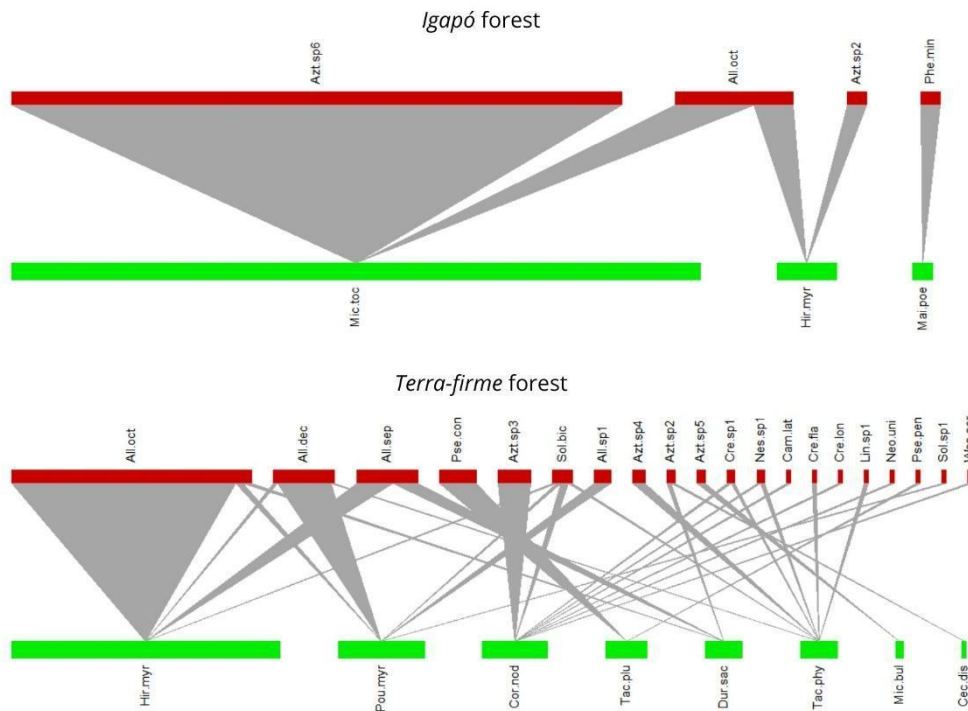


Figure 3. Obligatory ant-plant networks at Tatumã-Mirim. Links represent interactions between ants and plants mediated by domatias. Green bars indicate plant species, while red bars indicate ant species, in *igapó* (upper network) and *terra-firme* forests (lower network).

The composition of ant-plant associations differed between forest types for both facultative and obligate interactions (Figure 4). In facultative interactions involving EFN-bearing plants, species composition differed between *terra-firme* and *igapó* forests (PERMANOVA; $r^2 = 0.12$, $p = 0.003$). Similarly, obligate interactions between myrmecophytes and their resident ants also varied between forest types (PERMANOVA; $r^2 = 0.32$, $p = 0.008$). Obligatory networks exhibited clearer compositional separation between forest types, with minimal overlap between plots from different habitats (Figure

4). Facultative networks displayed greater within-habitat variability, particularly in *igapó*, indicating higher species turnover and more heterogeneous interaction patterns across plots.

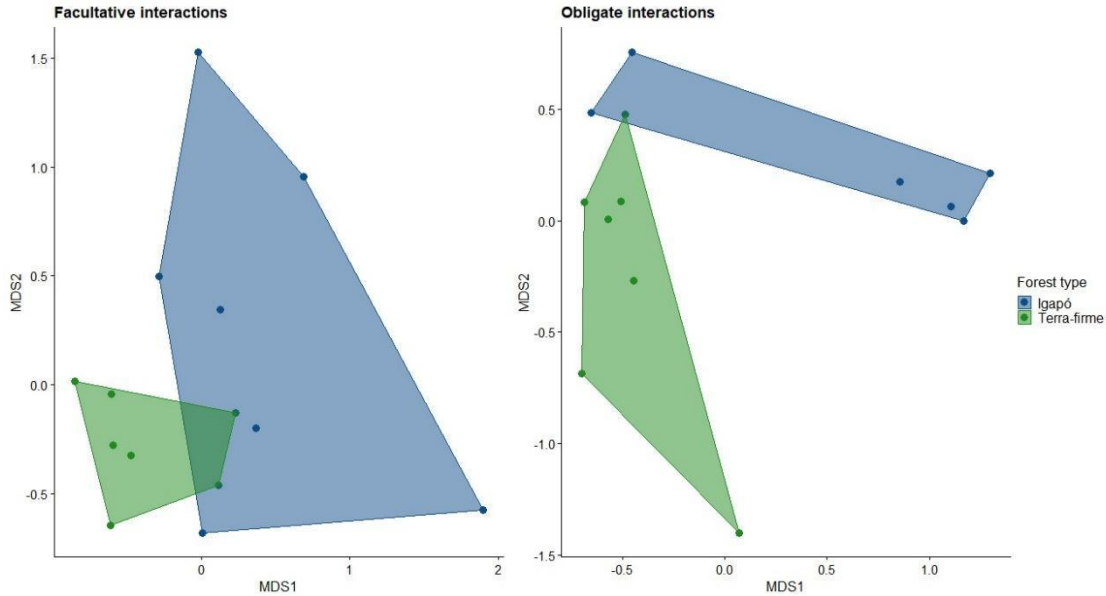


Figure 4. NMDS ordination represents the assemblage of facultative and obligatory interactions given the ant-plant distances (Bray-Curtis) at the network, for *terra-firme* (green dots) and *igapó* (blue dots) forests at Tarumã-Mirim.

We recorded 19 links by opportunistic ant species nesting in myrmecophytes, comprising 11 ant species across 10 plant species (Table S2). These associations were strongly biased toward *terra-firme* forests, where 18 of the 19 occurrences were recorded. In this forest type, *Solenopsis bicolor* was the most frequent opportunist, found nesting in four different myrmecophyte species, followed by *Azteca* sp. 2 and *Neoponera unidentata*. In contrast, a single ant-plant pair was registered in *igapó* forests, with *Azteca* sp. 2 found once on *Hirtella myrmecophila*. In *terra-firme* plots, myrmecophyte density was positively correlated with both opportunistic ant abundance ($p = 0.002$) and species

richness ($p < 0.001$) compared to *igapó* forests, indicating that increased availability of domatia may facilitate colonization by non-specialist ants (Figure 5).

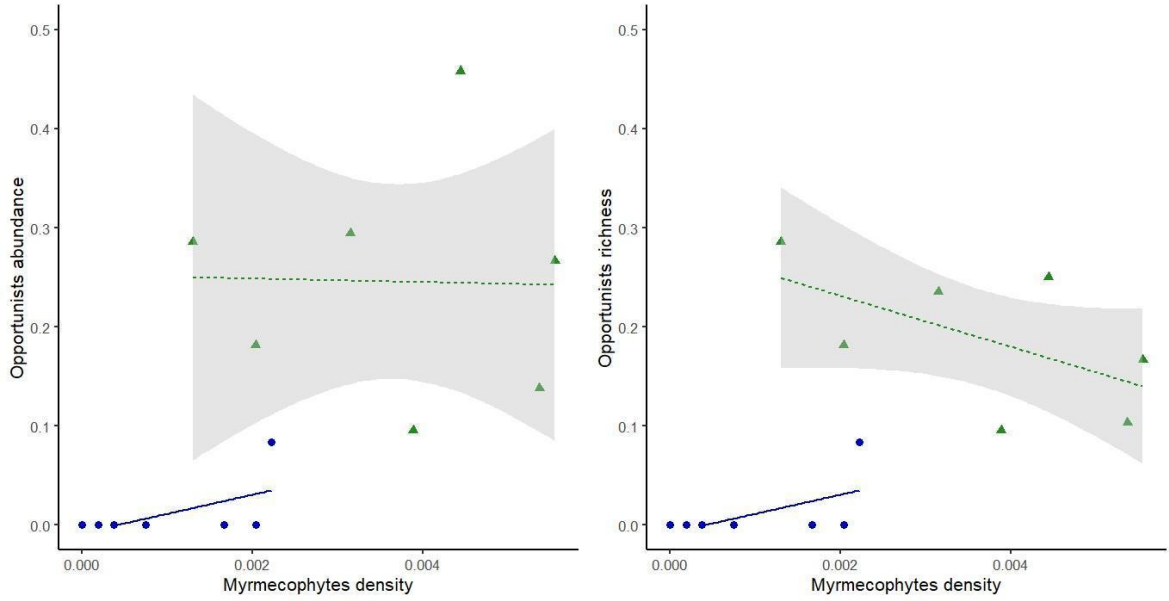


Figure 5. Comparison between the density of myrmecophytic plants and opportunistic ant species in *terra-firme* (green dots) and *igapó* (blue dots) forests at Tarumã-Mirim.

DISCUSSION

Our study shows that ant-plant mutualisms differ between seasonally flooded *igapó* forests and unflooded *terra-firme* forests, with contrasting patterns between facultative and obligate interactions. Facultative interactions involving EFN-bearing plants were more frequent and more strongly nested in *terra-firme* forests, where more stable conditions and complex vegetation structure are likely to enhance spatial overlap between generalist ants and plants. For obligate interactions, our results partially support our expectations, as ant-myrmecophyte networks were highly modular in both forest types, despite markedly lower ant and plant species richness and interaction frequency in *igapó* forests. Overall, these differences between forest types are consistent with the long-term influence of contrasting hydrological regimes on the structure and composition of ant-plant interaction networks.

Although species richness and interaction frequency declined abruptly in flooded forests, species composition showed a marked turnover between flooded and unflooded environments. As hypothesized, opportunistic ant species were almost entirely restricted to *terra-firme* forests, suggesting that seasonal flooding limits colonization by non-

specialist ants and reinforces the role of environmental filtering in structuring specialized interactions. These results highlight how disturbance regimes can modulate the architecture and composition of mutualistic networks by filtering species according to their ecological strategies and habitat tolerance.

Facultative interactions between ants and EFN-bearing plants displayed a significantly nested structure in *terra-firme* forest, but not in *igapós*, emphasizing the role of generalist species in maintaining network stability and interaction persistence despite specialist loss (Bascompte et al. 2006). Nestedness enhances ecological resilience by increasing redundancy, which allows lost links to be replaced under fluctuating conditions (Emer et al. 2013). Nevertheless, we interpret these findings cautiously, as sampling effort and network size, particularly in networks with low interaction frequency, may inflate nestedness estimates. In *igapó* forests, although networks of facultative interactions did not exhibit significant nestedness, the presence of weakly nested patterns may reflect seasonal shifts in foraging behavior. Ant species that typically nest in soil, litter, or lower vegetation strata may increase their use of plants even during the dry season (Adis and Junk 2002; Guimarães et al. 2006; Rico-Gray et al. 2012). In these flood-prone environments, extrafloral nectaries likely serve as vital foraging resources throughout wet and dry seasons, supporting the continuity of ant-plant interactions despite environmental constraints.

Our findings suggest that the nested structure observed in facultative interactions may confer robustness to periodic environmental perturbations, as it is characterized by species forming a core-periphery pattern in which highly connected species interact with many others (Guimarães et al. 2017). In contrast, the modularity observed in obligate interactions indicates that these associations are organized into cohesive subgroups of ants and myrmecophyte plants that interact more frequently within modules than between them (Olesen et al. 2007). Such compartmentalization suggests a structured pattern of interaction in which specialized pairs are clustered into relatively discrete subsets within the network (Guimarães et al. 2017).

Once dominated by few species, the stability of obligate interactions in flooded environments depends on the persistence of key species within modular compartments, a pattern consistent with broader ecological theories on mutualistic network resilience (Guimarães et al. 2017). In our study, *Miconia tococoronata* was the most abundant myrmecophyte plant in the *igapó* forests. This species is known to have adaptive strategies for survival in flooded areas, investing in rapid growth during early ontogenetic

stages through internode elongation to exceed the maximum flooding level (Izzo et al. 2018). Once the domatia are produced at a higher position, just above the flood line (Izzo et al. 2018), the disturbance does not interfere with the ants' ability to colonize and survive on *M. tococoronata*. Plants lacking a similar strategy would likely experience nest relocation or displacement of their ant colonies during floods.

Terra-firme forests are not subject to environmental filtering provided by flood and therefore, do not experience seasonal mortality of myrmecophytic plants and their associated ant colonies, which likely promotes the lower species richness observed in *igapó* forest. Opportunistic ants, which typically nest in the soil or leaf litter, tend to find plants by chance, unlike specialist queens that locate plants using chemical signals after nuptial flights (Blatrix and Mayer 2010). However, once opportunists enter a plant, they can persist due to priority effects (Fukami 2015), which at least partially inhibit colonization by specialists. In contrast, seasonal colony mortality in environments subject to periodic disturbances will lead to lower density and richness of opportunists, as observed.

Our results suggest that obligate interactions may be more strongly rewired across ecosystems than facultative interactions, given the substantial shift in the composition of EFN-bearing plants between flooded and unflooded forests. The composition of obligatory interactions exhibited a more pronounced divergence between environments, reflecting the restricted distribution of myrmecophytic plants and specialized ants in flooded areas (Emer et al. 2013). This difference may be explained by the dependence of specialized ants on their host plants, as the lower availability of myrmecophytes directly limits ant colonization (Fonseca and Ganade 1996, Dáttilo et al. 2013). In contrast, facultative interactions were more diverse across environments, likely due to the greater ecological flexibility of generalist ants, which can utilize a wider range of plants as food sources (Nogueira et al. 2020; Nogueira 2025).

The reduced richness and interaction frequency observed in obligatory ant-plant networks in flooded forests likely reflect strong environmental constraints on species establishment. However, the persistence of modularity and nestedness in these networks suggests that specialized ant-plant associations may retain structural cohesion despite biodiversity loss. Rather than being replaced by opportunistic species, as might be expected under chronic disturbance, obligate interactions in *igapó* forests appear to be maintained by a limited set of adapted specialists. This pattern underscores the importance of species-specific traits in sustaining mutualistic networks under environmental stress.

CONCLUSION

The contrasting responses of facultative and obligate interactions indicate that interaction types differ between seasonally flooded *igapó* forests and unflooded *terra-firme* forests. The persistence of structured obligate networks despite reduced diversity suggests that specialized associations can be maintained in flooded forest environments, whereas facultative interactions appear more sensitive to differences between forest types. Together, these findings highlight the importance of considering interaction type when assessing variation in ecological network structure across Amazonian forest environments. Future studies should investigate how the loss or persistence of key specialist interactions influences broader ecosystem functions, particularly in the face of ongoing hydrological changes driven by climate and land-use transformation in the Amazon.

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Data available upon request – The data that support the findings of this study are available, upon reasonable request, from the corresponding author Talitha Ferreira dos Santos.

Author Contributions – SANTOS, T. F.: Conceptualization, Project administration, Supervision, Software, Visualization, Investigation, Methodology, Data Curation, Formal analysis, Validation, Writing - Original draft, Writing - review & editing. PILCO, M. V.: Conceptualization, Investigation, Data curation, methodology, writing - review & editing. FARROÑAY, F.: Investigation, Data curation, methodology, writing - review & editing. IZZO, T. J.: Conceptualization, Validation, Writing - Original draft, Writing - review & editing. SANTOS, E. S.: Methodology, Data curation. BACCARO, F. B.: Conceptualization, Formal analysis, Funding acquisition, Resources, Supervision, Validation, Writing - Original draft, Writing - review & editing.

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SUPPLEMENTARY MATERIAL

Table S1. Summary of plot-level nestedness metrics (weighted NODF) for EFN-ant networks in *Terra-firme* and *Igapó* forests.

Plot	Forest type	NODF obs	NODF null mean	NODF null sd	P-value
1	<i>Terra-firme</i>	16.58	15.28	3.21	0.34
2		7.89	7.99	1.86	0.42
3		41.67	56.34	10.78	0.1
4		15.01	13.02	3.04	0.27
5		11.63	10.55	6.62	0.47
6		21.25	21.93	3.26	0.43
7		18.75	20.18	2.68	0.31
1	<i>Igapó</i>	16.67	7.77	8.32	0.47
2		19.35	33.15	10.98	0.07
3		51.15	47.53	9.09	0.42
4		0.0	0.0	0.0	0.0
5		0.0	26.28	17.18	0.0
6		25.0	18.13	7.9	0.31

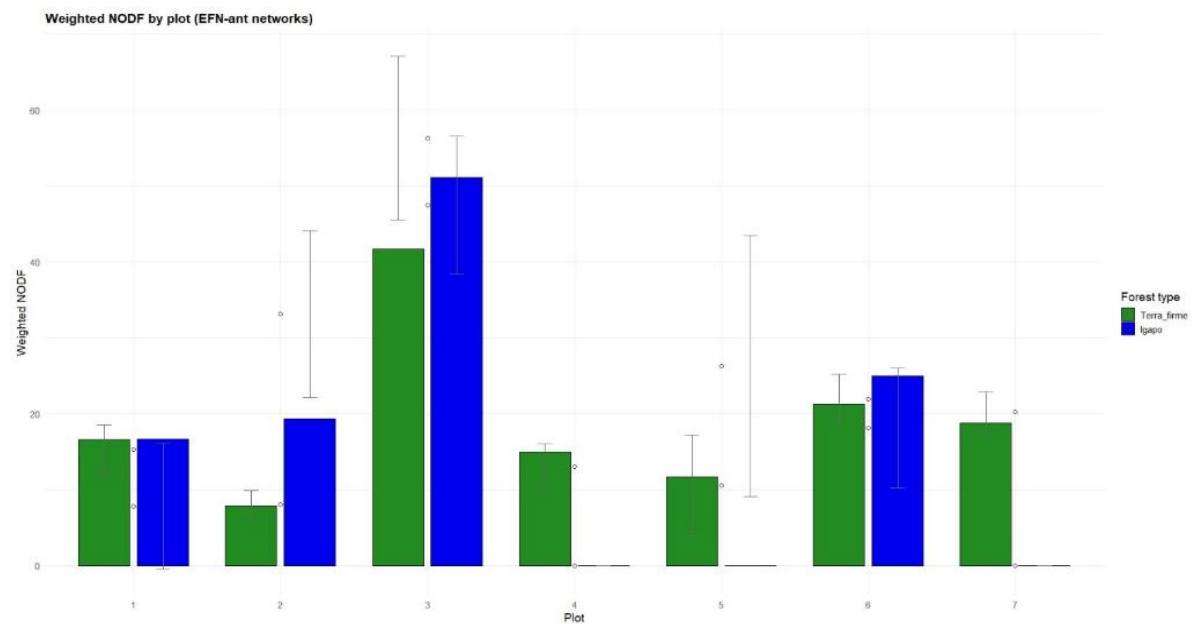


Figure S1. Observed weighted NODF values (bars) with null model means (dots) and standard deviations (error bars) for EFN-ant networks in each plot across *Terra-firme* and *Igapó* forests.

Table S2. Ant species associated with myrmecophytic plants in plots of *Terra-firme* and *Igapó* forests. The table presents the host plant and interacting ant species by forest type (TF = *Terra-firme*, I = *Igapó*), type of interaction (M = mutualist, O = opportunist), and observed interaction frequency.

Host plant	Ant species	Type of interaction	Forest type	Interaction frequency
<i>Cecropia distachya</i>	<i>Azteca</i> sp. 2	O	TF	1
<i>Cordia nodosa</i>	<i>Azteca</i> sp. 3	M	TF	8
	<i>Solenopsis bicolor</i>	O	TF	2
	<i>Camponotus latangulus</i>	O	TF	1
	<i>Crematogaster longispina</i>	O	TF	1
	<i>Crematogaster</i> sp. 1	O	TF	1
	<i>Neoponera unidentata</i>	O	TF	1
	<i>Nesomyrmex</i> sp. 1	O	TF	1
	<i>Wasmannia scrobifera</i>	O	TF	1
<i>Duroia saccifera</i>	<i>Allomerus septemarticulatus</i>	M	TF	6
	<i>Allomerus octoarticulatus</i>	M	TF	2
	<i>Azteca</i> sp. 2	O	TF	1
<i>Hirtella myrmecophila</i>	<i>Allomerus octoarticulatus</i>	M	TF	55
	<i>Allomerus septemarticulatus</i>	M	TF	9
	<i>Allomerus decemarticulatus</i>	M	TF	1
	<i>Solenopsis bicolor</i>	O	TF	1
	<i>Allomerus octoarticulatus</i>	M	IG	2
	<i>Azteca</i> sp. 2	O	IG	1
<i>Miconia alternidomatia</i>	<i>Pheidole minutula</i>	M	IG	1
<i>Miconia bullifera</i>	<i>Azteca</i> sp. 5	M	TF	2
<i>Miconia tococoronata</i>	<i>Azteca</i> sp. 6	M	IG	31
	<i>Allomerus octoarticulatus</i>	M	IG	4
<i>Pourouma myrmecophila</i>	<i>Allomerus decemarticulatus</i>	M	TF	13
	<i>Allomerus</i> sp. 1	M	TF	4
	<i>Allomerus octoarticulatus</i>	M	TF	2

<i>Tachigali physophora</i>	<i>Solenopsis bicolor</i>	O	TF	1
	<i>Solenopsis</i> sp. 1	O	TF	1
	<i>Azteca</i> sp. 4	M	TF	3
	<i>Allomerus decemarticulatus</i>	M	TF	1
	<i>Crematogaster flavosensitiva</i>	O	TF	1
	<i>Crematogaster</i> sp. 1	O	TF	1
	<i>Linepithema</i> sp. 1	O	TF	1
	<i>Nesomyrmex</i> sp. 1	O	TF	1
	<i>Solenopsis bicolor</i>	O	TF	1
	<i>Pseudomyrmex concolor</i>	M	TF	9
<i>Tachigali plumbea</i>	<i>Pseudomyrmex penetrator</i>	M	TF	1

CAPÍTULO 2: Morphological convergence is stronger in myrmecophyte-associated ants than in facultative EFN-foragers in the Brazilian Amazon

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Morphological convergence is stronger in myrmecophyte-associated ants than in facultative EFN foragers in the Brazilian Amazon

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Morphological convergence is stronger in myrmecophyte-associated ants than in facultative EFN-foragers in the Brazilian Amazon

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Author Contributions - T.F.S, F.B.B and T.J.I. conceived the ideas and designed methodology; R.R S, J.A.S and L.P.P. collected and curated the data; F.B.B., T.F.S. and T.J.I. analysed the data and led the writing of the manuscript; All authors contributed critically to the drafts and gave final approval for publication.

Statement on inclusion – This study synthesizes data from global sources, including studies conducted in the Brazilian Amazon. The authorship team includes researchers actively working in Amazonian ecosystems, contributing regional expertise and contextual interpretation of ecological patterns. We aimed to ensure balanced representation of studies across geographic regions, including research published in local and regional scientific outlets.

Data availability statement - Data will be archived in a public repository (e.g., Dryad) upon acceptance of the manuscript.

ABSTRACT

Ant-plant mutualisms span a continuum from facultative to highly specialized interactions, yet it remains unclear how the degree of interaction intimacy shapes morphological trait convergence in ant assemblages at broad spatial scales. Using a comprehensive trait-based dataset of arboreal ants from the Brazilian Amazon, we tested whether morphological convergence is stronger in ants associated with obligate myrmecophytes than in ants engaged in facultative interactions with extrafloral nectary (EFN)-bearing plants. We quantified and compared the functional trait spaces of EFN-associated and myrmecophyte-associated ants using multivariate hypervolume analyses, focusing on feeding- and mobility-related traits normalized by body size. Both interaction types occupied subsets of the overall arboreal ant morphospace, indicating ecological filtering rather than morphological innovation. However, myrmecophyte-associated ants exhibited markedly narrower and more clustered trait spaces for both mobility and feeding traits, reflecting strong morphological convergence consistent with structural constraints imposed by domatia. In contrast, EFN-associated ants showed broader and more diffuse trait distributions, although still significantly filtered relative to the general arboreal assemblage. Null model analyses confirmed that observed trait-space overlaps were lower than expected by chance for both interaction types, with the strongest departures in myrmecophyte-associated ants. Our results demonstrate that interaction intimacy modulates the strength of ecological filtering across trait dimensions, with obligate mutualisms driving pronounced functional clustering. These findings highlight how plant-derived resources and nesting architectures shape ant functional diversity and reveal enduring evolutionary imprints of ant-plant mutualisms in Brazilian Amazonian forests.

Keywords: Ant-plant mutualism; Extrafloral nectaries; Functional diversity; Morphological traits; Myrmecophyte plants.

INTRODUCTION

Ant-plant associations are remarkably diverse and have long been recognized as key systems for studying coevolutionary dynamics driven by biotic defenses (Heil & McKey, 2003; Weber & Agrawal, 2014; Nelsen et al., 2018). Mutualistic interactions between ants and plants occur along a continuum of specialization, from facultative interactions to highly specialized mutualisms (Guimarães et al., 2007; Del-Claro et al., 2018; Nogueira, 2025). Historically, such interactions likely evolved through the exploitation of plant-derived resources by terrestrial ants, initially for food and later for nesting opportunities (Moreau et al., 2006; Nelsen et al., 2018), a process reinforced by coevolution and morphological adaptations (Brouat et al., 2001; Guimarães et al., 2017).

From a theoretical perspective, ant-plant mutualisms provide insightful models for exploring ecological and evolutionary dynamics, including mechanisms of herbivore defense and resource competition (Heil & McKey, 2003; Rico-Gray & Oliveira, 2007; Juárez-Juárez et al., 2023; Nogueira, 2025). Plants bearing extrafloral nectaries (EFNs), for instance, typically engage in generalized mutualisms, attracting a wide array of ant species that exploit nectar as a readily available food source and as a substrate for tending hemipterans, in return for indirect protection against herbivores and other potential enemies (Heil & McKey, 2003; Calixto et al., 2018; Leal et al., 2023). On the other hand, ant-myrmecophyte interactions represent intimate partnerships shaped by ant-plant coevolution (Guimarães et al., 2006). Myrmecophyte plants provide structural nesting sites (domatia) for symbiotic ants, in exchange for defense against herbivores (Benson, 1985; Rico-Gray & Oliveira, 2007; Jyothi et al., 2025). In both cases, the way ants access and use shelter and nesting resources acts as a filter, favoring those groups or species that can reach the plants and obtain the greatest benefits (Guimarães et al., 2007; Dáttilo et al., 2014).

The long-term persistence of mutualistic associations is driven by the degree of trait matching between interacting partners (Bachmann & Drosel, 2025). Trait-based approaches provide valuable insights into the mechanisms that structure biodiversity in species-rich ecosystems, as morphological, physiological, and behavioral traits reflect how organisms acquire resources, maintain colony functioning, and adapt to ecological and evolutionary constraints (McGill et al., 2006; Violle et al., 2007; Kaspari & Weiser, 1999; Gibb et al., 2015; Parr et al., 2017; Sosiak & Barden, 2021). Particular ant traits may help us understand how ants occupy and use a given resource. When considered collectively within a multivariate morphological space, they can reveal the ecological and

evolutionary mechanisms shaping resource occupancy and dominance. In the case of ants, which are ancestral ground-dwelling insects (Lucky et al., 2013), the ability to access and exploit plant resources is certainly associated with morphological adaptations. For example, feeding-related traits, e.g., mandible and clypeus length, are associated with the ability of ants to exploit liquid food sources (Davidson et al., 2004; Weiser & Kaspari, 2006). Mobility-related attributes, such as larger transversal body dimensions and longer legs, may facilitate movement through plant surfaces but make it difficult to access plant cavities such as domatia (Davidson, 1989; Kaspari & Weiser, 1999). Morphological traits associated with particular interaction types can be understood within a filtering framework, in which host plants act as biotic microenvironmental filters that favor or exclude specific combinations of ant traits (Thakur & Wright, 2017; Keddy & Laughlin, 2021). Yet, most evidence so far comes from localized studies focused on particular systems, and it remains unclear whether these patterns of ecological filtering are consistent across multiple interaction types at broader regional scales.

The Amazon tropical forest is globally recognized as the most biodiverse biome on Earth and holds the largest continuous area of tropical moist forest, covering approximately 5.79 million km² (ter Steege et al., 2015). The Brazilian Amazon comprises a mosaic of forest types, flood regimes, and microclimates that sustain high levels of species richness and endemism (IBGE, 2004; Quesada et al., 2009). Furthermore, Amazon has acted as both a museum and cradle of ant diversity, and as a major center for the emergence and diversification of ant-plant mutualisms (Feitosa et al., 2022; Miranda et al., 2022; Dejean et al., 2025). Therefore, investigating the ant-plant associations at Amazon scale offers a unique model for understanding whether morphological convergence in ant assemblages mirrors the degree of specialization in different ant-plant interaction types.

In this study, we use a comprehensive trait-based dataset of arboreal ants from the Brazilian Amazon to test whether morphological convergence in ants is associated with the degree of specialization in ant-plant interactions, specifically in associations involving plants with extrafloral nectaries and myrmecophytes. We hypothesize that ant species associated with myrmecophyte plants exhibit greater morphological similarity, reflecting stronger morphological convergence than those engaged in facultative interactions, such as EFN-foraging. Specifically, we predict that: (1) ant assemblages associated with myrmecophytes will occupy a narrower region of morphospace, indicative of strong ecological filtering, whereas EFN-foraging ants will exhibit greater morphological

dispersion, more closely resembling the overall trait patterns of arboreal ants; (2) traits related to mobility will be more similar in myrmecophilic interactions (morphological convergence); and (3) feeding-related traits will be more similar in facultative interactions, such as those between ants and plants with extrafloral nectaries. These predictions aim to assess whether interaction specialization drives functional clustering within trait space and to determine whether convergence patterns vary according to the ecological function of the traits considered.

MATERIAL AND METHODS

Ant occurrence and interaction datasets

We used a validated database of ant diversity in the Brazilian Amazon (from 1817 to 2025), originally assembled by Andrade-Silva et al. (2022) and Andrade-Silva et al. (2024) through the Global Ant Biodiversity Informatics project (GABI; Guénard et al., 2017). The dataset includes expert-validated species names following the Online Catalog of the Ants of the World (Bolton, 2025), including only nominal ant taxa (species and subspecies); informal taxa (morphospecies) were not included. Andrade-Silva et al. (2022) also classified Amazonian ants by foraging stratum. Based on this previous classification, we selected all species belonging to two strata directly related to vegetation: (1) arboreal species, which forage primarily on vegetation, and (2) epigaeic + arboreal species, which use both arboreal and ground strata, totaling 475 species of the 1067 ant species.

From this database, we further classified ant species by nesting strata using taxonomic literature and online datasets. Nesting stratum reflects habitat use, trophic strategies, and microhabitat occupation by ants (Gibb et al., 2015; Andrade-Silva et al., 2022). It is particularly relevant for ant-plant interactions given that nesting location directly mediates access to plant-derived resources such as extrafloral nectar, trophobionts, and domatia (Davidson et al., 2004). Given the absence of natural history information for some species, we consulted experts to validate nesting strata not reported in the literature. Complementary, we compiled information on ant-plant mutualistic associations, focusing on interactions with extrafloral nectaries and/or trophobiosis with hemipterans, as well as associations with myrmecophyte plants (Figure 1). Plant species names were checked, corrected, and updated when necessary, following the International Plant Names Index (IPNI, 2025). Ecological interaction data were obtained primarily

from taxonomic articles and published monographs. When such information was unavailable, we used online databases and, ultimately, ecological studies on mutualistic interactions, which accounted for about 9% of all literature-based records.



Figure 1. Ant-mediated interactions with EFN-bearing and myrmecophytic plants. (A, B) *Pheidole biconstricta* and *Solenopsis* sp. visiting extrafloral nectaries of Bignoniaceae. (C) *Crematogaster brasiliensis* foraging on an extrafloral nectary located on the stem of *Inga* sp. (D, E) *Allomerus octoarticulatus* patrolling the domatia of *Miconia tococoronata* and *Hirtella myrmecophila*, respectively. (F) *Pseudomyrmex concolor* at the entrance of a domatium on *Tachigali plumbea*. Photo credit: F. Farroñay; T. Santos.

Morphological trait database

The morphological trait database comprises 15 continuous morphological traits widely recognized in the ant literature (Silva & Brandão, 2010, 2014, Del Toro et al., 2015). The morphological database was assembled from more than 3,000 high-definition images from AntWeb dataset and museum collections, complemented with measurements extracted directly from over 40 taxonomic publications when suitable images were unavailable. All measurements followed a standardized protocol implemented in ImageJ, prioritizing type material and using minor workers whenever possible to ensure

morphological consistency. Missing values due to absent views or damaged specimens were imputed using multivariate chained equations to maximize dataset completeness while retaining the structure of observed trait variation (see Andrade-Silva et al. 2022 for more details). For this study, we focused on ten morphological traits, grouped into two functional categories: feeding and mobility-related traits (Table 1). Feeding-related traits may reflect how ants acquire and process plant-derived resources (Fowler et al., 1991; Davidson et al., 2004; Weiser & Kaspari, 2006). Further, mobility attributes are expected to reflect body size and locomotion, which affect movement through vegetation and access to nesting sites (Kaspari, 1993; Gibb & Parr, 2013; Sosiak & Barden, 2021; Andrade-Silva et al., 2022).

Table 1. Morphological traits with functional categories and ecological roles associated with ant morphology used in the present study. Adapted from Silva and Brandão (2010).

Trait	Functional Role in Ant Ecology
Feeding	
Mandible length Mandible width	Prey capture, manipulation of resources (Fowler et al. 1991, Weiser & Kaspari, 2006).
Eye-mandible distance	Eye position might influence performance of visual predators (Fowler et al., 1991).
Eye length	Important character in food search (Weiser & Kaspari, 2006).
Scape length	Sensory perception. Longer scapes may facilitate the following pheromone trails (Weiser & Kaspari, 2006).
Clypeus length	Larger clypeus may be associated with liquid food-based diet (Davidson et al., 2004).
Mobility	
Head width Head length	While wider heads accommodate larger mandibular muscles that allow capture of larger or fiercer prey (Kaspari, 1993), head width and length is also correlated with body size and the ability to enter in smaller spaces.
Pronotum width	Wider pronotum are associated with the use of open or ground-level substrates, while narrower pronotum facilitate movement within confined spaces (Sosiak & Barden, 2021).
Weber's length	Body size indicator; body size is a key to many life history traits such as resource use (Kaspari and Weiser, 1999).
Hind femur length	A larger size favors agility, locomotion, and finding resources, but it makes it difficult to enter cavities and is unfavorable in more complex environments (Gibb & Parr, 2013).

Analysis

We quantified and compared the functional trait space of ant assemblages associated with myrmecophytes and EFNs using a multivariate hypervolume framework (*R* package hypervolume; Blonder et al. 2025). For each interaction type (Myrmecophyte-associated and ENF-associated ants), we constructed separate hypervolumes for mobility-related traits and feeding-related traits. To control for body size, all trait values were normalized by Weber's length (WL), a standard proxy for ant body size (Silva & Brandão, 2010). Subsequently, we applied a centered log-ratio (CLR) transformation to account for the compositional nature of the trait data (Aitchison, 1986; Greenacre, 2021). Data processing and CLR transformations were performed using the compositions package (van den Boogaart et al, 2022).

Trait-normalized data were analyzed using Principal Component Analysis (PCA) to reduce dimensionality and account for correlations among traits. Separate PCAs were conducted for feeding-related and mobility-related trait sets. The significance of PCA axes and trait loadings was assessed using the PCAtest function (PCAtest *R* package), based on 1,000 permutations of observations within each trait and 1,000 bootstrap resampling (Camargo 2022). PCA axes and loadings were interpreted as functional gradients associated with differences between ENF-associated and myrmecophyte-associated ant assemblages. These analyses indicated that the first three principal components captured a significant, non-random structure in trait variation and were therefore retained for subsequent hypervolume analyses. For feeding-related traits, the first three axes accounted for 76% of the variance, and for mobility-related traits, the first three axes accounted for 89% of the total variance and were selected for further analysis.

The first three PC axes were used to calculate hypervolumes using the Gaussian kernel method, with bandwidths optimized via cross-validation (Blonder et al., 2025). We then measured the pairwise intersection between the interaction-specific hypervolumes and the hypervolume representing the general arboreal ant assemblage. Intersection values were expressed as the proportion of trait space of Myrmecophyte-associated or ENF-associated ants shared with the baseline arboreal assemblage. Pairwise overlaps between hypervolumes were calculated using `hypervolume_set` and quantified via `hypervolume_overlap_statistics` functions from hypervolume package (Blonder et al., 2025). These metrics include the Sørensen overlap indice and absolute shared volume. To assess the robustness of volume estimates, we applied bootstrapping ($n = 100$ replicates) using the `hypervolume_resample` function (Blonder et al. 2025). We calculated the coefficient of variation (CV) of the bootstrapped volumes to evaluate the stability of

the estimation. A $CV < 10\%$ was considered indicative of stable volume estimates (Blonder et al., 2018).

To evaluate whether observed overlaps differed from random expectations, we implemented a null model for each trait and interaction type combination: (1) mobility and (2) foraging for Myrmecophyte-associated species and (3) mobility and (4) foraging for EFN-associated ant species. In each simulation/randomization, the species identities were randomly assigned to groups (i.e., Myrmecophyte-associated or general arboreal species), while maintaining the original sample size per group during 999 permutations. For each permutation, we recalculated the intersection proportion and compared it with the observed values. To visualize the structure of the observed functional spaces and their overlaps, we plotted 2D trait combinations using *ggplot2* (Wickham, 2016), overlaying kernel density contours for each group using *stat_density_2d*. All analyses were conducted in R (R Core Team 2025) version 4.3.2.

RESULTS

Taxonomic diversity

In total, we recorded mutualistic interactions for 302 species out of 475 arboreal and epigaeic arboreal ant species in the Brazilian Amazon, comprising 29 genera and seven subfamilies. Species classifications were compiled from an extensive survey of taxonomic and natural history literature, encompassing 181 published studies, allowing 84% of the species to be classified based on available information. As expected, no species were shared between the two mutualism categories. However, among the seven recorded subfamilies, all occurred in EFN-associated ants, whereas only four were recorded for myrmecophyte-associated species. At the genus level, six genera were shared between categories, indicating partial overlap between taxa, as expected for structurally distinct mutualisms that nonetheless involve within taxonomically related lineages.

Of the 302 mutualistic species, 217 belonging to 25 genera and seven subfamilies were categorized as ants engaged in EFN-bearing plants, representing 70% of all recorded ant-plant mutualisms. The most frequent genera were *Camponotus* (52 species), *Cephalotes* (47), *Crematogaster* (31), and *Dolichoderus* (27), which together accounted for approximately 72% of all EFN-associated ants (Supplementary material - Table S1).

A more restricted subset was identified for myrmecophytes, comprising 85 species distributed across 10 genera and four subfamilies in the Brazilian Amazon. The most frequent genera were *Azteca* (44 species), *Pseudomyrmex* (26), and *Allomerus* (6), representing about 91% of all records of ants nesting mutualistically in myrmecophytes. In contrast, six genera were represented by a single myrmecophilous species, such as *Crematogaster laevis*, *Myrcidris epicharis*, and *Pheidole minutula* (Supplementary material - Table S2).

Mobility-related traits

In general, the morphological space occupied by the traits of interacting ants was nested within the overall trait space of arboreal ants. For locomotory traits, EFN-associated ants exhibited a broader and more diffuse distribution, with a hypervolume spanning a larger portion of morphospace and overlapping substantially with the general arboreal assemblage (Figure 2). Nevertheless, null model comparisons revealed that the observed intersection between EFN-associated ants and the general assemblage was significantly lower than expected by chance (observed proportion = 0.769; $p = 0.017$).

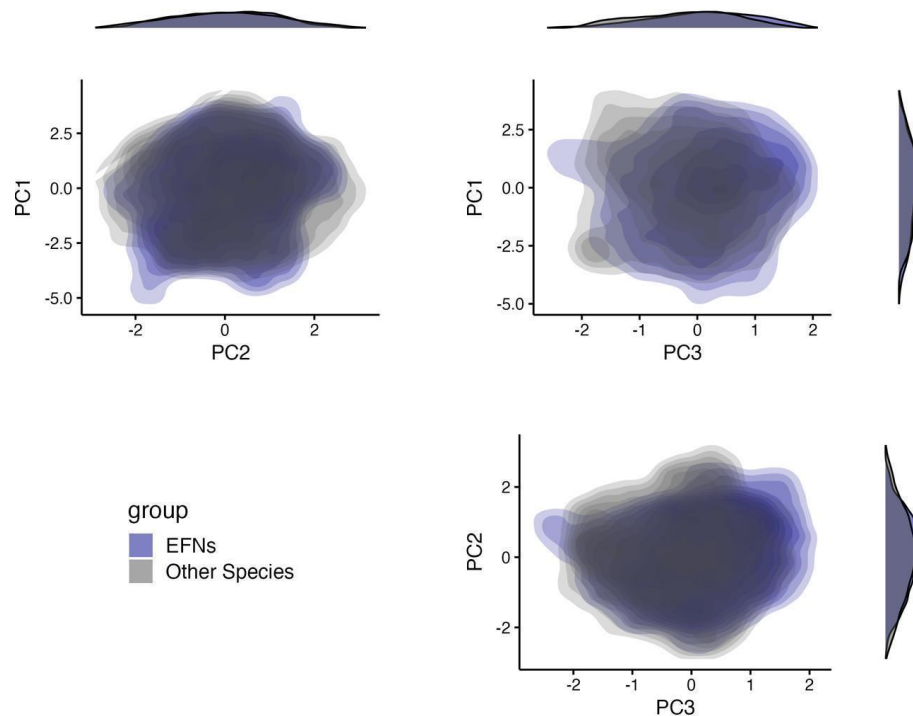


Figure 2. Morphospace of mobility-related traits for EFN-associated ants (blue) compared to the general arboreal ant assemblage (gray). Kernel density contours represent trait distributions across principal component axes.

By contrast, myrmecophyte-associated ants occupied a markedly narrower region of morphospace compared to EFN-associated ants and the general arboreal ant

assemblage (Figure 3). Their hypervolume showed limited dispersion and a high degree of internal overlap, indicating stronger morphological convergence within the group. Intersection analysis confirmed that myrmecophyte ants shared a significantly smaller proportion of trait space than expected under the null model (observed proportion = 0.447; $p = 0.001$).

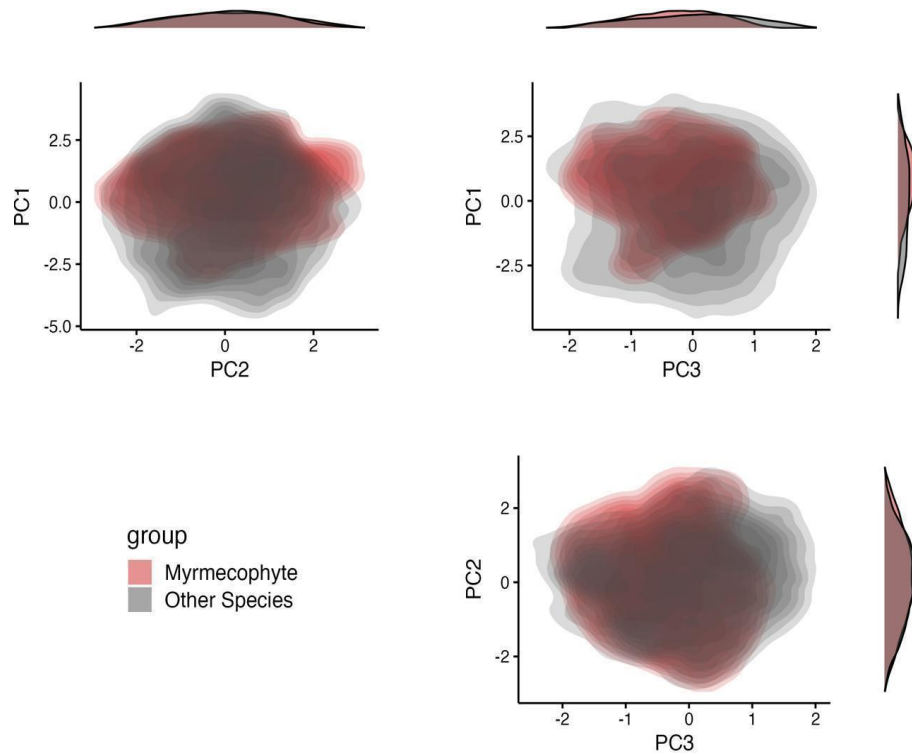


Figure 3. Morphospace of mobility traits for myrmecophyte-associated ants (red) compared to the general arboreal ant assemblage (gray). Kernel density contours represent trait distributions across principal component axes.

Feeding-related traits

For feeding-related traits, both interaction types occupied narrow morphospaces that differed significantly from the general arboreal ant assemblage. EFN-associated ants also displayed a reduced feeding trait space relative to the general arboreal assemblage (Figure 4). Their hypervolume showed a significantly lower intersection with the general assemblage than predicted by the null model (observed proportion = 0.628; $p = 0.003$).

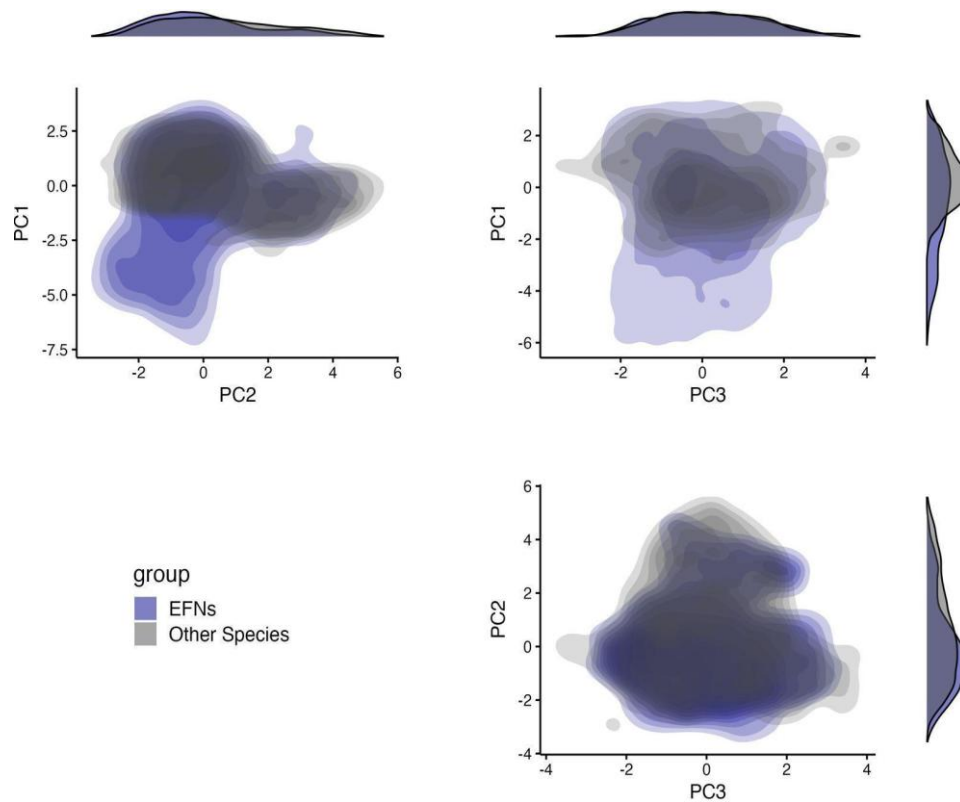


Figure 4. Morphospace of feeding-related traits for EFN-associated ants (blue; **216 spp.**) compared to the general arboreal ant assemblage (gray; **475 spp.**). Kernel density contours represent trait distributions across principal component axes.

Myrmecophyte-associated ants exhibited a constrained and well-defined trait space with low dispersion, indicating strong morphological convergence (Figure 5). Intersection analysis showed that they shared a substantially smaller proportion of trait space with the general assemblage than expected under the null model (observed proportion = 0.487; $p = 0.001$).

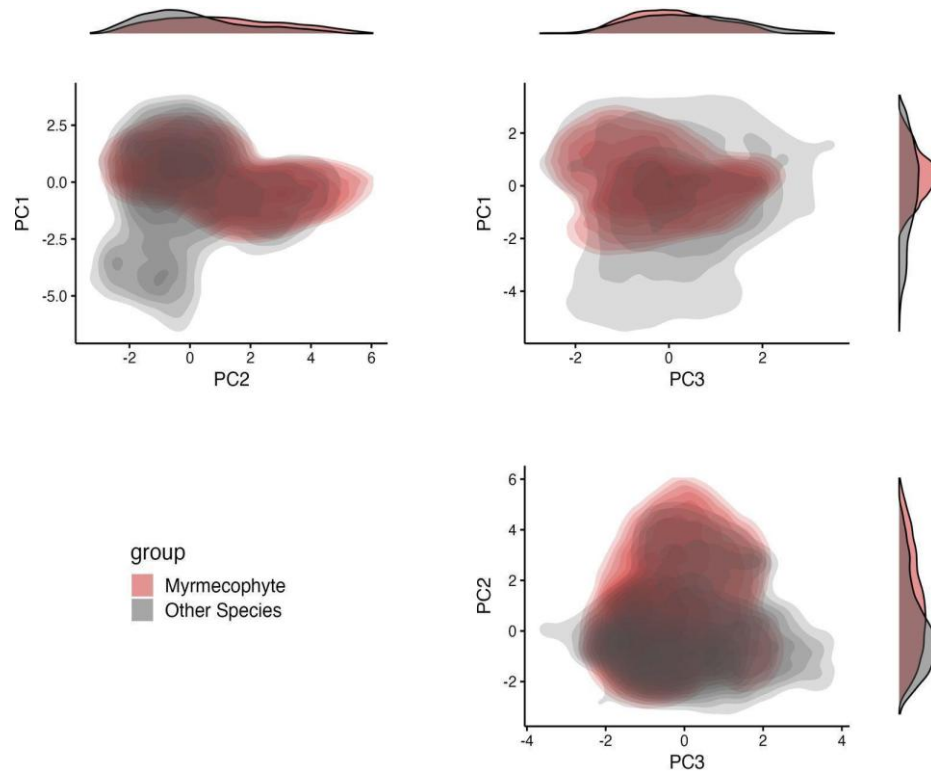


Figure 5. Morphospace of feeding-related traits for myrmecophyte-associated ants (red) compared to the general arboreal ant assemblage (gray). Kernel density contours represent trait distributions across principal component axes.

DISCUSSION

Taxonomic overview

Association with EFNs and myrmecophytes appears not to have driven the evolution of novel mobility or feeding phenotypes but instead reflects the trait-based structural and resource-mediated filtering of pre-existing morphological traits. The reduced morphological variation thus reflects the selective persistence of species whose traits are compatible with local conditions, rather than morphological innovation. In both cases, the taxonomic variance encompasses ants from phylogenetically distant clades. However, while the reduction of morphological variability in EFN-associated ants is relatively diffuse across both mobility and feeding-related traits, myrmecophyte-associated ants were taxonomically more specific and exhibited strong morphological convergence, occupying narrower and more restricted trait spaces. These differences suggest that the degree of interaction intimacy influences not only the taxonomic composition of ant assemblages but also the distribution of functional traits associated with mobility and feeding.

Our comprehensive database revealed that EFN-associated ants account for approximately 70% of all recorded ant-plant mutualisms in the Brazilian Amazon. In general, there are no genera exclusively associated with EFNs, which may explain the nested morphological structure within the trait space occupied by Amazonian arboreal ants. Despite the facultative and generalist nature of EFN associations, the involvement of lineages that are predominantly soil- and leaf-litter-associated remains particularly surprising. Only a small subset of species within these otherwise edaphic genera, such as *Strumigenys*, have evolved arboreal habits that allow them to exploit EFNs (Santos-Neto et al., 2024). Their occurrence, therefore, reflects infrequent evolutionary transitions toward arboreality within clades that are otherwise strongly associated with the litter-soil interface. However, previous studies indicate a frequent use of EFNs by certain groups such as *Camponotus*, *Cephalotes*, *Crematogaster*, and *Dolichoderus*, which were highlighted in our study. Some species of *Camponotus*, *Crematogaster*, and *Dolichoderus* are typically dominant and aggressive foragers that patrol EFN-bearing plants, deter potential herbivores and show a strong association with carbohydrate-rich resources (Anjos et al., 2016; Lange et al., 2017; Novais et al., 2025). Meanwhile, *Cephalotes* species exhibit a distinctive liquid-based diet, frequently visiting EFNs, floral nectaries, and pollen sources; although they are not always effective defenders, their presence can reduce herbivory pressure while enhancing colony nutrition (Byk & Del-Claro, 2010; Calixto et al., 2021).

In contrast, myrmecophyte-associated ants were taxonomically more restricted, with a total of 85 myrmecophilous species recorded in the Brazilian Amazon. The dominance of three genera with well-documented histories of associations with domatia-bearing plants is noteworthy: *Azteca* (Wheeler, 1929; Longino, 1991; Dejean et al., 2009), *Pseudomyrmex* (Ward, 1993; Fonseca, 1993; Ward, 1999), and *Allomerus* (Izzo & Vasconcelos, 2002; Izzo & Vasconcelos, 2005). Myrmecophilous ants typically nest in a limited number of myrmecophytic species or with exclusive partners, improving not only protection but also plant traits, such as relative growth rate (Fonseca 1999; Cárdenas et al. 2025). While plants evolve domatia into house protective ants, only a few clades have developed mutualistic connections with myrmecophytes, through physical and chemical adaptations for both partners (Chomicki et al., 2020). Importantly, two genera are exclusively associated with myrmecophytic plants: *Myrcidris* and *Allomerus*. *Myrcidris* is the sister genus to *Pseudomyrmex*, whereas *Allomerus* belongs to a lineage whose closest relatives (*Wasmannia* and *Blepharidatta*) are not myrmecophilous (Ward 1990;

Ward et al., 2015). These genera are morphologically similar and show no marked differentiation in the traits examined here. This pattern supports Fonseca and Ganade (1996), who reported that ant-plant associations in Amazonian forests are structured by ecological constraints rather than by phylogenetic or coevolutionary relationships. Accordingly, the known associations likely result from independent and repeated colonization events, with partner availability and replacement occurring over evolutionary time (Chomicki et al., 2015).

Mobility-related traits in symbiotic ants

EFN-associated ants exhibited broad and diffuse distributions of mobility-related traits, occupying a large portion of morphospace and substantially overlapping with the general arboreal assemblage. This broader morphological variation is consistent with the ecological flexibility inherent to facultative EFN associations, which accommodate species with diverse behavioral and defensive strategies (Heil & McKey, 2003). Moreover, this pattern reflects the nature of EFN-mediated interactions, where nectar rewards are accessible to a wide range of ant species (Nogueira et al., 2020). However, since extrafloral nectar is available on exposed plant tissues, larger-bodied ants tend to exhibit a higher degree of interaction with EFN-bearing plants (Weiser & Kaspari, 2006; Chamberlain & Holland, 2009; Miranda et al., 2024). Furthermore, ant species with longer legs may gain advantages in mobility across the arboreal substrate, enabling faster exploration and rapid response to enemies (i.e., herbivores, competitors and pathogens) (Gibb et al., 2015). Such traits combined with overall large body-sized may influence the ants' capacity to dominate exposed surfaces and monopolize nectar sources. Therefore, morphological attributes can mediate how efficiently ants exploit nectar resources and provide indirect plant protection.

Conversely to EFN systems, myrmecophyte-associated ants experience structural constraints imposed by domatia-bearing plants, demonstrated by the narrower functional space occupied by their morphological traits. Access to internal plant cavities requires specific body proportions that allow efficient movement and nesting within narrow spaces, favoring ants with compact bodies, shorter appendages, and increased maneuverability (Fonseca, 1993; Fonseca, 1999). Our study shows that morphological adaptations reduce the range of viable mobility traits, leading to a high degree of functional convergence among species inhabiting myrmecophytes. Such structural filtering likely represents a key ecological mechanism that drives specialization in

obligate mutualisms. By limiting access to arboreal species that can effectively navigate and occupy domatia, plants ensure the recruitment and stability of resident ant species, which are controlled by nesting space (Fonseca, 1999; Campbell et al., 2013). Over evolutionary time, this reciprocal selection may have reinforced the connection between plant architecture and ant morphology, leading to fine-tuned coadaptation in both partners (Brouat et al., 2001; Davidson & McKey, 1993). On the other hand, leg mobility suggests that some myrmecophyte-associated species have adapted to form highly mobile colonies, as observed in *Pseudomyrmex ferrugineus* group, which patrol and defend areas outside the nest continuously against intruders throughout the day and night (Sánchez-Rodríguez et al. 2025). Although our analyses were based on worker traits, queens of myrmecophilous ants may exhibit even stronger convergence in mobility-related morphology. Because queens are responsible for dispersal, host-plant location, and colony founding, they experience extreme selective pressures that canalize their morphology, patterns well documented for genera such as *Azteca*, where queens display pronounced morphological traits and high host specificity (Longino, 2007).

Feeding-related traits in symbiotic ants

Regarding feeding-related traits, EFN-associated ants also exhibited reduced trait spaces relative to the general arboreal assemblage. Extrafloral nectar is a readily available carbohydrate source that attracts species with varying degrees of trophic specialization and enhances ant colony fitness (Rudgers & Gardener, 2004; González-Teuber & Heil, 2009; Byk & Del-Claro, 2011). Dominant species found in this study, such as *Camponotus*, *Cephalotes*, and *Crematogaster* exhibit behavioral adaptations to arboreal environments, particularly within forest canopies, allowing them to forage extensively on carbohydrate-rich plant secretions and insect exudates (Blüthgen et al., 2000; Davidson et al., 2003; Ribas et al., 2010). Accordingly, clypeus measurements are often used as a proxy for liquid-feeding habits in worker ants (Davidson et al., 2004; Silva & Brandão, 2010). Moreover, arboreal species such as *Cephalotes pusillus* possess smaller mandibles and feed primarily on plant and insect exudates (Byk & Del-Claro, 2010). Thus, our study suggests that EFN-bearing plants may select for ants with morphological traits that enable efficient exploitation of liquid resources.

Myrmecophyte-associated ants exhibited an especially constrained feeding trait space, with low dispersion and high internal overlap. This pattern indicates strong morphological convergence associated with trophic adaptations that facilitate both

defense and obligatory plant association. From an evolutionary perspective, these ants initially exploited plant-derived resources (e.g., food bodies, nectar, and hemipteran honeydew) and later nested within plant cavities (Heil et al., 2010; Nelsen et al., 2018). Combined with mobility traits, their mandible and eye morphologies appear to have evolved for tasks such as extensive patrolling and manipulating confined structures, given that good vision, the ability to lick substrates and specialized use of jaws to cut trichomes reflect key behavioral components of co-evolutionary dynamics (Janzen, 1966; Dejean et al., 2005; Ward & Branstetter, 2017). Such integration exemplifies how ecological dependence within domatia systems drives both morphological and behavioral convergence in feeding-related traits.

CONCLUSION

Our findings demonstrate that degree of interaction intimacy is reflected in morphological patterns: obligate myrmecophyte interactions drive strong functional clustering, whereas facultative EFN interactions sustain broader trait diversity. These results support a general framework in which ecological filters act at multiple strengths and through distinct trait dimensions, depending on the type of resource offered by plants. This suggests that morphological convergence is not uniform across interaction types but reflects the ecological and evolutionary pressures imposed by different plant rewards. EFN-associated ants, and particularly those associated with myrmecophytes, have not developed morphological innovations in feeding or mobility-related traits throughout their evolution. Instead, their morphological quantitative traits appear to have converged toward a likely evolutionary optimum within the morphological space of Amazonian arboreal ants. Notably, several species from different subfamilies occupy a narrow morphological space, indicating strong ecological filtering and enduring evolutionary imprints on Amazonian arboreal ants.

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SUPPLEMENTARY MATERIAL

Table S1. List of ant species associated with extrafloral nectaries across the Brazilian Amazon Basin, including nesting stratum classification and number of species per genus.

Taxa	Nesting Stratum	Species number
Dolichoderinae		
<i>Dolichoderus</i>		27
<i>Dolichoderus abruptus</i> (Smith, 1858)	Arboreal	
<i>Dolichoderus andinus</i> (Kempf, 1962)	Arboreal	
<i>Dolichoderus attelaboides</i> (Fabricius, 1775)	Arboreal	
<i>Dolichoderus bidens</i> (Linnaeus, 1758)	Arboreal	
<i>Dolichoderus bispinosus</i> (Olivier, 1792)	Epigaeic/Arboreal	
<i>Dolichoderus cogitans</i> Forel, 1912	Arboreal	
<i>Dolichoderus debilis</i> Emery, 1890	Arboreal	
<i>Dolichoderus decollatus</i> Smith, 1858	Arboreal	
<i>Dolichoderus diversus</i> Emery, 1894	Arboreal	
<i>Dolichoderus fernandezi</i> MacKay, 1993	Arboreal	
<i>Dolichoderus ferrugineus</i> Forel, 1903	Arboreal	
<i>Dolichoderus ghilianii</i> Emery, 1894	Arboreal	
<i>Dolichoderus inermis</i> MacKay, 1993	Arboreal	
<i>Dolichoderus lamellosus</i> (Mayr, 1870)	Arboreal	
<i>Dolichoderus laminatus</i> (Mayr, 1870)	Arboreal	
<i>Dolichoderus longicollis</i> MacKay, 1993	Arboreal	
<i>Dolichoderus lugens</i> Emery, 1894	Arboreal	
<i>Dolichoderus lutosus</i> (Smith, 1858)	Arboreal	
<i>Dolichoderus mucronifer</i> (Roger, 1862)	Arboreal	
<i>Dolichoderus omacanthus</i> (Kempf, 1972)	Arboreal	
<i>Dolichoderus quadridenticulatus</i> (Roger, 1862)	Arboreal	
<i>Dolichoderus rufescens</i> Mann, 1912	Arboreal	
<i>Dolichoderus rugosus</i> (Smith, 1858)	Arboreal	
<i>Dolichoderus septemspinosus</i> Emery, 1894	Arboreal	
<i>Dolichoderus setosus</i> (Kempf, 1959)	Arboreal	
<i>Dolichoderus spinicollis</i> (Latreille, 1817)	Arboreal	
<i>Dolichoderus voraginosus</i> MacKay, 1993	Arboreal	

<i>Linepithema</i>	2
<i>Linepithema angulatum</i> (Emery, 1894)	Epigaeic/Arboreal
<i>Linepithema iniquum</i> (Mayr, 1870)	Arboreal
<i>Tapinoma</i>	1
<i>Tapinoma melanocephalum</i> (Fabricius, 1793)	Epigaeic/Arboreal
Ectatomminae	
<i>Ectatomma</i>	2
<i>Ectatomma brunneum</i> Smith, 1858	Epigaeic/Arboreal
<i>Ectatomma tuberculatum</i> (Olivier, 1792)	Epigaeic/Arboreal
<i>Holcoponera</i>	1
<i>Holcoponera moelleri</i> Forel, 1912	Arboreal
Formicinae	
<i>Camponotus</i>	52
<i>Camponotus ager</i> (Smith, 1858)	Epigaeic/Arboreal
<i>Camponotus alboannulatus</i> Mayr, 1887	Arboreal
<i>Camponotus apicalis</i> (Mann, 1916)	Arboreal
<i>Camponotus arboreus</i> (Smith, 1858)	Arboreal
<i>Camponotus atriceps</i> (Smith, 1858)	Epigaeic/Arboreal
<i>Camponotus bidens</i> Mayr, 1870	Arboreal
<i>Camponotus brevis</i> Forel, 1899	Epigaeic/Arboreal
<i>Camponotus canescens</i> Mayr, 1870	Arboreal
<i>Camponotus chartifex</i> (Smith, 1860)	Arboreal
<i>Camponotus cingulatus</i> Mayr, 1862	Epigaeic/Arboreal
<i>Camponotus crassicornis</i> Emery, 1920	Arboreal
<i>Camponotus crassus</i> Mayr, 1862	Arboreal
<i>Camponotus crassus amazonicus</i> Santschi, 1922	Arboreal
<i>Camponotus crassus delabiatus</i> Santschi, 1925	Arboreal
<i>Camponotus cressoni</i> André, 1887	Arboreal
<i>Camponotus depressus</i> Mayr, 1866	Arboreal
<i>Camponotus femoratus</i> (Fabricius, 1804)	Arboreal
<i>Camponotus fastigatus</i> Roger, 1863	Arboreal
<i>Camponotus folicola</i> Forel, 1904	Arboreal
<i>Camponotus hippocrepis</i> Emery, 1920	Arboreal

<i>Camponotus latangulus</i> Roger, 1863	Epigaeic/Arboreal
<i>Camponotus lespesii</i> Forel, 1886	Arboreal
<i>Camponotus leydigi</i> Forel, 1886	Terrestrial
<i>Camponotus macrocephalus</i> Emery, 1894	Arboreal
<i>Camponotus melanoticus</i> Emery, 1894	Arboreal
<i>Camponotus mirabilis</i> Emery, 1903	Arboreal
<i>Camponotus mocsaryi</i> Forel, 1902	Arboreal
<i>Camponotus mus</i> Roger, 1863	Arboreal
<i>Camponotus nidulans</i> (Smith, 1860)	Arboreal
<i>Camponotus novogranadensis</i> Mayr, 1870	Arboreal
<i>Camponotus pittieri</i> Forel, 1899	Arboreal
<i>Camponotus pittieri fuscogaster</i> Emery, 1920	Arboreal
<i>Camponotus planatus</i> Roger, 1863	Epigaeic/Arboreal
<i>Camponotus propinquus</i> Mayr, 1887	Arboreal
<i>Camponotus rapax</i> (Fabricius, 1804)	Arboreal
<i>Camponotus rectangularis</i> Emery, 1890	Arboreal
<i>Camponotus renggeri</i> Emery, 1894	Arboreal
<i>Camponotus rufipes</i> (Fabricius, 1775)	Arboreal
<i>Camponotus sanctaefidei</i> Dalla Torre, 1892	Arboreal
<i>Camponotus sanctaefidei convexinodis</i> Wheeler, 1934	Arboreal
<i>Camponotus sanctaefidei coronatus</i> Santschi, 1922	Arboreal
<i>Camponotus senex</i> (Smith, 1858)	Epigaeic/Arboreal
<i>Camponotus sericeiventris</i> (Guérin-Méneville, 1838)	Arboreal
<i>Camponotus sericeiventris satrapus</i> Wheeler, 1931	Arboreal
<i>Camponotus substitutus</i> Forel, 1899	Arboreal
<i>Camponotus tenuiscapus</i> Roger, 1863	Arboreal
<i>Camponotus textor</i> Forel, 1899	Arboreal
<i>Camponotus traili</i> Mayr, 1878	Arboreal
<i>Camponotus trapeziceps</i> Forel, 1908	Arboreal

<i>Camponotus trapezoideus</i> Mayr, 1870	Arboreal
<i>Camponotus urichi</i> Forel, 1899	Arboreal
<i>Camponotus urichi sculnus</i> Forel, 1904	Arboreal
Gigantiops	1
<i>Gigantiops destructor</i> (Fabricius, 1804)	Epigaeic/Arboreal
Myrmelachista	1
<i>Myrmelachista bambusarum</i> Forel, 1903	Arboreal
Myrmicinae	
Cardiocondyla	1
<i>Cardiocondyla obscurior</i> Wheeler, 1929	Arboreal
Cephalotes	46
<i>Cephalotes adolphi</i> (Emery, 1906)	Arboreal
<i>Cephalotes atratus</i> (Linnaeus, 1758)	Arboreal
<i>Cephalotes basalis</i> (Smith, 1876)	Arboreal
<i>Cephalotes betoi</i> De Andrade, 1999	Arboreal
<i>Cephalotes bohlsi</i> (Emery, 1896)	Arboreal
<i>Cephalotes bruchi</i> (Forel, 1912)	Arboreal
<i>Cephalotes christopherseni</i> (Forel, 1912)	Arboreal
<i>Cephalotes clypeatus</i> (Fabricius, 1804)	Arboreal
<i>Cephalotes coffeae</i> (Kempf, 1953)	Arboreal
<i>Cephalotes columbicus</i> (Forel, 1912)	Arboreal
<i>Cephalotes complanatus</i> (Guérin-Méneville, 1844)	Arboreal
<i>Cephalotes conspersus</i> (Smith, 1867)	Arboreal
<i>Cephalotes cordatus</i> (Smith, 1853)	Arboreal
<i>Cephalotes cordiae</i> (Stitz, 1913)	Arboreal
<i>Cephalotes depressus</i> (Klug, 1824)	Arboreal
<i>Cephalotes duckei</i> (Forel, 1906)	Arboreal
<i>Cephalotes eduarduli</i> (Forel, 1921)	Arboreal
<i>Cephalotes fiebrigi</i> (Forel, 1906)	Arboreal
<i>Cephalotes grandinosus</i> (Smith, 1860)	Arboreal
<i>Cephalotes inaequalis</i> (Mann, 1916)	Arboreal
<i>Cephalotes klugi</i> (Emery, 1894)	Arboreal
<i>Cephalotes laminatus</i> (Smith, 1860)	Arboreal

<i>Cephalotes maculatus</i> (Smith, 1876)	Arboreal
<i>Cephalotes manni</i> (Kempf, 1951)	Arboreal
<i>Cephalotes minutus</i> (Fabricius, 1804)	Arboreal
<i>Cephalotes oculatus</i> (Spinola, 1851)	Arboreal
<i>Cephalotes opacus</i> Santschi, 1920	Arboreal
<i>Cephalotes pallens</i> (Klug, 1824)	Arboreal
<i>Cephalotes pallidoides</i> De Andrade, 1999	Arboreal
<i>Cephalotes pallidus</i> De Andrade, 1999	Arboreal
<i>Cephalotes palustris</i> De Andrade, 1999	Arboreal
<i>Cephalotes pavonii</i> (Latreille, 1809)	Arboreal
<i>Cephalotes pellans</i> De Andrade, 1999	Arboreal
<i>Cephalotes persimilis</i> De Andrade, 1999	Arboreal
<i>Cephalotes persimplex</i> De Andrade, 1999	Arboreal
<i>Cephalotes placidus</i> (Smith, 1860)	Arboreal
<i>Cephalotes pusillus</i> (Klug, 1824)	Epigaeic/Arboreal
<i>Cephalotes quadratus</i> (Mayr, 1868)	Arboreal
<i>Cephalotes ramiphilus</i> (Forel, 1904)	Arboreal
<i>Cephalotes serraticeps</i> (Smith, 1858)	Arboreal
<i>Cephalotes simillimus</i> (Kempf, 1951)	Arboreal
<i>Cephalotes solidus</i> (Kempf, 1974)	Arboreal
<i>Cephalotes spinosus</i> (Mayr, 1862)	Arboreal
<i>Cephalotes targionii</i> (Emery, 1894)	Arboreal
<i>Cephalotes trichophorus</i> De Andrade, 1999	Arboreal
<i>Cephalotes umbraculatus</i> (Fabricius, 1804)	Arboreal

Crematogaster

31

<i>Crematogaster abstinens</i> Forel, 1899	Arboreal
<i>Crematogaster acuta</i> (Fabricius, 1804)	Arboreal
<i>Crematogaster amapaensis</i> Kempf, 1960	Arboreal
<i>Crematogaster arcuata</i> Forel, 1899	Arboreal
<i>Crematogaster boliviana</i> (Wheeler, 1922)	Arboreal
<i>Crematogaster brasiliensis</i> Mayr, 1878	Arboreal
<i>Crematogaster bryophilia</i> Longino, 2003	Arboreal
<i>Crematogaster carinata</i> Mayr, 1862	Arboreal

<i>Crematogaster crinosa</i> Mayr, 1862	Arboreal
<i>Crematogaster curvispinosa</i> Mayr, 1862	Arboreal
<i>Crematogaster distans</i> Mayr, 1870	Arboreal
<i>Crematogaster egregior</i> Forel, 1912	Arboreal
<i>Crematogaster erecta</i> Mayr, 1866	Arboreal
<i>Crematogaster evallans</i> Forel, 1907	Arboreal
<i>Crematogaster huberi</i> (Forel, 1907)	Arboreal
<i>Crematogaster jardinero</i> Longino, 2003	Arboreal
<i>Crematogaster levior</i> Longino, 2003	Arboreal
<i>Crematogaster limata</i> Smith, 1858	Arboreal
<i>Crematogaster longispina</i> Emery, 1890	Arboreal
<i>Crematogaster moelleri</i> Forel, 1912	Arboreal
<i>Crematogaster montezumia</i> Smith, 1858	Arboreal
<i>Crematogaster nigropilosa</i> Mayr, 1870	Arboreal
<i>Crematogaster obscurata</i> Emery, 1895	Arboreal
<i>Crematogaster quadriiformis</i> Roger, 1863	Arboreal
<i>Crematogaster rochai</i> Forel, 1903	Arboreal
<i>Crematogaster stollii</i> Forel, 1885	Arboreal
<i>Crematogaster sumichrasti</i> Mayr, 1870	Arboreal
<i>Crematogaster tenuicula</i> Forel, 1904	Arboreal
<i>Crematogaster torosa</i> Mayr, 1870	Arboreal
<i>Crematogaster victima</i> Smith, 1858	Arboreal
<i>Crematogaster wardi</i> Longino, 2003	Arboreal
Cyphomyrmex	2
<i>Cyphomyrmex minutus</i> Mayr, 1862	Epigaeic/Arboreal
<i>Cyphomyrmex rimosus</i> (Spinola, 1851)	Epigaeic/Arboreal
Daceton	2
<i>Daceton armigerum</i> (Latreille, 1802)	Arboreal
<i>Daceton boltoni</i> Azorsa & Sosa-Calvo, 2008	Arboreal
Megalomyrmex	2
<i>Megalomyrmex balzani</i> Emery, 1894	Epigaeic/Arboreal
<i>Megalomyrmex foreli</i> Emery, 1890	Epigaeic/Arboreal
Monomorium	1

<i>Monomorium floricola</i> (Jerdon, 1851)	Epigaeic/Arboreal	
Nesomyrmex		2
<i>Nesomyrmex asper</i> (Mayr, 1887)	Arboreal	
<i>Nesomyrmex spininodis</i> (Mayr, 1887)	Arboreal	
Pheidole		3
<i>Pheidole biconstricta</i> Mayr, 1870	Epigaeic/Arboreal	
<i>Pheidole gauthieri</i> Forel, 1901	Arboreal	
<i>Pheidole mendicula</i> Wheeler, 1925	Epigaeic	
Procryptocerus		13
<i>Procryptocerus attenuatus</i> (Smith, 1876)	Arboreal	
<i>Procryptocerus convexus</i> Forel, 1904	Arboreal	
<i>Procryptocerus goeldii</i> Forel, 1899	Arboreal	
<i>Procryptocerus gracilis</i> (Smith, 1858)	Arboreal	
<i>Procryptocerus hirsutus</i> Emery, 1896	Arboreal	
<i>Procryptocerus hylaeus</i> Kempf, 1951	Arboreal	
<i>Procryptocerus marginatus</i> Borgmeier, 1948	Arboreal	
<i>Procryptocerus paleatus</i> Emery, 1896	Arboreal	
<i>Procryptocerus pictipes</i> Emery, 1896	Arboreal	
<i>Procryptocerus scabriusculus</i> Forel, 1899	Arboreal	
<i>Procryptocerus spiniperdus</i> Forel, 1899	Arboreal	
<i>Procryptocerus striatus</i> (Smith, 1860)	Arboreal	
<i>Procryptocerus subpilosus</i> (Smith, 1860)	Arboreal	
Solenopsis		1
<i>Solenopsis richteri</i> Forel, 1909	Epigaeic/Arboreal	
Strumigenys		2
<i>Strumigenys epinotalis</i> Weber, 1934	Arboreal	
<i>Strumigenys fairchildi</i> Brown, 1961	Arboreal	
Paraponerinae		
Paraponera		1
<i>Paraponera clavata</i> (Fabricius, 1775)	Epigaeic/Arboreal	
Ponerinae		
Leptogenys		1
<i>Leptogenys wheeleri</i> Forel, 1901	Arboreal	

Neoponera		6
<i>Neoponera crenata</i> (Roger, 1861)	Arboreal	
<i>Neoponera globularia</i> (MacKay & MacKay, 2010)	Arboreal	
<i>Neoponera inversa</i> (Smith, 1858)	Arboreal	
<i>Neoponera rugosula</i> Emery, 1902	Arboreal	
<i>Neoponera theresiae</i> (Forel, 1899)	Arboreal	
<i>Neoponera villosa</i> (Fabricius, 1804)	Arboreal	
Odontomachus		2
<i>Odontomachus bauri</i> Emery, 1892	Epigaeic/Arboreal	
<i>Odontomachus panamensis</i> Forel, 1899	Arboreal	
Pseudomyrmecinae		
Pseudomyrmex		12
<i>Pseudomyrmex caeciliae</i> (Forel, 1913)	Arboreal	
<i>Pseudomyrmex filiformis</i> (Fabricius, 1804)	Arboreal	
<i>Pseudomyrmex ita</i> (Forel, 1906)	Arboreal	
<i>Pseudomyrmex maculatus</i> (Smith, 1855)	Arboreal	
<i>Pseudomyrmex phyllophilus</i> (Smith, 1858)	Arboreal	
<i>Pseudomyrmex pisinnus</i> Ward, 1989	Arboreal	
<i>Pseudomyrmex pupa</i> (Forel, 1911)	Arboreal	
<i>Pseudomyrmex simplex</i> (Smith, 1877)	Arboreal	
<i>Pseudomyrmex subater</i> (Wheeler & Mann, 1914)	Arboreal	
<i>Pseudomyrmex tenuissimus</i> (Emery, 1906)	Arboreal	
<i>Pseudomyrmex unicolor</i> (Smith, 1855)	Arboreal	
<i>Pseudomyrmex venustus</i> (Smith, 1858)	Arboreal	
Total of species		215

Table S2. List of arboreal ant species associated with myrmecophyte plants across the Brazilian Amazon Basin.

Taxa	Myrmecophyte associated	Reference
<i>Allomerus brevipilosus</i> Fernández, 2007	<i>Gleasonia uaupensis</i> Ducke	Fernandez, 2007
<i>Allomerus decemarticulatus</i> Mayr, 1878	<i>Hirtella physophora</i> Mart. & Zucc., <i>Duroia</i> sp., <i>Tococa</i> sp.	Fernandez, 2007
<i>Allomerus maietae</i> Fernández, 2007	<i>Miconia alatiflora</i> Michelang.	Fernandez, 2007
<i>Allomerus octoarticulatus</i> Mayr, 1878	<i>Hirtella myrmecophila</i> Pilg.	Fernandez, 2007
<i>Allomerus septemarticulatus</i> Mayr, 1878	<i>Duroia saccifera</i> (Schult. & Schult.f.) K.Schum.	Fernandez, 2007
<i>Allomerus vogeli</i> Kempf, 1975	<i>Miconia macrosperma</i> (Mart.) Michelang.	Fernandez, 2007
<i>Azteca alfari</i> Emery, 1893	<i>Cecropia obtusa</i> Trécul., <i>C. adenopus</i> Mart., <i>C. leucocoma</i> Miq.,	Longino, 2007
<i>Azteca angusticeps</i> Emery, 1893	<i>Cordia alliodora</i> (Ruiz & Pav.) Oken; <i>Duroia petiolaris</i> Spruce ex K.Schum.,	Wheeler, 1942
<i>Azteca aurita</i> Emery, 1893	<i>Cecropia</i> sp.	Longino, 2007
<i>Azteca australis</i> Wheeler, 1942	<i>Cecropia</i> sp.	Longino, 1991
<i>Azteca bequaerti</i> Wheeler & Bequaert	<i>Cecropia hispidissima</i> Cuatrec.; <i>Tococa guianensis</i> Aubl.	Wheeler, 1929; Dejean et al., 2009
<i>Azteca brevicornis</i> (Mayr, 1878)	<i>Cecropia hispidissima</i> Cuatrec.	Wheeler, 1942
<i>Azteca coussapoeae</i> Forel, 1904	<i>Cecropia</i> sp.	Wheeler, 1942
<i>Azteca crassicornis</i> Emery, 1893	<i>Cordia nodosa</i> Lam.	Emery, 1893
<i>Azteca delpini</i> Emery, 1893	<i>Cordia nodosa</i> Lam.	Wheeler, 1942
<i>Azteca depilis</i> Emery, 1893	<i>Cordia nodosa</i> Lam.	Wheeler, 1942
<i>Azteca duckei</i> Forel, 1906	<i>Duroia hirsuta</i> (Poepp.) K.Schum.	Wheeler, 1929
<i>Azteca duroiae</i> Forel, 1904	<i>Duroia</i> sp.; <i>Cecropia</i> sp.	Wheeler, 1929
<i>Azteca emeryi</i> Forel, 1904	<i>Cecropia</i> sp.; <i>Cordia alliodora</i> (Ruiz & Pav.) Oken	Wheeler, 1929
<i>Azteca fasciata</i> Emery, 1893	<i>Cecropia</i> sp.	Arruda et al., 2016

<i>Azteca fasciata similis</i> Mann, 1916	<i>Cecropia</i> sp.	Arruda et al., 2016
<i>Azteca goeldii</i> Forel, 1906	<i>Cecropia</i> sp.	Wheeler, 1942
<i>Azteca huberi</i> Forel, 1906	<i>Cecropia</i> sp.	Wheeler, 1942
<i>Azteca instabilis</i> (Smith, 1862)	<i>Cecropia</i> sp.	Longino, 2007
<i>Azteca isthmica</i> Wheeler, 1942	<i>Cecropia</i> sp.	Wheeler, 1942
<i>Azteca jelskii</i> Emery, 1893	<i>Cecropia</i> sp.	Longino, 2007
<i>Azteca lallemandi</i> Forel, 1899	<i>Cecropia</i> sp.	Longino, 2007
<i>Azteca minor</i> Forel, 1904	<i>Cecropia ficifolia</i> Warb. & Snethl.	Wheeler, 1929
<i>Azteca muelleri</i> Emery, 1893	<i>Cecropia adenopus</i> Mart. ex Miq.	Wheeler, 1929
<i>Azteca muelleri terminalis</i> Mann, 1916	<i>Cecropia adenopus</i> Mart. ex Miq.	Wheeler, 1929
<i>Azteca olitrix</i> Forel, 1904	<i>Cordia nodosa</i> Lam.	Wheeler, 1929
<i>Azteca ovaticeps</i> Forel, 1904	<i>Cecropia</i> sp.	Longino, 2007
<i>Azteca paraensis</i> Forel, 1904	<i>Cecropia</i> sp.	Bondar, 1930
<i>Azteca sapii</i> Forel, 1912	<i>Cecropia</i> sp.	Longino, 1996
<i>Azteca schimperi</i> Emery, 1893	<i>Cecropia leucocoma</i> Miq.	Longino, 2007
<i>Azteca schumannii</i> Emery, 1893	<i>Tachigali</i> sp.	Wheeler, 1942
<i>Azteca schumannii dubia</i> Mann, 1916	<i>Tachigali</i> sp.	Wheeler, 1942
<i>Azteca schumannii taediosa</i> Forel, 1904	<i>Tachigali</i> sp.	Wheeler, 1942
<i>Azteca stanleyuli</i> Forel, 1921		Wheeler, 1942
<i>Azteca trailii</i> Emery, 1893	<i>Tococa</i> sp.	Wheeler, 1929
<i>Azteca trailii filicis</i> Forel, 1904	<i>Tococa</i> sp.	Wheeler, 1929
<i>Azteca trailii tococae</i> Forel, 1904	<i>Tococa formicaria</i> Mart. ex DC.	Wheeler, 1929
<i>Azteca trigona</i> Emery, 1893	<i>Cecropia</i> sp.	Longino, J.T. Ants of the World database
<i>Azteca trigona mathildae</i> Forel, 1906	<i>Cecropia</i> sp.	Longino, J.T. Ants of the World database
<i>Azteca trigona subdentata</i> Forel, 1904	<i>Cecropia</i> sp.	Longino, J.T. Ants of the World database

<i>Azteca ulei</i> Forel, 1904	<i>Cordia nodosa</i> Lam.; <i>Duroia saccifera</i> (Mart.) Hook.f. ex K.Schum.	Wheeler, 1929
<i>Azteca ulei cordiae</i> Forel, 1904	<i>Cordia nodosa</i> Lam.	Wheeler, 1929
<i>Azteca ulei nigricornis</i> Forel, 1904	<i>Cordia nodosa</i> Lam.	Wheeler, 1929
<i>Azteca velox</i> Forel, 1899	<i>Cordia nodosa</i> Lam.	Longino, 2007
<i>Azteca xanthochroa</i> (Roger, 1863)	<i>Cecropia</i> sp.	Wheeler, 1929
<i>Brachymyrmex heeri</i> Forel, 1874	<i>Duroia saccifera</i> (Mart.) Hook.f. ex K.Schum.	Wheeler, 1942
<i>Brachymyrmex pictus</i> Mayr, 1887	<i>Tachigali paniculata</i> Aubl.	Ortiz-Sepulveda et al. 2019
<i>Camponotus balzani</i> Emery, 1894	<i>Cecropia</i> sp.	Fonseca & Ganade, 1996
<i>Camponotus blandus</i> (Smith, 1858)	<i>Cecropia</i> sp.	McClure et al., 2008
<i>Crematogaster laevis</i> Mayr, 1878	<i>Maieta guianensis</i> Aubl.	Vasconcelos & Davidson, 2000
<i>Myrcidris epicharis</i> Ward, 1990	<i>Myrcia madida</i> McVaugh	Ward, 1990
<i>Myrmelachista nigella</i> (Roger, 1863)	<i>Duroia hirsuta</i> (Poepp.) K.Schum.	Longino, 2006
<i>Pheidole minutula</i> Mayr, 1878	<i>Maieta guianensis</i> Aubl., <i>M. poeppigii</i> Mart. ex Triana	Vasconcelos, 1993
<i>Pseudomyrmex acanthobius</i> (Emery, 1896)	<i>Acacia</i> sp.	Wild, 2007
<i>Pseudomyrmex boopis</i> (Roger, 1863)	<i>Acacia</i> sp.	Ward, 1993
<i>Pseudomyrmex concolor</i> (Smith, 1860)	<i>Tachigali paniculata</i> Aubl.	Ward, 1999
<i>Pseudomyrmex cubaensis</i> (Forel, 1901)	<i>Cordia alliodora</i> (Ruiz & Pav.) Oken	Ward, 1989
<i>Pseudomyrmex curacaensis</i> (Forel, 1912)	<i>Triplaris</i> sp.	Ward, 1989
<i>Pseudomyrmex deminutus</i> Ward, 1999	<i>Triplaris</i> sp.	Ward, 1999
<i>Pseudomyrmex dendroicus</i> (Forel, 1904)	<i>Triplaris</i> sp.	Ward, 1999
<i>Pseudomyrmex elongatus</i> (Mayr, 1870)	<i>Triplaris cumingiana</i> Fisch. & C.A.Mey.	Ward, 1999
<i>Pseudomyrmex ferox</i> Ward, 1999	<i>Tachigali</i> sp.; <i>Tachigali ptychophysca</i> Spruce ex Benth.	Ward, 1999
<i>Pseudomyrmex gracilis</i> (Fabricius, 1804)	<i>Acacia</i> sp.	Ward, 1993
<i>Pseudomyrmex insuavis</i> Ward, 1999	<i>Tachigali</i> sp.	Ward, 1999

<i>Pseudomyrmex kuenckeli</i> (Emery, 1890)	<i>Tachigali</i> sp.	Ward, 1999
<i>Pseudomyrmex longior</i> (Forel, 1904)	<i>Triplaris</i> sp.	Sanchez, 2015
<i>Pseudomyrmex malignus</i> (Wheeler, 1921)	<i>Tachigali</i> sp.	Ward, 1999
<i>Pseudomyrmex penetrator</i> (Smith, 1877)	<i>Tachigali</i> sp.	Ward, 1999
<i>Pseudomyrmex pictus</i> (Stitz, 1913)	<i>Tachigali</i> sp.	Ward, 1999
<i>Pseudomyrmex rubiginosus</i> (Stitz, 1913)	<i>Triplaris</i> sp.; <i>Tachigali</i> sp.	Ward, 1999
<i>Pseudomyrmex sericeus</i> (Mayr, 1870)	<i>Triplaris</i> sp.	Ward, 1999
<i>Pseudomyrmex sericeus cordiae</i>	<i>Cordia alliodora</i> (Ruiz & Pav.) Oken	Ward, 1999
<i>Pseudomyrmex tachigaliae</i> (Forel, 1904)	<i>Tachigali</i> sp.	Ward, 1999
<i>Pseudomyrmex tenuis</i> (Fabricius, 1804)	<i>Tachia guianensis</i> Aubl.	Kempf, 1960
<i>Pseudomyrmex triplaridis</i> (Forel, 1904)	<i>Triplaris</i> sp.	Ward, 1999
<i>Pseudomyrmex triplarinus</i> (Weddell, 1850)	<i>Triplaris</i> sp.	Ward, 1999
<i>Pseudomyrmex urbanus</i> (Smith, 1877)	<i>Cordia longituba</i> Chodat & Vischer	Ward, 1989
<i>Pseudomyrmex viduus</i> (Smith, 1858)	<i>Triplaris</i> sp.	Wheeler, 1929
<i>Pseudomyrmex vinneni</i> (Forel, 1906)	<i>Tachigali</i> sp.	Wheeler, 1929
<i>Strumigenys tococae</i> Wheeler Bequaert, 1929	<i>Tococa</i> sp.	Wheeler, 1929

CONSIDERAÇÕES GERAIS

No primeiro capítulo, demonstramos que a inundação sazonal atua como um forte filtro ambiental na organização das interações mutualistas entre formigas e plantas nas florestas amazônicas. O regime de inundação influenciou simultaneamente a composição de espécies e a estrutura das redes formiga-planta, além da menor prevalência de espécies oportunistas em áreas inundáveis, resultando em comunidades de formigas mais especializadas em florestas inundáveis, ainda que em menor frequência. Esses resultados evidenciam que gradientes hidrológicos não apenas moldam a distribuição das assembleias, mas também reorganizam as interações ecológicas, com potenciais implicações para a estabilidade dos mutualismos em ambientes sujeitos a distúrbios naturais recorrentes.

No capítulo 2, estudamos como as interações com plantas mirmecófitas e com plantas portadoras de nectários extraflorais estão associadas a conjuntos distintos de traços morfológicos de formigas arbóreas em escala amazônica, revelando padrões de convergência morfológica (funcional) entre espécies que exploram cada tipo de recurso vegetal. Formigas associadas a mirmecófitas apresentaram um espaço funcional mais restrito, consistente com maior especialização ecológica, enquanto aquelas associadas a nectários extraflorais exibiram maior amplitude morfológica. Esses resultados indicam que correspondências funcionais entre parceiros mutualistas desempenham papel central na estruturação das interações formiga-planta, refletindo adaptações aos diferentes modos de ocupação e exploração das plantas hospedeiras.

Em conjunto, esta tese demonstra que a distribuição e a organização das interações formiga-planta nas florestas amazônicas emergem da ação integrada de filtros ambientais e de correspondências funcionais entre parceiros. Ao integrar abordagens de redes ecológicas e diversidade funcional em escala regional, nossos resultados representam o primeiro esforço em larga escala baseado em traços aplicado a mutualismos formiga-planta na Amazônia Brasileira e fornecem uma base para abordagens macroecológicas da diversidade de formigas na Bacia Amazônica. Em um contexto de mudanças climáticas e possíveis alterações no regime hidrológico amazônico, compreender como gradientes ambientais e atributos funcionais moldam interações mutualistas torna-se essencial para prever respostas das comunidades e orientar estratégias de conservação que considerem

não apenas espécies isoladas, mas também as interações que sustentam o funcionamento dos ecossistemas.

OUTROS ARTIGOS PUBLICADOS DURANTE O PERÍODO DO DOUTORADO

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4. Gaem, P. H., Farroñay, F., **Santos, T. F.**, Cabello, N. B., Mazine, F. F., & Vicentini, A. (2019). First record of *Myrcia magna* (Myrtaceae) as a myrmecophyte host for *Myrcidris epicharis* (Formicidae: Pseudomyrmecinae). *Sociobiology*, 66, 592.
5. Aline Nobre Guindani, Talitha Ferreira dos Santos, Isabela Freitas Oliveira, Diego Rodrigues Guilherme, Janderson Batista Rodrigues Alencar, Torbjørn Haugaasen, Fabricio Beggiato Baccaro. Effects of seasonal flooding on ant species richness, assemblage composition and functional diversity in central Amazonian forests. (nesse caso, artigo submetido para a revista *Insect Conservation and Diversity*, em dezembro de 2025).

DIVULGAÇÃO CIENTÍFICA

Durante o período do doutorado, participei de duas edições do **Curso de História Natural do Alto Cuieiras**, realizado pelo Projeto Museu na Floresta do Instituto Nacional de Pesquisas da Amazônia (INPA), nos anos de 2019 e 2022, na Base do Alto Cuieiras, localizada na Área de Proteção Ambiental Margem Esquerda do Rio Negro. O curso aborda a história natural de diferentes grupos biológicos, incluindo plantas, insetos e mamíferos, integrando pesquisa científica e atividades de formação em campo. Em ambas as edições, atuei, juntamente com a Dra. Flávia Santana, na liderança das atividades relacionadas ao tema Interações Ecológicas, com enfoque principalmente em interações inseto-planta e inseto-fungo. Ao final da edição de 2019, desenvolvemos coletivamente uma cartilha de divulgação científica direcionada às comunidades do entorno da base, com o objetivo de compartilhar conhecimentos sobre biodiversidade e interações ecológicas de forma acessível.



Além disso, em 2022, fui convidada a participar do capítulo *Formigas da Amazônia*, da série documental *Amazônia do Macro ao Micro*, produzida pela TV Cultura em parceria com a UnivespTV e o Museu da Amazônia (MUSA). O documentário tem como objetivo apresentar a floresta amazônica em diferentes escalas, das grandes paisagens aos organismos microscópicos que sustentam o funcionamento do ecossistema. O episódio *Formigas da Amazônia* também contou com a participação do Dr. Fabricio Baccaro e da Dra. Amanda Batista e abordou o papel ecológico das formigas na Amazônia, destacando sua diversidade, organização social e importância para a sociedade. Durante o episódio, apresentei aspectos relacionados ao tema do meu doutorado, especialmente sobre interações ecológicas e relação das formigas e plantas mirmecófitas. O material encontra-se disponível na plataforma YouTube por meio do seguinte link: <https://www.youtube.com/watch?v=aD6QYIqunN0>.



