Original Article

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* tended to be lower than in white-sand forests. In contrast, alpha diversity of ground-dwelling ants was similar in both habitats of the studied regions. The species composition of arboreal ants of white-sand *campinas* and white-sand forests was highly 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, whereas ground-dwelling ants are more influenced by regional conditions, underscoring the complex interplay of ecological and historical factors in these habitats.

Keywords: 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, because 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 many 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, such as 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 (WSEs), 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 flooded seasonally (Adeney *et al.* 2016). Locally, WSE consists of heterogeneous and distinctive habitats distributed along gradients from

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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 biogeographical 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, Capurucho *et al.* 2023, De Oliveira *et al.* 2023).

Despite being considered 'species-poor' habitats, WSEs make 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 1000 species have been catalogued on antmaps.org/? (Janicki et al. 2016, GABI: Guénard et al. 2017, Andrade-Silva et al. 2022). This diversity is a crude underestimate, because several areas and habitats of the region remain poorly sampled (Andrade-Silva et al. 2022, Schmidt et al. 2022), including WSEs (Andrade-Silva et al. 2022, Carvalho et al. 2023). The high diversity of ants in the Amazon is partly linked to microhabitat stratification (Klimes et al. 2015), which influences the distribution of ants. The forest understorey and canopy layers provide more reliable resources for nesting and feeding in comparison to the 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 (Davidson and Patrell-Kim 1996, Vasconcelos and Vilhena 2006, Klimes et al 2015, da Silva de Oliveira and Schmidt 2019).

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 functional traits of ants might help in understanding 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 WSEs. 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, can contract or expand depending on habitat complexity and resource availability, reflecting the selective pressures imposed by local conditions (Mouchet et al. 2010). For example, traits related to mobility, such as femur length, or to resource acquisition, such as mandible size, might be filtered in

structurally complex habitats, such as forests, where competition and niche differentiation are intensified (Guillherme *et al.* 2019). Conversely, in simpler environments, such as open *campinas*, functional space might narrow, favouring traits that optimize survival in exposed conditions, such as enhanced vision for predator detection (Weiser and Kaspari 2006).

Here, we compare 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 kilometres of continuous habitat, whereas in the other, the WSE is composed of small and isolated patches. We expect that the contrasting habitat structure and landscape configuration will influence the taxonomic and functional structure of ant assemblages and propose the following predictions: (i) ant alpha diversity will be higher in white-sand forest owing to its more complex vegetation structure in comparison to open white-sand vegetation in both studied regions; (ii) ant alpha diversity will be greater in regions with large, continuous habitats in comparison 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 in comparison 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 WSEs is 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 m) growing in sand soils as white-sand forest (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 (latitude -3.003, longitude -60.693) and Parque Nacional do Viruá (hereafter, Parna Viruá), situated at Roraima state (latitude 1.282, longitude –61.111). The WSE in the RDS Rio Negro is found as patches of low- to high-canopy forests with open understorey (WSF) or as small patches (18-29 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 WSCs in RDS Rio Negro are often restricted to areas of shallow water table that can be flooded temporarily after heavy rains. In sharp contrast, WSE with its different physiognomies occupies $\sim 1 \times 10^6$ ha of the Parna Viruá (ICMBio 2014). Approximately 255 000 ha are represented by open/shrubby *campina* (WSC), and the several physiognomies of WSFs cover >700 000 ha in



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 an 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. E, white-sand forest 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.

Parna Viruá (ICMBio 2014). The WSCs in Parna Viruá are also restricted to areas with the shallowest water table in the land-scape, 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 June 2019 (4 in WSC and 10 in WSF) and 12 plots in Parna Viruá in February 2022 (6 in WSC and 6 in WSF) following the RAPELD sampling design (Magnusson *et al.* 2013). The plots were 250 m long and distributed regularly at every 1 km in the landscape. Each plot contained 10 sampling stations with four pitfall traps (two on the ground and two in the vegetation) spaced at 25 m intervals, totalling 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 h. Collected ants were preserved in 70% alcohol. Our sampling effort resulted in 1040 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 has been updated constantly (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



Figure 2. Study sites: white-sand *campinas* (yellow diamonds) and white-sand forests (red diamonds) from Viruá National Park in RDS Rio Negro.

type specimens, and IMAGEJ software was used for image-based analysis when direct examination of specimens 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). From 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):

- (i) Eye length (EL) and distance from the eye to the mandible insertion (DEM): eye size is related to food-seeking behaviour 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).
- (ii) 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).
- (iii) 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).
- (iv) Mandible length (ML): larger mandibles enable access to prey of different shapes and sizes, and 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 0 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 owing to the relatively long distance between sampling stations (Baccaro and Ferraz 2013). Preliminary analysis indicated that the assemblage patterns were similar using only nominal species or using all species (nominal species and morphospecies); hence, we opted to include all sampled ants in the analysis. Ant species were classified as grounddwelling or arboreal specialists when recorded in only one of these strata or as habitat generalists if collected in both grounddwelling 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 analysis and PERMANOVA were run in the VEGAN package (Oksanen *et al.* 2023). 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 in two complementary ways. In both cases, we used only the nominal species, given that we did not have morphological information for morphospecies. First, community weight means (CWMs) 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, which measures the average distance of species from the centroid of the functional space; functional evenness, which assesses how evenly species fill the functional space; and functional divergence, 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 (Supporting Information, Table S1), distributed across 57 genera and nine subfamilies, with 146 species (53% of the total) nominally identified (Supporting Information, Table S2). The most species-rich subfamily (see species-rich habitats in the RDS Rio Negro and Parna Viruá regions; Supporting Information, Table S2) was the Myrmicinae (150 species), followed by the Ponerinae (42 species) and Formicinae (36 species). We sampled 130 ant species in WSC and 236 in WSF, with 40 species recorded exclusively 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 (Supporting Information, Table S1).

Species richness of arboreal ants in WSF was similar in both studied regions, as was also observed in WSC (Fig. 3A). Species richness of arboreal ants in WSC tended to be lower than in WSF,

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

Ground-dwelling specialists (i.e. collected only in this stratum) were proportionally more diverse in WSF than in WSC in both studied regions (two-way ANOVA, P = .03 for habitat effect) and more varied in both habitats in RDS Rio Negro compared with Parna Viruá (two-way ANOVA, P = .03 for site effect; Fig. 4A). Ant diversity in WSC and WSF was similar among the arboreal specialists (two-way ANOVA, P = .89 for habitat effect; Fig. 4B). However, WSC and WSF of Parna Viruá had proportionally more arboreal species than RDS Rio Negro (two-way ANOVA, P = .0012 for site effect). Diversity of generalist species (i.e. recorded in both sampling strata) was higher in WSC than WSF in both regions (Fig. 4C), especially in RDS Rio Negro (two-way ANOVA, P = .008 for site effect and P = .01 for habitat effect).

Ant assemblage beta diversity and indicator species

The species composition of arboreal ants of WSC was highly distinct between study regions, as in WSF (Fig. 5A). However, we did not find differences in WSC and WSF species composition within each region (PERMANOVA, P = .87 for habitat effect and P = .001 for site effect). In contrast, we found strong effects of habitats and site location (PERMANOVA, P = .001 for habitat effect and P = .001 for site effect) in the species composition of ground-dwelling ants (Fig. 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 harboured 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. The distance from the eye to the mandible insertion tended to be higher in arboreal ants in the WSC of Parna Viruá compared with the same habitat in RDS Rio Negro (P = .02). However, no differences between habitats were detected in this trait (Fig. 6A). Arboreal ants in WSF tended to have longer femurs (P = .001) than ants in WSC in both regions (Fig. 6C). Likewise, arboreal ants in WSF tended to have a longer mandible than WSC ants (P = .06; Fig. 6E). A habitat effect was observed among the ground-dwelling ants (P = .001), with the distance from the eye to the mandible being longer in WSC than in WSF in both regions (Fig. 6F). Also, the eye of ground-dwelling ants was longer in WSC than in WSF (P = .004) in RDS Rio Negro and Parna Viruá (Fig. 6G).



Figure 3. Sample-based rarefaction and extrapolation curves using the Hill number separated by arboreal ant species (A–C) and ground-dwelling ants (D–F): species richness or q = 1 (A and D), Shannon indices or q = 2 (B and E), and Simpson indices or q = 3 (D and F).



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

Among the arboreal ants, functional dispersion was higher in WSF than in WSC (Fig. 7A), especially in RDS Rio Negro (two-way ANOVA, P = .03 for habitat effect and P = .05 for site). Functional divergence in arboreal ants was also more accentuated in WSF than WSC (P = .03 for habitat effect) in both study regions (Fig. 7B). Functional evenness in arboreal ants was higher in RDS Rio Negro compared with Parna Viruá (P = .02 for site effect) in both sampled habitats (Fig. 7C). Among ground-dwelling ants, the functional dispersion (P = .009) and regularity (P = .002) were much lower in Parna Viruá than in RDS Rio Negro in both WSF and WSC (Fig. 7D, F).



Figure 5. Ordinations of sampling sites based on Jaccard indices of arboreal (A) and ground-dwelling (B) ants represented on two axes of nonmetric multidimensional scales (MDS).



Figure 6. Box plots of community weighted means (CWMs) of ant assemblages sampled in white-sand *campina* (WSC) and white-sand forest (WSF) calculated with data of five morphological traits.

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 geographical 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 in WSC, in agreement with the habitat heterogeneity hypothesis, which 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). 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 geographical location. This



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

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 gain a better understanding of these habitats, which remain underexplored despite their ecological significance, and to protect them.

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 to 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 (Gibb and Parr 2013, Parr *et al.* 2017). For instance, this approach could clarify whether species within similar functional roles exhibit redundancy or whether 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 is apparently associated with landscape dynamics. In addition to extremely low fertility, soils in WSEs are frequently inundated by groundwater (Damasco *et al.* 2013, Mendonça *et al.* 2014, Adeney *et al.* 2016). The extent and duration of the flooding regime in WSEs are highly variable and depend on the local relief (Damasco *et al.* 2013). For example, some spots in WSEs 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 are likely to 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 its large and continuous expanses of WSE, which would be consistent with the species-area relationship and habitat availability 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 with Parna Viruá, which is precisely the opposite of the expected pattern. In contrast, arboreal ants of WSF and WSC were more diversified in Parna Viruá. We hypothesized that the intensity and duration of flooding could also explain the relatively low diversity of grounddwelling 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 might explain the higher proportional diversity of arboreal specialists observed in WSC and WSF at the Parna Viruá compared with 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 with 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. Although the relative proportion of ground-dwelling species was higher in the RDS Rio Negro in both habitats, the proportion of arboreal species was 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 might 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 in comparison to geographical location. Arboreal ant similarity among habitats was 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 importance of site location 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 (Ribas *et al.* 2003, Vasconcelos *et al.* 2004, De Oliveira *et al.* 2023).

The landscape of each study region is strongly contrasting in terms of habitat availability, and this configuration is likely to be 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 tectonic 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 might 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 longer in WSF than in WSC, suggesting the more structurally complex habitat filter traits associated with mobility. Likewise, 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 with WSF. Bigger and more separated eyes might reflect adaptations to a more exposed environment, where vision plays a crucial role in detecting prey and predators.

Arboreal ants in WSF exhibited greater functional dispersion than in WSC, possibly owing 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 with RDS Rio Negro, indicating that regional factors also have a more important role in functional diversity than habitat structure. Thus, the functional diversity of ground-dwelling ants is more sensitive to regional conditions, whereas that of arboreal ants is more related to habitat complexity. Our results demonstrate that the origins of each habitat in distinct biogeographical regions affects not only the taxonomic but also the functional diversity response of ants to variability in habitat structure.

CONCLUSION

Ant diversity is shaped significantly 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 WSEs. 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 conservation strategies to reduce habitat disturbance in white-sand ecosystems (WSEs). 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 crucial for advancing our understanding of how habitat complexity and biogeographical history interact to shape the structure and function of tropical biodiversity.

SUPPLEMENTARY DATA

Supplementary data is available at *Biological Journal of the Linnean Society* online.

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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.

APPENDIX 1.LIST OF ANT SPECIES SIGNIFI-CANTLY ASSOCIATED WITH A PARTICULAR HABITAT IN THE TWO STUDY REGIONS.

Indicator Value (IndVal) varies from zero to one, and *P*-values were obtained with 999 permutations. Abbreviations: RDS Rio Negro, Reserva de Desenvolvimento Sustentável do Rio Negro; WSC, white-sand *campina*; WSF, white-sand forests.

Taxon	Indicator of	IndVal	P-value
Dolichoderus imitator	WSC RDS Rio Negro	0.842	.001
Pseudomyrmex oculatus	WSC RDS Rio Negro	0.791	.001
Ectatomma tuberculatum	WSC RDS Rio Negro	0.753	.001
Camponotus (Tanaemyrmex) sp. 1	WSC RDS Rio Negro	0.748	.001
Camponotus (Tanaemyrmex) testaceus	WSC RDS Rio Negro	0.688	.002
Pheidole sp.4	WSC RDS Rio Negro	0.658	.005
Wasmannia auropunctata	WSC RDS Rio Negro	0.658	.006
Camponotus (Myrmaphaenus) cf. vagulus	WSC RDS Rio Negro	0.612	.004
Pheidole sp. 33	WSC RDS Rio Negro	0.612	.002
Neoponera globularia	WSC RDS Rio Negro	0.607	.002
Brachymyrmex sp. 1	WSC RDS Rio Negro	0.589	.004
Camponotus (Myrmocladoecus) rectangularis	WSC RDS Rio Negro	0.587	.005
Cephalotes atratus	WSC RDS Rio Negro	0.581	.01
Crematogaster torosa	WSC RDS Rio Negro	0.5	.023
Camponotus (Myrmobrachys) senex	WSC RDS Rio Negro	0.5	.03
Dorymyrmex sp. 1	WSC RDS Rio Negro	0.481	.03
Camponotus (Myrmobrachys) sp. 18	WSC RDS Rio Negro	0.463	.035
Brachymyrmex sp. 2	WSC RDS Rio Negro	0.456	.044
Camponotus (Myrmaphaenus) sp. 8	WSC RDS Rio Negro	0.456	.047
Paratrachymyrmex diversus	WSF RDS Rio Negro	0.734	.001
Pheidole sp. 1	WSF RDS Rio Negro	0.665	.002
Camponotus (Myrmaphaenus) sp. 1	WSF RDS Rio Negro	0.645	.004
Blepharidatta brasiliensis	WSF RDS Rio Negro	0.632	.003

Taxon	Indicator of	IndVal	P-value
Crematogaster sotobosque	WSF RDS Rio Negro	0.548	.008
Gnamptogenys horni	WSF RDS Rio Negro	0.544	.033
Camponotus (Myrmobrachys) crassus	WSC Parna Viruá	0.833	.001
Cephalotes pusillus	WSC Parna Viruá	0.831	.001
Camponotus (Myrmothrix) atriceps	WSC Parna Viruá	0.671	.006
Pseudomyrmex termitarius	WSC Parna Viruá	0.645	.002
Crematogaster nr. acuta	WSC Parna Viruá	0.626	.007
Dolichoderus diversus	WSC Parna Viruá	0.611	.007
Ectatomma brunneum	WSC Parna Viruá	0.605	.015
Solenopsis cf. saevissima	WSC Parna Viruá	0.587	.013
Pseudomyrmex venustus	WSC Parna Viruá	0.5	.025
Cephalotes pavonii	WSC Parna Viruá	0.474	.034
Pseudomyrmex gracilis	WSC Parna Viruá	0.468	.039
Camponotus rapax	WSF Parna Viruá	0.788	.001
Azteca sp. 1	WSF Parna Viruá	0.744	.001
Azteca chartifex	WSF Parna Viruá	0.732	.001
Pheidole diligens	WSF Parna Viruá	0.687	.001
Labidus praedator	WSF Parna Viruá	0.609	.002
Nylanderia sp. 3	WSF Parna Viruá	0.588	.028
Crematogaster flavomicrops	WSF Parna Viruá	0.577	.003
Pheidole biconstricta	WSF Parna Viruá	0.577	.013
Pheidole sp. 11	WSF Parna Viruá	0.577	.008
Camponotus (Tanaemyrmex) lespesii	WSF Parna Viruá	0.554	.014
Cephalotes placidus	WSF Parna Viruá	0.543	.021
Neoponera apicalis	WSF Parna Viruá	0.542	.031
Dolichoderus laminatus	WSF Parna Viruá	0.542	.009
Azteca cf. ulei	WSF Parna Viruá	0.538	.017
Pheidole radoszkowskii	WSF Parna Viruá	0.5	.019
Acromyrmex octospinosus	WSF Parna Viruá	0.5	.021

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