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ESTRUTURA DE ASSEMBLEIAS DE FORMIGAS EM ECOSSISTEMAS DE AREIA BRANCA EM DIFERENTES ESCALAS ESPACIAIS NA AMAZÔNIA

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Manaus, Amazonas

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Tese apresentada ao Programa de Pós Graduação em Zoologia, da Universidade Federal do Amazonas/Instituto Nacional de Pesquisas da Amazônia, como parte dos requisitos para obtenção do título de Doutora em Zoologia.

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"I Come as one but I stand as ten Thousand".

(Maya Angelou)

Resumo

A Amazônia, o bioma terrestre mais diverso do planeta, é moldada por eventos históricos e pela heterogeneidade ambiental. Plantas e animais especializaram-se em diferentes tipos de vegetação, como florestas de terra-firme, florestas inundadas e ecossistemas de areia branca (White Sand Ecosystems – WSE). Estes, com solos pobres em nutrientes e baixa produtividade, abrigam espécies altamente adaptadas e muitas vezes endêmicas. No entanto, a diversidade de formigas nesses ambientes é ainda pouco conhecida. Dada sua importância ecológica, as formigas são um grupo ideal para estudar as interações entre espécies e suas respostas às variações ambientais. Esta tese examinou a estrutura e composição de assembleias de formigas em WSEs da Amazônia brasileira em diferentes escalas espaciais. No **primeiro capítulo**, investigamos como a diversidade de formigas terrestres e arbóreas é influenciada pela estrutura da vegetação ao longo de um gradiente de vegetação de areia branca. No **segundo capítulo** explorou como a estrutura do habitat e os processos biogeográficos afetam assembleias de formigas em campinas abertas e florestas de areia branca em duas regiões. Para o **terceiro capítulo**, apresentamos o primeiro levantamento abrangente de formigas arbóreas e terrestres em campinas. Descobrimos que a diversidade beta foi dominada pela substituição de espécies, e a estrutura do habitat influenciou a composição de formigas terrestres e arbóreas. Essas conclusões reforçam a necessidade de estratégias de conservação que levem em consideração a complexidade e heterogeneidade dos ecossistemas de areia branca para preservar sua biodiversidade.

Palavras- chave: Floresta Amazônica, Ecossistemas de Areia Branca (WSEs), Diversidade de Formigas, Gradiente Ambiental, Estrutura do Habitat, Conservação.

Abstract

The Amazon, the most diverse terrestrial biome on the planet, is shaped by historical events and environmental heterogeneity. Plants and animals have specialized in different types of vegetation, such as terra-firme forests, flooded forests, and white-sand ecosystems (WSEs). These ecosystems, characterized by nutrient-poor soils and low productivity, harbor highly adapted and often endemic species. However, ant diversity in these environments remains largely unknown. Given their ecological importance, ants are an ideal group to study species interactions and their responses to environmental variations. This thesis investigated the structure and composition of ant assemblages in WSEs of the Brazilian Amazon at different spatial scales. In the first chapter, we examined how the diversity of ground-dwelling and arboreal ants is influenced by vegetation structure along a white-sand vegetation gradient. The second chapter explored how habitat structure and biogeographic processes affect ant assemblages in open campinas and white-sand forests across two regions. In the third chapter, we presented the first comprehensive survey of arboreal and ground-dwelling ants in campinas. We found that beta diversity was dominated by species turnover, and habitat structure influenced the composition of both ground-dwelling and arboreal ants. These findings highlight the need for conservation strategies that consider the complexity and heterogeneity of white-sand ecosystems to preserve their biodiversity.

Keywords: Amazon Rainforest, White-Sand Ecosystems (WSEs), Ant Diversity, environmest gradient, Habitat Structure, Conservation.

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Introdução geral

A Amazônia é o bioma terrestre mais diverso do planeta, e sua diversidade é estruturada por eventos históricos e pela heterogeneidade ambiental da região (Haffer 1969; Emilio et al. 2010; Householder et al. 2021). Longe de ser uma paisagem homogênea de floresta, a Amazônia é um mosaico de ambientes distintos, que variam desde densas florestas de terra-firme até áreas sazonalmente inundadas por águas brancas (Várzeas) e águas pretas (Igapós), bem como ecossistemas mais abertos, semelhantes a savanas (Junk et al. 2011) conhecidas como Ecossistemas de areia branca. Nesse bioma, espécies de plantas e animais tornaram-se total ou parcialmente especializadas nesses diferentes tipos de vegetação e manchas de vegetação não florestal (Fadini et al. 2021; Adeney et al. 2016; Borges et al. 2016a; Oliveira et al. 2023). Assim, os gradientes ambientais associados a esses diferentes tipos de vegetação afetam a distribuição das espécies, contribuindo de forma essencial para os padrões de beta-diversidade na região amazônica (Tuomisto e Ruokolainen 2006; Graça et al. 2017; Guilherme et al. 2019).

Os Ecossistemas de areia branca na Amazônia (White sand Ecossystems; WSE) são considerados singulares na América do Sul Tropical (IBGE 2012, Adney et al. 2016) e têm abrangência nos estados do Acre, Amazonas, Pará, Rondônia e Roraima, podendo se estender ainda pela Colômbia, Venezuela, Guiana Francesa, Guiana, Suriname e Peru (IBGE, 2012). Conhecidas no Brasil como Campina e Campinaranas (Stropp et al. 2011, Vicetinni, 2016), em outras regiões como complexo vegetacional sobre areia branca (Silveira 2003), esses ecossistemas são caracterizados por baixa produtividade, diversidade reduzida e solos com alto oligotrofismo e acidez, quando comparados às florestas de terra-firme (Anderson 1981). A vegetação dos ecossistemas de areia branca inclui campinas arbustivas abertas e campinaranas arbóreas densas ou florestadas (Anderson 1981; IBGE 2012; Daly et al. 2016; Silveira 2003; Adney et al. 2016), e sua estrutura varia conforme a origem geológica, topografia, textura do solo, fertilidade, hidrologia, profundidade do lençol freático e regime de fogo (Anderson 1981; Adeney et al. 2016; Fine e Bruna 2016).

A combinação de fatores ambientais presentes nos ecossistemas de areia branca resulta em modificações profundas na estrutura e composição das assembleias de plantas e animais em comparação com as florestas de terra-firme adjacentes. As campinas e campinaranas são menos diversas e apresentam uma composição florística distinta, composta por vegetação mais esclerófila e com elevada ocorrência de endemismo (Anderson 1981; Daly et al. 2016; Fine et al. 2010; Stroop et al. 2011). O número de espécies de plantas endêmicas associado à variação geográfica e isolamento desses ecossistemas sugere que eles contribuem para a diversidade regional de espécies amazônicas (Fine et al. 2016). Esse padrão também é observado em assembleias de animais, como aves (Borges et al. 2016). Além disso, as composições diferenciadas de espécies de plantas nesses ecossistemas, afetam diretamente a abundância de polinizadores, dispersores de sementes e predadores, muitos dos quais são insetos (Laurance e Bierregaard 1997; Didham et al. 1996).

Entre os insetos, as formigas são particularmente interessantes como espécies de estudo, pois desempenham várias funções ecológicas, como predação, dispersão e controle de herbívoros (Bihn et al. 2010; Lach et al. 2010), interagindo com seu ambiente em múltiplas escalas (Spiesman & Cumming 2008). Elas nidificam e forrageiam em diferentes estratos florestais, como camadas superficiais do solo, serapilheira, troncos de arbustos e árvores, além do dossel (Blüthgen e Feldhaar 2010). A heterogeneidade ambiental, portanto, tende a estar associada a um maior número de espécies de formigas, devido à oferta mais diversificada de recursos (Ribas et al. 2003; Pacheco e Vasconcelos 2012). Apesar do Ecossistema de Areia branca apresentar grande variação na disponibilidade de recursos, poucos trabalhos investigaram como características ambientais estruturam as assembleias de formigas nos ecossistemas de areia branca na Amazônia. A maioria dos estudos sobre formigas em ambientes amazônicos não florestados concentra-se em áreas de savana (cerrados amazônicos), que possuem uma história evolutiva e estrutura ambiental distintas (Vasconcelos e Vilhena 2006; Vasconcelos et al. 2008; Peixoto et al. 2010).

Categorizar escalas e agrupar espécies com base em seus grupos funcionais, ou seja, nas funções que desempenham nos ecossistemas, tem sido uma tendência crescente na ecologia devido à sua capacidade de prever ou explicar a estrutura das comunidades (McGill et al. 2006; Philpott et al. 2010). A força dessas relações varia de acordo com as características do ambiente em questão (Giacomini 2007). Assim, as assembleias de formigas fornecem um sistema de estudo ideal para examinar diferentes níveis de tolerância às variações de recursos, condições e perturbações nos ecossistemas terrestres (Leal et al. 2012; Baccaro et al, 2013, Solar et al. 2016). Os ecossistemas de areia branca na Amazônia ainda são muito pouco estudados. A maioria dos estudos sobre formigas em ambientes amazônicos não florestados são restritas as áreas de savana (cerrados amazônicos) que apresentam uma história evolutiva e estrutura ambiental distintas (Peixoto et al. 2010). Entretanto, como conhecemos pouco sobre história de vida e da ecologia das espécies de formigas, sabemos pouco o que regem mudança na riqueza e abundância de espécies entre locais com cobertura vegetal diferente. Nesse contexto, a presente tese investigou a estrutura e a composição de assembleias de formigas em ecossistemas de areia branca em diferentes escalas espaciais na Amazônia brasileira. Os resultados estão organizados em três capítulos:

Capítulo 1: Investigamos o efeito da estrutura da vegetação na diversidade de formigas em dois estratos ao longo de um gradiente natural de vegetação de areia branca na Amazônia central.

Capítulo 2: Investigamos a influência da estrutura do habitat e da biogeografia na diversidade taxonômica e funcional de assembleias de formigas em ecossistema de areia branca na Amazônia

Capítulo 3: Realizamos o primeiro levantamento de espécies de formigas arbóreas e terrestres de Campinas na Amazôna brasileira

CAPÍTULO 1

Beta diversity and microhabitat use of ant assemblages in a white-sand vegetation gradient in central Amazonia.

Amanda Batista da Silva de Oliveira, Sérgio Henrique Borges, Alessander Turibio Paes, Rafaela Caroline dos Santos Pereira, Ramiro Dário Melinski, Albertina Pimentel Lima, William E. Magnusson, Fabricio Beggiato Baccaro

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REVIEW PAPER

Beta diversity and microhabitat use of ant assemblages in a white-sand vegetation gradient in central Amazonia

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Abstract Much of the remarkable beta diversity of the Amazon biome is associated with the variety of vegetation types and other broad environmental gradients. We investigated ant assemblages in white-sand vegetation, one of the most distinctive vegetation types in the Amazon. Using pitfall traps in trees and on the ground, we comprehensively surveyed the ant assemblages along a natural gradient of vegetation structure, quantified with ground-LiDAR measurements. We collected individuals of 212 ant species/morphospecies distributed across 53 genera and nine subfamilies. Alpha diversity was not correlated with vegetation complexity, but beta diversity varied widely along the vegetation gradient. Species replacement was the predominant beta-diversity component, with smaller contributions from richness differences and nestedness. Terrestrial species composition was affected by vegetation structure, but arboreal species were more uniformly distributed along the vegetation-complexity gradient. Many habitat-generalist species (sampled in terrestrial and arboreal stratum) were sampled in less-complex parts of the gradient, suggesting that vertical stratification is diluted in more open vegetation. Our data indicate that the high species replacement in a small area increases the conservation value of this vegetation type by allowing much greater overall diversity than would be predicted by local alpha diversity.

Implications for insect conservation Our study demonstrates a remarkable ant-species replacement along a gradient of white-sand vegetation and highlights the importance of conserving this fragile environment, which is threatened by fire, deforestation, and mining.

Keywords Formicidae · White-sand · Replacement · Vertical stratification · Environmental gradient

Introduction

The Amazon is the most diverse terrestrial biome, and its diversity is structured through historical events and the environmental heterogeneity of the region (Haffer 1969; Emilio et al. 2010; Householder et al. 2021). In the Amazon, animal and plant species have become totally or partially specialized in different vegetation types, such as flooded forests, *terra firme* forests, and patches of non-forest vegetation (Fadini et al. 2021; Adeney et al. 2016; Borges et al. 2016a; Oliveira et al. 2023). Thus, the environmental gradients associated with different vegetation types affect the species distribution, making an essential contribution to beta-diversity patterns in the Amazon region (Tuomisto and Ruokolainen 2006; Graça et al. 2017; Guilherme et al. 2019).

Beta diversity takes into account the turnover and the gain/loss of species, which may lead to replacement and nested patterns, respectively (Podani and Schmera 2011). Understanding how beta diversity is partitioned into these components is relevant for understanding the organization of Amazonian biota, as they are related to distinct ecological and historical processes. For instance, species replacement

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can be affected by environmental gradients or historical contingencies (Qian et al. 2009). In contrast, nestedness (i.e., species assemblages from sites with a smaller number of species are subsets richer sites) can result from colonization or extinction events (Gaston and Blackburn 2000; Ulrich and Gotelli 2007). However, differences in species richness between sites do not always result in nested patterns (Baselga 2010; Carvalho et al. 2012). In these cases, the effect of environmental gradients may be more relevant to explaining richness differences between sites (Podani and Schmera 2011, Heino et al. 2017).

One of the most unique vegetation types found in the Amazon is the white-sand vegetation that grows on nutrient-poor sandy soils with superficial water tables (Anderson 1981). The white-sand vegetation occupies only 1.6% of the Amazon basin, distributed as patches of different sizes and degrees of isolation (Adeney 2016; Borges et al. 2016b). In addition, this vegetation is distributed along environmental gradients that vary from forests with open canopies and low densities of large trees (white-sand *campinarana*) to open vegetation similar to heathlands (white-sand *campina*) (Anderson 1981; Adeney et al. 2016). The habitat structure and floristic composition of white-sand *campinas* and *campinaranas* are distinct from adjacent forests and Amazonian savannas (Anderson 1981; Daly et al. 2016; Silveira 2003; Stropp et al. 2011).

White-sand vegetation poses numerous challenges to the survival of animals and plants due to their spatial constraints, nutrient-poor soils, and open vegetation structure (Anderson 1981; Daly et al. 2016; Fine et al. 2010; Stropp et al. 2011). The environmental filters represented by these restrictive conditions select biological assemblages that are “poor” in alpha diversity but with a high degree of endemism. Several biological groups have been recently studied in white-sand vegetation, including plants (Fine and Baraloto 2016; Vicentini 2016), insects (Lamarre et al. 2016; Graça et al. 2017; Vasconcelos et al. 2004), birds (Capurucho et al. 2013; Borges et al. 2016a) and frogs (Fraga et al. 2018; Carvalho et al. 2018; Ferrão et al. 2022). All these authors call attention to white-sand vegetation’s contribution to the Amazon’s regional beta diversity (Costa et al. 2020; Borges et al. 2016a; Capurucho et al. 2020; Fine and Baraloto 2016).

Birds and plants are the most studied organisms in white-sand vegetation (e.g., Capurucho et al. 2020; Fine et al. 2010, Costa et al. 2020), which limits our understanding of the contribution of these habitats to the diversity of other organisms, especially megadiverse groups such as arthropods (Lamarre et al. 2016). Among arthropods, ants are excellent study models since they are easy to sample, nest and forage in different forest strata and perform essential ecosystem functions, such as nutrient cycling, soil aeration, seed dispersal, and predation (Agosti et al. 2000; Spiesman and Cumming 2008; Blüthgen and Feldhaar 2010; Bihn et al. 2010; Lach et al. 2010).

Vertical microhabitat differentiation in the vegetation strongly affects ant-species distribution (Kaspari and Yanoviak 2001). Arboreal vegetation provides more predictable resources for nesting and food than soil (Yanoviak and Kaspari 2000). In contrast, the vegetation microclimate is more variable than soil or litter (Vasconcelos and Vilhena 2006). Due to the characteristics of these microhabitats, ant assemblages are markedly different between the arboreal and terrestrial strata (Yanoviak and Kaspari 2000; Arruda et al. 2021; Vasconcelos and Vilhena 2006). However, this vertical stratification is better documented in ant assemblages from forests or savannas with well-defined arboreal and terrestrial strata (Yanoviak and Kaspari 2000; Ribas et al. 2003; Vasconcelos and Vilhena 2006; Da Silva and Schmidt 2019).

Most studies of ant assemblages in non-forest vegetation in the Amazon have been conducted in savanna enclaves (e.g., Peixoto et al. 2010; Vasconcelos and Vilhena 2006; Siqueira and Silva 2021), with white-sand vegetation remaining relatively neglected by researchers. Here, we aim to fill this gap by investigating ant assemblages along an environmental gradient in white-sand vegetation in Central Amazonia. We aimed to answer the following questions: (i) How are species richness, abundance, and composition of arboreal and terrestrial ants distributed along the environmental gradient in a white-sand ecosystem?; (ii) What is the contribution of species replacement and nestedness to the patterns of beta diversity of arboreal and terrestrial ants in white-sand ecosystems?; (iii) How do variations in vegetation structure along environmental gradients affect species microhabitat use in the white-sand ecosystem? We expect a marked difference between species composition between strata but a strong relationship between ant species richness and habitat complexity, with fewer species and abundance in more open habitats for both terrestrial and arboreal strata. We also expected that the vegetation structure along the white-sand forests would work as a filter with nestedness dominating the beta-diversity patterns, especially for the terrestrial species (i.e., the assemblages of more open areas will be subsets of more closed sites). Given that forest structure varies greatly along the gradient in white sand forests, we expect to find proportionately more habitat generalist species in more open and sparsely vegetated sites.

Materials and methods

Study area

Ants were collected in the white-sand vegetation of the Rio Negro Sustainable Development Reserve (RDS Rio Negro), a protected area of 102,979 hectares located on the lower course of the Rio Negro (Fig. 1). The RDS Rio Negro is part of a mosaic of protected areas distributed along the lower course of the Rio Negro, covering more than eight million hectares (FVA 2011).

The climate in the region is tropical humid (mean annual rainfall of 2300 mm), with most rain falling between January and April and a drier period from July to September. The average temperature oscillated around 27 ºC, with relative humidity above 80%. The vegetation of the RDS Rio Negro comprises various forest types, including upland forests, black-water flooded forests (*igapó* forests), and white-sand vegetation. Each vegetation type has distinct ecological characteristics and harbors different animal and plant assemblages (PGRDS 2017).

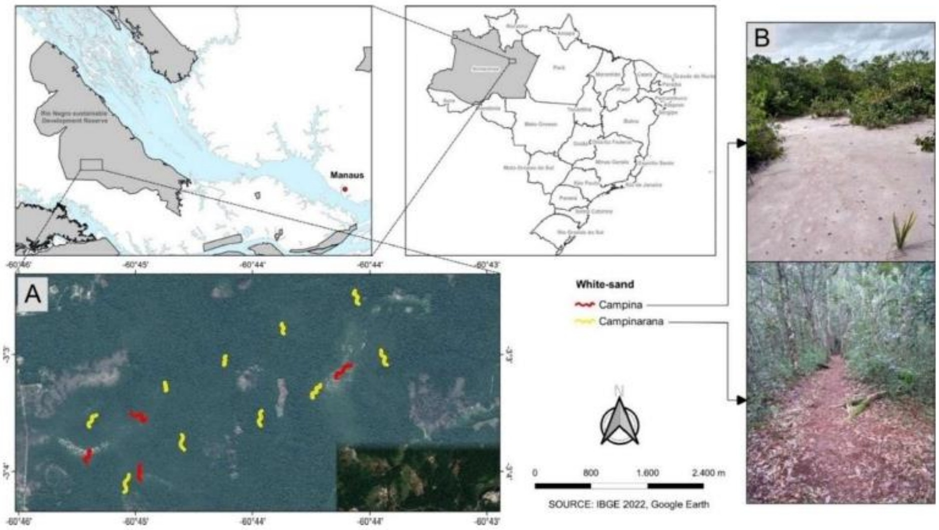
Environmental gradient

Five variables related to vegetation structure that potentially influence ant diversity and abundance were quantified: canopy maximum height (m), canopy average height (m), canopy cover (%), fraction of gaps computed at 10 m height, and leaf area index in the vertical profile. These vegetation variables were obtained using portable ground LiDAR (Laser Detection and Ranging) equipment (Riegl LD90-3100VHS-FLP). LiDAR is a practical and low-cost remote-sensing system used to measure distances from structures as a function of the time elapsed between the emission and return of a laser ray (Lefsky et al. 2002; Parker et al. 2004). Vegetation measurements using LiDAR were obtained while the researchers walked at constant speed on the 250 m centerline in each sampling plot. The five target variables were calculated using standard R scripts (R Core Team 2022).

Ant sampling

Ants were collected in ten 250-meter-long permanent plots installed in white-sand *campinas* and *campinaranas*. in the RDS Rio Negro following the RAPELD sampling design (Magnusson et al. 2013). The plots were separated from each other by approximately one kilometer and followed the contour of the terrain to minimize edaphic variation within the sampling unit (Magnusson et al. 2013). Four additional plots were installed in white-sand *campina* vegetation, totaling 14 plots encompassing a wide natural range of vegetation growing on sandy soils in the study area. We installed 10 sampling stations spaced at 25 m intervals in each plot. We placed two terrestrial and two arboreal pitfall traps (~ 2 m apart) in each sampling station, resulting in 560 ant samples (280 from the arboreal traps and 280 from the terrestrial traps).

The pitfall traps consisted of a 500 ml plastic cup (height: 12 cm, diameter: 9 cm) installed on the soil surface to collect terrestrial ants or fixed in tree or shrub branches at approximately 2.5 m to capture arboreal ants. Terrestrial traps were established with the cup border level with the soil surface, containing a solution of water and sodium chloride (Bestelmeyer et al. 2000). Arboreal traps were baited with human urine diluted in water, which is very attractive for arboreal ant species (Powell et al. 2011). Also, a small amount of detergent was added to the traps to break the surface tension of the water. The traps remained in operation for 48 h



SOURCE: IBGE 2022, Google Earth

Fig. 1 Map of the study site (A) showing the variation in vegetation structure along the white-sand vegetation gradient, from open areas (B) (*campina*) to dense white-sand forests (*campinarana*) in June 2019, and the collected individuals were conserved in 70% alcohol.

The sampled ants were identified at the genus level following Baccaro et al. (2015) and at the species level using several taxonomic keys (Brandão 1990; Fernández 2003; Longino 2003; MacKay and MacKay 2010). In addition, the collected ants were compared with identified specimens deposited in the invertebrate collections of the Universidade Federal do Amazonas (UFAM) and the Instituto Nacional de Pesquisas da Amazônia (INPA). The identity of some species was confirmed by Itanna Fernandes from INPA and Rodrigo Feitosa from the Ant Systematics and Biology Laboratory at the Universidade Federal do Paraná (UFPR).

Data analysis

Vegetation structure

The environmental gradient represented by the vegetation-structure variables of each plot was summarized using a Principal Component Analysis (PCA). We used the five LiDAR measurements standardized to mean zero and one standard deviation. We calculated the loadings of each original metric with PC1 and PC2 to describe better the structural change detected by LiDAR with individual variables.

Ant diversity

Plots were used as sampling units in all analyses. Because most ant species are colonial, we used the frequency of occurrence ranging from zero to 10 (the number of sampling stations per plot) to estimate relative abundance per plot and strata. The frequency of occurrence is a useful index of the number of colonies in a plot due to the relatively long (25 m) distance between traps (Baccaro and Ferraz 2013). Ant species were classified as terrestrial or arboreal when recorded in only one of these strata or habitat generalists if recorded in both terrestrial and arboreal traps.

We used sample-based species-accumulation curves to compare overall species richness between microhabitat strata. We also calculated sampling coverage by stratum, which provides a more standardized comparison between effort and sampling coverage (Chao and Jost 2012). These analyses were done in the iNEXT statistical package (Hsieh and Chao 2016).

The relationships between ant species richness or abundance with vegetation structure at the plot level were analyzed using generalized linear models (GLM). The first component (PC1), based on five LiDAR variables, which accounted for ~ 88% of the variance, was used as the vegetation-structure descriptor in this analysis.

The dissimilarity in species composition of ant assemblages between strata was assessed using non-metric multidimensional scaling (NMDS) based on the Bray-Curtis measure for relative abundance and with the Sørensen index for presence-absence data. The robustness of the groups formed by NMDS was assessed by a non-parametric Permutation-based MANOVA (PERMANOVA) with 999 randomizations. The NMDS and PERMANOVA were calculated using the vegan package (Oksanen et al. 2015).

To test the hypothesis that variation in ant-species composition was affected by changes in vegetation structure along the environmental gradient, we also used PERMANOVA tests for each stratum separately. For this analysis, we used the Bray-Curtis dissimilarity distance matrix based on relative abundance and Sørensen index for presence and absence data as the response variable and the vegetation structure complexity (PC1) as the predictor variable. We also created a direct ordination graph for each stratum showing the ant species occurrence along the vegetation gradient (PC1).

We applied the Podani and Schmera (2011) approach to partitioning pairwise gamma diversity between plots into species similarity, species replacement, and richness differences. This approach also provides relativized measurements of beta diversity, nestedness and richness differences. These components are measured through relativized indices and presented in ternary plots (Podani and Schmera 2011). The ternary plots contrast beta diversity versus similarity, species replacement versus nestedness, and richness difference versus richness agreement. Richness agreement refers to the largest subset of species for which the two sites being compared would be equally rich. In contrast, Richness difference is the sum of richness difference values for pairs of sites with no species in common. The indices were computed using the SDRSimplex program (Podani andSchmera 2011), and the results were displayed with graphs prepared with SYN-TAX 2000 package (Podani 2001).

We also used generalized linear models (GLM) to investigate the relationships between the richness and the relative abundance of habitat generalist species along the vegetation-structure gradient (PC1). All analyses, except the beta-diversity partitioning, were done in the R language (version 4.2.1; R Core Development Team 2020).

Results

Vegetation structure

The first (PC1) and second (PC2) principal components represented 87.5% and 6.9% of the variation in vegetation structure, respectively (supplementary material SM1). Lower values of PC1 were strongly correlated with lower

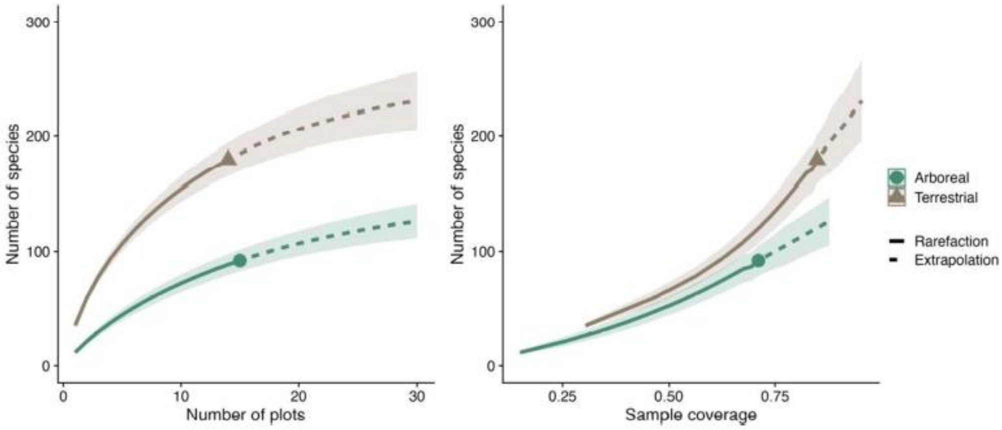


Fig. 2 Ant species accumulation curves **(a)** and sampling coverage **(b)** for arboreal and terrestrial strata. The shaded area around the continuous lines represents 95% confidence intervals

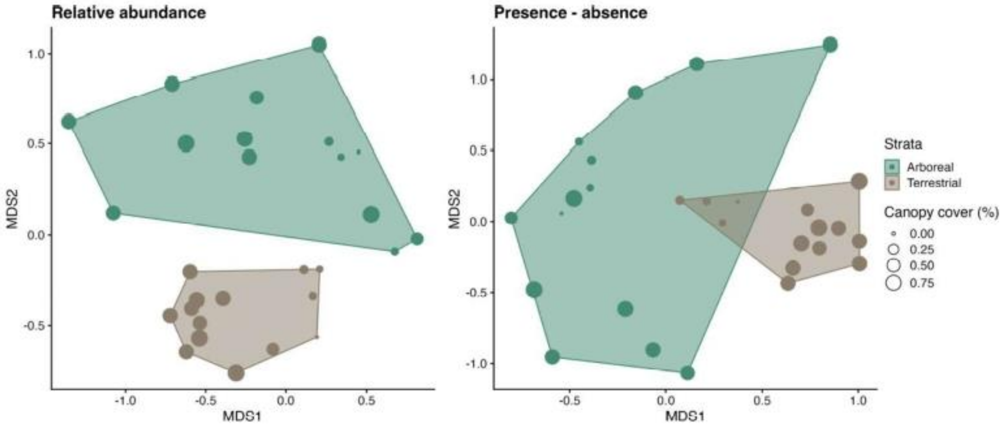


Fig. 3 NMDS ordination of the ant assemblages among strata at RDS Rio Negro, central Amazonia, Brazil

canopy, more gaps, and higher leaf area. In comparison, higher PC1 values indicate sites with higher canopy, fewer gaps, and larger leaf area index (supplementary material SM2 - Table 1).

Differences in ant assemblages between strata

We collected 212 ant species/morphospecies belonging to 53 genera and nine subfamilies (Supplementary material SM3- Table 2). Myrmicinae (105 species), Formicinae (39) and Ponerinae (33 species) had the highest numbers of species and Dolichoderinae, Pseudomyrmecinae, Ectatomminae, Dorylinae, Amblyoponinae and Paraponerinae were represented by only 1 to 12 species. The genera with the higher numbers of species collected were *Pheidole* (31 species), followed by *Camponotus* (30), *Crematogaster* (15) and *Hypoponera* (11), *Solenopsis* (8) and *Pseudomyrmex* (7). The most widely distributed species in the study area were *Crematogaster tenuicula* (48), sampled in seven sampling plots, *Paratrachymyrmex diversus* (78), sampled in ten plots, followed by *Pheidole* sp.1 (51), sampled in ten plots.

A total of 178 ant species were collected only in terrestrial pitfalls, 92 only in arboreal pitfalls, and 58 were found in both strata (Fig. 2). Species accumulation curves indicated that ant species richness was higher in the ground stratum than the arboreal stratum (Fig. 2). However, the sampling coverage of the arboreal stratum was lower (0.71) than the sampling coverage in the terrestrial pitfalls (0.85), even using samples with standardized collection effort by strata.

The species composition differed between the terrestrial and arboreal strata, for both presence-absence and relative-abundance data (Fig. 3). Additionally, the species composition of ground-dwelling ants was moderately related to the forest structure ($R^2 = 25\%$ using relative-frequency data per plot and $R^2 = 20\%$ using presence-absence data); there was no relation between the arboreal-species composition along the forest structure gradient (Fig. 3).

Species replacement was the predominant component of beta diversity considering all ant species and for analyses with only the arboreal or terrestrial species (Fig. 4). Species similarity, richness differences, and nestedness had a low contribution to beta diversity. In addition, the species turnover (or replacement) was stronger for the arboreal assemblage than the ground strata (Fig. 4).

Ant assemblages along the vegetation gradient

Ant species richness was not associated with variations in vegetation structure summarized by the first PCA component

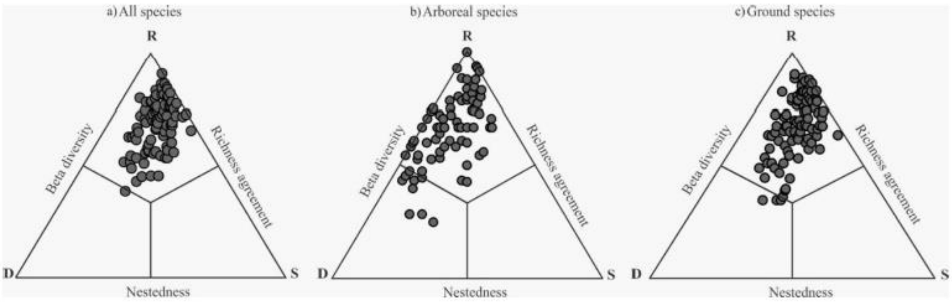


Fig. 4 Ternary plots showing ant beta-diversity components of similarity (S), differences in species richness (D), and replacement (R). The dots represent relativized pairwise scores for all possible site comparisons. The analyses were separated by all species **(a)**, only arboreal **(b)**, and only terrestrial **(c)** species. Each point represents relativized pairwise comparisons between plots. Points at the triangle border lines indicate maximum values for the respective metric

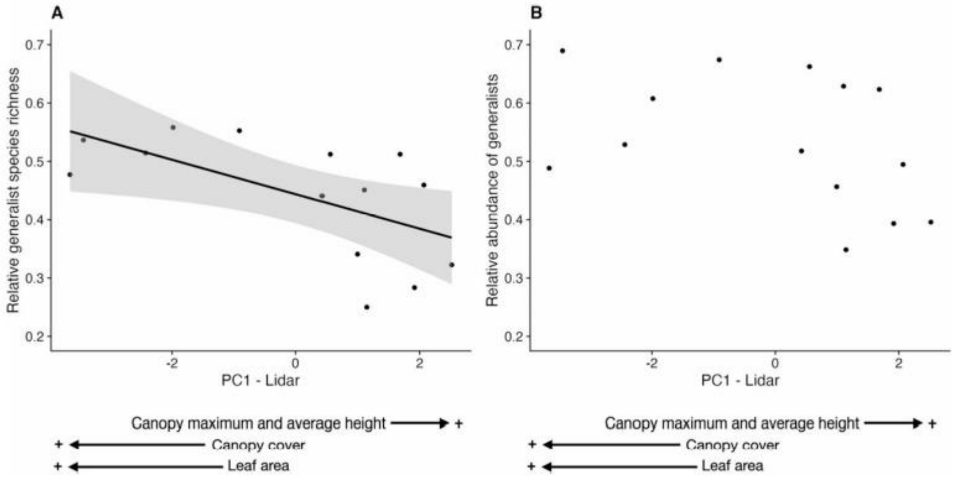


Fig. 5 Relative number **(A)** and abundance **(B)** of generalist species along the main vegetation structure gradient (LiDAR – PC1).

(PC1) for either arboreal ($r^2 = 0.023$, df = 12, P = 0.598) or ground strata ($r^2 = 0.006$ df = 12, P = 0.785). In contrast, ground-species composition was affected by vegetation structure measured by PC1 (PERMANOVA, $R^2 = 0.25$, P = 0.001). Arboreal species tended to occupy the gradient more uniformly since species composition did not correlate with PC1 (PERMANOVA, $R^2 = 0.08$, P = 0.248). Even so, the relative abundance of some terrestrial and arboreal ant species appears to be higher in different parts of the vegetation gradient (supplementary material SM4 and SM5).

The proportion of habitat-generalist species was related to PC1 ($F_{1,12} = 6.772$, P = 0.023), indicating that white-sand *campina* harbor more habitat-generalist species than areas with a more closed canopy. However, no significant relationship was found between ant relative-abundance data ($F_{1,12} = 2.601$, P = 0.132) and the vegetation gradient (Fig. 5).

Discussion

Our study demonstrates the importance of environmental gradients within white-sand vegetation for understanding ant species distribution and vertical stratification. As expected, the number of ant species sampled on the ground was higher than those sampled in the vegetation (Arruda et al. 2021; Vasconcelos and Vilhena 2006; Vasconcelos et al. 2004). However, there were other differences between strata. Although replacement dominated beta diversity in both strata, arboreal assemblages showed a stronger pattern, with higher species replacement among plots. The higher replacement of species in the arboreal stratum was unrelated to the main vegetation structure gradient, as found for the terrestrial species. In addition, proportionally more habitat-generalist species were found in more open areas. Our results suggest that ant-assemblage stratification weakens along the vegetation-structure gradient. However, this dilution occurs more due to decreased typically arboreal species in the more open and less complex areas of the white-sand vegetation gradient.

The structure and organization of ant assemblages that forage and nest in vegetation and soil are often distinct since the species are exposed to different conditions and respond differently to environmental gradients (Powell et al. 2011; Arruda et al. 2021; Neves et al. 2021; Yanoviak and Kaspari 2000; Blüthgen and Feldhaar 2010). For example, ants receive higher solar incidence in the arboreal stratum and are subject to higher and more variable temperatures and relatively fewer nitrogen-rich resources. Conversely, microclimatic conditions are more stable in the soil layer where the availability of nitrogen-rich resources is higher (Kaspari et al. 2015). Our data suggest that these ecological differences between arboreal and ground strata can restrict the distribution of some species to distinct parts of the environmental gradient. Moreover, a relatively large number of generalist species were sampled in less-forested plots, suggesting that the vertical stratification is diluted in more open areas, where the resources are presumed to be scarcer.

The ant alpha diversities in the arboreal and ground strata were not related to the vegetation-complexity gradient. In contrast, the beta-diversity components of the ant assemblage showed more consistent differentiation along the gradient. Ground-ant species composition was correlated with vegetation complexity along the sampling gradient, while arboreal species were little affected by vegetation-structure variation. This pattern may be explained by the variation in ant species richness associated with the complexity of the white-sand vegetation (Siqueira and Silva 2021). The low influence of nestedness related to the lack of relation with species richness indicates that ordered species impoverishment/enrichment is weak in this system.

In continuous white-sand *campinarana* forests, canopy height ranges from 15 to 20 m, and emergent trees may reach up to 30 m in height (IBGE 2012; Silveira 2003). The *campinarana* vegetation structure, particularly the canopy cover, favors the establishment of typical arboreal ants, as our results have shown. In contrast, the white-sand *campina* is limited to a small strip of vegetation, with a dense herbaceous layer dominated by patches of exposed sand. Small trees with coriaceous, stiff, sclerophyllous leaves, shrubs, and twisted trunks grow very close to each other, with bushes that rarely exceed two meters in height (Anderson 1981). These characteristics allow greater light penetration, which may limit the occurrence of some forest species. Furthermore, our results show that open white-sand *campina* harbor many habitat generalist species with broader habitat requirements that are presumably more capable of dealing with a wide range of food sources and microclimate variation.

The predominance of the replacement component of beta diversity in ant assemblages may also be related to variations in microclimatic changes and food resources along the studied gradient. Despite the higher species richness in the ground strata, overall beta diversity was higher in the arboreal ant assemblages, but only the terrestrial ant assemblages were related to vegetation structure. Likely, the variability in ecological conditions acts as an environmental filter sorting distinct species assemblies finely tuned along the vegetation gradient. In particular, the high turnover between white-sand *campina* and nearby upland forests on more clayey soils contributes to increased beta diversity in the region (Vasconcelos et al. 2004). Vegetation heterogeneity seems to be an essential promoter of arboreal (Ribas et al. 2003) and ground (Vasconcelos et al. 2023) ant diversity in non-forested environments. Our results echo these previous studies, expanding these findings to the white-sand vegetation complex.

Implications for conservation

Although Amazonian white-sand vegetation is famous for its poverty in fauna and flora, we document a rich assemblage of ants in these habitats. White-sand vegetation harbors many endemic bird and plant species. Still, the degree of endemism of ant species associated with white-sand vegetation could not be evaluated due to the scarcity of arthropod studies in these habitats. Nonetheless, our data indicate that several ant species are restricted to short parts of the vegetation gradient, resulting in replacement being the predominant component of the beta diversity. Thus, to conserve a larger portion of the ant diversity, protecting the entire vegetation gradient, including the small and isolated patches of white-sand *campina*, will be necessary.

Human activities, such as deforestation and mining, threaten Amazonian white-sand vegetation. Patches of white-sand *campina* have been destroyed for sand extraction for civil construction (Ferreira et al. 2013), and the vegetation is susceptible to fire (Flores and Holmgren 2021). Moreover, the white-sand vegetation covers a small portion of the Amazon region and, due to the poverty of its soils, has limited regeneration capacity (Anderson 1981), making this fragile habitat much more endangered than the larger and continuous forests growing over better-structured soils. Greater sampling of ants and other invertebrates in white-sand vegetation must be prioritized since these endangered habitats could host endemic species with small distributions (Ferreira et al. 2014; Borges et al. 2014). Such studies are fundamental to expanding the current Amazonian protected area system, including larger expanses of white-sand vegetation and its unique biodiversity.

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Authors' contributions A.B.S.O: Conceptualization, methodology, validation, formal analysis, data curation, writing – original draft, writing – review & editing. S.H.B: Conceptualization, writing – review & editing. A.T.P: ant sorting and material preparation, R.C.S.P and R.D.M: LiDAR field sampling and modeling, writing – review & editing. A.P.L: funding, writing – review & editing. W.E.M: funding, writing – review & editing. F.B.B: Conceptualization, Formal analysis, writing – review & editing, visualisation.

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Data Availability The data that support the findings of this study are available in supplemental material.

Declarations

Ethical approval The sampling was authorized by ICMBio, license N. 72174-1.

Competing interests The authors declare no competing interests.

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Supplementary material

Table 1- Loadings for Correlation PCA for the LiDAR vegetation descriptors data.

	PC1	PC2
canopy maximum height (m)	0.97	0.02
canopy average height (m)	0.97	0.17
canopy openness (%)	-0.93	0.11
fraction of gaps computed at 10 meters height	-0.87	0.44
leaf area index in the vertical profile	0.93	0.33

Table 2. Occurrence and frequency of species and morphospecies of ants sampled in the arboreal and terrestrial strata in the Rio Negro Sustainable Development Reserve, Amazonas, Brazil.

Taxa	**Arboreal**	**Terrestrial**	**Total**
AMBLYOPONINAE			
Prionopelta minuta Ladino & Feitosa, 2020	-	1	1
DOLICHODERINAE			
Azteca sp.1	5	2	7
Azteca sp.2	-	1	1
Azteca sp.3	3	-	3
Azteca sp.4	4	-	4
Dolichoderus bispinosus Olivier, 1792	8	1	9
Dolichoderus imitator Emery, 1894	9	9	18
Dolichoderus laminatus Mayr, 1870	2	-	2
Dorymyrmex sp.1	-	7	7
Forelius sp.1	-	1	1
Tapinoma sp.1	2	2	4
DORYLINAE			
Eciton vagans Olivier, 1792	-	2	2
Labidus coecus Latreille, 1802	-	45	45
Neivamyrmex cristatus André, 1889	-	3	3
Neivamyrmex sp.1	-	1	1
ECTATOMMINAE			
Ectatomma tuberculatum Olivier, 1792	8	11	19

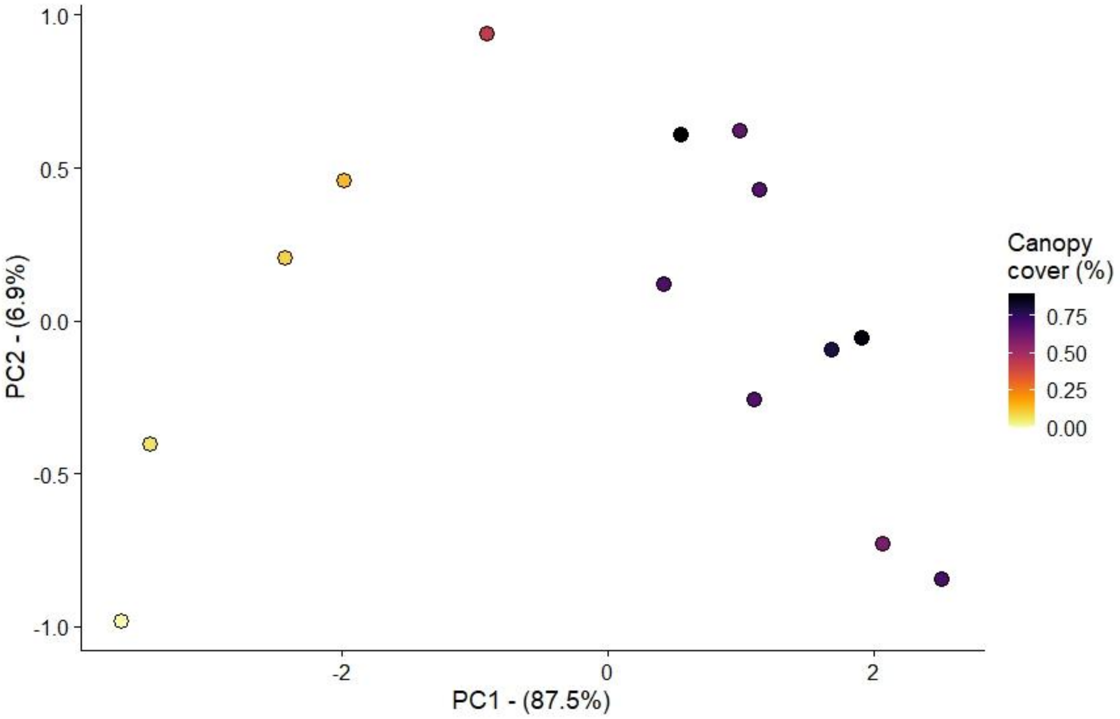
Ectatomma brunneum Smith, 1858	-	23	23
Ectatomma edentatum Roger, 1863	-	1	1
Ectatomma lugens Emery, 1894	-	17	17
Gnamptogenys fernandezi Lattke, 1990	1	1	2
Gnamptogenys horni Santschi, 1929	-	16	16
Gnamptogenys kempfi Lenko, 1964	-	1	1
Gnamptogenys sulcata Smith, 1858	-	4	4
Gnamptogenys tortuolosa Smith, 1858	-	2	2
Holcoponera moelleri Forel, 1912	-	2	2
Holcoponera relicta Mann, 1916	-	1	1
Holcoponera striatula Mayr, 1884	3	2	5
FORMICINAE			
Acropyga sp.1	-	3	3
Brachymyrmex sp.1	2	4	6
Brachymyrmex sp.2	1	2	3
Brachymyrmex sp.3	-	1	1
Brachymyrmex sp.4	-	1	1
Camponotus chartifex Smith, 1860	-	1	1
Camponotus sp.15	1	-	1
Camponotus sp.18	2	2	4
Camponotus ager Smith, 1858	4	1	5
Camponotus atriceps Smith, 1858	31	8	39
Camponotus burtoni Mann, 1916	1	-	1
Camponotus cameranoi Emery, 1894	16	12	28
Camponotus compositor Santschi, 1922	3	18	21
Camponotus cf genatus	1	-	1
Camponotus cf prox tastigatus vagulatus	-	1	1
Camponotus leydigi Forel, 1886	-	3	3
Camponotus rapax Fabricius, 1804	1	3	4
Camponotus rectangularis Emery, 1890	9	2	11
Camponotus sp.1	3	6	9
Camponotus sp.11	-	1	1
Camponotus sp.16	-	2	2
Camponotus sp.17	1	-	1
Camponotus sp.19	2	-	2
Camponotus sp.2	2	4	6
Camponotus sp.3	1	-	1
Camponotus sp.35	1	-	1
Camponotus sp.4	1	-	1
Camponotus sp.5	1	-	1
Camponotus sp.6	2	9	11
Camponotus sp.7	3	-	3
Camponotus sp.8	1	-	1
Camponotus sp.9	2	-	2
Camponotus cf tanaemyrmex	18	18	36
Camponotus testaceus Emery, 1894	13	4	17

Nylanderia sp.1	-	11	11
Nylanderia sp.2	4	8	12
Nylanderia sp.3	5	12	17
Tranopelta gilva Mayr, 1866	-	1	1
MYRMICINAE			
Allomerus septemarticulatus Mayr, 1878	2	1	3
Apterostigma sp.1	-	2	2
Apterostigma sp.2	-	2	2
Apterostigma sp.3	-	2	2
Atta sexdens Linnaeus, 1758	3	7	10
Blepharidatta brasiliensis Wheeler, 1915	-	20	20
Carebara brevipilosa Fernández, 2004	-	1	1
Cephalotes atratus Linnaeus, 1758	10	4	14
Cephalotes grandinosus Smith, 1860	1	-	1
Cephalotes minutus Fabricius, 1804	4	1	5
Cephalotes opacus Santschi, 1920	3	1	4
Cephalotes pallens Klug, 1824	1	-	1
Cephalotes pallidus De Andrade, 1999	1	-	1
Cephalotes placidus Smith, 1860	3	-	3
Cephalotes pusillus Klug, 1824	1	-	1
Cephalotes umbraculatus Fabricius, 1804	1	-	1
Crematogaster brasiliensis Mayr, 1878	5	7	12
Crematogaster carinata Mayr, 1862	2	1	3
Crematogaster curvispinosa Mayr, 1862	-	1	1
Crematogaster evallans Forel, 1907	4	3	7
Crematogaster flavosensitiva Longino, 2003	2	5	7
Crematogaster limata Smith, 1858	-	2	2
Crematogaster longispina Emery, 1890	-	6	6
Crematogaster nigropilosa Mayr, 1870	1	3	4
Crematogaster sotobosque Longino, 2003	-	11	11
Crematogaster sp.2	-	1	1
Crematogaster sp.3	2	-	2
Crematogaster sp.4	1	-	1
Crematogaster sp.5	-	1	1
Crematogaster tenuicula Forel, 1904	19	29	48
Crematogaster torosa Mayr, 1870	2	1	3
Cyphomyrmex minutus Mayr, 1862	-	16	16
Cyphomyrmex sp.3	-	2	2
Cyphomyrmex sp.4	-	3	3
Daceton armigerum Latreille, 1802	-	3	3
Hylomyrma blandiens Kempf, 1961	-	1	1
Hylomyrma immanis Kempf, 1973	-	1	1
Megalomyrmex ayri Brandão, 1990	-	1	1
Megalomyrmex incisus Smith, 1947	-	1	1
Megalomyrmex pr silvestrii	-	1	1
Monomorium sp.1	2	3	5

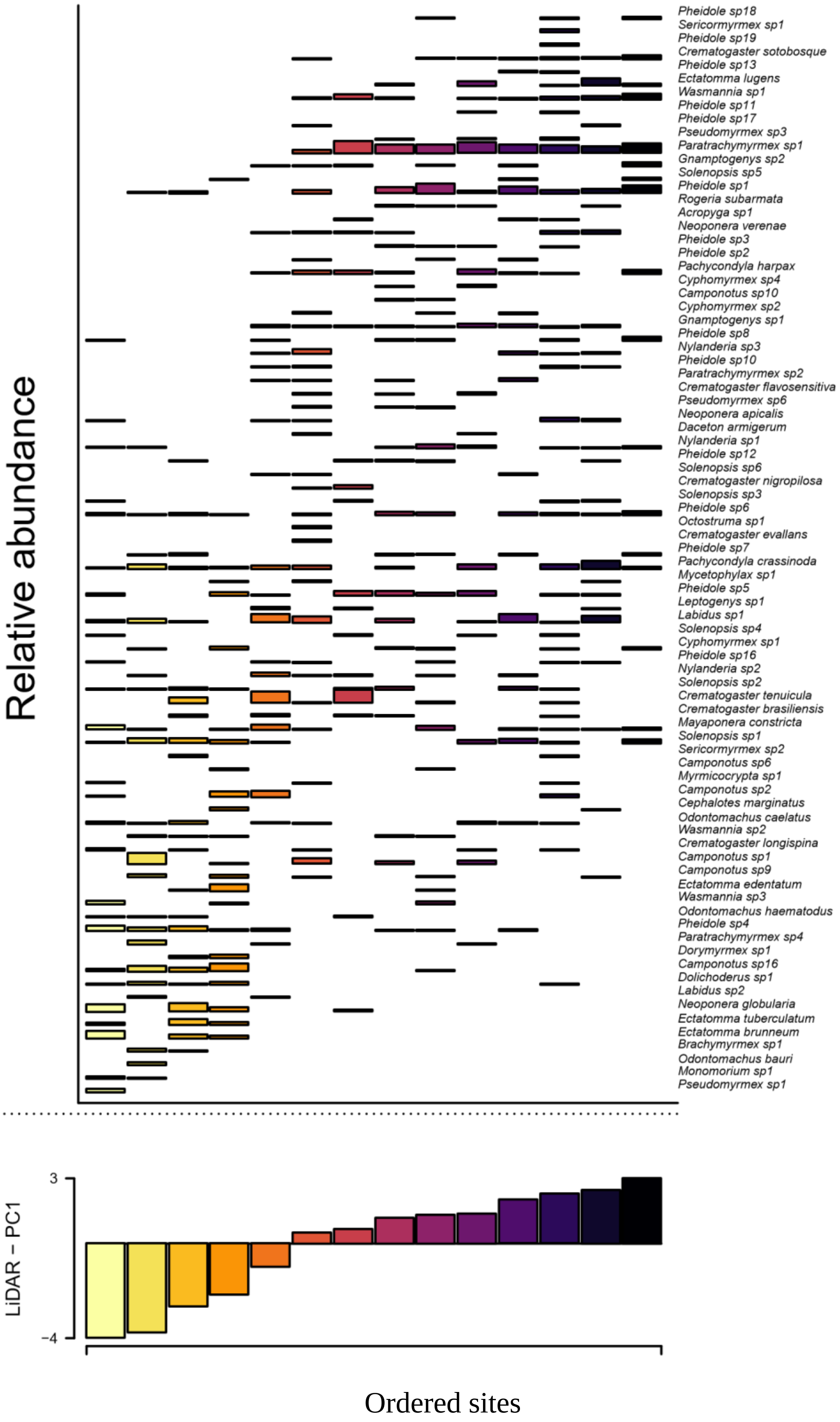
Monomorium sp.2	1	1	2
Mycetophylax lectus Forel, 1911	-	2	2
Mycetophylax sp.3	-	1	1
Myrmicocrypta sp.1	-	3	3
Myrmicocrypta sp.2	-	1	1
Ochetomyrmex semipolitus Mayr, 1878	-	22	22
Octostruma balzani Emery, 1894	-	1	1
Octostruma betschi Perrault, 1988	-	3	3
Paratrachymyrmex bugnioni Forel, 1912	-	7	7
Paratrachymyrmex diversus Mann, 1916	2	76	78
Paratrachymyrmex mandibularis Weber, 1938	-	1	1
Paratrechina sp.1	-	1	1
Pheidole fimbriata Roger, 1863	-	3	3
Pheidole micros Wilson, 2003	-	2	2
Pheidole sp.1	8	43	51
Pheidole sp.10	-	9	9
Pheidole sp.13	-	2	2
Pheidole sp.14	1	1	2
Pheidole sp.16	1	4	5
Pheidole sp.17	1	3	4
Pheidole sp.18	-	2	2
Pheidole sp.19	-	2	2
Pheidole sp.2	4	1	5
Pheidole sp.20	-	2	2
Pheidole sp.21	-	1	1
Pheidole sp23	-	3	3
Pheidole sp.24	-	1	1
Pheidole sp.25	-	1	1
Pheidole sp.26	-	2	2
Pheidole sp.28	-	1	1
Pheidole sp.29	-	2	2
Pheidole sp3	-	5	5
Pheidole sp30	-	1	1
Pheidole sp.31	-	2	2
Pheidole sp.32	-	10	10
Pheidole sp.33	-	4	4
Pheidole sp.4	-	11	11
Pheidole sp.5	-	25	25
Pheidole sp.6	-	1	1
Pheidole sp.7	-	4	4
Pheidole sp.8	-	9	9
Pheidole sp.9	-	2	2
Pheidole vorax Fabricius, 1804	-	6	6
Procryptocerus sp.1	1	-	1
Rogeria subarmata Kempf, 1961	1	6	7
Sericormyrmex sp.1	-	4	4

Sericormyrmex sp.2	-	4	4
Sericormyrmex sp.3	-	1	1
Solenopsis sp.1	-	26	26
Solenopsis sp.2	2	12	14
Solenopsis sp.3	2	6	8
Solenopsis sp.4	-	5	5
Solenopsis sp.5	-	3	3
Solenopsis sp.6	1	3	4
Solenopsis sp.7	-	2	2
Solenopsis sp.8	1	-	1
Strumigenys denticulata Mayr, 1887	1	2	3
Strumigenys elongata Roger, 1863	-	1	1
Strumigenys sp.3	-	1	1
Strumigenys sp.4	1	-	1
Wasmannia auropunctada Roger, 1863	1	16	17
Wasmannia rochai Forel, 1908	-	1	1
Xenomyrmex sp.1	1	-	1
Xenomyrmex sp.2	1	-	1
Xenomyrmex sp.1	3	-	3
Xenomyrmex sp.2	1	-	1
PARAPONERINAE			
Paraponera clavata Fabricius, 1775	1	1	2
PONERINAE			
Anochetus horridus Kempf, 1964	-	2	2
Anochetus sp.1	-	1	1
Anochetus sp.2	-	1	1
Centromyrmex sp.1	-	1	1
Hypoponera sp.1	1	1	2
Hypoponera sp.10	-	1	1
Hypoponera sp.11	-	1	1
Hypoponera sp.2	-	1	1
Hypoponera sp.3	-	1	1
Hypoponera sp.4	-	1	1
Hypoponera sp.5	-	1	1
Hypoponera sp.6	-	1	1
Hypoponera sp.7	1	-	1
Hypoponera sp.8	-	1	1
Hypoponera sp.9	-	1	1
Leptogenys acadêmica López-Muñoz et al., 2018	-	1	1
Leptogenys sp.1	-	4	4
Mayaponera constricta Mayr, 1884	1	19	2-
Neoponera apicalis Latreille, 1802	-	11	11
Neoponera globularia MacKay & MacKay, 2010	-	22	22
Neoponera sp.1	-	1	1
Neoponera sp.2	1	-	1
Neoponera unidentata Mayr, 1862	1	-	1

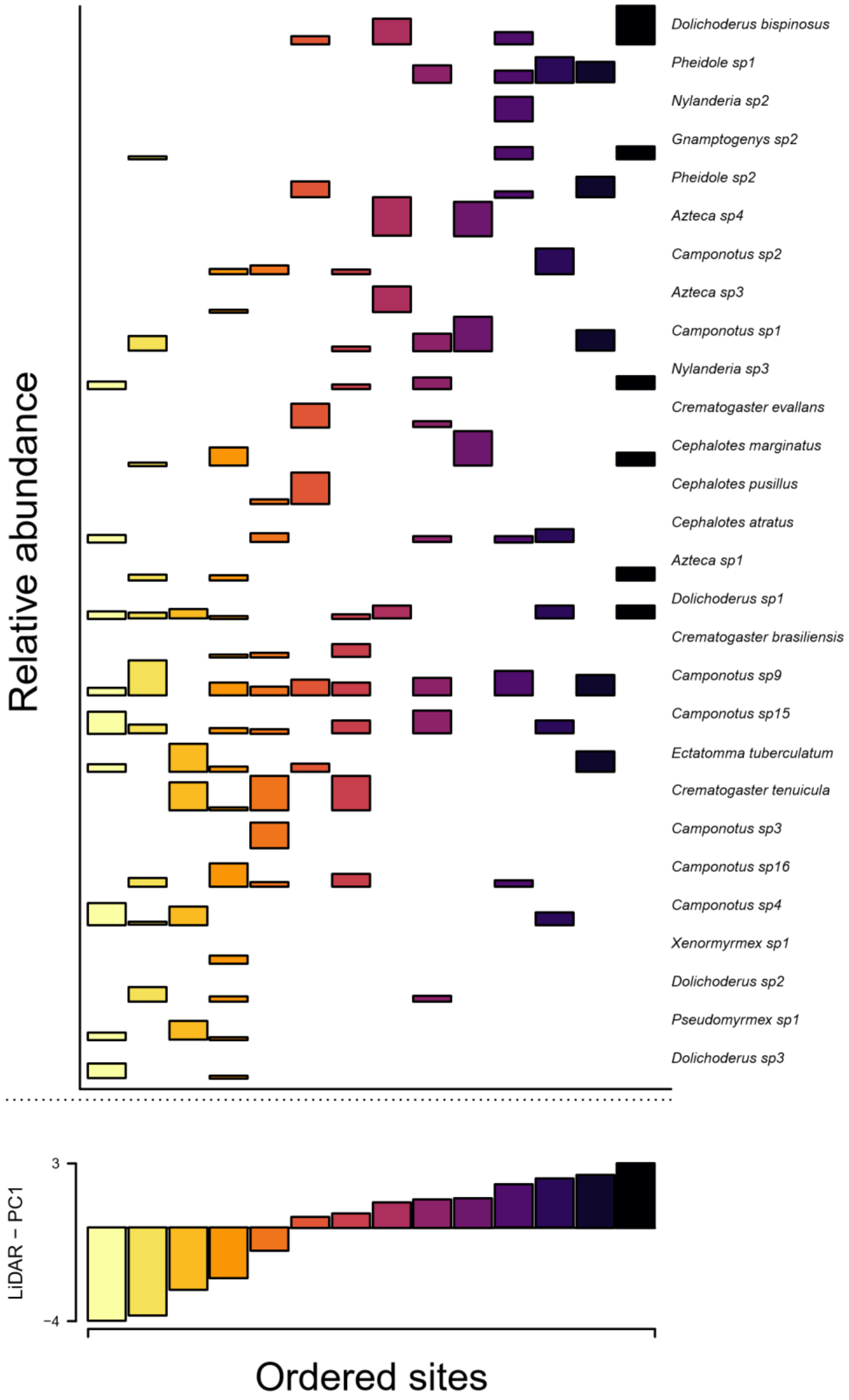
Neoponera verenae Forel, 1922	-	13	13
Neoponera villosa Fabricius, 1804	-	2	2
Odontomachus bauri Emery, 1892	-	3	3
Odontomachus caelatus Brown, 1976	-	12	12
Odontomachus haematodus Linnaeus, 1758	1	4	5
Odontomachus sp.1	-	1	1
Odontomachus sp.2	1	-	1
Pachycondyla crassinoda Latreille, 1802	1	41	42
Pachycondyla fuscoatra Roger, 1861	-	1	1
Pachycondyla harpax Fabricius, 1804	-	17	17
PSEUDOMYRMICINAE			
Pseudomyrmex boopis Roger, 1863	1	5	6
Pseudomyrmex oculatus Smith, 1855	4	4	8
Pseudomyrmex sp.4	1	2	3
Pseudomyrmex sp.5	-	1	1
Pseudomyrmex sp.6	2	-	2
Pseudomyrmex sp.7	1	-	1
Pseudomyrmex tenuis Fabricius, 1804	1	6	7



SM1. Principal Component Axis for the LiDAR vegetation descriptors along natural white-sand vegetation structure gradient.



SM4. Distribution of terrestrial ant species along a white-sand vegetation gradient in the RDS Rio Negro, Manacapuru and Novo Airão Municipality, Brazil. The plots (represented as columns) are ordered by LiDAR PC1 values.



SM5. Distribution of arboreal ant species along a white-sand vegetation gradient in the RDS Rio Negro, Manacapuru and Novo Airão Municipality, Brazil. The plots are ordered by LiDAR PC1 values.

CAPÍTULO 2

Habitat structure shapes ant diversity in Amazonian white-sand ecosystems

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Habitat structure shapes ant diversity in Amazonian white-sand ecosystems

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ABSTRACT

White-sand ecosystems are one of the most distinctive vegetation types of the Amazon but their arthropod diversity remains poorly studied. We compared ant assemblages of open white-sand *campinas* and white-sand forests in two regions in the northern Brazilian Amazon to examine the influence of habitat structure and location on taxonomic and functional diversity of these organisms. Alpha diversity of arboreal ants in white-sand *campinas* tends to be lower than in white-sand forests. In contrast, alpha diversity of ground-dwelling ants was similar in both habitats of studied regions. The species composition of arboreal ants of white-sand *campinas* and white-sand forests was very distinct between the study regions. In contrast, arboreal assemblages of these habitats were similar within each region. Species composition of ground-dwelling ants was strongly affected by habitat and region. Functional space of arboreal and ground-dwelling ants was also affected by region and habitat structure, with morphological traits related to vision (eye size), mobility (femur length), and prey manipulation (mandible lengths) filtered mainly by habitat independently of region. Our results highlight that structural complexity in white-sand forests promotes greater arboreal ant diversity while ground-dwelling ants are more influenced by regional conditions, underscoring the complex interplay of ecological and historical factors in these habitats.

KEY WORDS: Open vegetation, ant assemblage, tree ants, taxonomic and functional diversity

INTRODUCTION

Habitats are defined by the biotic and abiotic conditions necessary for organisms to survive and reproduce (Southwood 1977, Stadtmann and Seddon 2020). These conditions are spatially variable since similar habitats could be subject to distinct geological and climatic events, affecting the species diversity and composition (Lomolino *et al.* 2017). Thus biological assemblages living in similar habitats in different biogeographical regions provide good models for understanding how species diversity and assemblage structure evolve across time and space (Ricklefs and Schluter 1993, Rosenzweig 1995, Fine 2015).

The Amazon is the largest rainforest in the world, and part of its astonishing biological diversity is explained by the variability in soils and vegetation types that provide habitats for a large number of species (Pires and Prance 1985, Quesada *et al.* 2009, Tuomisto *et al.* 2019, Oliveira-Filho *et al.* 2021). Also, the Amazon basin was subject to complex past events like river formation, climate changes, and tectonism that affect landscapes and their associated habitats and species (Val *et al.* 2021). One of the most distinctive vegetation types of the Amazon is the white-sand ecosystems (WSE), which serve as habitats for a unique conjunct of species of plants and vertebrates (Anderson 1981, Pires and Prance 1985).

Amazonian white-sand ecosystems grow on sandy soils (podzols and spodosoils), which are nutrient-poor and generally distributed in low parts of the terrain that can be seasonally flooded (Adeney *et al.* 2016). Locally, WSE consists of heterogeneous and distinctive habitats distributed along gradients from open and grassy vegetation, resembling savannas, to high canopy forests with dense thin trees (Anderson 1981, Adeney *et al.* 2016). WSE is distributed in different biogeographic regions and found as isolated patches or large and continuous habitats (Adeney *et al.* 2016, Capurucho *et al.* 2020, Rego *et al.* 2024). Some studies suggest that the areas occupied by Amazonian

WSE are dynamic, with evidence for expansion and retraction in the past (Ritter *et al.* 2021, Capurucho *et al.* 2023). Landscape configuration, local differences in the habitat structure, and historical contingencies affect the diversity of animal and plant assemblages in WSE (Borges *et al.* 2016a, Costa *et al.* 2020, De Oliveira *et al.* 2023, Capurucho *et al.* 2023).

Despite being considered "species-poor" habitats, WSE had a remarkable contribution to Amazonian beta diversity, as demonstrated for birds and plants (Fine and Baraloto 2016, Vicentini 2016, Capurucho *et al.* 2023). Unfortunately, the arthropod diversity of WSE is poorly characterized despite recent advances (e.g., Lamarre *et al.* 2016, Siqueira and Silva 2021, De Oliveira *et al.* 2023). Protection and continuous investigation of the WSE biodiversity are priorities since these fragile ecosystems are impacted by anthropogenic activities (e.g., fires, sand extraction), which threaten their unique biota (Ferreira *et al.* 2013, Flores and Holmgren 2021).

Despite being considered ‘species-poor’ habitats, WSEs have a notable contribution to Amazonian beta diversity, as demonstrated for birds and plants (Fine and Baraloto, 2016, Vicentini, 2016, Capurucho *et al.* 2023). Unfortunately, arthropod diversity in WSEs is still poorly characterized, despite recent advances (e.g. Lamarre *et al.* 2016, Siqueira and Silva, 2021; De Oliveira *et al.* 2023). Even ubiquitous and abundant invertebrate taxa, such as ants, are very little investigated in these environments (Andrade-Silva *et al.* 2024).

Ants play essential roles in tropical ecosystems, particularly in the Amazon region, where nearly 1,000 species have been cataloged on www.Antmaps.org (Janicki *et al.* 2016, GABI: Guénard *et al.* 2017, Andrade-Silva *et al.* 2022). This diversity is a crude underestimate since several areas and habitats of the region remain poorly sampled (Andrade-Silva *et al.* 2022, Schmidt *et al.* 2022), including WSE (Carvalho *et al.* 2023, Andrade-Silva *et al.* 2022). The high diversity of ants in the Amazon is partially associated with microhabitat stratification (Klimes et al. 2015), which affects ants' distribution. Forest understory and canopy layers offer more predictable resources for nesting and feeding than ground stratum (Yanoviak and Kaspari 2000, Vasconcelos and Vilhena 2006). Consequently, ant species compositions differ between the arboreal and terrestrial strata in most studied habitats (Vasconcelos and Vilhena 2006, da Silva de Oliveira and Schmidt 2019, Davidson and Patrell-Kim 1996; Klimes *et al* 2015).

Ant assemblages are also influenced by ecological and biogeographical processes, reflecting the interaction between local and regional changes (Ribas *et al.* 2003, Campos *et al.* 2011, Pacheco and Vasconcelos 2012, Schmidt *et al.* 2017). Local environmental conditions often act as filters, allowing only species with determined traits to survive in a given habitat (Guilherme *et al.* 2019, Siqueira and Silva 2021). Although the ants' functional traits may help to understand species responses to environmental gradients (Gibb *et al.* 2015, Parr *et al.* 2017), the role of local habitat heterogeneity in the functional structuring of Amazonian ant assemblages is scarcely assessed (Guilherme *et al.* 2019), especially in WSE. Convergence in trait composition can result from similar selective pressures, shedding light on the mechanisms that promote and maintain biodiversity in different areas (Cornwell and Ackerly 2009). Additionally, the functional space, defined as the range of trait combinations within a community, may contract or expand depending on habitat complexity and resource availability, reflecting the selective pressures imposed by local conditions (Mouchet *et al.* 2010, Villéger *et al.* 2010). For example, traits related to mobility, such as femur length, or resource acquisition, such as mandible size, may be filtered in structurally complex habitats like forests, where competition and niche differentiation are intensified (Guillherme *et al.* 2019). Conversely, in simpler environments such as open campinas, functional space might narrow, favoring traits that optimize survival in exposed conditions, such as enhanced vision for predator detection (Weiser and Kaspari 2006).

Here, we compared the ant assemblages of the open white-sand vegetation and closed canopy white-sand forests distributed in two biogeographical regions. In one of those regions, the WSE occupies thousands of square kilometers of continuous habitat, while in the other, the WSE is composed of small isolated patches. We expect that the contrasting habitat structure and landscape configuration will influence ant assemblages' taxonomic and functional structure and proposed the following predictions: (i) ant alpha diversity will be higher in white-sand forests due to its more complex vegetation structure compared to open white-sand vegetation in both studied regions; (ii) ant alpha diversity will be greater in regions with large, continuous habitats compared to regions where these habitats are smaller and isolated; (iii) alpha diversity of ground-dwelling and arboreal ants will be more affected by local vegetation heterogeneity and the beta diversity of these ecological groups will be more responsive to site effect; (iv) ant species turnover will be high between both habitat structure and site location and; (v) functional space will be higher in white-sand forests compared to open white-sand vegetation and different components of functional diversity will be affected only by habitat structure, but not by site location (i.e., functional convergence in different regions).

MATERIALS AND METHODS

Sampling habitats and study regions

The vegetation of WSE is quite variable in structure and plant species composition (Anderson 1981, Ferreira 2009, Costa *et al.* 2020 – Fig. 1). In this study, we used the habitat classification proposed by Borges *et al.* (2016b) that categorized open fields with grass and scrub areas as white-sand *campina* (WSC) and low to high-canopy forests (10-

30 meters) growing in sand soils as white-sand forests (WSF). WSE is used here as a general term that includes all variations in the structure and floristics of this vegetation type (Fig.1).

We sampled ants in two protected areas located in the northern Brazilian Amazon (Fig. 2): Reserva de Desenvolvimento Sustentável do Rio Negro (hereafter RDS Rio Negro), located in Amazonas state (Lat: -3.003; Long: -60.693) and Parque Nacional do Viruá (hereafter Parna Viruá), situated at Roraima state (Lat: 1.282; Long: -61.111). The WSE in the RDS Rio Negro is found as patches of low to high-canopy forests with open understory (WSF) or as small patches (18 to 29 ha) of open to shrub vegetation growing in exposed sandy soil (WSC). Both WSF and WSC are surrounded by upland *terra firme* forests that dominate the regional landscape. The WSC in RDS Rio Negro are often restricted to areas of shallow water table, that can be temporally flooded after heavy rains. In sharp contrast, WSE with its different physiognomies occupies about one million hectares of the Parna Viruá (ICMBio 2014). Approximately 255,000 hectares are represented by open/shrubby *campina* (WSC), and the several physiognomies of white-sand forests (WSF) cover more than 700,000 hectares in Parna Viruá (ICMBio 2014). The WSC in Parna Viruá are also restricted to areas with the shallowest water-table in the landscape, but given the size, some WSC areas can remain flooded for several months (Damasco *et al.* 2013).

Ant collection and identification

Ants were collected in 14 plots in RDS Rio Negro in in June 2019 (four in WSC and 10 in WSF) and 12 plots in Parna Viruá in in February 2022 (six in WSC and six in WSF) following the RAPELD sampling design (Magnusson *et al.* 2013). The plots were 250 m long and regularly distributed at every 1 km in the landscape. Each plot contained ten sampling stations with four pitfall traps (two on the ground and two in the vegetation) spaced at 25 m intervals, totaling 40 traps per plot. Ground traps contained water and sodium chloride solution, and the arboreal traps were placed ~2 m high and were filled with diluted human urine (Bestelmeyer *et al.* 2000, Powell *et al.* 2011), and operated for 48 hours. Collected ants were preserved in 70% alcohol. Our sampling effort resulted in 1.040 pitfall samples (520 from the arboreal traps and 520 from the ground-dwelling traps).

The ants were sorted and identified at the genus level following Baccaro *et al.* (2015) and at the species resolution using taxonomic keys of Brandão (1990), Fernández (2003), Longino (2003), MacKay and MacKay (2010), and Oliveira *et al* (2021). The collected ants were also compared with identified specimens deposited in the invertebrate collections of the Universidade Federal do Amazonas (UFAM), the National Institute of Amazonian Research (INPA), and Systematics and Biology of Ants Laboratório de Sistemática e Biologia de Formigas da Universidade Federal do Paraná (UFPR). Specimens were deposited in the Zoological Collection Prof. Paulo Bührnheim (CZPB–UFAM) and invertebrate collections of INPA and Coleção Entomológica Padre Jesus Santiago Moure - DZUP.

Functional traits

We used a morphological trait database of Amazonian ants that have been constantly updated (Andrade-Silva *et al.* 2022, Andrade-Silva *et al.* 2024). In short, morphological traits of ant species were measured using high-resolution images and selected publications. Measurements were standardized by prioritizing type specimens, and ImageJ software was employed for image-based analysis when direct specimen examination was not feasible. Missing data were addressed through imputation methods. Given the high number of species and measurements, only one specimen was measured per species. For detailed protocols see Andrade-Silva *et al.* (2022) and Andrade-Silva *et al.* (2024). Among the database, we selected the following five continuous morphological traits associated with different aspects of ant biology and related to open or forested environments (see the Global Ant Traits Database, Parr *et al.* 2017):

- **Eye length (EL) and distance from eye to the mandible insertion (DEM)**: eye size is related to food-seeking behavior and periods of activity (Weiser and Kaspari 2006). The distance from the compound eye to the mandibular insertion can influence visual performance in predator species (Silva and Brandão 2014).
- **Femur length (FL)**: the size of the femur is linked to the complexity of the environment. Proportionally shorter femurs are advantageous for navigating complex interstitial habitats by allowing better access to small crevices and resources on the leaf litter (Kaspari and Weiser 1999).
- **Head length (HL)**: used as an indicator of body mass and related to the foraging strategies. Ants with larger heads support larger mandibles to attack prey with different body sizes (Kaspari and Weiser 1999).
- **Mandible length (ML)**: larger mandibles enable access to prey of different shapes and sizes, while longer mandibles allow for the predation of larger prey (Fowler *et al.* 1991, Weiser and Kaspari 2006).

DATA ANALYSIS

Plots were the sampling units in the analyses, and the occurrence frequency ranging from zero to 10 (the number of sampling stations per plot and stratum) was used to estimate the relative abundance of ants. Occurrence frequency is a helpful index of the number of ant colonies in a plot due to the relatively long distance between sampling stations (Baccaro and Ferraz 2013). Preliminary analysis indicates that the assemblage patterns were similar using only nominal species or using all species (nominal species and morphospecies). Then, we opted to include all sampled ants in the analysis. Ant species were classified as ground-dwelling or arboreal specialists when recorded in only one of these strata or as habitat generalists if collected in both ground-dwelling and arboreal traps.

Ant alpha diversity of the two habitats (WSC and WSF) and two regions (RDS Rio Negro and Parna Viruá) was compared through sample-based cumulative curves extrapolated for a common sampling effort (12 samples in each habitat) using the statistical package iNEXT (Chao and Jost 2012, Colwell *et al.* 2012, Hsieh and Chao 2016). In the cumulative curves, we used the Hill numbers with coefficients (q) that emphasize rare species (q = 0, species richness), neither rare nor abundant species (q = 1, exponential of Shannon's entropy), and the most abundant species (q = 2, inverse of Simpson index) (Hill 1973, Chao *et al.* 2014, Roswell *et al.* 2021). The cumulative curves were built by sampling stratum (ground-dwelling or arboreal). We also used a two-way ANOVA to test for differences in species richness of specialists and generalists across habitat (WSC and WSF) and region (RDS Rio Negro and PARNA Viruá).

Non-metric multidimensional scaling (NMDS) based on the Jaccard distance was used to assess the dissimilarity in species composition of ant assemblages between habitats and regions. The statistical significance of the previously defined groups based on habitats and regions was evaluated by a permutation (PERMANOVA) with 999 randomizations. The NMDS and PERMANOVA analysis were run in the vegan package (Oksanen *et al.* 2024). In addition to assemblage ordination, we performed an indicator species analysis to identify ant species significantly associated with a particular habitat and region (De Cáceres and Legendre 2009).

Ant functional diversity was assessed using two complementary ways. First, community weight means (CWM) were calculated to identify which particular morphological trait was filtered by habitat types in each study region. Additionally, three indices that represent different aspects of the functional structure of ant assemblages (Mouchet *et al.* 2010) were used: functional dispersal (Fdis), which measures the average distance of species from the centroid of the functional space; functional evenness (FEve), which assesses how evenly species fill the functional space; and functional divergence (Fdiv), which evaluates how species are distributed within the functional space, focusing on those with extreme traits.

These indices were calculated using standardized functional traits where each trait was divided by Weber's length of the species, a standard measure of ant size. Therefore, the three indices compare differences in form, while the CWM compares relative size values (but Weber's length). Differences among habitats and regions were tested using two-way ANOVA in both cases. The CWM and functional indices were calculated using the FD package (Laliberté *et al.* 2014).

RESULTS

Ant assemblage - alpha diversity

We documented the presence of 276 species or morphospecies in our study sites (Table S1), distributed across 57 genera and nine subfamilies, with 146 species (53% of the total) nominally identified (Table S2). The most species-rich subfamily (see species-rich habitats in the RDS Rio Negro and Parna Viruá regions, Table 1) was Myrmicinae (150 species), followed by Ponerinae (42 species) and Formicinae (36 species). We sampled 130 ant species in WSC and 236 in WSF, with 40 species exclusively recorded in WSC, 146 found only in WSF, and 90 species collected in both habitats. Additionally, we recorded new distribution records for 30 species in the state of Roraima, two of which also represent the first records for Amazonas, and four species were recorded for the first time in Brazil (Table S1).

Species richness of arboreal ants of WSF was similar in both studied regions as happened with arboreal ants in WSC (Fig. 3A). Species richness of arboreal ants in WSC tends to be lower than in WSF, despite a slight overlap in confidence interval observed between WSC and WSF in RDS Rio Negro (Figure 3A). The same general patterns were recovered with the Shannon ($q = 1$) and Simpson ($q = 2$) indices (Figure 3B, C), except that the arboreal richness of the dominant species was lower in WSC in Viruá National Park compared with other habitats (Figure 3C). Among the ground-dwelling ants, WSF in both regions and WSC in RDS Rio Negro had similar alpha diversity (Figure 3D, E, F). In contrast, the alpha diversity of ground-dwelling ants of WSC in Parna Viruá was remarkably lower than all other habitats (Figure 3D, E, F, Figure S1).

Ground-dwelling specialists (i.e., collected only in this stratum) were proportionally more diverse in WSF than WSC in both studied regions (Two-way ANOVA, $P = 0.03$ for habitat effect) and more varied in both habitats in RDS Rio Negro compared to Parna Viruá (Two-way ANOVA, $P = 0.03$ for site effect, Figure 4A). Ant diversity in WSC and WSF was similar among the arboreal specialists (Figure 4B) (Two-way ANOVA, $P = 0.89$ for habitat effect). However, WSC and WSF of Parna Viruá had proportionally more arboreal species than RDS Rio Negro (Two-way ANOVA, $P = 0.0012$ for site effect). Diversity of generalist species (i.e., recorded in both sampling strata) was higher in WSC than WSF in both regions (Figure 4C), especially in RDS Rio Negro (Two-way ANOVA, $P = 0.008$ for site effect and $P = 0.01$ for habitat effect).

Ant assemblage - beta diversity and indicator species

The species composition of arboreal ants of WSC was very distinct between study regions, just like in WSF (Figure 5A). However, we did not find differences in WSC and WSF species composition within each region (PERMANOVA, $P = 0.87$ for habitat effect and $P = 0.001$ for site effect). In contrast, we found strong effects of habitats and site location (PERMANOVA, $P = 0.001$ for habitat effect and $P = 0.001$ for site effect) in the species composition of ground-dwelling ants (Figure 5B).

We identified 52 species/morphospecies significantly associated with a specific habitat (WSC and WSF) within the studied regions (Appendix 1). Nineteen species were indicators of WSC in RDS Rio Negro, and 11 species were significantly associated with the same habitat in Parna Viruá. WSF in Parna Viruá harbors a higher number of indicator species (n = 16) than the same habitat in RDS Rio Negro (n = 6).

Ant assemblage - functional diversity

Habitats and regions filtered some morphological traits. Distance from eye to the mandible insertion tends to be higher in arboreal ants in the WSC of Parna Viruá compared to the same habitat in RDS Rio Negro ($P = 0.02$). However, no differences between habitats were detected in this trait (Figure 6A). Arboreal ants in WSF tend to have larger femur length ($P = 0.001$) than ants in WSC in both regions (Figure 6C). Similarly, arboreal ants in WSF tend to have larger mandible length than WSC ants ($P = 0.06$) (Figure 6E). A habitat effect was observed among the ground-dwelling ants ($P = 0.001$), with the distance from eye to the mandible being larger in WSC than in WSF in both regions (Figure 6F). Also, the eye length of ground-dwelling ants are larger in WSC than in WSF ($P = 0.004$) in RDS Rio Negro and Parna Viruá (Figure 6G).

Among the arboreal ants, functional dispersion (FDis) was higher in WSF than WSC (Figure 7A), especially in RDS Rio Negro (Two-way ANOVA, $P = 0.03$ for habitat effect and *P* = 0.05 for site). Functional divergence (FDiv) in arboreal ants was also more accentuated in WSF than WSC (*P* = 0.03 for habitat effect) in both study regions (Figure 7B). Functional evenness in arboreal ants was higher in RDS Rio Negro compared to Parna Viruá (*P* = 0.02 for site effect) in both sampled habitats (Figure 7C). Among ground-dwelling ants, the functional dispersion (*P* = 0.009) and regularity (*P* = 0.002) were much lower in Parna Viruá than RDS Rio Negro in both WSF and WSC (Figure 7 D, F).

DISCUSSION

The alpha and beta diversity of arboreal and ground-dwelling ants varied significantly between WSF and WSC and among the regions, indicating that habitat type and geographic location are determinants in the structure of ant assemblages. Furthermore, the observed differences in morphological characteristics and functional space underscore the importance of considering multiple ecological scales to understand functional diversity patterns in this unique Amazonian ecosystem.

Taxonomic diversity

We predicted that ant alpha diversity would be higher in WSF than WSC in agreement with the habitat heterogeneity hypothesis that suggests that structurally complex habitats provide more resources and diversified niches with a concomitant increase in the local species diversity (MacArthur and MacArthur 1961, Ribas *et al.* 2005). Indeed, the alpha diversity of arboreal ants in WSF was superior to WSC in both study regions, suggesting that the habitat structure plays an important role in species diversity independent of geographic location. This suggests that the physical and biological characteristics of WSF provide a consistent environment and resources for the colonization and survival of arboreal ants, maintaining greater local species diversity (De Oliveira *et al.* 2023).

Among the recorded species, at least one endangered species and others rarely documented in Amazonian ecosystems were identified. These findings highlight the taxonomic and conservation value of white-sand ecosystems, emphasizing their role in housing unique and vulnerable biodiversity. Such records reinforce the necessity of further studies to better understand and protect these habitats, which remain underexplored despite their ecological significance.

We found higher alpha diversity in the ground than in the arboreal stratum, as observed in other studies (Vasconcelos and Vilhena 2006, Schmidt *et al.* 2013, da Silva de Oliveira and Schmidt 2019). However, in contrast with arboreal ants, the local diversity of ground-dwelling ants was similar among WSF and WSC, except for WSC in Parna Viruá. The similar alpha diversity among habitats in the ground-dwelling ant assemblages indicates that the variability in soil habitat (e.g., litter density and soil porosity) apparently does not influence the local diversity of ants that live on the ground, which is surprising given the great contrast in vegetation biomass between WSF and WSC. Adding a functional group or guild classification to ground-dwelling ants could further elucidate how these assemblages partition habitat resources and respond to environmental heterogeneity (Parr *et al.* 2017; Gibb *et al*. 2015). For instance, this approach could clarify whether species within similar functional roles exhibit redundancy or if certain guilds are more sensitive to habitat variations, thus providing a deeper understanding of the ecological processes driving assemblage composition in these contrasting habitats.

The remarkable lower ant alpha diversity in WSC at the Parna Viruá apparently is associated with landscape dynamics. In addition to extremely low fertility, soils in WSE are frequently inundated by groundwater (Adeney 2016, Mendonça *et al.* 2014, Adeney *et al.* 2016, Damasco *et al.* 2013). The extension and duration of the flooding regime in WSE are highly variable and depend on the local relief (Damasco *et al.* 2013). For example, some spots in WSE could remain flooded for several months in Parna Viruá (Damasco *et al.* 2013). The magnitude and duration of flooding in the WSC patches in RDS Rio Negro are much lower than in the large areas of WSC in Parna Viruá. The recurrent floods are natural disturbances for ground-dwelling ants (Baccaro *et al.* 2013) and likely restrict local diversity in regions with long-duration and large-scale flooding, such as Parna Viruá.

We predicted that ant alpha diversity would be greater in Parna Viruá with their large and continuous expanses of WSE which would be consistent with species area-diversity and habitat amount hypotheses (Fahrig 2013). However, species taxonomic diversity does not show consistent patterns among ant groups. The richness of ground-dwelling specialist ants was higher in RDS Rio Negro compared to Parna Viruá, which is precisely opposed expected pattern. In contrast, arboreal ants of WSF and WSC are more diversified in Parna Viruá. We hypothesized that the intensity and duration of flooding could also explain the relatively low diversity of ground-dwelling specialist ants in Parna Viruá.

Seasonal floods also force ants to migrate to the arboreal stratum to survive (Adis *et al.* 2001). This forced migration to trees during flooding periods may explain the higher proportional diversity of arboreal specialists observed in WSC and WSF at the Parna Viruá compared to the same habitats in RDS Rio Negro. In contrast, flooding restricts local diversity by limiting the availability of microhabitats and resources necessary for the survival of ants that nest in the soil (Seal and Tschinkel 2010, Tschinkel *et al.* 2012, Baccaro *et al.* 2013). The smaller patches of WSC in RDS Rio Negro probably experience faster recolonization after periodic flooding than the larger and almost continuous WSC of Parna Viruá. In addition, the higher diversity of generalist species in WSC compared to WSF in both regions suggests that vertical stratification can be diluted in more open vegetation (De Oliveira *et al.* 2023).

The most striking patterns we found were (i) the consistent difference between the proportion of species associated with the terrestrial or arboreal stratum between regions and (ii) the inversion of the pattern between strata. While the relative proportion of ground-dwelling species is higher in the RDS Rio Negro in both habitats, the proportion of arboreal species is higher in the Parna Viruá, also in both habitats. These results reinforce a marked effect of the region, probably associated with the landscape configuration resulting from distinct historical contexts. The extensive area of WSC in the Parna Viruá may function as a species source for the WSF. At the same time, the large extension of WSF that dominates the landscape of the RDS Rio Negro provides propagules (species) for the WSC in the region. Similar patterns have been proposed to explain differences between Brazilian and Australian savannas (Neves *et al.* 2024).

The species composition of arboreal ants was similar between WSC and WSF within each region, suggesting that the contrasting vegetation structure between these habitats has a low influence on the beta diversity compared to geographical location. Arboreal ant similarity among habitats is still stronger in RDS Rio Negro where WSF dominates the landscape. In sharp contrast, the composition of arboreal ant species in WSC and WSF differed between the studied regions, reflecting the site location's importance in determining beta diversity. In turn, habitat structure and site location strongly affected the species composition of ground-dwelling ants. Habitat diversity found along gradients from open fields (WSC) to forests (WSF) promotes higher species turnover within each region (De Oliveira *et al.* 2023, Ribas *et al.* 2003, Vasconcelos *et al.* 2004).

The landscape of each study region is strongly contrasting in terms of habitat availability, and this configuration is likely associated with WSE origins in each region. The extensive WSE in the Parna Viruá are formed by sediments deposited in large distributary fluvial systems (megafans), which could have originated from tectonism disturbance during the Late Pleistocene and Holocene (Rossetti *et al.* 2012, Zani and Rossetti 2012). In contrast, the small white sand patches in the RDS Rio Negro result from local degradation of the clay component of the soil (podsolization) (Dubroeucq *et al.* 1991, Mafra *et al.* 2002). These contrasting historical trajectories may result in distinct habitat distribution and configuration, affecting the taxonomic diversity of WSE ant assemblages.

Functional diversity

As we predicted, most morpho-functional traits were filtered by the vegetation structure instead of site location (Almeida *et al.* 2023). Among the arboreal ants, the femur length was larger in WSF than in WSC, suggesting the more structurally complex habitat filter traits associated with mobility. Similarly, the longer mandible in arboreal ants in WSF suggests a higher diversity of prey available in these habitats (Fowler *et al.* 1991, Yamamoto *et al.* 2009,). Among ground-dwelling ants, traits associated with vision were selected in WSC compared to WSF. Bigger and more separated eyes may reflect adaptations to a more exposed environment, where vision plays a crucial role in detecting prey and predators.

Arboreal ants in WSF exhibit greater functional dispersion than in WSC, possibly due to the higher structural heterogeneity and availability of resources in these habitats. In addition, the higher functional evenness in arboreal ants in RDS Rio Negro, regardless of habitat, highlights the regional influence on functional diversity. Ground-dwelling ants in

Parna Viruá showed lower functional dispersion and regularity compared to RDS Rio Negro, indicating that regional factors also have a important role on functional diversity than habitat structure. Thus, the functional diversity of ground-dwelling ants is more sensitive to regional conditions, while that of arboreal ants more related with habitat complexity. Our results demonstrate that the origins of each habitat in distinct biogeographic regions affect not only the taxonomic but also the functional diversity response of ants to variability in habitat structure.

Ant diversity is significantly shaped by habitat structure and geographical location, whose influence was highly variable across habitats (opens vs. forest), habitats (ground vs. arboreal), and morphological traits. These findings have important implications for biodiversity conservation and ecosystem management in Amazonian white-sand ecosystems. By highlighting the role of habitat-specific filters and regional processes in shaping ant diversity, our results emphasize the need to protect and manage the structural complexity of these habitats. Furthermore, our study provides a framework for understanding how ant diversity responds to environmental gradients, offering insights that can inform strategies to habitat disturbance on WSE. Future research should expand on these findings by incorporating long-term monitoring to assess temporal dynamics in ant assemblages and exploring the interplay between functional and phylogenetic diversity. Additionally, integrating experimental approaches to test the resilience of functional traits under varying environmental pressures could provide deeper insights into the mechanisms driving biodiversity patterns in these highly dynamic ecosystems. Such studies will be critical for advancing our understanding of how habitat complexity and biogeographic history interact to shape the structure and function of tropical biodiversity.

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CONFLICT OF INTEREST

None declared.

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DATA AVAILABILITY

The data on which this article is based are available as Supporting Information

AUTHOR CONTRIBUTION

A.B.O., F.B. and S.H.B contributed to the study conception and design. Fieldwork was performed by A.B.O. Data analyses were performed by A.B.O. and F.B. J.A.S., R.R.S. and F.A.S provides the ants functional traits. R.M.F. gave support in the ant identification The first manuscript version was prepared by A.B.O. and S.H.B. All authors commented on revised versions and approved the final manuscript version.

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Appendix 1. List of ant species significantly associated to a particular habitat (white-sand campina WSC or white-sand forests WSF) in the two study regions (RDS Rio Negro and Parna Viruá). IndVal varies from 0 to 1 and P values were obtained with 999 permutations.

Taxons	**Indicator of**	**IndVal**	**P value**
Dolichoderus imitator	WSC RDS Rio Negro	0.842	0.001
Pseudomyrmex oculatus	WSC RDS Rio Negro	0.791	0.001
Ectatomma tuberculatum	WSC RDS Rio Negro	0.753	0.001

Camponotus (Tanaemyrmex) sp01	WSC RDS Rio Negro	0.748	0.001
Camponotus (Tanaemyrmex) testaceus	WSC RDS Rio Negro	0.688	0.002
Pheidole sp.4	WSC RDS Rio Negro	0.658	0.005
Wasmannia auropunctata	WSC RDS Rio Negro	0.658	0.006
Camponotus (Myrmaphaenus) cf *vagulus*	WSC RDS Rio Negro	0.612	0.004
Pheidole sp.33	WSC RDS Rio Negro	0.612	0.002
Neoponera globularia	WSC RDS Rio Negro	0.607	0.002
Brachymyrmex sp.1	WSC RDS Rio Negro	0.589	0.004
Camponotus (Myrmocladoecus) rectangularis	WSC RDS Rio Negro	0.587	0.005
Cephalotes atratus	WSC RDS Rio Negro	0.581	0.01
Crematogaster torosa	WSC RDS Rio Negro	0.5	0.023
Camponotus (Myrmobrachys) senex	WSC RDS Rio Negro	0.5	0.03
Dorymyrmex sp. 1	WSC RDS Rio Negro	0.481	0.03
Camponotus (Myrmobrachys) sp. 18	WSC RDS Rio Negro	0.463	0.035
Brachymyrmex sp.2	WSC RDS Rio Negro	0.456	0.044
Camponotus (Myrmaphaenus) sp. 8	WSC RDS Rio Negro	0.456	0.047
Paratrachymyrmex diversus	WSF RDS Rio Negro	0.734	0.001
Pheidole sp. 1	WSF RDS Rio Negro	0.665	0.002
Camponotus (Myrmaphaenus) sp. 1	WSF RDS Rio Negro	0.645	0.004
Blepharidatta brasiliensis	WSF RDS Rio Negro	0.632	0.003
Crematogaster sotobosque	WSF RDS Rio Negro	0.548	0.008
Gnamptogenys horni	WSF RDS Rio Negro	0.544	0.033
Camponotus (Myrmobrachys) crassus	WSC Parna Viruá	0.833	0.001
Cephalotes pusillus	WSC Parna Viruá	0.831	0.001
Camponotus (Myrmothrix) atriceps	WSC Parna Viruá	0.671	0.006
Pseudomyrmex termitarius	WSC Parna Viruá	0.645	0.002
Crematogaster nr *acuta* sp. 5	WSC Parna Viruá	0.626	0.007
Dolichoderus diversus	WSC Parna Viruá	0.611	0.007
Ectatomma brunneum	WSC Parna Viruá	0.605	0.015

Solenopsis cf. *saevissima*	WSC Parna Viruá	0.587	0.013
Pseudomyrmex venustus	WSC Parna Viruá	0.5	0.025
Cephalotes pavonii	WSC Parna Viruá	0.474	0.034
Pseudomyrmex gracilis	WSC Parna Viruá	0.468	0.039
Camponotus rapax	WSF Parna Viruá	0.788	0.001
Azteca sp. 1	WSF Parna Viruá	0.744	0.001
Azteca chartifex	WSF Parna Viruá	0.732	0.001
Pheidole diligens	WSF Parna Viruá	0.687	0.001
Labidus praedator	WSF Parna Viruá	0.609	0.002
Nylanderia sp. 3	WSF Parna Viruá	0.588	0.028
Crematogaster flavomicrops	WSF Parna Viruá	0.577	0.003
Pheidole biconstricta	WSF Parna Viruá	0.577	0.013
Pheidole sp.11	WSF Parna Viruá	0.577	0.008
Camponotus (Tanaemyrmex) lespesii	WSF Parna Viruá	0.554	0.014
Cephalotes placidus	WSF Parna Viruá	0.543	0.021
Neoponera apicalis	WSF Parna Viruá	0.542	0.031
Dolichoderus laminatus	WSF Parna Viruá	0.542	0.009
Azteca cf. *ulei*	WSF Parna Viruá	0.538	0.017
Pheidole radoszkowskii	WSF Parna Viruá	0.5	0.019
Acromyrmex octospinosus	WSF Parna Viruá	0.5	0.021

LEGENDS OF FIGURES AND TABLES

Figure 1. Variation in the vegetation structure of Amazonian White-sand ecosystems: A) open white-sand campina with grassy aspect in Parque Nacional do Viruá, B) low canopy white-sand forest in Parque Nacional do Viruá, C) white-sand forest in Parque Nacional do Viruá, note the small diameters of trees, D) shrubby white-sand campina growing in exposed patch of sandy soil in Reserva de Desenvolvimento Sustentável do Rio Negro, E) white-sand forest in Reserva de Desenvolvimento Sustentável do Rio Negro. Photographs taken by Amanda Batista de Oliveira.

Figure 2. Study sites: White sand campinas (yellow) and White sand forests (red) from Viruá National Park an RDS Rio Negro

Figure 3. Sample-based rarefaction and extrapolation curves using Hill number separated by arboreal ant species (upper panel) and ground-dwelling ants (lower panel): species richness or q1 (A and D), Shannon indices or q2 (B and E), and simpson indices or q3 (D and F).

Figure 4. Box-plots of species richness of ant specialist in ground (A) and arboreal (B) layers and generalist species (C) in white-sand ecosystems habitats and regions. Numbers of species are represented proportionally.

Figure 5. Ordinations of sampling sites based in Jaccard indices of arboreal (A) and ground-dwelling (B) ants represented in two axis of non-metric multidimensional scales

Figure 6. Box-plots of community weight means (CWM) of ant assemblages sampled in white-sand campina (WSC) and white-sand forests (WSF) calculated with data of five morphological traits.

Figure 7. Box-plots of functional indices separated by stratum, habitat and regions: functional dispersion (FDis), functional divergence (FDiv), and functional evenness (FEve).

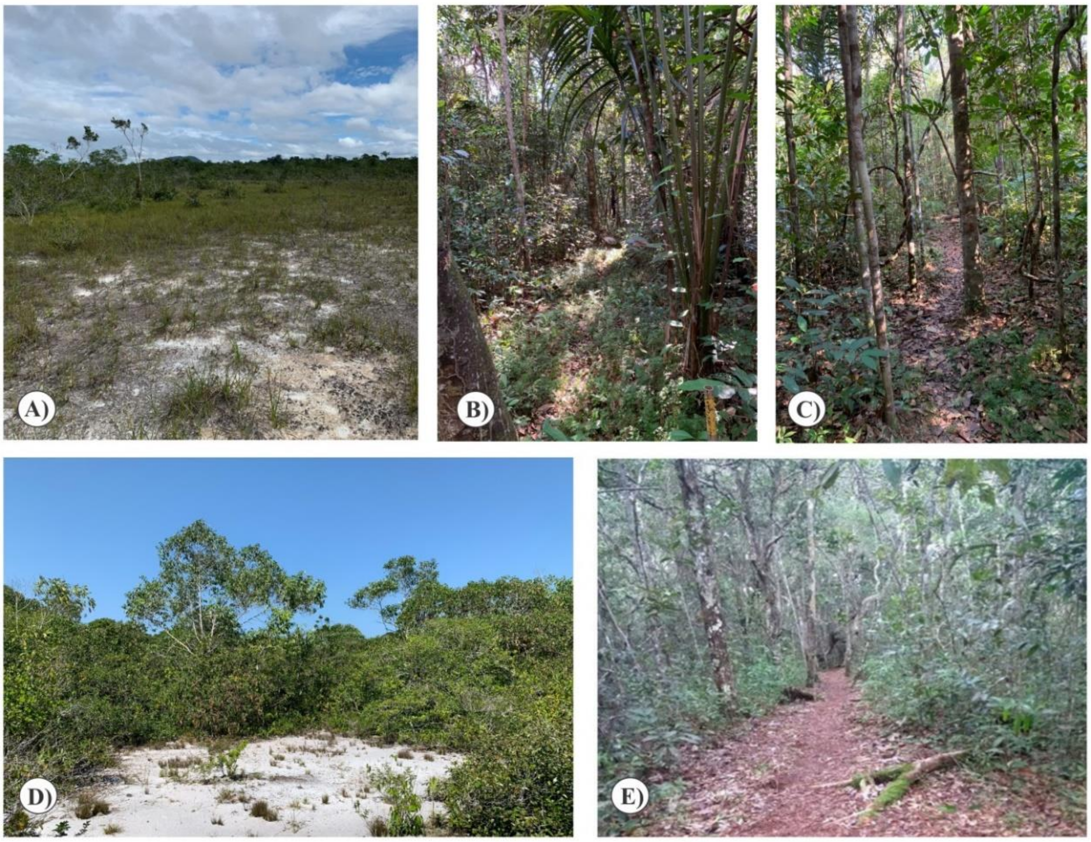

Figure 1. Variation in the vegetation structure of Amazonian White-sand ecosystems: A) open white-sand campina with grassy aspect in Parque Nacional do Viruá, B) low canopy white-sand forest in Parque Nacional do Viruá, C) white-sand forest in Parque Nacional

do Viruá, note the small diameters of trees, D) shrubby white-sand campina growing in exposed patch of sandy soil in Reserva de Desenvolvimento Sustentável do Rio Negro, E) white-sand forest in Reserva de Desenvolvimento Sustentável do Rio Negro. Photographs taken by Amanda Batista de Oliveira.

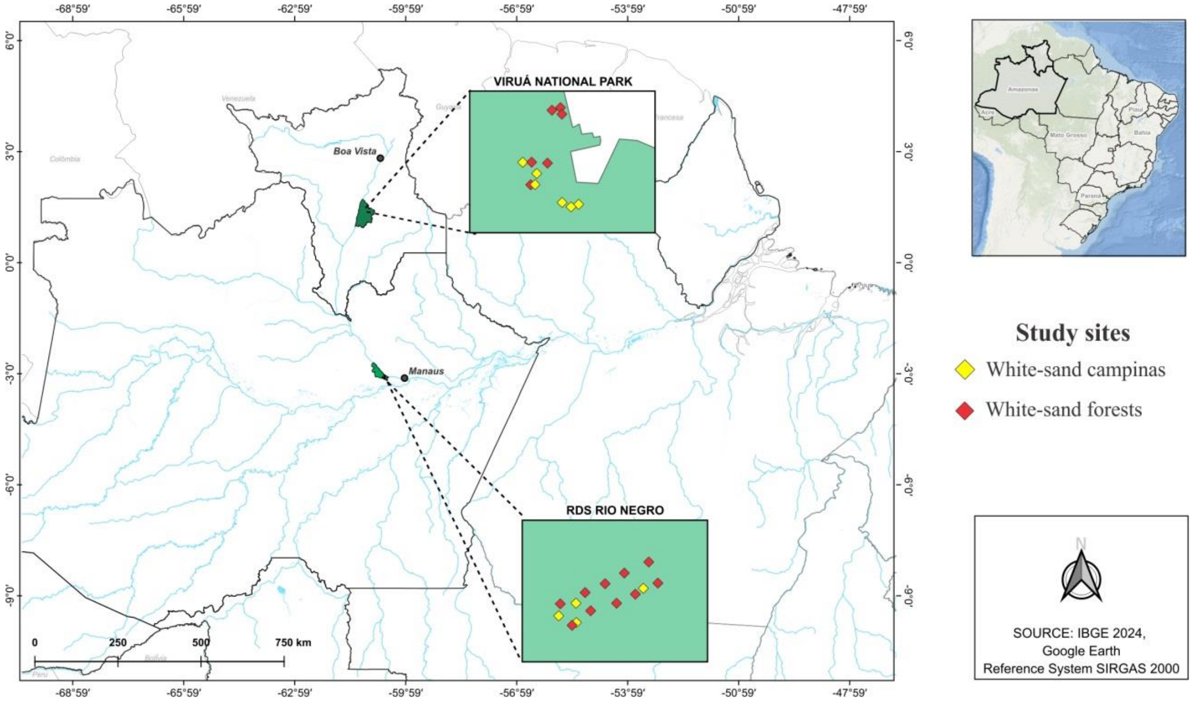

Figure 2. Study sites: White sand campinas (yellow) and White sand forests (red) from Viruá National Park an RDS Rio Negro

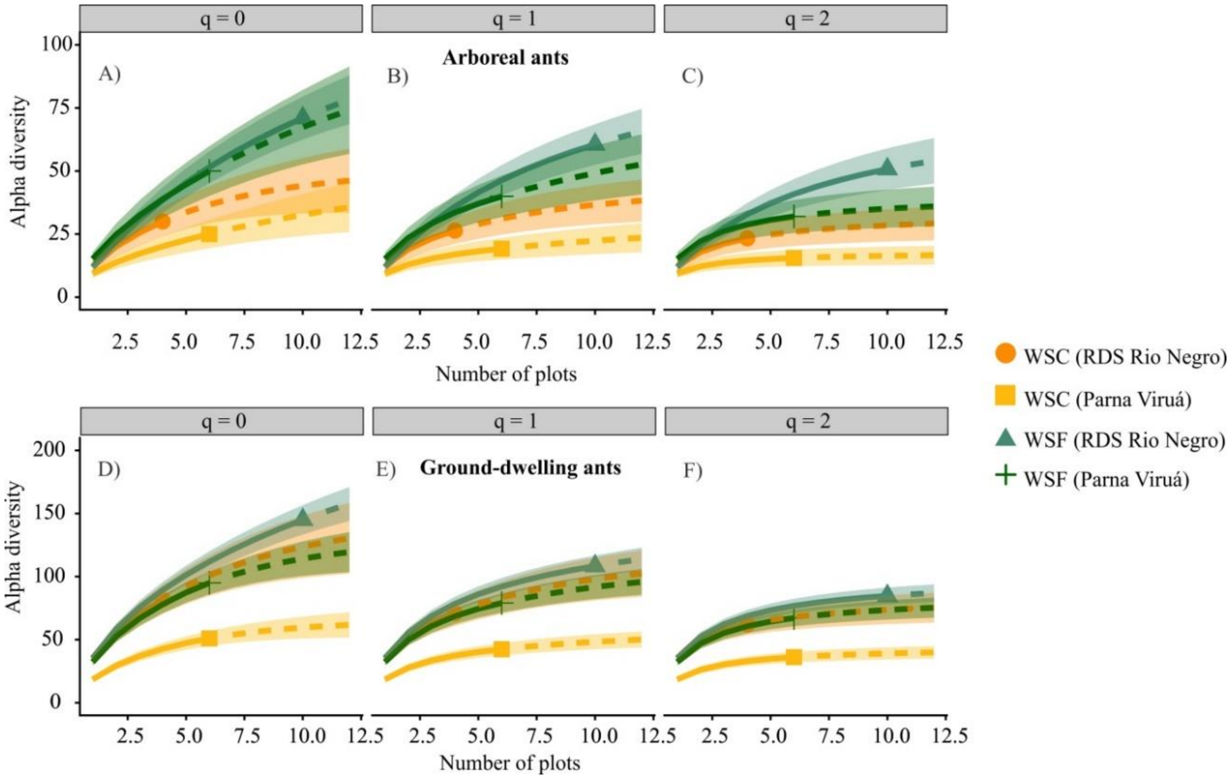

Figure 3. Sample-based rarefaction and extrapolation curves using Hill number separated by arboreal ant species (upper panel) and ground-dwelling ants (lower panel): species richness or q1 (A and D), Shannon indices or q2 (B and E), and simpson indices or q3 (D and F).

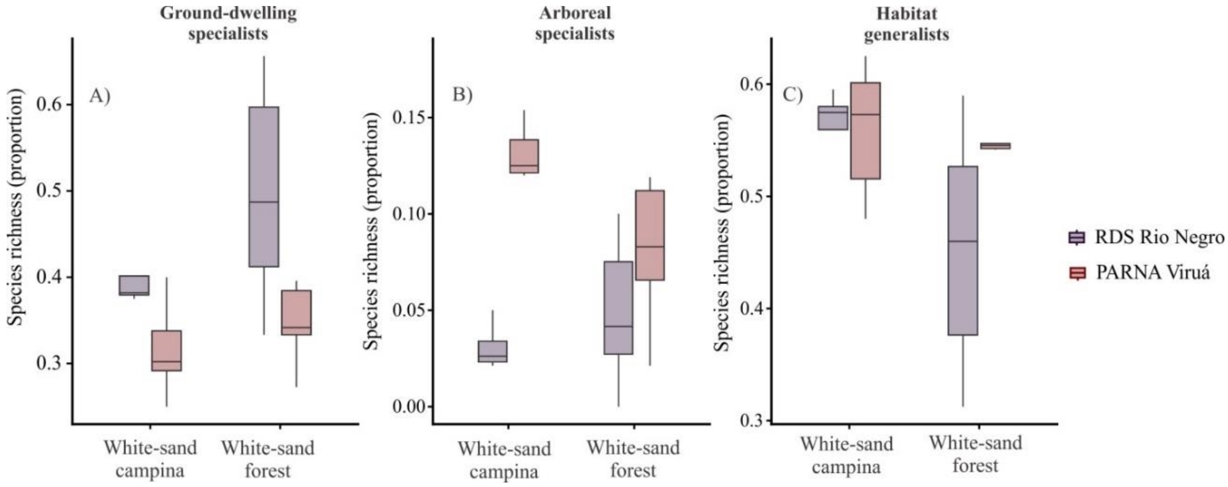

Figure 4. Box-plots of species richness of ant specialist in ground (A) and arboreal (B) layers and generalist species (C) in white-sand ecosystems habitats and regions. Numbers of species are represented proportionally.

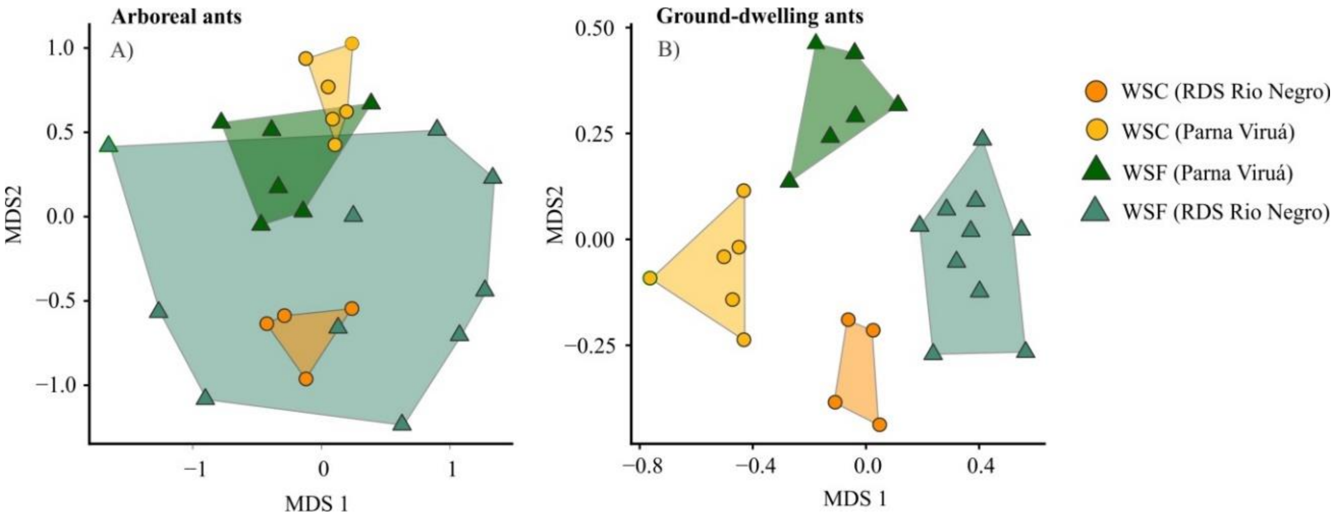

Figure 5. Ordinations of sampling sites based in Jaccard indices of arboreal (A) and ground-dwelling (B) ants represented in two axis of non-metric multidimensional scales

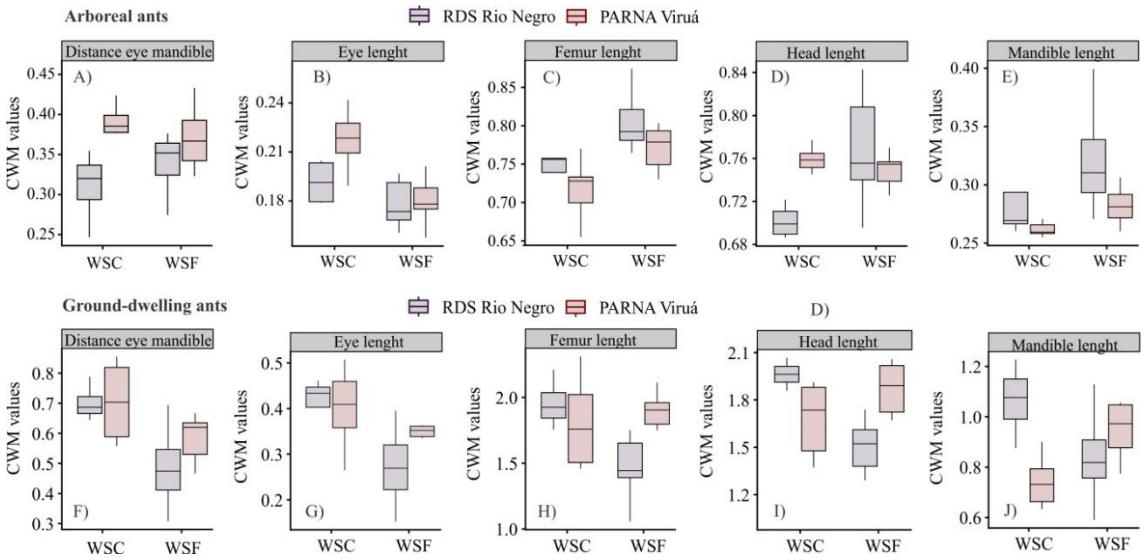

Figure 6. Box-plots of community weight means (CWM) of ant assemblages sampled in white-sand campina (WSC) and white-sand forests (WSF) calculated with data of five morphological traits.

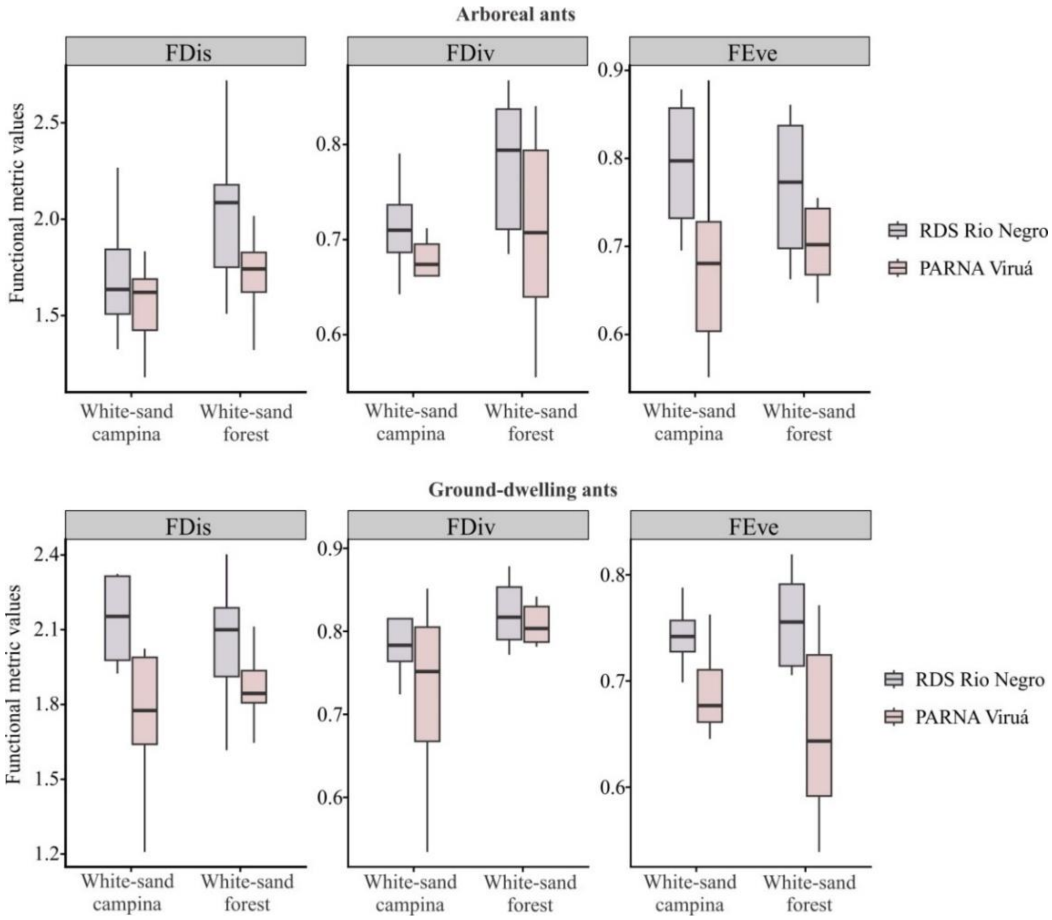

Figure 7. Box-plots of functional indices separated by stratum, habitat and regions: functional dispersion (FDis), functional divergence (FDiv), and functional evenness (FEve).

Table S2. Numbers of ant genera (out of the parentheses) and species (in parentheses) in the subfamilies, collected in two distinct habitats in the RDS Rio Negro and Parna Viruá regions.

Subfamilies	**White-sand campina**		**White-sand forest**	
	RDS Rio Negro	**Parna Viruá**	**RDS Rio Negro**	**Parna Viruá**
Myrmicinae	15 (38)	9 (33)	25 (98)	12 (63)
Formicinae	4 (20)	2 (10)	4 (23)	(2) (13)
Ponerinae	5 (16)	5 (9)	8 (26)	6 (18)
Dolichoderinae	5 (7)	2 (3)	4 (8)	2 (12)
Pseudomyrmecinae	1 (4)	1(6)	1 (6)	1 (2)
Ectatomminae	2 (4)	2 (2)	3 (11)	2 (5)
Dorylinae	3 (3)	2 (3)	2 (2)	2 (3)
Amblyoponinae	0 (1)	0	1 (1)	0
Paraponerinae	0	0	1 (1)	0

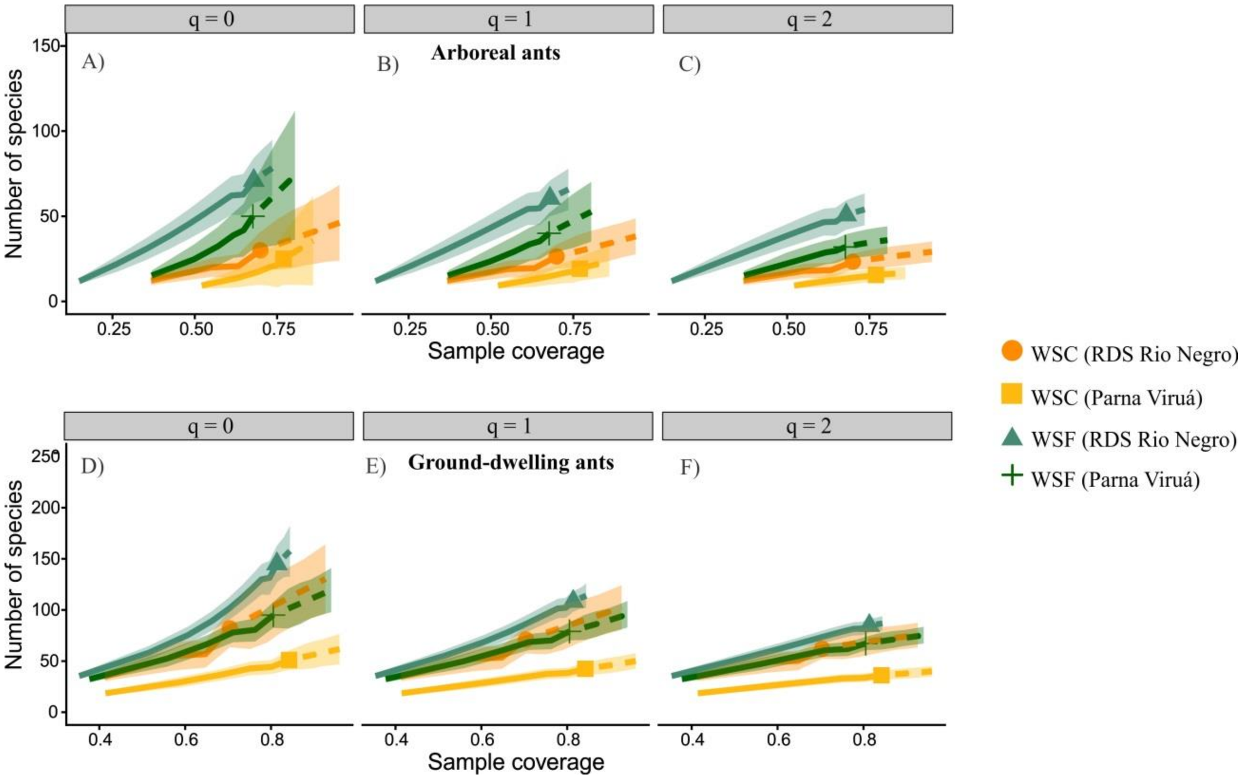

Fig. S1. Sample-coverage rarefaction and extrapolation curves using Hill number separated by arboreal ant species (upper panel) and ground-dwelling ants (lower panel): species richness or q1 (A and D), Shannon indices or q2 (B and E), and simpson indices or q3 (D and F).

SUPLEMENTARY MATERIAL

HABITAT STRUCTURE SHAPES ANT DIVERSITY IN AMAZONIAN WHITE-SAND ECOSYSTEMS

Amanda Batista de Oliveira, Sérgio Henrique Borges, Joudellys Andrade-Silva, Rodrigo Machado Feitosa, Rogério R. Silva, Fernando Augusto Schmidt, Fabricio Beggiato Baccaro

Table S1: List of species from Amazonian white-sand ecosystems with frequency of occurrence. First record for Roraima[1], Amazonas[2] , Amazônia[3] e Brazil[4] .

	Number of occurrences RDS do Rio Negro		Number of occurrences Parna Viruá		Number of occurrences RDS do Rio Negro		Number of occurrences Parna Viruá	
	Strata				**Habitat**			
Taxa	pitfall arboreal	Pitfall soil	pitfall arboreal	Pitfall soil	WSC	WSF	WSC	WSF
Amblyoponinae								
Prionopelta sp. 1		1				1		
Dolichoderinae								
Azteca chartifex Forel, 1896	4		14	6		4	2	18
Azteca sp. 4			1					1
Azteca cf. *ulei*	1	1	11	3	1	1		14
Azteca lallemandi Forel, 1899 [1]			1	1				2
Azteca sp. 1	7	4	25	7	7	4		32
Azteca sp. 4			1					1
Dolichoderus attelaboides Fabricius, 1775 [1]			2					2
Dolichoderus bispinosus Olivier, 1792	8	1	3	1		9		4
Dolichoderus debilis Emery, 1890 [1]			2					2
Dolichoderus diversus Emery, 1894 [1]			19				17	2
Dolichoderus imitator Emery, 1894	9	9	2	3	13	5	3	2
Dolichoderus laminatus Mayr, 1870 [1]	2		9			2		9
Dorymyrmex sp. 1		6			5	1		
Dorymyrmex sp. 3		1			1			
Forelius sp.1		1			1			
Tapinoma sp.1	2	2			1	3		
Dorylinae								
Eciton vagans Olivier, 1792 [1]		2		2	2		2	

Labidus coecus Latreille, 1802		45		12	8		4	8
Labidus praedator Smith, 1858		3	2	8			1	9
Neivamyrmex cristatus André, 1889						3		
Neivamyrmex sp. 1		1			1			
Nomamyrmex esenbeckii Westwood, 1842 [1]				2				2
Ectatomminae								
Ectatomma brunneum Smith, 1858		23	3	38	22	1	41	
Ectatomma edentatum Roger, 1863		1			1			
Ectatomma lugens Emery, 1894		17		13		17		13
Ectatomma sp. 3				3				3
Ectatomma tuberculatum Olivier, 1792	8	11	4	3	17	2		7
Gnamptogenys fernandezi Lattke, 1990 [1]	1	1	1		1	1		
Gnamptogenys horni Santschi, 1929		16		5		16		5
Gnamptogenys kempfi Lenko, 1964		1				1		
Gnamptogenys sulcata Smith, 1858		4				4		
Gnamptogenys tortuolosa Smith, 1858		2		2		2		2
Holcoponera moelleri Forel, 1912		2				2	2	
Holcoponera relicta Mann, 1916		1				1		
Holcoponera striatula Mayr, 1884 [1]	3	2		8		5	2	
Formicinae								
Acropyga sp. 1						3		
Brachymyrmex sp. 1	2	4			5	1		
Brachymyrmex sp. 2	1	2			2	1		
Brachymyrmex sp. 3		1			1			
Camponotus (Myrmobrachys) nr. *formiciformis* [4]	2					2		
Camponotus (Tanaemyrmex) testaceus Emery, 1894[2]	14	4			10	8		
Camponotus (Dendromyrmex) nidulans Smith, 1860[1]	1					1		

Camponotus (Myrmaphaenus) nr. *vagulus* [3]	1	2			3			
Camponotus (Myrmaphaenus) helleri Emery, 1903 [4]	3					3		
Camponotus (Myrmaphaenus) leydigi Forel, 1886		3		1	2	1	1	
Camponotus (Myrmaphaenus) sp. 1	5	15	1			20	1	
Camponotus (Myrmaphaenus) sp. 2	5	23	20	14	11	17	10	24
Camponotus (Myrmaphaenus) sp. 8	1	2			2	1		
Camponotus (Myrmaphaenus) sp. 11		1			1			
Camponotus (Myrmepomis) sericeiventris Guérin-Méneville, 1838	1		5				4	9
Camponotus (Myrmobrachys) crassus Mayr, 1862	16	12	102	57	21	7	135	24
Camponotus (Myrmobrachys) senex Smith, 1858	2				2			
Camponotus (Myrmobrachys) sp. 3	1					1		
Camponotus (Myrmobrachys) sp. 18	2	2	1		4			1
Camponotus (Myrmocladoecus) rectangularis Emery, 1890	9	2			9	2		
Camponotus (Myrmosphincta) sexguttatus Fabricius, 1793 [1]			3				3	
Camponotus (Myrmothrix) atriceps Smith, 1858	31	8	122	59	22	17	110	71
Camponotus (Tanaemyrmex) lespesii Forel, 1886[1]	1		5	2		1		7
Camponotus (Tanaemyrmex) sp. 1	22	19	1		33	8	1	
Camponotus (Tanaemyrmex) sp. 2			1					1
Camponotus burtoni Mann, 1916	1					1		
Camponotus chartifex Smith, 1860		1			1			
Camponotus rapax Fabricius, 1804	1	3	13	20		4		33
Camponotus sp. 5	1					1		
Nylanderia fulva Mayr, 1862[1]			1	11			7	5
Nylanderia sp. 1		11	1	4	2	9		4

Nylanderia sp. 2	4	8		12	1	11	6	6
Nylanderia sp. 3	5	12	1	24	1	16		25
Nylanderia sp. 5				1				1
Myrmicinae								
Acromyrmex octospinosus Kempf, 1972[1]			1	2				3
Allomerus septemarticulatus Mayr, 1878	2	1				3		
Apterostigma sp. 1		2				2		
Apterostigma sp. 2		2				2		
Apterostigma sp. 3		2				2		
Apterostigma urichii Forel, 1893				1				1
Atta sexdens Linnaeus, 1758	3	7		2	2	8		2
Blepharidatta brasiliensis Wheeler, 1915		20				20		
Carebara brevipilosa Fernández, 2004		1				1		
Cephalotes atratus Linnaeus, 1758	10	4			11	3		
Cephalotes grandinosus Smith, 1860	1					1		
Cephalotes minutus Fabricius, 1804	4	1	9	3	1	4	4	8
Cephalotes opacus Santschi, 1920	3	1	1	1	1	3		2
Cephalotes pallens Klug, 1824	1		1			1	3	
Cephalotes pallidus De Andrade, 1999	1					1		
Cephalotes pavonii Latreille, 1809			9	1			9	1
Cephalotes placidus Smith, 1860	3		13	1		3		14
Cephalotes pusillus Klug, 1824	1		37	7		1	37	7
Cephalotes sp.1			1			1		1
Cephalotes sp. 2			1				1	
Cephalotes sp. 3				1				1
Cephalotes umbraculatus Fabricius, 1804	1		2					2
Crematogaster brasiliensis Mayr, 1878	5	7	3	15	3	9		18
Crematogaster carinata Mayr, 1862[1]	2	1		1		3		1

Crematogaster curvispinosa Mayr, 1862		1				1		
Crematogaster evallans Forel, 1907 [2]	4	1				5		
Crematogaster flavomicrops Longino, 2003 [1]				5				5
Crematogaster flavosensitiva Longino, 2003	3	5	1	3		8		2
Crematogaster gr. *Limata* sp. 2		1				1		
Crematogaster gr. *Limata* sp. 3			1					1
Crematogaster limata Smith, 1858	1	2				3		
Crematogaster longispina Emery, 1890		6			3	3		
Crematogaster nigropilosa Mayr, 1870	1	3				4		
Crematogaster nr. *acuta*			7	16			18	5
Crematogaster nr. *brasiliensis*		1				1		
Crematogaster nr. *crinosa* sp. 1		2				2		
Crematogaster nr. *flavosensitiva*			1					1
Crematogaster sotobosque Longino, 2003		10				10		
Crematogaster sp. 5				3				3
Crematogaster sp. 6				1				1
Crematogaster sp. 9				3			2	1
Crematogaster sp. 11	1					1		
Crematogaster sp. 13			2	3				3
Crematogaster sp. 14				1			1	
Crematogaster sp. 15			2	6				6
Crematogaster tenuicula (Forel, 1904)	19	30	2		10	39	1	1
Crematogaster torosa Mayr, 1870	2	1			3			
Cyphomyrmex minutus Mayr, 1862		16			4	12		
Cyphomyrmex rimosus Spinola, 1851				4			1	3
Cyphomyrmex sp.3		2				2		
Cyphomyrmex sp. 4		3				3		
Daceton armigerum Latreille, 1802		3				3		

Hylomyrma blandiens Kempf, 1961		1				1		
Hylomyrma immanis Kempf, 1973		1				1		
Megalomyrmex ayri Brandão, 1990		1				1		
Megalomyrmex incisus Smith, 1947		1				1		
Megalomyrmex nr. *silvestrii*		1				1		
Megalomyrmex symmetochus Wheeler, 1925				3				3
Megalomyrmex wallacei Mann, 1916				12			5	7
Monomorium sp. 1	2	3			3	2		
Monomorium sp. 2	1	1				2		
Mycetophylax lectus Forel, 1911[2]		2			2			
Mycetophylax sp. 3		1				3		
Myrmicocrypta sp. 1		3			1	2		
Myrmicocrypta sp. 2		1				1		
Ochetomyrmex semipolitus Mayr, 1878		2				2		
Octostruma balzani Emery, 1894		1				1		
Octostruma betschi Perrault, 1988		3				3		
Paratrachymyrmex bugnioni Forel, 1912		7			4	3		
Paratrachymyrmex diversus Mann, 1916	2	76		1		78		1
Paratrachymyrmex mandibularis Weber, 1938		1				1		
Paratrechina longicornis		1			1			
Pheidole biconstricta Mayr, 1870				19				19
Pheidole cf. *exigua*		7	1	10	2	5	2	9
Pheidole diligens Smith, 1858[1]			2	68			4	66
Pheidole fimbriata Roger, 1863		3				3		
Pheidole microps Wilson, 2003[1]/[2]		2		1		2		1
Pheidole radoszkowskii Mayr, 1884			1	4				5
Pheidole sp. 1	8	44		6	3	49		6

Pheidole sp. 10		9	2		1	8		2
Pheidole sp. 11			1	12				13
Pheidole sp. 12				7				7
Pheidole sp. 13		2		1		2		1
Pheidole sp. 14	1				1			
Pheidole sp. 15				3			3	
Pheidole sp. 16		1				1		
Pheidole sp. 17	2	3				5		
Pheidole sp. 18		3				3		
Pheidole sp. 19		1				1		
Pheidole sp. 2	4	2		19		6	3	16
Pheidole sp. 20		2				2		
Pheidole sp. 21		1		1		1		1
Pheidole sp. 22				4				4
Pheidole sp. 23		2		2	2		2	
Pheidole sp. 24		1				1		
Pheidole sp. 25		1				1		
Pheidole sp. 26		2				2		
Pheidole sp. 27		1		8		1	3	5
Pheidole sp. 29				3				3
Pheidole sp. 3		5				5		
Pheidole sp. 30				3				3
Pheidole sp. 31				1				1
Pheidole sp. 32								3
Pheidole sp. 33		4		3	4			
Pheidole sp. 34				6			3	3
Pheidole sp. 35			2					2
Pheidole sp. 36				1			1	

Pheidole sp. 37		1				1		
Pheidole sp. 4		18			13	5		
Pheidole sp. 42		1				1		
Pheidole sp. 45				1				1
Pheidole sp. 49		3			1	2		
Pheidole sp. 5		27			6	11		
Pheidole sp. 50		2				2		
Pheidole sp. 51		1				1		
Pheidole sp. 6		13			4	9		
Pheidole sp. 7		7			3	4		
Pheidole sp. 8		9		6	1	8		6
Pheidole sp. 9		2				2		
Pheidole vorax Fabricius, 1804		6		3	1	5		3
Procryptocerus sp. 1	1					1		
Rogeria subarmata Kempf, 1961 [1]/ [2]	1	6		2		7	1	1
Sericormyrmex sp. 1		4				4		
Sericormyrmex sp. 2		4			2	2		
Sericormyrmex sp. 3		1				1		
Solenopsis cf. *saevissima*				29			24	5
Solenopsis globularia Smith, 1858 [1]				2				2
Solenopsis picea Emery, 1896 [1]				3				3
Solenopsis sp. 1		23		30	15	8	19	11
Solenopsis sp. 2	2	13		8	4	11	8	
Solenopsis sp. 3	2	7		13	1	8	1	12
Solenopsis sp. 4	1	3				4		
Solenopsis sp. 5		1		5	1		1	4
Solenopsis sp. 6		2				2		

Solenopsis sp. 7			1	13	1		1	13
Solenopsis sp. 8		1		1			1	
Solenopsis sp. 9		1		15		1	11	4
Solenopsis substituta Santschi, 1925		2		3	2		3	
Solenopsis virulens Smith, 1858 [1]		4		11		4	7	4
Strumigenys denticulata Mayr, 1887		2				3		
Strumigenys elongata Roger, 1863	1	1		1		1		1
Strumigenys sp. 3		1				1		
Strumigenys sp. 4	1			1	1		1	
Strumigenys sp. 5				1				2
Tranopelta gilva Mayr, 1866		1			1			
Wasmannia auropunctata Roger, 1863	1	16		2	12	5	5	
Wasmannia rochai Forel, 1908		1			1			
Xenomyrmex sp. 1	3				3			
Xenomyrmex sp. 2	1					1		
Xenomyrmex sp. 3	1					1		
Paraponerinae								
Paraponera clavata Fabricius, 1775	1	1				2		
Ponerinae								
Anochetus diegensis Forel, 1912		1				1		
Anochetus horridus Kempf, 1964		2				2		
Centromyrmex brachycola Roger, 1861		1				1		
Hypoponera opaciceps Mayr, 1887 [1]				5			5	
Hypoponera sp. 1	1	1		3	2			3
Hypoponera sp. 10		1				1		
Hypoponera sp. 2				1				1
Hypoponera sp. 3		1		1		1		1
Hypoponera sp. 4		1		2		1		2

Hypoponera sp. 5		1				1		
Hypoponera sp. 7	1	1				1		
Hypoponera sp. 8		1				1		
Hypoponera sp. 9		1				1		
Hypoponera trigona cauta Forel, 1912 [1]/[2]		1		1		1	1	
Leptogenys gaigei Wheeler, 1923		1				1		
Leptogenys linearis Smith, 1858 [2]		2				2		
Leptogenys sp. 1		1				1		
Leptogenys sp. 2		1				1		
Mayaponera arhuaca Forel, 1901				1				1
Mayaponera constricta Mayr, 1884	1	19	1	11	7	13	1	11
Neoponera apicalis Latreille, 1802		11		18	1	10		18
Neoponera carinulata Roger, 1861	1					1		
Neoponera curvinodis Forel, 1899	1	2			1	2		
Neoponera globularia MacKay & MacKay, 2010		22			21	1		
Neoponera unidentata Mayr, 1862			1					1
Neoponera verenae Forel, 1922		13		3		13		3
Neoponera villosa Fabricius, 1804		1			1			
Odontomachus bauri Emery, 1892		1		7	1		3	4
Odontomachus caelatus Brown, 1976		13		3	6	7	2	1
Odontomachus cf. *bradleyi*		1			1			
Odontomachus cf. *ruginodis*		1		11	1			
Odontomachus haematodus Linnaeus, 1758	1	4		7	3	1	5	2
Odontomachus hastatus Fabricius, 1804	1				1			
Odontomachus ruginodis Wheeler, 1908 [4]							1	10
Odontomachus sp. 1		1			1			
Pachycondyla crassinoda Latreille, 1802	1	41		63	10	32	3	60

Pachycondyla harpax Fabricius, 1804		17		17		17		17
Pachycondyla impressa Roger, 1861		1		1	1			1
Pachycondyla procidua Emery, 1890				3				3
Pachycondyla striata Smith, 1858		1				1		
Pseudoponera stigma Fabricius, 1804			1					1
Pseudomyrmecinae								
Pseudomyrmex boopis Roger, 1863	1	5			1	5		
Pseudomyrmex gracilis Fabricius, 1804 [1]			1				7	1
Pseudomyrmex oculatus Smith, 1855	4	4			8			
Pseudomyrmex sp. 14			2					2
Pseudomyrmex sp. 4	1	2			1	2		
Pseudomyrmex sp. 5		1				1		
Pseudomyrmex sp. 6	2		1			2	1	
Pseudomyrmex sp. 7	1					1		
Pseudomyrmex sp. 9			2				2	
Pseudomyrmex tenuis Fabricius, 1804	1	6		16	1	6		
Pseudomyrmex termitarius Smith, 1855			1				17	
Pseudomyrmex unicolor Smith, 1855 [1]			1				1	
Pseudomyrmex venustus Smith, 1858 [1]			3				3	

CAPÍTULO 3

Beyond the Forest: Ants (Hymenoptera: Formicidae) of the White-Sand Campinas in the Amazon, Brazil

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Manuscrito em preparação

Beyond the Forest: Ants (Hymenoptera: Formicidae) of the White-Sand Campinas in the Amazon, Brazil

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ABSTRACT

Amazonian ecosystems are globally recognized for their extraordinary biodiversity, with many habitats supporting species adapted to various environmental conditions. Among these habitats, white-sand ecosystems, locally known as campinas, are unique due to their edaphic and microenvironmental characteristics. Amazonian campinas, characterized by oligotrophic soils and harsh environmental conditions, have been underestimated in biodiversity, particularly concerning ant fauna. These ecosystems exhibit a distinct ecological composition, favoring the occurrence of species adapted to nutrient-poor, seasonally flooded soils. This study aimed to conduct the first detailed survey of ant species in Amazonian campinas, focusing on arboreal and ground-dwelling species. Ant samples were collected from 12 campinas distributed across Acre, Amazonas, and Roraima, using ground and arboreal traps in permanent plots following the RAPELD protocol. Species were identified using taxonomic keys and compared with reference collections. The study recorded 172 ant species, with 21 new occurrences for the Amazon, including the first record of Hypoponera trigona cauta. Diversity was highest in the Acre, and RDS Rio Negro areas, and ground-dwelling ants exhibited greater species richness than arboreal ants. The findings suggest that Amazonian campinas, although often overlooked, are essential for conserving specialized species. The discovery of new occurrences and high diversity underscores the need for conservation strategies that account for the geological and ecological heterogeneity of these ecosystems.

Keywords: Ants, Campinas, WSE, Amazon, Biodiversity, Conservation

INTRODUCTION

In Brazil, open or non-forest vegetation ecosystems cover approximately 27% of the country’s surface area (Overbeck et al. 2022). Among these, the White-Sand Ecosystem (WSE) in the Amazon, known as campinas and campinaranas, stands out, covering an area of 334,879 km² (Adeney et al., 2016), particularly concentrated in the Rio Negro Basin. The WSE is notable for its oligotrophic soils, which support a distinct community of species adapted to nutrient-poor conditions. These ecosystems exemplify the Amazon’s ecological complexity, hosting many endemic species (Ferreira, 2009; Capurucho et al. 2020; Costa et al. 2020). The origin of the WSE is often attributed to sedimentation from ancient river systems (Rossetti et al. 2012) and podzolization processes in flooded areas (Dubroeucq et al. 1991; Mafra et al. 2002).

Within the WSE, campinas are characterized by low vegetation, with shrubs and trees rarely exceeding 4 meters in height. These areas feature open canopies and are composed of small fragments surrounded by white sand, often covered by bromeliads, orchids, and lichens (Adeney et al. 2016; Capurucho et al. 2020). Their distribution varies across regions due to geological factors (Anderson, 1981; Adeney et al. 2016; Fine and Bruna, 2016), resulting in irregularly scattered fragments of different sizes. Although the upper Rio Negro region is recognized for the extensive presence of these ecosystems (Ducke and Black, 1953), smaller patches can be found throughout the Brazilian Amazon, particularly in areas receiving over 2,000 mm of annual precipitation (Adeney et al. 2016).

Compared to the adjacent upland forests, the vegetarion of campina grow on low-fertility sandy soils and are subject to seasonal flooding, which leads to significant changes in plant and animal community composition (Anderson, 1981; Fine et al., 2010; Fine et al., 2016). These characteristics make WSEs globally unique ecosystems (Adeney et al. 2016; Capurucho et al. 2023). However, these areas have received little attention for conservation and are often altered by human activities such as burning and sand extraction, compromising their ecological integrity (Demachi et al., 2019; Montero, 2023). Few studies have explicitly focused on campinas, underscoring the need to understand the fauna that survive in these stressful environments.

Ants (Formicidae) serve as crucial ecological models due to their roles in nutrient cycling and seed dispersal, and they are especially abundant in tropical forests (Schultheiss et al., 2022). The Amazon is distinguished by exceptional ant diversity (Guénard et al. 2017), and ants are essential for maintaining regional biodiversity and ecosystem functions. However, many areas remain unexplored (Andrade-Silva et al. 2022; Carvalho et al. 2023). Ant diversity is shaped by microhabitat stratification, with distinct species adapted to arboreal and terrestrial layers (Vasconcelos and Vilhena, 2006). Additionally, ant community composition is shaped by environmental processes working on different spatial scales, illustrating the interplay between local and regional changes (Campos et al. 2011). Ants are also sensitive bioindicators, responding to environmental variations such as temperature shifts and resource availability (Pacheco and Vasconcelos, 2012; Baccaro et al., 2013; Solar et al., 2016). Despite their ecological importance, studies of ants in Amazonian white-sand ecosystems, especially on the most stressfull campina environment, are scarce, representing an understudied area in ant ecology.

Identifying ant species in these ecosystems is vital to addressing the Linnean shortfall, which refers to the gap between the total number of species and those formally described, and the Wallacean shortfall, which pertains to the lack of information on species' geographic distributions (Brown and Lomolino, 1998; Whittaker et al. 2005). Many species remain undiscovered or unnamed, limiting our understanding of biodiversity and ecological interactions in WSEs (Carvalho et al. 2023). Therefore, detailed investigation and description of ant species in campinas areas are essential to filling these knowledge gaps and promoting effective conservation of these unique ecosystems. This study presents the first species list of ants recorded across different open vegetation campinas configuration. Our aim was to conduct the first dedicated survey of arboreal and ground-dwelling ant species in these areas to unravel their ant diversity and emphasize their importance for biodiversity conservation.

MATERIALS AND METHODS

Our study was conducted across 12 WSE campinas in the WSE campinas located In southwestern Amazonia, within the state of Acre, isolated patches of white-sand ecosystems extend through the municipalities of Mâncio Lima and Cruzeiro do Sul (Acre, 2010; Brito et al., 2017). One campina was studied in a vegetational complex over white sand (07°28'18.88" S, 72°54'14.43" W), located 20 km from Mâncio Lima, near BR-307 (Figure S1). Average temperature is 24.4 °C, with annual rainfall between 1,600 mm and 2,750 mm (Acre, 2006).

In central Amazonia, these ecosystems are concentrated around the Rio Negro basin. One campina was selected at the ATTO site (02°10'58.58" S, 59°01'19.85" W), located in the Uatumã Sustainable Development Reserve (RDS-Uatumã), in the municipalities of São Sebastião do Uatumã and Itapiranga, within the Uatumã River basin (Figure S1). The site has an average temperature of 28 °C and annual rainfall of 2,376 mm (IDESAM, 2009). Five campinas are located in the RDS of Rio Negro (03°02'50.68" S, 60°43'43.93" W). The RDS Rio Negro is part of a protected mosaic along the lower Rio Negro, covering over eight million hectares (FVA, 2011). The average annual temperature is 27 °C, with 2,300 mm of rainfall (PGRDS, 2017).

At the same time, in northern Amazonia, the Viruá National Park, located in the municipality of Caracaraí in southern Roraima, encompasses a mosaic of alluvial forests, campinas, campinaranas, and terra firme forests (Figure S1). Six campinas were studied in Viruá National Park (01°25'31.02" N, 60°59'11.93" W), located in the municipality of Caracaraí, south-central Roraima. The park consists of a mosaic of alluvial forests, campinas, campinaranas, and upland forests. Annual temperatures range from 24 °C to 28 °C (INMET, 2008), with rainfall around 2,000 mm and an altitude between 60 and 360 meters (Silva et al., 2015; Schaefer et al., 2009).

Ant Sampling

Ant samples were collected from 12 permanent plots, each 250 meters long, established in WSE open vegetation campinas, following the RAPELD sampling design (Magnusson et al. 2013). In each plot, 10 sampling stations were distributed, with four pitfall traps at each station (two ground traps and two arboreal traps). The ground traps contained a solution of water and sodium chloride (Bestelmeyer et al. 2000), while the arboreal traps contained diluted human urine (Powell et al. 2011). The collected individuals were preserved in 70% alcohol, and the traps remained active for 48 hours. The sampling resulted in 480 ant samples, 240 from arboreal traps and 240 from ground traps, collected in 2019, 2020, and 2022.

Data Processing and Analysis

The samples were processed at the Community Ecology Laboratory of the Federal University of Amazonas (UFAM) in Manaus, Brazil. The ants were classified, mounted, and identified at the genus level using Baccaro et al. (2015) and at the species level using various taxonomic keys: Brandão (1990); Fernández (2003); Longino (2003); MacKay and MacKay (2010); Fernández (2008); Lattke et al. (2007); Camacho et al. (2020); Longino and Oliveira et al. (2021). They were compared with specimens from UFAM and INPA, and experts from INPA and UFPR confirmed the identification. When identification to the species level was impossible, the ants were treated as morphospecies. The specimens were deposited in the Prof. Paulo Bührnheim Zoological Collection (CZPB–UFAM) and the invertebrate collections of INPA and UFPR. All collections were conducted under the authorization of the Chico Mendes Institute for Biodiversity Conservation (ICMBIO; SISBIO/72174-1).

To compare the species richness and overall diversity across the four areas (Acre, RDS Uatumã, RDS do Rio Negro, and PARNA do Viruá) and to compare the overall species richness between arboreal and ground strata, we fitted interpolation and extrapolation curves for Hill numbers (Chao et al., 2014). To assess our sampling efficiency, species accumulation curves were built using interpolation (i.e., rarefaction) and extrapolation. These curves were generated with the R package 'iNEXT' (Hsieh et al., 2016; R Core Team, 2019) based on 120 samples, and 95% confidence intervals were estimated with 1,000 permutations.

RESULTS

Ant Diversity

We recorded 172 ant species in the WSE campinas. During the collection, we found 147 species in ground traps and 69 species in tree traps (Table S1). Out of the 172 sampled species, 86 were identified, representing 50% of the total. In total, we recorded 92 ant species in the campinas of the Rio Negro RDS, 65 in the campinas of Viruá

National Park, 58 in Acre, and 34 in the campina at the Atto site (Fig. 3, Table S1). The average species richness per stratum was similar across all studied areas. However, Acre showed significant variation in the average number of species between its strata (Fig. 3b). Acre stood out for having the highest diversity of species and genera. In comparison, diversity was lower at the Atto site and PARNA do Viruá (Fig. 2a). Additionally, species accumulation curves showed that ant species richness was greater in the ground stratum compared to the arboreal stratum (Fig. 2b). Of these, 104 species were collected exclusively from the ground, 25 were collected solely from trees, and 43 were collected from both strata.

The WSE campinas comprise 45 ant genera and eight subfamilies (Table S1). The most represented subfamily in the samples was Myrmicinae, with 109 genera, Formicinae with 33 genera, and Ponerinae with 20 genera (Table S1). The genus *Pheidole* Westwood, 1839, was the richest in species with 25 species, followed by *Camponotus* Mayr, 1861 (22) and *Crematogaster* Lund, 1831 (17). The most frequently encountered species were *Camponotus (Myrmobrachys) crassus* (164), *Camponotus (Myrmothrix) atriceps* (145), *Ectatomma brunneum* (78), and *Camponotus (Tanaemyrmex)* sp. 1 (36), which were sampled in all campinas areas (Fig. 3). Our study revealed 21 new species occurrences in the campinas areas (Table S1). Among those, we recorded *Hypoponera trigona cauta* (Forel, 1912) for the first time in the Brazilian Amazon (Fig. 3 a, available at https://antmaps.org/?).

DISCUSION

Traditionally, WSE campinas have been associated with lower species richness than other Amazonian ecosystems (Stropp et al., 2011). However, our research, which focused exclusively on campinas, substantial diversity in an oligotrophic environment characterized by nutrient-poor sandy soils. Despite their seemingly homogeneous structure, these areas support a functional diversity of micro-habitats that favor a distinct ant assemblage (Siqueira and Silva 2021).

The studied areas exhibit significant differences in habitat availability, attributed to the distinct origins of white-sand ecosystems (WSE). In Viruá National Park, the WSE formed from fluvial sediments deposited by megafans associated with tectonic disturbances (Rossetti et al. 2012; Zani and Rossetti 2012). In the RDS Rio Negro, the WSE resulted from the podzolization of clayey soils (Dubroeucq et al. 1991; Mafra et al. 2002). In Acre, the WSE developed on sandstone sediments, remnants from the Guiana and Brazilian Shields, transported by rivers toward the Pacific before the Andean uplift (Silveira, 2003; Daly et al., 2016). The higher diversity observed in areas such as RDS Rio Negro and Acre, possibly influenced by the proximity of terra firme forests, suggests that these areas act as species sources that adapt to and colonize the savannas. These geological variations shape the distribution of habitats and, consequently, influence the taxonomic diversity of ants in each region. This biological richness, however, contrasts sharply with the significant knowledge gaps imposed by the Linnean and Wallacean deficits. These deficits refer, respectively, to the lack of knowledge about the total number of species (Linnean) and the absence of detailed information regarding species' geographic distributions (Wallacean). Despite strong taxonomic efforts, only about 50% of species have been formally identified. In regions like the Amazon, where biodiversity is immense and many areas remain difficult to access, cataloging species and understanding their biogeography pose considerable challenges (Andrade-Silva et al. 2024). Although *campinas* cover only about 5% of the Amazon (Adeney et al. 2016), the logistical challenges of reaching many open-vegetation areas have resulted in a lack of information about the ecological patterns of ant richness and abundance in these habitats.

The taxonomic analysis revealed that white-sand ecosystems harbor 67 genera and nine subfamilies of ants (Figure S4), emphasizing the importance of these areas as crucial habitats for significant species diversity. The subfamilies Myrmicinae, Formicinae, and Ponerinae were the most abundant, which was expected due to their strong presence in tropical regions (Ward et al. 2014, 2016). The most frequently sampled species was Camponotus crassus Mayr, 1862, which often interacts with plants equipped with extrafloral nectaries and trophobiont insects, playing an essential role in plant-ant interactions (Lange et al. 2019). This ant, with high ecological flexibility, adapts to different environments, primarily nesting in the soil and foraging during the day, and is common in open and seasonal ecosystems. Camponotus atriceps Smith, 1858 (Figure S4), widely distributed in South America (Oliveira and Brandão 1991; Schoereder et al. 2010), was found in all campina areas, both in the soil and arboreal strata. The genus Camponotus Mayr, one of the largest among ants, shows great diversity, with colonies that can house thousands of individuals in various locations, such as soil, trunks, and tree canopies, as well as symbiotic interactions with other arthropods and ants (Lange et al. 2019).

The diversity observed in regions such as Acre, ATTO, RDS Rio Negro, and Viruá National Park, along with the identification of 21 new species occurrences and the first record of Hypoponera trigona cauta in the Amazon, highlights the need for continued conservation efforts and research in these regions. The sandy soils of the campinas (Podzols or Spodosols), characterized by low nutrient levels and seasonal water saturation, are limiting factors that shape a highly specialized biota, marked by phylogenetic endemism and a floristic composition distinct from other Amazonian ecosystems (Anderson, 1981, Borges et al. 2016; Prata et al. 2018; Costa et al. 2020). These factors create unique conditions that favor the development of specialized species, further emphasizing the role of campinas in the conservation of Amazonian biodiversity (Adeney et al. 2016). Further taxonomical studies are needed to investigate how many endemic and new species are among the 86 morphospecies sampled in these areas. The unique ecological and geological characteristics of the Amazon's white-sand ecosystems underscore the urgency of addressing existing knowledge gaps in species identification and distribution. Expanding taxonomical efforts and ecological research in these areas is essential for preserving both the known and yet-to-be-discovered biodiversity, particularly in specialized habitats like the campinas.

These savannas still harbor many unknown species, underscoring the urgent need for their conservation. Preserving these environments is crucial not only for protecting known species but also for safeguarding those yet to be described, ensuring the continuation of essential ecological processes in the Amazon. Geological and environmental variations among the white-sand ecosystems (WSE) in different studied regions shape habitat distribution and ant taxonomic diversity, reinforcing the importance of conservation strategies that account for this heterogeneity to maintain the high biodiversity observed.

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LEGENDS AND FIGURES

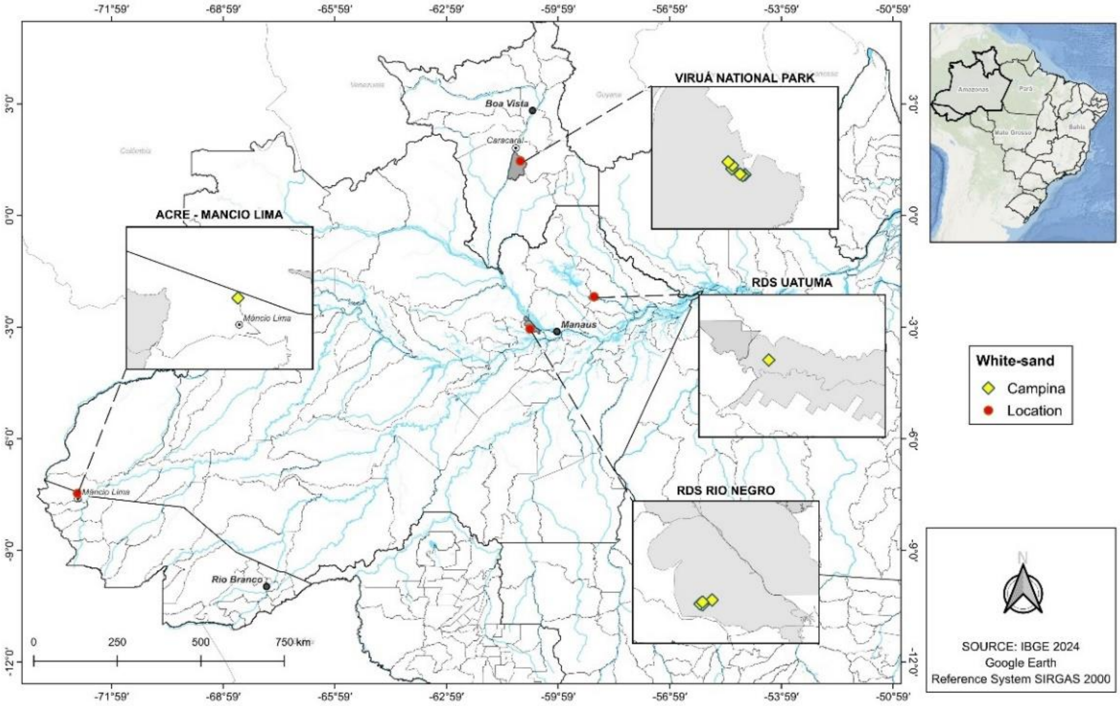

Figure 1. Map of the Campinas White-sand Ecossystems-WSE (yellow) the Brazilian Amazon basin.

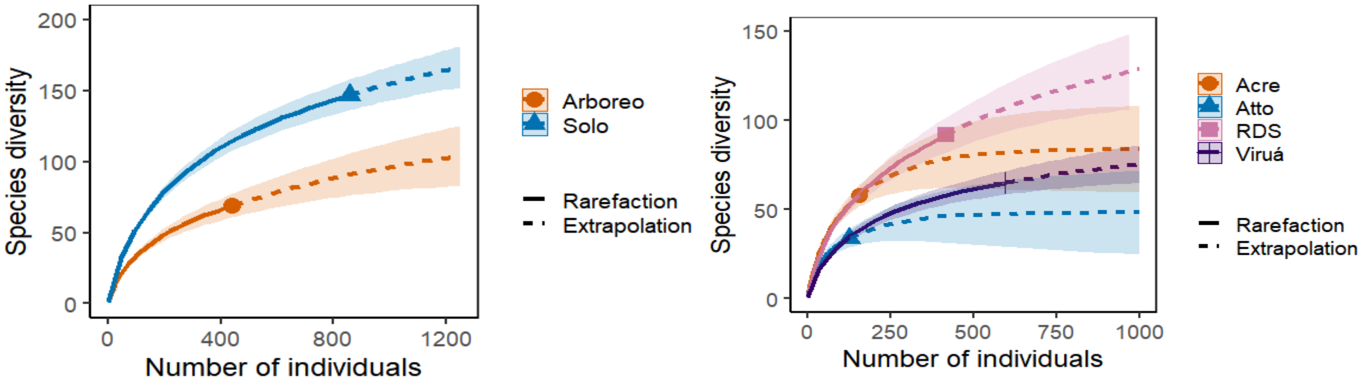

Figure 2. Sample-based rarefaction and extrapolation curves using Hill numbers, separated by ant frequency: (a) arboreal and ground strata, and (b) campina areas.

Figure 3. Frontal and lateral views of (a) *Hypoponera trigona cauta*, (b) *Ectatomma brunneum*, (c) *Camponotus crassus, (d) Camponotus atriceps* and (e) *Camponotus* (*Tanaemyrmex*) sp. 1. The first species is newly recorded from the Brazilian Amazon, while the remaining four species have been recorded Campinas (WSE) of the Brazilian Amazon.

Supplementary material

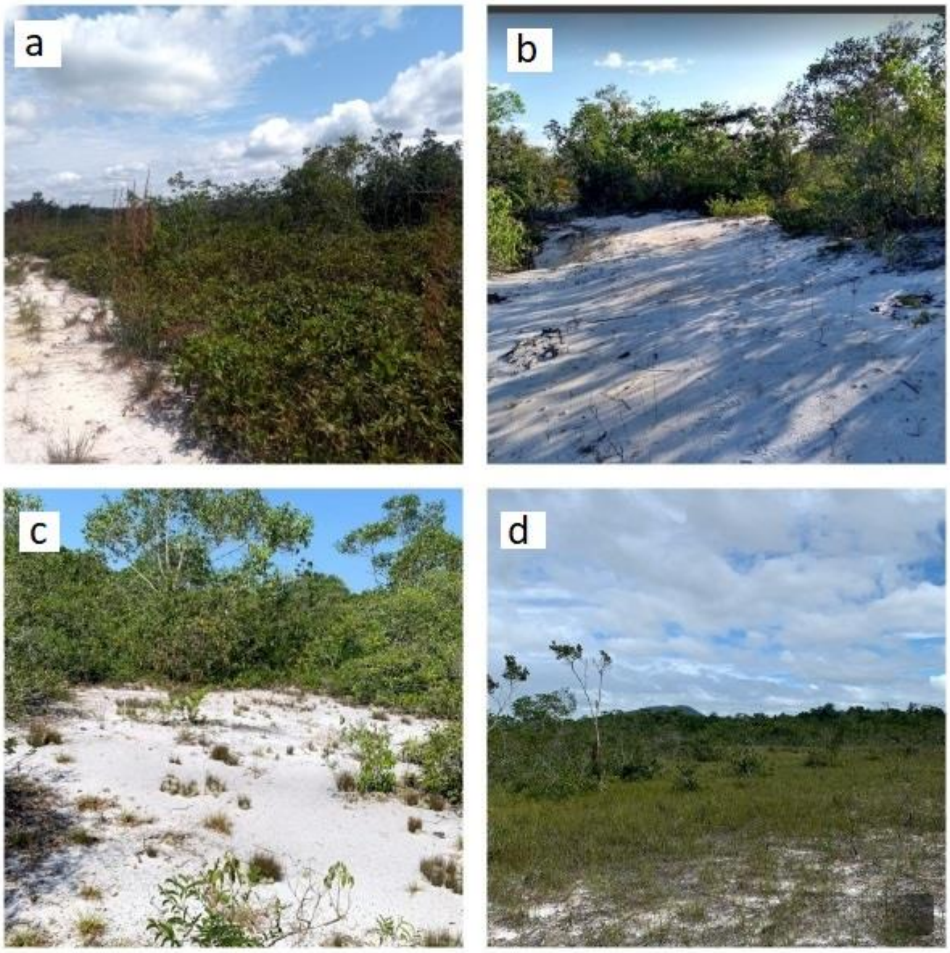

Figure S1. Campinas em WSE: (a) Campina Acre, (b) Campina Atto, (c) Campina da RDS do Rio Negro e (d) Campina do Parna viruá. Photoghaphs taken by ABSO

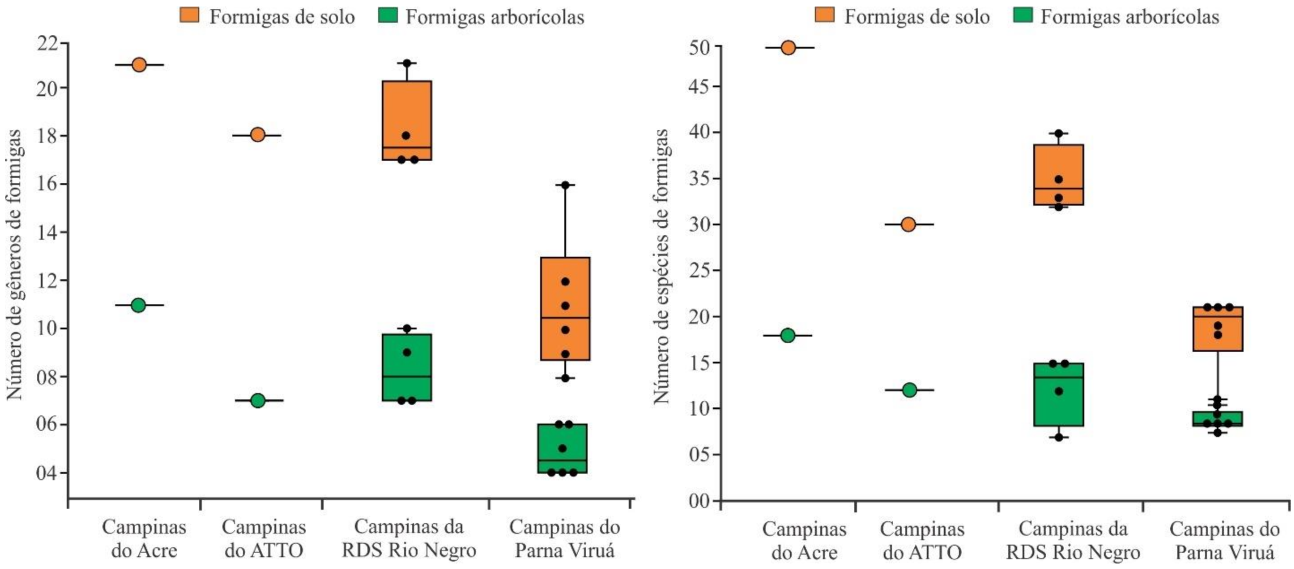

Figure S2. Average ant species richness per transect. (a) Number of ant genera in ground and arboreal strata, and (b) Number of ant species in ground and arboreal strata.

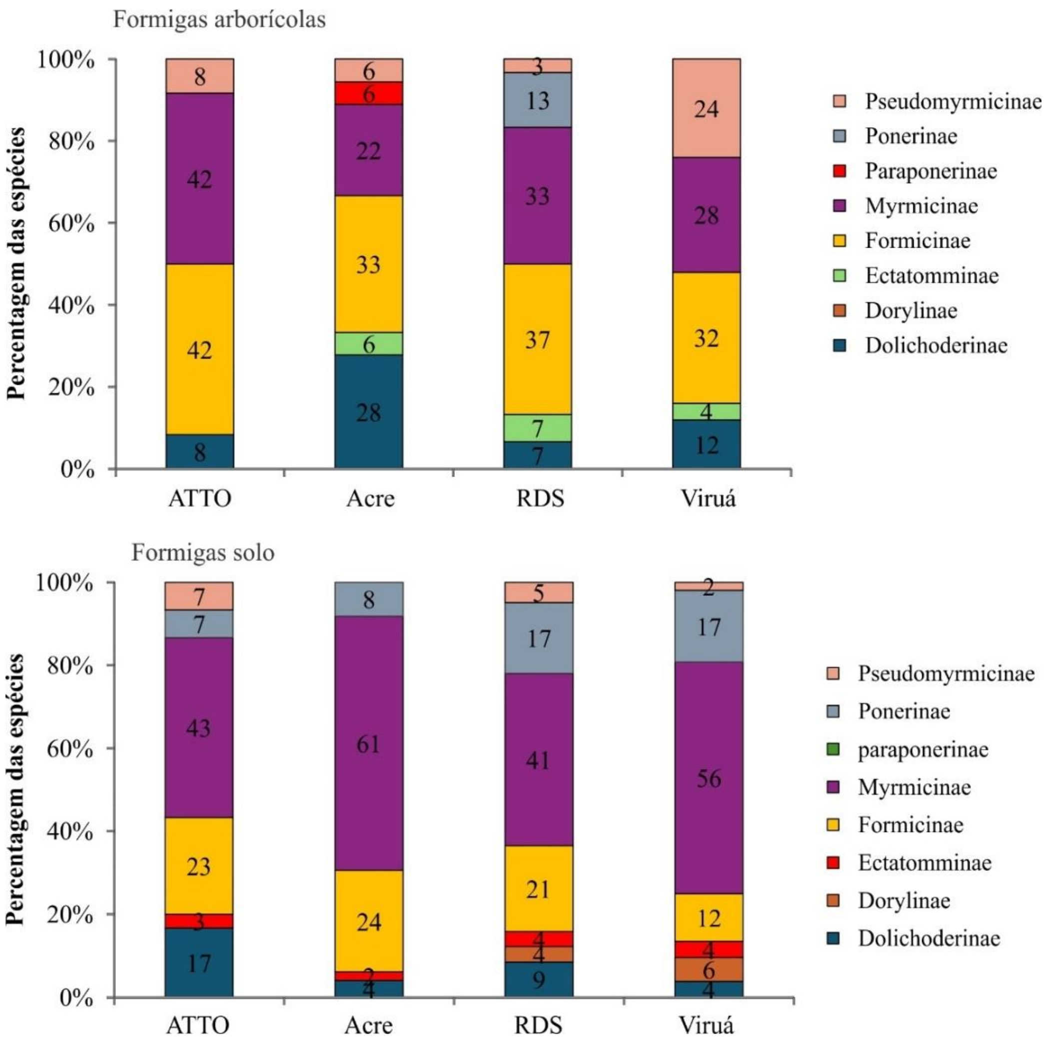

Figure S3. Number of occurrences of ant species subfamilies per transect. (a) Tree ants (b) Ground ants

Table S1: List of species with frequency of occurrence in WSE Campinas. First record for Roraima(*), Amazônia (**) and Brazil (***).

Taxa	Sítio WSE_ Campinas			
	Acre	ATTO (AM)	RDS do Rio negro (AM)	Parna do Viruá (RR)
DOLICHODERINAE	**18**	**11**	**29**	**22**
Azteca chartifex Forel, 1896	1			2
Azteca cf *ulei*			1	
Azteca sp. 1	9		7	
Brachymyrmex sp. 1		1		
Dolichoderus diversus Emery, 1894				17
Dolichoderus imitator Emery, 1894			13	3
Dolichoderus lutosus Smith, 1858	2			
Dolichoderus rugosus Smith, 1858	3*			
Dorymyrmex sp. 1		2	5	
Dorymyrmex sp. 2		3		
Dorymyrmex sp. 3		2	1	
Forelius sp. 1		3	1	
Linepithema angulatum Emery, 1894	3*			
Tapinoma sp. 1			1	
DORYLINAE			**11**	**7**
Eciton vagans Olivier, 1792			2	2*
Labidus coecus Latreille, 1802			8	4
Labidus praedator Smith, 1858)				1
Neivamyrmex sp. *1*			1	
ECTATOMMINAE	**4**	**11**	**41**	**43**
Ectatomma brunneum Smith, 1858	4	11	22	41
Ectatomma edentatum Roger, 1863			1	

Ectatomma tuberculatum Olivier, 1792			17	
Gnamptogenys fernandezi (Lattke, 1990			1	1
Holcoponera striatula Mayr, 1884				2*
FORMICINAE	**34**	**41**	**134**	**278**
Camponotus (Myrmaphaenus) cf *vagulus*	1			
Brachymyrmex sp. 1			5	
Brachymyrmex sp. 2			2	
Brachymyrmex sp. 3		2	1	
Camponotus (Tanaemyrmex) testaceus	2*		10	
Camponotus (Myrmaphaenus) blandus		4		
Camponotus (Myrmaphaenus) cf *vagulus*	2		3	
Camponotus (Myrmaphaenus) leydigi			2	1
Camponotus (Myrmaphaenus) sp. 1				1
Camponotus (Myrmaphaenus) sp. 2	3		11	10
Camponotus (Myrmaphaenus) sp. 8	1		2	
Camponotus (Myrmaphaenus) sp. 11		3	1	
Camponotus (Myrmobrachys) crassus Mayr, 1862	2	6	21	135
Camponotus (Myrmobrachys) senex Smith, 1858			2	
Camponotus (Myrmobrachys) sp. 26		1		
Camponotus (Myrmobrachys) sp. 18			4	
Camponotus (Myrmobrachys) sp. 24	2			
Camponotus (Myrmocladoecus) rectangularis Emery, 1890	3		9	
Camponotus (Myrmosphincta) sexguttatus Fabricius, 1793)				3*
Camponotus (Myrmothrix) atriceps Smith, 1858)		13	22	110
Camponotus (Tanaemyrmex) sp. 1	1	1	33	1
Camponotus chartifex Smith, 1860			1	

Camponotus rapax Fabricius, 1804	6			
Camponotus sericeiventris Wheeler, 1935		3		4
Camponotus sp. 24	1			
Gigantiops destructor Fabricius, 1804	1			
Nylanderia fulva (Mayr, 1862	1			7
Nylanderia sp. 1	2		2	
Nylanderia sp. 2			1	6
Nylanderia sp. 3			1	
Nylanderia sp. 5	5	8		
Nylanderia sp. 6	1			
Tranopelta gilva Mayr, 1866			1	
MYRMICINAE	**88**	**52**	**134**	**188**
Apterostigma urichii Forel, 1893	1*			
Atta sexdens Linnaeus, 1758			2	
Blepharidatta sp. 1	2			
Cephalotes atratus Linnaeus, 1758		1	11	
Cephalotes minutus Fabricius, 1804			1	4
Cephalotes opacus Santschi, 1920			1	
Cephalotes pallens Klug, 1824				3
Cephalotes pavonii Latreille, 1809				9
Cephalotes placidus Smith, 1860	5			
Cephalotes pusillus Klug, 1824		2		37
Cephalotes sp. 2				1
Crematogaster brasiliensis Kempf, 1972	4		3	
Crematogaster flavomicrops Longino, 2003	3*			
Crematogaster flavosensitiva Longino, 2003	4			

Crematogaster gr. *Limata* sp. 3	2			
Ccrematogaster longispina Emery, 1890	4		3	
Crematogaster nr. *flavosensitiva*				2
Crematogaster nr. *Acuta* sp. 5				18
Crematogaster sp. 4	1			
Crematogaster sp. 7	6			
Crematogaster sp. *8*	1			
Crematogaster sp. *9*				2
Crematogaster sp. *10*	1			
Crematogaster sp. *11*		1		
Crematogaster sp. *14*				1
Crematogaster sp. *18*	1			
Crematogaster tenuicula Forel, 1904			10	1
Crematogaster torosa Mayr, 1870			3	
Cyphomyrmex minutus Mayr, 1862			4	
Cyphomyrmex rimosus Spinola, 1851	2	1		1
Cyphomyrmex salvini Forel, 1899	1			
Cyphomyrmex sp. 9		4		
Megalomyrmex balzani Emery, 1894	2			
Megalomyrmex sp. 8		1		
Megalomyrmex wallacei Mann, 1916				5
Monomorium sp. 1			3	
Mycetomoellerius farinosus Emery, 1894	5			
Mycetophylax lectus Forel, 1911			2*	
Myrmicocrypta sp. 1			1	
Paratrachymyrmex bugnioni Forel, 1912	1		4	

Paratrachymyrmex diversus Mann, 1916	9*			
Paratrechina sp.1			1	
Pheidole cf. *exigua*			2	2
Pheidole diligens Smith, 1858				4*
Pheidole gertrudae Forel, 1886		1*		
Pheidole radoszkowskii Mayr, 1884	5	16		
Pheidole sp. 1			3	
Pheidole sp. 10	3		1	
Pheidole sp. 14			1	
Pheidole sp. 15				3
Pheidole sp. 16	1			
Pheidole sp. 2		1		3
Pheidole sp. 23			2	2
Pheidole sp. 27		4		3
Pheidole sp. 28		1		
Pheidole sp. 33			4	
Pheidole sp. 34				3
Pheidole sp. 36				1
Pheidole sp. 4			13	
pheidole sp. 43	1			
Pheidole sp. 44	3			
Pheidole sp. 45	1			
Pheidole sp. 49			1	
Pheidole sp. 5			6	
Pheidole sp. 6			4	
Pheidole sp. 7			3	

Pheidole sp. 8			1	
Pheidole vorax Fabricius, 1804	1		1	
Rogeria subarmata Kempf, 1961		3		1
Sericormyrmex sp. 2			2	
Solenopsis cf *saevissima*				24
Solenopsis globularia Smith, 1858		5		
Solenopsis sp. 1			15	19
Solenopsis sp. 2	1		4	8
Solenopsis sp. 3			1	1
Solenopsis sp. 5			1	1
Solenopsis sp. 7				1
Solenopsis sp. 8			1	1
Solenopsis sp. 9				11
Solenopsis substituta Santschi, 1925	10*		2	3
Solenopsis virulens Smith, 1858	6*			7
Strumigenys sp. 4			1	1
Tetramorium bicarinatum Nylander, 1846		1		
Wasmannia auropunctata Roger, 1863	1	10	12	5
Wasmannia rochai Forel, 1908			1	
Xenormyrmex sp. 1			3	
PARAPONERINAE	**4**			
Paraponera clavata Fabricius, 1775	4			
PONERINAE	**9**	**7**	**59**	**27**
Holcoponera striatula Mayr, 1884	2			6*
Hypoponera opaciceps Mayr, 1887				5*
Hypoponera sp. 1			2	

Hypoponera sp. 7			1	
Hypoponera trigona cauta Forel, 1912				1**
Mayaponera constricta Mayr, 1884	1		7	1
Neoponera apicalis Latreille, 1802			1	
Neoponera curvinodis Forel, 1899			1	
Neoponera globularia			21	
Neoponera villosa Fabricius, 1804			1	
Odontomachus bauri Emery, 1892			1	3
Odontomachus caelatus Brown, 1976			6	2
Odontomachus cf *bradleyi*			1	
Odontomachus cf *ruginodis*	1		1	
Odontomachus haematodus Linnaeus, 1758		2	3	5
Odontomachus hastatus Fabricius, 1804			1**/***	
Odontomachus ruginodis Wheeler, 1908				1
Odontomachus sp. 1			1	
Pachycondyla crassinoda Latreille, 1802	5	5	10	3
Pachycondyla impressa Roger, 1861			1	
PSEUDOMYRMICINAE	**1**	**5**	**11**	**31**
Pseudomyrmex boopis Roger, 1863			1	
Pseudomyrmex gracilis Fabricius, 1804				7*
Pseudomyrmex oculatus Smith, 1855			8	
Pseudomyrmex sp. 17	1	1		
Pseudomyrmex sp. 18		4		
Pseudomyrmex sp. 4			1	
Pseudomyrmex sp. 6				1
Pseudomyrmex sp. 9				2

Pseudomyrmex tenuis Fabricius, 1804	1	
Pseudomyrmex termitarius Smith, 1855		17
Pseudomyrmex unicolor Smith, 1855 *		1*
Pseudomyrmex venustus Smith, 1858 *		3*

CONSIDERAÇÕES FINAIS

Os resultados obtidos nesta tese reforçam a importância dos Ecossistemas de areia branca na Amazônia (WSE), destacando como este estudo ampliou o entendimento sobre a influência da estrutura da vegetação das WSE na diversidade de formigas em diferentes escalas. Em escala local, demonstrei como a complexidade da vegetação afeta a diversidade ao longo de um gradiente natural, revelando padrões marcantes de substituição de espécies. Em escala regional, ao comparar campinas e florestas de areia branca em diferentes regiões da Amazônia, evidenciei os efeitos combinados da estrutura do habitat e da biogeografia na diversidade taxonômica e funcional das formigas.

Este estudo também trouxe uma contribuição significativa para o conhecimento zoológico dos invertebrados na Amazônia, com foco nas formigas, ampliando o conhecimento sobre a distribuição geográfica desses organismos e revelando as espécies que sobrevivem e se adaptam às condições extremas dessa região complexa. Além disso, meu trabalho resultou em diversos novos registros para os estados do Acre, Roraima e Amazonas, destacando a importância de explorar áreas menos estudadas para entender melhor a rica biodiversidade da Amazônia.

Por fim, este estudo reforça o quanto ainda há para ser descrito e conhecido sobre a vasta biodiversidade da Amazônia, e como os padrões ecológicos observados influenciam a distribuição desses organismos em áreas singulares da bacia Amazônica. Este trabalho contribui para preencher lacunas de conhecimento sobre a distribuição geográfica das espécies e ressalta a necessidade urgente de preservar as interações ecológicas nesses habitats únicos e frágeis, que abrigam uma diversidade essencial e ameaçada, demandando esforços crescentes de conservação.

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Divulgação Científica

O primeiro capítulo da minha tese foi realizado na Reserva de Desenvolvimento Sustentável (RDS) do Rio Negro, onde investiguei a diversidade de formigas ao longo de um gradiente natural de campinas campinarana. Posteriormente, retornei à comunidade para compartilhar os resultados da pesquisa, promovendo a divulgação científica e desenvolvendo uma cartilha educativa intitulada "Conhecendo as Formigas que não Dão no Açúcar da RDS do Rio Negro". Essa cartilha tem o objetivo de apresentar as formigas da região, destacando a importância ecológica desses insetos no ecossistema local.

Como parte de um esforço contínuo para integrar a ciência e o ecoturismo, participei da Oficina de Condutores de Turismo Ecológico na RDS Rio Negro, um curso oferecido pelo edital Nº 007/2021 - BIODIVERSA/FAPEAM, com o título "Biodiversidade e Turismo na RDS Rio Negro". O curso aconteceu entre os dias 21 e 23 de abril de 2023 no ramal Vale Dourado, no km 50 da estrada de Novo Airão, com o objetivo de capacitar guias turísticos da região sobre a biodiversidade local, com enfoque na fauna, flora e fungos.

Durante o evento, ministrei uma palestra com o tema "Conhecendo as formigas que não dão no açúcar", abordando a ecologia das formigas e sua relevância para a manutenção da biodiversidade da RDS. Além disso, foram realizadas oficinas e atividades práticas, como trilhas que exploraram aspectos da fauna local, incluindo répteis, sapos e fungos, com a participação de crianças e adultos. Esse tipo de interação fortalece a conscientização ambiental e promove o envolvimento das comunidades locais na preservação dos recursos naturais.

A capacitação dos guias turísticos e o envolvimento das comunidades com a ciência contribuem diretamente para o ecoturismo sustentável na RDS, gerando benefícios econômicos e sociais, ao mesmo tempo em que promove a preservação da biodiversidade. A divulgação científica através de cartilhas e oficinas é essencial para fomentar o conhecimento e a conservação dos ecossistemas únicos da Amazônia.

A oficina contou com a participação de especialistas como o Dr. William Magnusson e a Dra. Kely Cruz, e foi organizada pelo Centro de Estudos Integrados da Biodiversidade Amazônica (CENBAM/INPA), destacando-se como um projeto fundamental para o fortalecimento da educação ambiental e do turismo ecológico na região.

Eciton burchellii

Amanda de Oliveira
Fabricio Baccaro

CONHECENDO AS FORMIGAS QUE NÃO DÃO NO AÇÚCAR

DA RESERVA DE DESENVOLVIMENTO SUSTENTAVÉL (RDS) RIO NEGRO

VOCÊ SABIA?

CONHECENDO AS FORMIGAS QUE NÃO DÃO NO AÇÚCAR

DA RESERVA DE DESENVOLVIMENTO SUSTENTAVÉL (RDS) RIO NEGRO

Existem mais de 13.000 espécies de formigas no mundo e mais de 1.700 espécies no Brasil.

As formigas representam entre 30 a 50% da biomassa animal terrestre de toda floresta amazônica.

Quem são elas?

As formigas são insetos encontrados em praticamente todos os ambientes terrestres, com exceção dos polos. São insetos muito comuns, e frequentemente encontrados dentro das nossas casas. Geralmente encontramos as formigas dentro do açucareiro, mas elas estão praticamente em qualquer lugar que tenha comida.

As formigas estão presentes em número considerável, mas é nas florestas tropicais que apresentam maior abundância, frequência e diversidade. Para se ter uma ideia, é estimado que as formigas, representam de 30 a 50% da biomassa animal terrestre de toda floresta amazônica. Nos trópicos como um todo, é impossível olhar para um metro quadrado de solo de floresta e não encontrar ao menos uma formiga.

Formigas da espécie *Tapinoma melanocephalum*, se esbaldando em um prato de doce. (foto: Baccaro et a. 2015)

As formigas que vemos andando por ai, representam entre 10 a 20% do total de formigas de um formigueiro!!

VOCÊ SABIA?

As formigas possuem três pares de pernas e todas elas são eussociais, ou seja, todas elas vivem em colônias (formigueiros).

Uma Rainha do gênero *Atta*. (foto: Alex Wild)

- As formigas são insetos sociais e apresentam uma clara divisão de tarefas necessárias à manutenção das colônias.
- Na época do acasalamento, a rainha realiza o chamado "voo nupcial", durante o qual se acasala com os machos, que costumam morrer pouco tempo depois.
- A comunicação entre as formigas é vital e se beneficia essencialmente dos feromônios. Mas as formigas também usam sons para se comunicar a curta distância.

Onde as formigas vivem?

Formigas do gênero *Eciton*, ou formigas de correição (foto: Alex Wild)

Os ninhos ou formigueiros podem ser estabelecidos desde o subsolo até as copas das árvores. Uma fração importante das formigas nidifica na superfície do solo, seja na serapilheira, cavidades naturais, gravetos e troncos caídos. Outras preferem ocos de troncos e gravetos de árvores. Existe ainda, espécies que constroem seus próprios ninhos, como algumas espécies de *Azteca*, também conhecidas como "tapibas".

Formigueiro de Tapibas (*Azteca*). (foto: Amanda Batista)

VOCÊ SABIA?

Uma única árvore em uma floresta tropical pode ter mais espécies que um país europeu de tamanho médio, como Portugal.

O que as formigas comem?

Apesar do hábito alimentar de boa parte das espécies ser desconhecido, acredita-se que a maior parte das espécies de formigas são onívoras. Isto é, a espécie se alimenta de diversos tipos de recursos. Esse fato é facilmente observado em nossas casas, onde a mesma espécie visita o açucareiro, o lixo e procura por restos de comida onde quer que seja.

Uma formiga do gênero *Pheidole*, se alimentando de néctar extrafloral. (Foto: Talitha Ferreira)

Formigas comendo formigas; várias operárias do gênero *Pheidole* dominaram e estão carregando um indivíduo bem maior de *Cephalotes atratus*. (foto: Phillip Klauvin))

As formigas chamadas de "cortadeiras“, são frequentemente vistas carregando pedaços de folhas. Na realidade, elas se alimentam de um fungo que criam no interior dos formigueiros. As folhas que elas cortam e carregam, às vezes por longas distâncias, servem como alimento para esses fungos.

Uma formiga do gênero *Paratrachymyrmex*, que também corta folhas que são utilizadas no cultivo de fungos. (foto: Alex Wild)

Importância ecológica!

As formigas são muito abundantes e desempenham papéis importantes nos ecossistemas. Elas podem agir como polinizadoras, dispersoras de sementes, atacam insetos herbívoros, servem de alimento para outros organismos e são sensíveis a mudanças ambientais.

As formigas fornecem um sistema de estudo ideal para examinar diferentes níveis de tolerância às variações ambientais, respondendo de forma rápida às mudanças que acontecem no ecossistema.

Conhecendo as formigas do Ramal do Uga-Uga- RDS do Rio Negro

A Reserva de Desenvolvimento Sustentável (RDS) Rio Negro é uma Unidade de Conservação (UC) que abrange os municípios de Manacapuru, Iranduba e Novo Airão. Encontra-se em meio a um mosaico de unidades de conservação de diferentes categorias, formando um gradiente vegetacional natural de campina e campinarana conhecido como Ecossistemas de Areia Branca (figura A e B). Essas áreas ficam próximas com ambiente de terra-firme, formando uma cobertura vegetal diferente e com alta importância para a conservação da fauna e flora. As informações e registros das espécies de formigas da RDS foram realizadas em 2019 no módulo do Programa de Pesquisas em Biodiversidade (PPBio) situado no Ramal do Uga-Uga (figura C).

Figura A: campina e **B**: Campinarana. (foto: Amanda Batista)

Figura C: Estudante de doutorado Amanda Batista (esquerda) e o morador da comunidade Jânio Junior (direita) coletando formigas nas áreas de campinaranas. (foto: Amanda Batista)

Existem vários métodos de coletas de formigas como por exemplo: coleta direta, iscas, pitfalls... Na RDS todas as formigas foram coletadas por armadilhas de queda do tipo "pitfall".

VOCÊ SABIA?

Quando é descoberta uma nova espécie, os cientistas escolhem um nome científico único.

Formigas do Ramal Uga-Uga

Já foram coletadas no módulo de pesquisas do PPBio no ramal Uga-Uga, 200 espécies de formigas pertencentes a 54 gêneros. Abaixo apresentamos os principais gêneros e espécies encontrados na RDS.

DOLICHODERINAE

Azteca


Azteca constructor

As operárias facilmente reconhecidas em campo pela agressividade com que defendem seu território e pelo odor característico que liberam quando pressionadas entre os dedos. São arborícolas, construindo seus ninhos na copa das árvores e em cavidades na madeira viva ou morta. Algumas espécies são conhecidas como “Tapibas”.

VOCÊ SABIA?

Algumas espécies de Azteca têm uma relação mutualista com a árvore embaúba (Cecropia).

DOLICHODERINAE

Dolichoderus

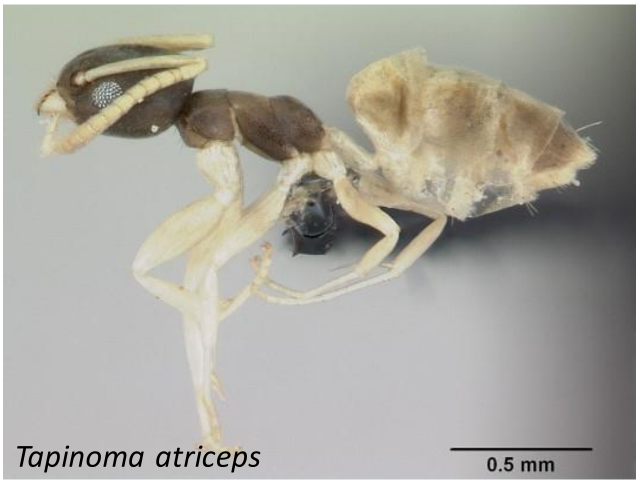
Dolichoderus bispinosus

São formigas muito ativas durante o dia. São arborícolas, mas a espécie Dolichoderus bispinosus (coletada no ramal Uga-Uga) pode construir seus ninhos no solo. São comuns em florestas tropicais, e também liberam odor característico quando pressionadas.

Referência: BACCARO, Fabricio B. et al. Guia para os gêneros de formigas do Brasil. **Manaus: Editora INPA**, v. 388, 2015.

DOLICHODERINAE

Tapinoma



Tapinoma atriceps

As espécies de *Tapinoma* utilizam uma grande variedade de locais de nidificação, por exemplo solo, com ou sem cobertura vegetal, em árvores e em troncos em decomposição.

VOCÊ SABIA?

As espécies de *Tapinoma* são abundantes em áreas urbanas.

DORYLINAE

ECITON

Eciton burchellii

Popularmente chamadas de "formigas de correição" ou "formigas legionárias" por estarem boa parte do tempo em movimento e não construírem ninhos fixos. As operárias maiores podem ter mandíbulas enormes em forma de gancho. Elas são caracterizadas por ninhos enormes, hábito nômade, e são predadoras vorazes.

VOCÊ SABIA?

Existe até uma família de aves nas Américas do Sul e Central especializada em seguir correições aproveitando os insetos e outros pequenos animais que tentam escapar do ataque das formigas.

Referência: BACCARO, Fabricio B. et al. Guia para os gêneros de formigas do Brasil. **Manaus: Editora INPA**, v. 388, 2015.

DORYLINAE

Labidus

Labidus praedator

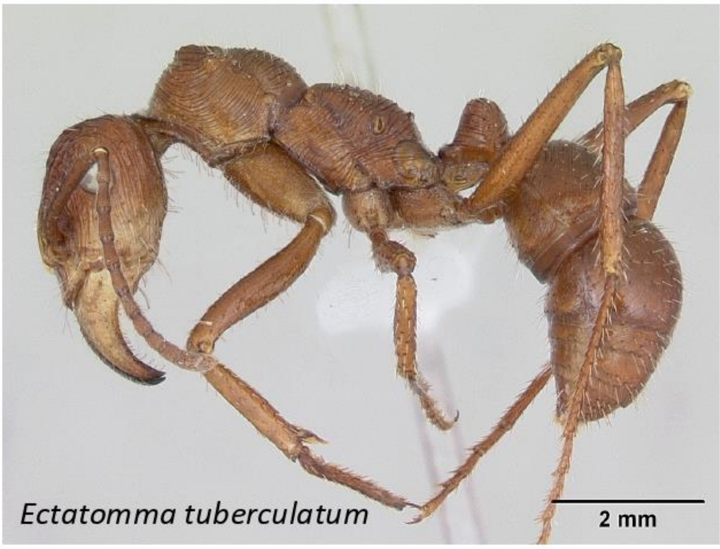
Labidus são frequentemente as formigas de correição mais comuns e formam colônias com milhares de indivíduos, vivem em ambientes florestados e nidificam principalmente no subsolo.

VOCÊ SABIA?

Durante a busca por alimentos na superfície as colônias formam uma massa fervilhante de indivíduos que predam pequenos artrópodes e recolhem diversos tipos de alimentos (como sementes e frutas).

ECTATOMMINAE

ECTATOMMA



Ectatomma tuberculatum

A maioria dessas espécies é relativamente comum em diversos habitats (floresta úmida, floresta seca e savana).

VOCÊ SABIA?

Ectatomma tuberculatum faz ninhos na base das árvores, mas forrageia na vegetação.

Referência: BACCARO, Fabricio B. et al. Guia para os gêneros de formigas do Brasil. **Manaus: Editora INPA**, v. 388, 2015.

FORMICINAE

CAMPONOTUS

Camponotus atriceps

Camponotus é um gênero dominante e fácil de ser notado. É conhecido também como formigas carpinteiras, porque muitas espécies constroem seus formigueiros em madeira.

VOCÊ SABIA?

Algumas espécies desse gêneros gostam de estabelecer ninhos em aparelhos eletrônicos! Outras fazem ninhos em batentes das portas ou outras estruturas de madeira comuns.

Camponotus crassus

MYRMICINAE

ATTA

Atta laevigata

Atta é um gênero de formiga "cortadeira", conhecidas como saúvas. Usam folhas e outras partes vegetais para cultivar o fungo que serve de alimento para a colônia.

VOCÊ SABIA?

Que uma rainha de Atta pode viver por até 30 anos produzindo mais de 200 ovos por dia.

Referência: BACCARO, Fabricio B. et al. Guia para os gêneros de formigas do Brasil. **Manaus: Editora INPA**, v. 388, 2015.

MYRMICINAE

CEPHALOTES

Cephalotes atratus

Cephalotes é um gênero conhecido como formigas-tartaruga. Recebem esse nome porque tem o exoesqueleto (casca) bem duro. São exclusivamente arborícolas.

VOCÊ SABIA?

Em algumas espécies de *Cephalotes*, as operárias maiores usam a cabeça para bloquear a entrada do ninho.

MYRMICINAE

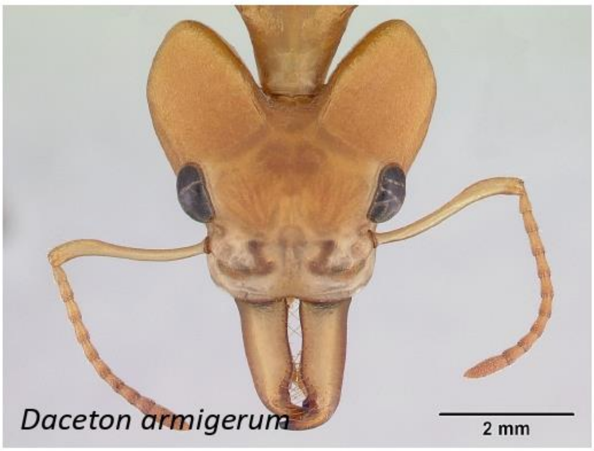
DACETON

Daceton nidificam em cavidades de troncos construídas por outros insetos e as colônias podem conter até 2.500 indivíduos. Forrageiam em árvores, mas eventualmente podem descer para a serapilheira.

Daceton armigerum

VOCÊ SABIA?

Daceton estão entre as poucas espécies de formigas que conseguem virar a cabeça para cima.



Daceton armigerum

Referência: BACCARO, Fabricio B. et al. Guia para os gêneros de formigas do Brasil. **Manaus: Editora INPA**, v. 388, 2015.

MYRMICINAE

CREMATOGASTER

Crematogaster tenuicula

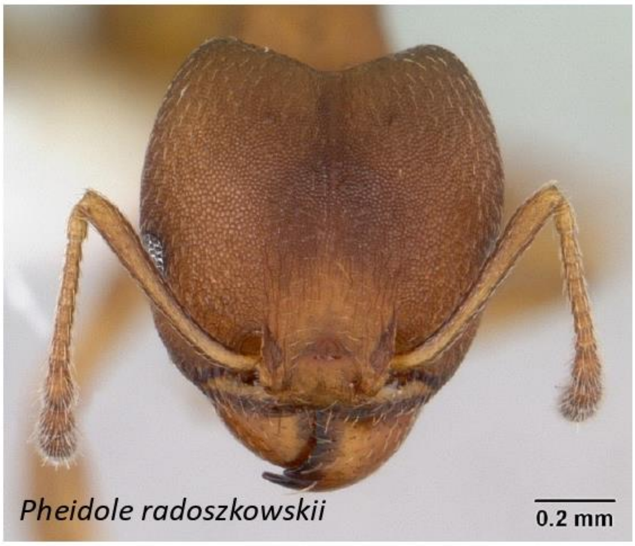
Crematogaster, tem o gáster (abdome) em forma de coração. Espécies desse gênero são encontradas em qualquer lugar, desde florestas até áreas urbanas.

VOCÊ SABIA?

Crematogaster, gosta de visitar estruturas nas plantas que liberam néctar e consome excretas açucarados produzidos por cigarrinhas.

MYRMICINAE

PHEIDOLE



Pheidole radoszkowskii

Pheidole, conhecida como formiga “cabeçuda”. É um gênero hiperdiverso, com mais de 2000 espécies descritas podendo ser encontradas nos mais diversos ambientes.

Pheidole radoszkowskii

VOCÊ SABIA?

Algumas espécies de *Pheidole*, possui uma grande importância ecológica na dispersão de sementes e controle das populações de outros artrópodes.

Referência: BACCARO, Fabricio B. et al. Guia para os gêneros de formigas do Brasil. **Manaus: Editora INPA**, v. 388, 2015.

MYRMICINAE

SOLENOPSIS


Solenopsis saevissima

Solenopsis é um gênero conhecido popularmente como como ”formigas de fogo” e “lava-pés” por possuir uma ferroada dolorosa. São consideradas pragas em cidades.

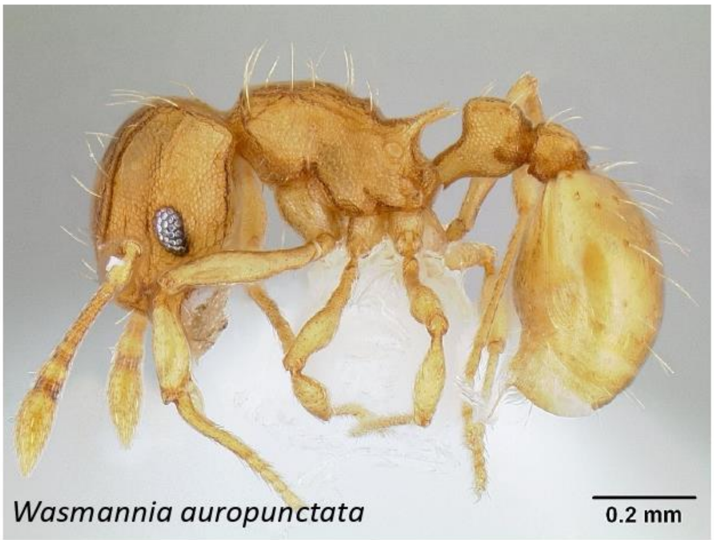

Solenopsis saevissima

VOCÊ SABIA?

Algumas espécies de *Solenopsis*, são consideradas vetores de bactérias em hospitais, podendo constituir problema de saúde publica.

MYRMICINAE

WASMANNIA


Wasmannia auropunctata

Wasmannia, também conhecida como “jiquitaia” na região, é famosa pela ferroada doida. Fora do Brasil, ela é conhecida como “pequena formiga de fogo”

VOCÊ SABIA?

A espécie *Wasmannia auropunctata*, é uma espécie invasora que causa danos severos aos ecossistemas não nativos.

Referência: BACCARO, Fabricio B. et al. Guia para os gêneros de formigas do Brasil. **Manaus: Editora INPA**, v. 388, 2015.

PARAPONERINAE

PARAPONERA

Paraponera clavata

A *Paraponera clavata* é única espécie da subfamilia, conhecida popularmente por “Tucandeira”. Constroem seus ninhos na base de árvores, mas forrageiam na vegetação.

VOCÊ SABIA?

As tucandeiras são conhecidas por produzir ferroadas extremamente dolorosas, com sintomas que podem durar até 24 horas. Essa espécie é usada em rituais indígenas presas a luvas.

PONERINAE

PACHYCONDYLA

Pachycondyla harpax

As *Pachycondylas conhecida por formiga-de-ferrão e geralmente são grandes e negras,* algumas espécies buscam alimentos no chão da floresta.

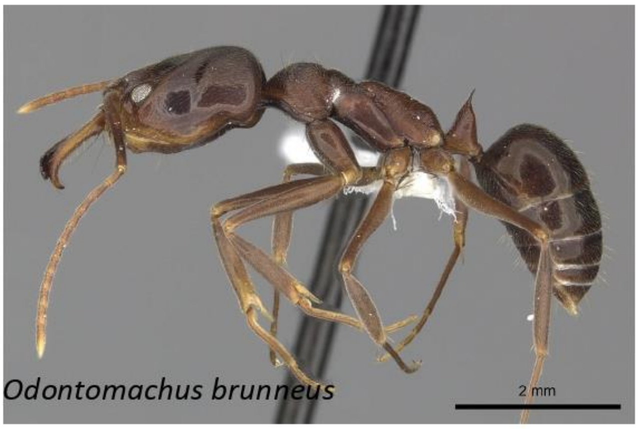
VOCÊ SABIA?

Possuem hábito de procurar alimentos solitário ou em dupla.

Referência: BACCARO, Fabricio B. et al. Guia para os gêneros de formigas do Brasil. **Manaus: Editora INPA**, v. 388, 2015.

PARAPONERINAE

ODONTOMACHUS


Odontomachus brunneus

São conhecidas como formigas estalo, pelo som que a batida de suas mandíbulas faz quando são importunadas.

VOCÊ SABIA?

Ao caçar, mantêm suas mandíbulas altamente modificadas abertas a 180° e as fecham com extrema força e velocidade.

PSEUDOMYRMECINAE

PSEUDOMYRMECINAE

A maioria das espécies desse gênero possui hábito arborícola que vivem em galhos e buscam seus alimentos predominantemente na vegetação.

VOCÊ SABIA?

Essas formigas são conhecidas na região como "tachi", por sua ferroada doída.

Referência: BACCARO, Fabricio B. et al. Guia para os gêneros de formigas do Brasil. **Manaus: Editora INPA**, v. 388, 2015.
ANTWEB. Disponível em: <http://www.antweb.org>. Acessado em: 07 abr. 2022.
ANTWIKI. Disponível em: <http://www.antwiki.org/wiki/Welcome_to_AntWiki>. Acessado em: 07 abr. 2022

Ficha de observação em campo

Participante: ______________________________________

1. Local das Trilhas: Marque um (x) no tipo de ambiente na RDS.

( ) Terra firme ( ) Campinarana ( ) Campina

2. Qual formiga observei na trilha?

a) Local: Solo ( )

( ) grande: nº de formigas ______________________

( ) pequena: nº de formigas______________________

b) Local: plantas ( )

( ) grande: nº de formigas ______________________

( ) pequena: nº de formigas______________________

3. Você saberia dizer o nome de algumas formigas que você observou?

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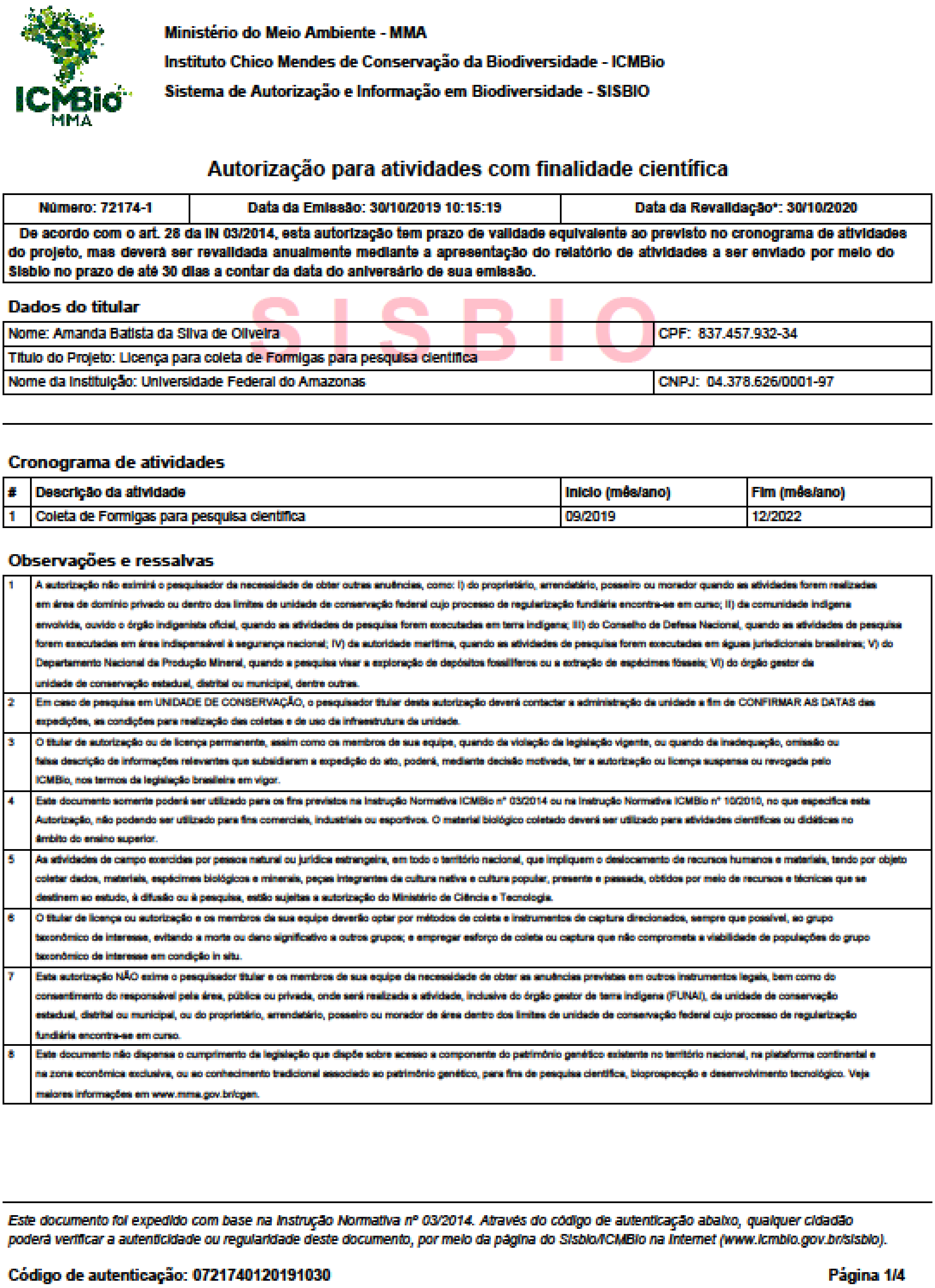
Anexo



Ministério do Meio Ambiente - MMA
Instituto Chico Mendes de Conservação da Biodiversidade - ICMBio
Sistema de Autorização e Informação em Biodiversidade - SISBIO

Autorização para atividades com finalidade científica

Número: 72174-1	Data da Emissão: 30/10/2019 10:15:19	Data da Revalidação*: 30/10/2020

De acordo com o art. 28 da IN 03/2014, esta autorização tem prazo de validade equivalente ao previsto no cronograma de atividades do projeto, mas deverá ser revalidada anualmente mediante a apresentação do relatório de atividades a ser enviado por meio do Sisbio no prazo de até 30 dias a contar da data do aniversário de sua emissão.

Dados do titular

Nome: Amanda Batista da Silva de Oliveira	CPF: 837.457.932-34
Título do Projeto: Licença para coleta de Formigas para pesquisa científica	
Nome da Instituição: Universidade Federal do Amazonas	CNPJ: 04.378.626/0001-97

Cronograma de atividades

#	Descrição da atividade	Início (mês/ano)	Fim (mês/ano)
1	Coleta de Formigas para pesquisa científica	09/2019	12/2022

Observações e ressalvas

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