



# 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 °C, 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

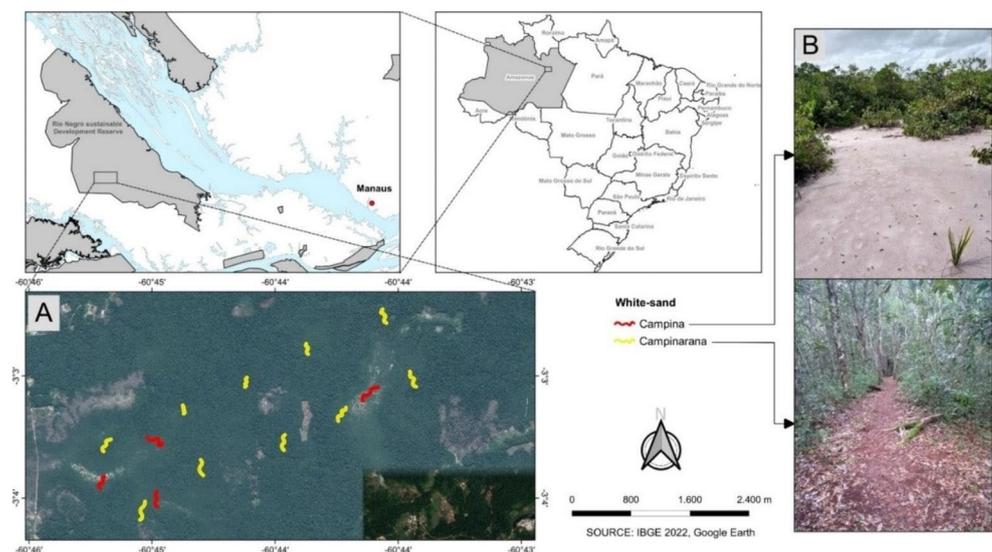
et al. 2004). Vegetation measurements using LiDAR were obtained while the researchers walked at constant speed on the 250 m centerline in each sampling plot. The five target variables were calculated using standard R scripts (R Core Team 2022).

### 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

**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 and Schmera 2011), and the results were displayed with graphs prepared with SYN-TAX 2000 package (Podani 2001).

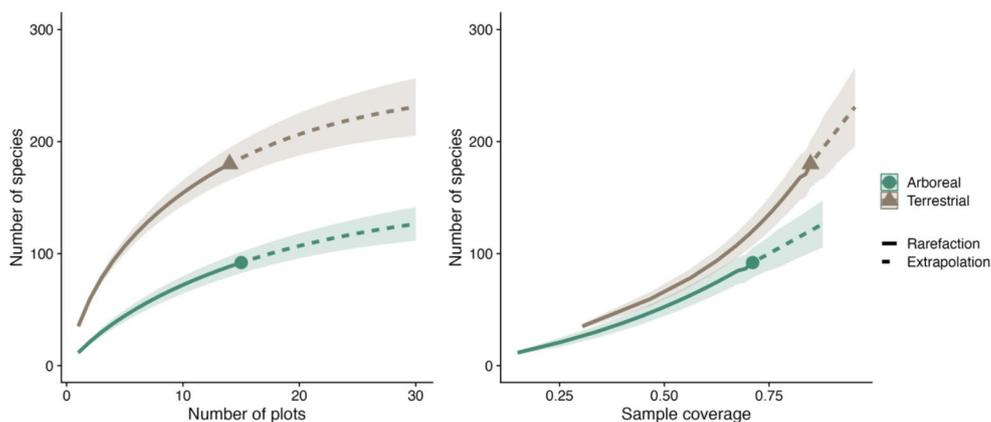
We also used generalized linear models (GLM) to investigate the relationships between the richness and the relative abundance of habitat generalist species along the vegetation-structure gradient (PC1). All analyses, except the beta-diversity partitioning, were done in the R language (version 4.2.1;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

## Results

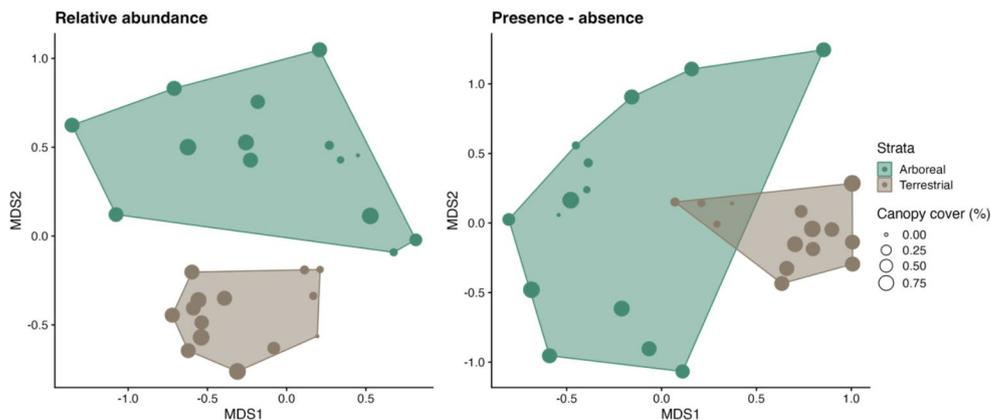
### Vegetation structure

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

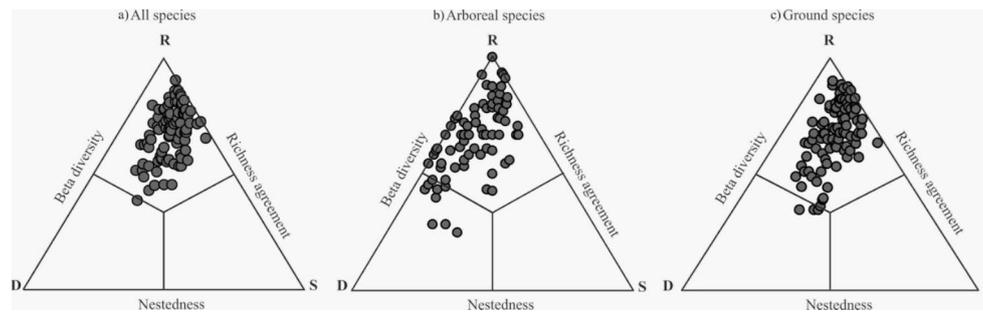
that ant species richness was higher in the ground stratum than the arboreal stratum (Fig. 2). However, the sampling coverage of the arboreal stratum was lower (0.71) than the sampling coverage in the terrestrial pitfalls (0.85), even using samples with standardized collection effort by strata.

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

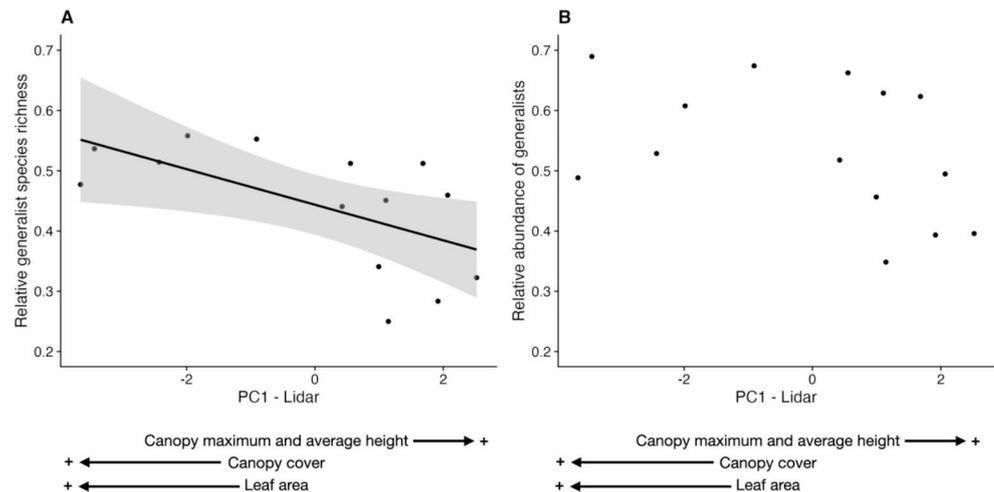
Ant species richness was not associated with variations in vegetation structure summarized by the first PCA component



**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.

**Supplementary Information** The online version contains supplementary material available at <https://doi.org/10.1007/s10841-023-00517-4>.

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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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