ECOGRAPHY

Research article

Macroecological patterns of functional and phylogenetic diversity vary between ground and arboreal assemblages in Neotropical savanna ants

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Ecography
2024: e07122
doi: 10.1111/ecog.07122
Subject Editor:
Jose Alexandre Felizola Diniz-Filho
Editor-in-Chief: Miguel Araújo
Accepted 26 April 2024

Macroscale environmental gradients can have contrasting effects on organisms that occupy different vertical niches, but we have little understanding of how this might result in different macroscale diversity patterns in ground and arboreal communities. We also have little understanding of how different dimensions of diversity, such as functional and phylogenetic diversity, vary along macroscale environmental gradients. Here we examine latitudinal and elevational patterns of different dimensions of diversity for both ground and arboreal assemblages in Neotropical savanna ants. The study was based on ant species occurring at 32 sites covering a 22° range of latitude and > 1000 m range in elevation in Brazil. Functional and phylogenetic richness were positively correlated with species richness, all increasing with latitude. However, the greater phylogenetic richness on the ground than in trees did not simply reflect differences in species richness. The mean functional and phylogenetic divergence among species was also greater on the ground than in trees, indicating a stronger role of competition. Both mean functional and phylogenetic divergence showed negative correlations with elevation in trees but not on the ground. In trees, the standardized effect size (taking into account differences in species richness) of mean functional divergence was negatively related to elevation and mean phylogenetic divergence was negatively related to both latitude and elevation. These findings suggest that as temperature decreases the relative importance of environmental filtering in arboreal but not ground communities increases (and that of competition and niche partitioning decreases). Overall, we show that the macroecological patterns of ant species richness that have previously been reported for Brazilian savannas do not adequately represent other dimensions of diversity, and that the representativeness differs between vertical strata. Macroecological patterns of functional and phylogenetic divergence indicate that the relative importance of competition and environmental filtering also differs between vertical strata.

Keywords: cerrado, community assembly, Formicidae, functional traits, geographic diversity gradients, vertical stratification

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Introduction

A key goal of ecology is to understand how biological diversity is distributed along environmental gradients and the mechanisms structuring local communities. Latitudinal and elevational climatic gradients are widely recognized as key factors driving species distributions (Field et al. 2009). In many terrestrial habitats, verticality is also an important environmental gradient regulating species distributions as climatic conditions in the canopy can be very different from those on the ground (Basset et al. 2003, Scheffers et al. 2013). However, we know relatively little about how ground and arboreal organisms respond differentially to macroscale climatic gradients, even though there is mounting evidence that such gradients can have contrasting effects on organisms that occupy different vertical niches (Scheffers et al. 2013, Oliveira and Scheffers 2019, Leahy et al. 2021).

A wide variety of taxa are highly stratified vertically, having very different arboreal and ground communities (Roisin et al. 2005, Wilkie et al. 2010, Acharya and Vijayan 2017, Camargo et al. 2018). However, most studies that have looked at the influence of vertical stratification on diversity patterns have considered taxonomic diversity only, when important insights into the mechanisms that shape ecological communities can be also obtained by considering functional diversity (i.e. considering functional traits) and phylogenetic diversity (i.e. taking into account evolutionary relationships) (Webb et al. 2002, Cavender-Bares et al. 2009, Swenson et al. 2012, Stevens and Tello 2014). Functional diversity provides information about the ecological niches and the functional roles that species play in ecosystems (Swenson and Weiser 2014), and phylogenetic diversity addresses whether species are drawn from similar or from distantly related lineages. These complementary measures of diversity are required for a more comprehensive understanding of the structure and dynamics of biological communities (Webb et al. 2002, Cadotte et al. 2013, Zhao et al. 2020). Moreover, there can be substantial spatial mismatches between the different dimensions of diversity, which can have important implications for conservation management (Devictor et al. 2010). Ground and arboreal faunas are often distinct from each other both functionally and phylogenetically (Blaimer et al. 2015, Almeida et al. 2023), and therefore might be expected to show different macroecological patterns of functional and phylogenetic diversity.

Measures of functional and phylogenetic variation can also provide important insights into the mechanisms structuring biological communities (Cadotte et al. 2013). If communities are structured primarily by competition, then one would expect to find high levels of functional and phylogenetic divergence among community members. In contrast, if communities are structured primarily through environmental filtering (as is often the case where climatic conditions are harsher), then one would expect to find high levels of functional and phylogenetic clustering.

Several recent studies have analyzed the functional and/or phylogenetic diversity of communities of ants (Blaimer et al. 2015, Smith et al. 2015, Liu et al. 2016, Arnan et al. 2017, Agavekar et al. 2019), a dominant insect group that regulates a wide variety of ecosystem services, such as seed dispersal, decomposition, nutrient cycling, and biological control (Del Toro et al. 2012). Many of these studies have documented how the different dimensions of diversity vary among habitat types (Liu et al. 2016, Agavekar et al. 2019) or along environmental gradients (Smith et al. 2015, Arnan et al. 2017, Neves et al. 2019, Neves et al. 2023). Vertical stratification is a common feature of ant assemblages, especially in the tropics (Brühl et al. 1998, Vasconcelos and Vilhena 2006, Wilkie et al. 2010, Antoniazzi et al. 2021, Leponce et al. 2021, Leahy et al. 2022, Xing et al. 2023). However, our understanding of how different dimensions of ant diversity vary vertically is very limited, even though previous studies have pointed out that the arboreal fauna may not play by the same set of rules as their conspecifics living below them on the ground' (Basham et al. 2019).

Similarly, there is little information on the extent to which ant communities associated with different vertical strata respond differentially to macroscale climatic gradients, or on potential differences in the relative importance of competition versus environmental filtering as mechanisms structuring ground and arboreal communities. Arboreal and ground-dwelling ant communities occupy distinct habitats, which differ from each other in many aspects, such as in microclimate (Scheffers et al. 2013, Leahy et al. 2022), food resources (Yanoviak and Kaspari 2000, Blüthgen et al. 2003, Vieira et al. 2021), and nesting substrates (Almeida et al. 2023). Furthermore, arboreal and ground-dwelling ants show differences in their thermal tolerances (Leahy et al. 2022) and in the extent to which they can adapt to climatic variation through flexible foraging along the vertical gradient (Leahy et al. 2022, Vasconcelos et al. 2023).

We have previously described how ground and arboreal ant assemblages in Brazilian savannas show different macroecological patterns of species richness and composition and, consequently, how the vertical stratification of these assemblages varies at large spatial scales (Vasconcelos et al. 2023). Savanna ant species richness is much greater on the ground than in trees (Almeida et al. 2023, Vasconcelos et al. 2023). Furthermore, species richness on the ground increases with latitude at a faster rate than in trees (Vasconcelos et al. 2018, 2023).

In this study we compare macroecological patterns of diversity in ground versus arboreal ants in Neotropical savannas and evaluate the degree of congruence between multiple dimensions of diversity. In particular, we investigate the extent to which vertical (i.e. between strata) and horizontal (i.e. along latitudinal and elevational gradients) patterns of ant species richness correlate with those of functional and phylogenetic diversity. In addition, we evaluate the extent to which the mechanisms of ant community assembly vary along the vertical and horizontal dimensions. We hypothesized that the marked difference in taxonomic richness between the arboreal and ground faunas, both vertically and horizontally, results in concomitant differences in functional and phylogenetic diversity. Since arboreality is a derived lifestyle among ants (Lucky et al. 2013, Blaimer et al. 2015) and occurs in a very limited subset of ant genera (Blaimer et al. 2015), we also expected to find communities that are both less diverse and more clustered, both functionally and phylogenetically, in trees than on the ground. Finally, we expected to find differences in the way that communities from different strata are structured along large-scale climatic gradients. Arboreal ants are less cold tolerant than are ants that forage on the ground (Leahy et al. 2021), and so environmental filtering can be expected to play a stronger role in the assembly of the arboreal communities as latitude and/or elevation increases and thus as temperature decreases. On the other hand, at warmer sites interspecific competition and niche partitioning may be of greater importance for the arboreal than for the ground communities. This is because although the proportion of arboreal species found foraging on the ground remains constant along a latitudinal temperature gradient, that of ground-dwelling species foraging in trees tend to increase as latitude decreases (Vasconcelos et al. 2023).

Material and methods

Data set and study region

Our data set derives from previous sampling of the arboreal and ground-foraging ant fauna at 32 sites in Brazil (Vasconcelos et al. 2018, 2023). Except for two sites in the Amazon region and one in semi-arid Caatinga, all sampling sites were located in the Cerrado (savanna) biome of central Brazil (Vasconcelos et al. 2023) (Fig. 1). Ants were sampled in the dominant savanna vegetation of the study region (locally known as cerrado sensu stricto) characterized by a relatively open canopy of trees 3–8 m tall and a ground layer composed of grasses, herbs, and small shrubs (Oliveira-Filho and Ratter 2002).

The study region encompasses 22° of latitude and 18° of longitude, and the sites sampled vary in elevation from 24 to 1130 m a.s.l (Fig. 1). The mean annual temperature within this region ranges from 18.1 to 26.6°C, and the mean annual rainfall from 860 to 2000 mm. The mean annual temperature decreases significantly as both site elevation ($r = -0.846$, $p < 0.001$) and latitude ($r = -0.772$, $p < 0.001$) increase, whereas mean annual rainfall did not show a significant correlation with elevation or with latitude ($r = -0.270$ and -0.322, respectively). However, as latitude increases, both rainfall during the wettest quarter ($r = 0.840$, $p < 0.001$) and net primary productivity ($r = 0.837$, $p < 0.001$) also increase (Vasconcelos et al. 2019, 2023).

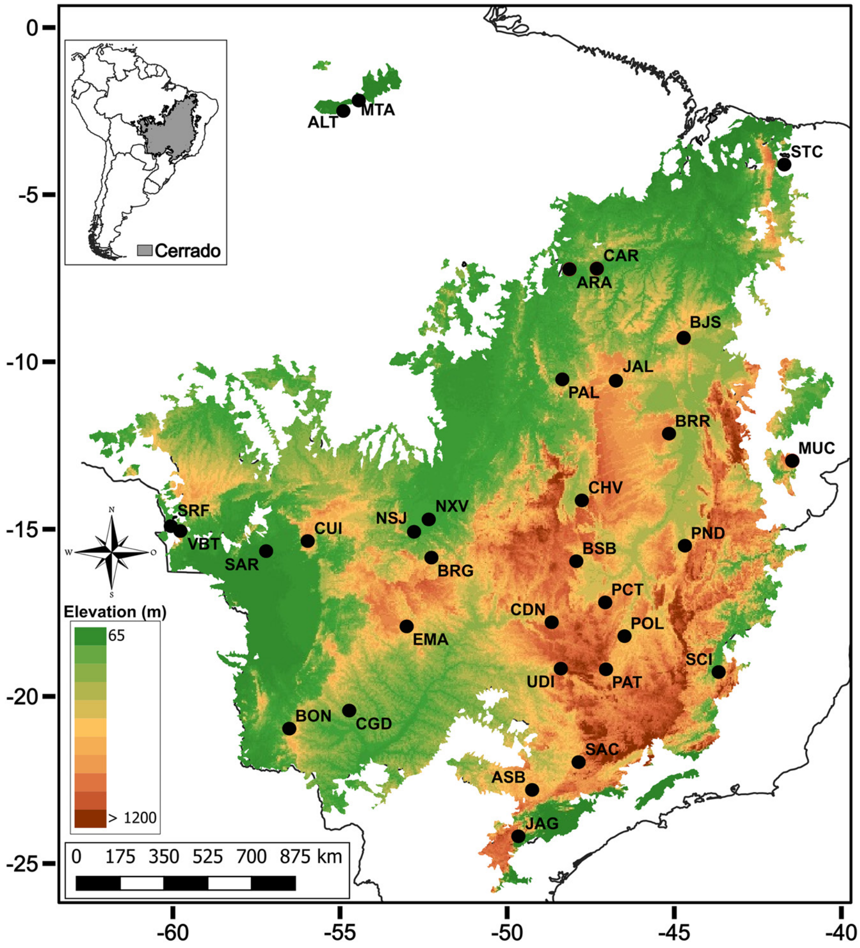

Figure 1. Map showing the location of the 32 sampling sites in the savanna dominated landscape (Cerrado) of Brazil. Site acronyms are found in the Supporting information.

At each site, ants had been sampled along three linear transects (~ 1 km apart from each other) using pitfall traps. Along each transect, we marked 20 sampling points (spaced at 20 m intervals), with alternate points used to sample ants that forage on the soil surface and on trees. To collect ants foraging on the ground, a set of four pitfall traps, arranged in a square grid of approximately 2.5 × 2.5 m, was installed at each sampling point. To collect ants foraging in the arboreal vegetation, four pitfall traps were fixed on the branches of the tree that was located nearest to each sampling point. Arboreal traps were positioned approximately 2 m above the ground (range: ~ 1.5 to 3 m) and baited with human urine (diluted 1:2 in water), which is a highly attractive bait for arboreal ants (Vasconcelos et al. 2014). Ground pitfall traps were not baited because this is not necessary for obtaining large catches. All pitfall traps, plastic cups 7.8 cm in diameter, were operated for 48 h. Sampling dates are provided in the Supporting information.

A total of 439 species from 76 genera were collected (Supporting information), 391 species (from 75 genera) on the ground and 195 species (from 42 genera) in trees. Voucher specimens of all species are held in the Zoological Collection of the Federal University of Uberlândia (UFU) and the Entomological Collection Padre Jesus Santiago Moure (DZUP) from the Federal University of Paraná (UFPR).

Functional traits

For each species we measured five morphological traits commonly used in studies of ant functional diversity (Martello et al. 2018, Agavekar et al. 2019). At least five ant workers from each species were measured and average values were calculated for the measurements of each trait; when fewer than five workers were available, we measured all specimens. For species with worker dimorphism or polymorphism, only minor workers were measured. Whenever possible, the measured individuals were from different sampling sites. A detailed account of the hypothesized functions of each trait can be found in Parr et al. (2017) and Martello et al. (2018) but, briefly: 1) Weber's length is a measure of body size and is correlated with metabolic characteristics; 2) eye length is indicative of food searching behavior; 3) inter-ocular distance is involved in the perception of habitat complexity and the performance of visual predators; 4) femur length is indicative of locomotory abilities and foraging behavior; 5) mandible length is indicative of diet. We relativized the last four traits by dividing them by Weber's length. All trait measures were then standardized to zero mean and unit variance. In addition, we obtained information on the main diet, nest location, foraging stratum, and recruitment type of each species (Supporting information), as these traits are all highly relevant to the functional organization of ant communities, including in Brazilian savanna (Silvestre et al. 2003, Silva et al. 2015).

All nine functional traits (five morphological and four behavioural) were used to calculate the Gower distance between pairs of species. The matrix of distances between species was then used to construct a functional dendrogram (according to species occurrence) through UPGMA, as a basis for measuring functional diversity in a way consistent with that for phylogenetic diversity (Mammola et al. 2021). Functional distance was calculated using the 'Daisy' function implemented by the 'cluster' package (Maechler et al. 2022) in R (www.r-project.org).

Phylogenetic tree

For phylogenetic analysis, we obtained DNA sequences of ultraconserved elements (UCEs) for 357 of our 439 species (one representative of each), using the methodology detailed in Neves et al. (2023). We then used these sequences to construct a maximum-likelihood tree with IQTREE ver. 1.6.12 (Nguyen et al. 2015) to reflect phylogenetic relatedness. We added the other 82 species that lacked UCE data through the Yule process, using the *genus.to.species.tree* function available in the 'phytools' package (Revell 2012). A total of 1000 simulated trees were generated to account for the uncertainty associated with the phylogenetic positions of the additional species. Finally, we built a maximum clade credibility (MCC) tree consisting of a consensus among the 1000 simulated trees (Supporting information). The MCC tree was built using the *maxCladeCred* function incorporated in the 'ape' package (Paradis and Schliep 2019). All analyzes were performed in R.

Functional and phylogenetic diversity

We used the topology of the functional dendrogram for analyses of functional diversity, and the topology of the phylogenetic tree for analyses of phylogenetic diversity. We considered two metrics of diversity: one that measures 'richness' and the other 'divergence' between community members (Tucker et al. 2017). As a measure of phylogenetic richness, we calculated the diversity index that sums branch lengths connecting species within a community for phylogenetic richness (PD) (Faith 1992) and its functional equivalent for functional richness (FD) (Petchey and Gaston 2002). As a measure of divergence, we used the mean pairwise phylogenetic distance (MPD) among all species from the community (Webb et al. 2002), and its functional equivalent MFD (Petchey and Gaston 2002). The MFD and MPD metrics were based on abundance data, where abundance represented the total number of sampling points in which the species was recorded.

We compared the observed values of the functional and phylogenetic diversity metrics with the values generated through 999 randomizations of the community matrix using the 'independent swap' algorithm. Finally, we calculated the standardized effect sizes (SES) of all of the above metrics. Standardized richness (ses.FD and ses.PD) indicates departure from random expectation given species richness, and standardized divergence (ses.MFD and ses.MPD) provides insights into the relative importance of different processes influencing community assembly. Higher than expected standardized MFD and MPD are indicative of dispersion due to niche partitioning, whereas lower than expected values indicate clustering due to environmental filtering (Webb 2000, Webb et al. 2002, Swenson and Weiser 2014). We used the formula: SES = (Obs – $\text{Mean}_{\text{null}}$)/$\text{S.D.}_{\text{null}}$, where Obs is the observed functional or phylogenetic diversity in a given community, $\text{Mean}_{\text{null}}$ = is the mean of the 999 randomly generated values, and $\text{S.D.}_{\text{null}}$ is the SD. Analyses were performed in the R package 'picante' (Kembel et al. 2010), which provides the significance of the difference between each observed SES score and those generated by the null model, as based on the rank of the observed score in relation to the scores generated by 999 randomizations of the community matrix. Conventionally, SES values > 1.96 or < −1.96 are regarded as significant ($\alpha = 0.05$) (Webb et al. 2002).

Statistical analyses

For the statistical analyses, we pooled ant data for the three transects at each site. All analyses were performed using R . We used linear models (analysis of covariance) to test for the effects of species richness and vertical strata on the observed (i.e. non-standardized) metrics of functional and phylogenetic diversity. In these models, vertical stratum was treated as a fixed factor and species richness (SR) as a covariate. The response variable represented the diversity (functional or phylogenetic) recorded in each of the two vertical strata (arboreal or ground) in each site. In this way, we were able to determine the extent to which eventual differences in the observed diversity metrics were independent of SR differences between strata. Separate analyses were performed for each non-standardized diversity metric. As in no case did we detect a significant interaction between species richness and vertical strata, we proceeded with the analyses without the interaction term.

Differences between vertical strata in the standardized effect size (SES) of the functional and phylogenetic diversity metrics were assessed using linear models (one-way Anova). In addition, we made inferences about the mechanisms of community assembly in each vertical stratum using one sample *t*-tests, given that significance values generated through the null model approach are conservative (Götzenberger et al. 2016). For each stratum we tested if the mean of the SES values (n = 32 sites) was significantly different from zero. Means above zero were regarded as indicative of (functional or phylogenetic) overdispersion, whereas means below zero were regarded as indicative of clustering (Agavekar et al. 2019).

The relative influence of latitude and elevation on the metrics of functional of functional and phylogenetic diversity (observed and standardized) was evaluated using a multimodel averaging approach using the R package 'MuMIn' (Bartoń 2023). Separate models were run for the arboreal and the ground-dwelling communities and for each metric. We checked for multicollinearity between the predictor variables using the variance inflation factor (VIF), but as VIF was low (1.52) we retained both latitude and elevation as predictors in our models. We also checked for outliers with large influence on regression parameters and whenever necessary removed the outlier value from the analysis (Zuur et al. 2010).

Results

Functional and phylogenetic diversity

Both functional and phylogenetic richness (FD and PD) were strongly and positively related to species richness (FD: $F_{1,61} = 270.6$, $p < 0.001$; PD: $F_{1,61} = 1108.2$, $p < 0.001$), which was on average 2.3 times greater on the ground than in trees (Fig. 2). On average, FD was 1.67 times greater on the ground than in trees, whereas PD was two times greater. The observed difference in FD between the arboreal and the ground communities was not significant after accounting for species richness differences (i.e. when using species richness as a covariate) ($F_{1,61} = 0.63$, $p = 0.429$) (Fig. 2a). In contrast, we found significantly more PD on the ground than in trees ($F_{1,61} = 68.6$, $p < 0.001$), even when accounting for higher species richness (Fig. 2b).

Variation in the mean pairwise functional dissimilarity (MFD) as well as in the mean pairwise phylogenetic dissimilarity (MPD) among community members were independent of the observed variation in SR within each stratum (MFD: $F_{1,61} = 0.09$, $p = 0.76$; MPD: $F_{1,61} = 1.71$, $p = 0.19$; Fig. 2c, d). MFD was on average 1.06 times greater on the ground ($F_{1,61} = 19.6$, $p < 0.001$), compared with 1.14 times greater for MPD ($F_{1,61} = 45.9$, $p < 0.001$). The variability in both MFD and MPD was much lower on the ground than in trees (Coefficient of variation: MFD trees = 9.8%, MFD ground = 4.9%, MPD trees = 5.8%, MPD ground = 1.7%) (Fig. 2c, d).

On average, we did not find any significant difference between the arboreal and the ground stratum when looking at the standardized effect size (SES) of the functional and phylogenetic diversity metrics (ses.FD: $F_{1,62} = 0.16$, $p = 0.69$; ses.PD: $F_{1,62} = 0.24$, $p = 0.62$; ses.MFD: $F_{1,62} = 0.46$, $p = 0.50$; ses.MPD: $F_{1,62} = 0.002$, $p = 0.96$). In addition, both on the ground and in trees, the mean SES values were not significantly different from zero and this was true for all the functional and phylogenetic diversity metrics analyzed (one-sample *t*-tests, $p \geq 0.14$ in all comparisons).

Relationship with elevation and latitude

Species richness (SR) and functional (FD) and phylogenetic (PD) richness were all positively correlated with latitude, both on the ground and in trees (Fig. 3a). Similarly, on the ground (but not in trees), the phylogenetic divergence among community members (MPD) tended to increase with latitude (Fig. 3a). Elevation was not a significant correlate for SR or for any of the observed metrics of functional and phylogenetic diversity in the ground stratum. On the other hand, in trees, FD, PD, MFD and MPD were all negatively correlated with elevation (Fig. 3b).

In general, neither latitude nor elevation presented a significant relationship with the standardized metrics of functional and phylogenetic diversity of the ground-dwelling ant communities (Fig. 3c, d). The only exception was ses.PD (on the ground), which tended to increase with latitude (Fig. 3c, 4e). In trees, we found a negative relationship between both

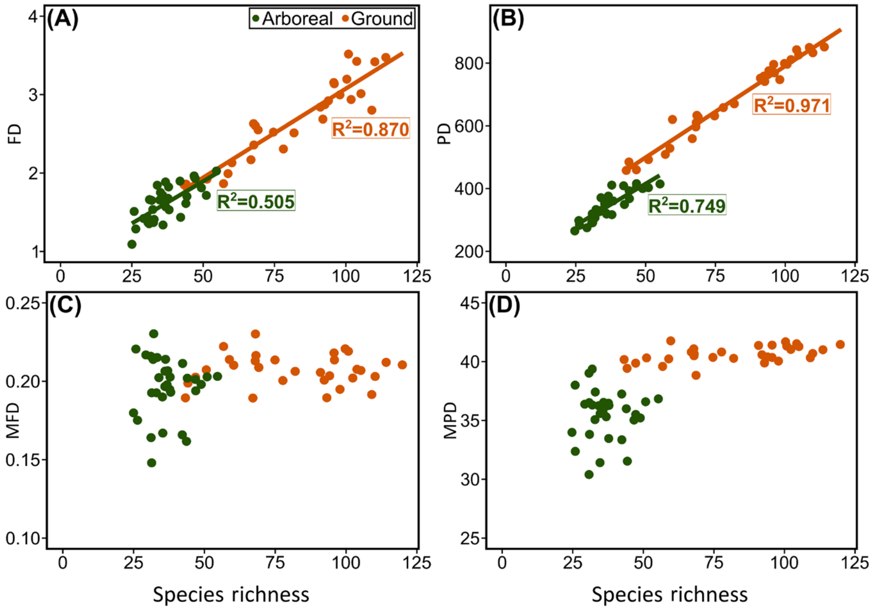

Figure 2. Relationship between species richness and the non-standardized metrics of functional and phylogenetic richness (FD and PD) and divergence (MFD and MPD) for ant communities from the arboreal and the ground stratum.

ses.FD and ses.MFD (Fig. 3d, 4b, d) and elevation, whereas the arboreal ses.MPD was negatively correlated with elevation and latitude (Fig. 3d, 4g, h).

Discussion

Functional and phylogenetic diversity are important components of biodiversity but are routinely overlooked in community ecology and conservation management. Our study examines differences in the macroecological relationships among functional diversity, phylogenetic diversity, and species richness between ground and arboreal ant communities in Brazilian savannas. In addition, we use the macroecological relationships to provide insights into how mechanisms of community assembly vary between vertical strata and along latitudinal and elevational climatic gradients.

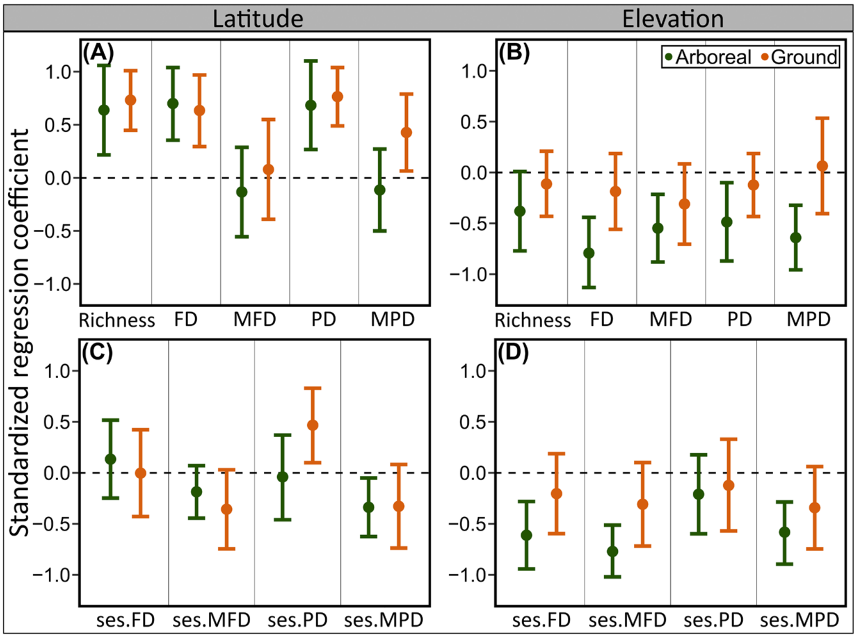

Figure 3. Standardized regression coefficients (and their 95% confidence intervals) of the models that evaluated the influence of latitude and elevation on the non-standardized metrics of functional and phylogenetic richness (FD and PD) and divergence (MFD and MPD), and on the standardized effect size (SES) of these same metrics, for ant communities in the arboreal or the ground stratum. Coefficients whose 95% CI are above or below the dashed line are significantly different from zero.

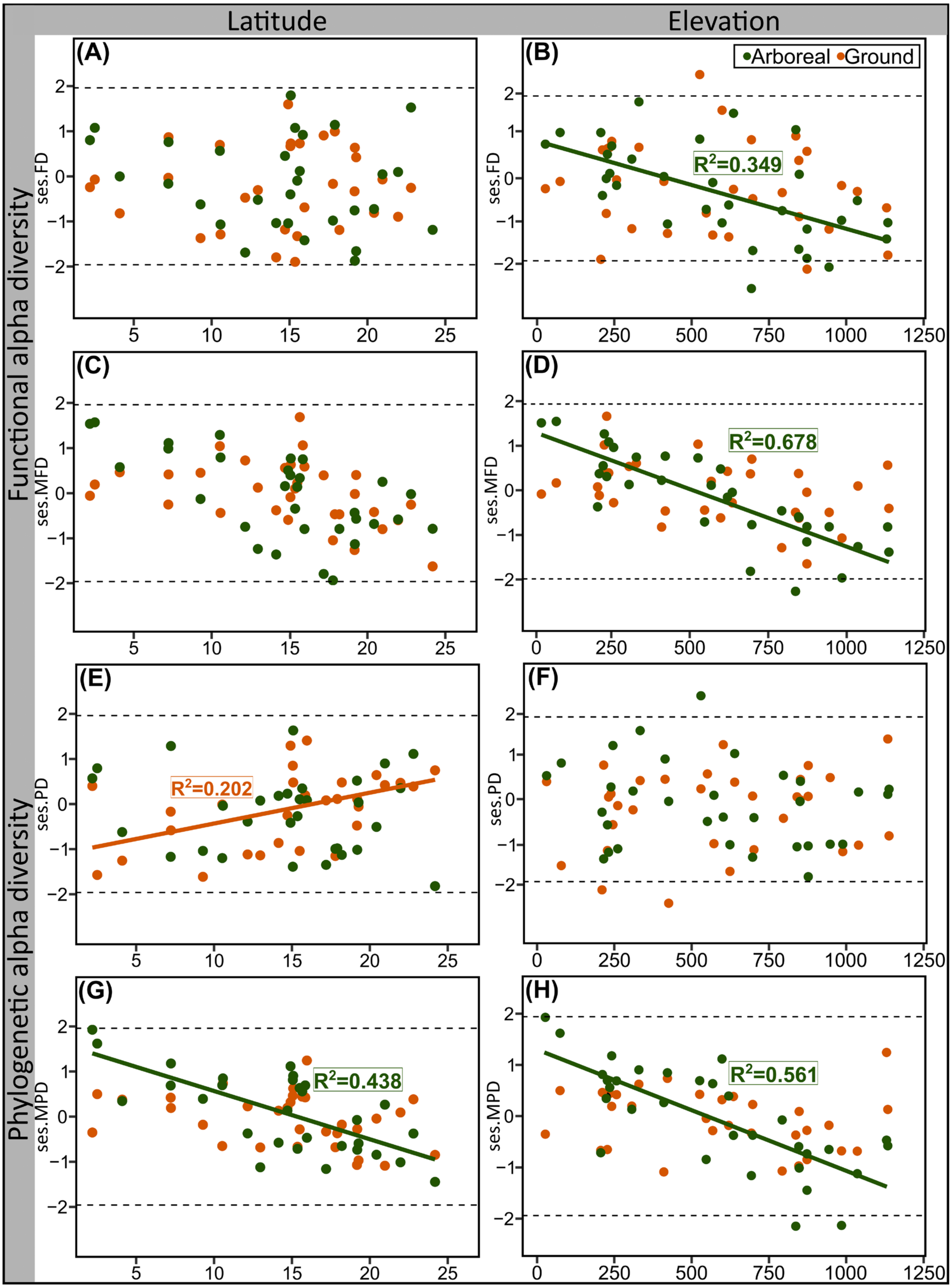

Figure 4. Scatterplot of the relationship between latitude, elevation (in meters), and the standardized effect size (SES) of the metrics of functional and phylogenetic richness and divergence for ant communities in the arboreal or the ground stratum. The dashed lines represent SES values above 1.96 or below – 1.96.

Functional and phylogenetic diversity on the ground and in trees

We expected that the marked difference in taxonomic richness between the arboreal and the ground-dwelling communities (Almeida et al. 2023, Vasconcelos et al. 2023) would result in concomitant differences in functional and phylogenetic diversity. Indeed, ant species richness (SR) was much greater on the ground than in trees and both functional and phylogenetic richness (FD and PD) were strongly and positively correlated with SR. However, while the difference in FD between vertical strata was associated only with the difference in SR, PD was greater on the ground than in trees even after accounting for differences in SR. This reflects the fact that arboreality has evolved in only a relatively small number of ant clades (Lucky et al. 2013, Blaimer et al. 2015).

We found no significant influence of SR on the functional and phylogenetic divergence (MFD and MPD) among members of the sampled communities. This is to be expected because such divergences represent means rather than sums as is the case for both FD and PD (Tucker et al. 2017). Despite this, both MFD and MPD were higher on the ground than in trees. MPD measures phylogenetic divergence at deeper nodes (Tucker et al. 2017), and the greater MPD on the ground likely reflects not only more ant lineages but also more representatives from older lineages (such as Dorylinae and Ponerinae) on the ground than in trees (Lucky et al. 2013, Blaimer et al. 2015). Interestingly, the magnitude of the difference in functional divergence between arboreal and ground communities was smaller than that for phylogenetic divergence, which suggests that many of the phylogenetically distinct species found on the ground may be playing similar functional roles.

Relationship with elevation and latitude

Given that FD and PD were both correlated with species richness (SR), macroecological patterns of FD and PD largely mirrored those of SR (Vasconcelos et al. 2023), increasing with latitude on both the ground and in trees. Interestingly, FD and PD were negatively correlated with elevation in trees but not on the ground.

When we looked at standardized effect sizes of the of functional and phylogenetic richness (ses.FD and ses.PD) a different pattern emerged, as in most cases these two metrics did not show any consistent variation across the gradients of latitude and elevation. However, in trees we did find a trend towards lower than expected ses.FD values as elevation increased, whereas on the ground higher-than-expected ses.PD values as latitude increased. This latter finding is probably associated with the greater incidence of forest-associated taxa at higher than at lower latitudes (Vasconcelos et al. 2018), since many of these taxa, such as the Ponerinae, belong to relatively old clades (Lucky et al. 2013, Blaimer et al. 2015). The increased presence of older ant lineages at higher than at lower latitudes (Vasconcelos et al. 2018) also helps to explain why we found a positive correlation between latitude and phylogenetic divergence (MPD).

Mechanisms of species assembly

On average, the standardized metrics of functional and phylogenetic divergence (ses.MFD and ses.MPD) did not differ from random expectation in both the arboreal and ground communities. However, the two communities showed different macroecological patterns with respect to these metrics, indicating different mechanisms of community assembly in the two strata. On the ground, neither ses.MFD or ses.MPD varied with latitude or elevation, indicating that mechanisms of community assembly are geographically consistent. However, in trees ses.MFD was negatively related to elevation and ses.MPD negatively related to both latitude and elevation. This suggests that as temperatures decrease with elevation and/or latitude, the importance of competition and niche partitioning in structuring arboreal communities decreases, while the role of habitat filtering becomes increasingly important.

Ground and arboreal ant communities are defined by place of foraging rather than nesting, as many species do not forage exclusively where they nest (Majer 1990, Leahy et al. 2021, Vasconcelos et al. 2023). In Brazilian savannas, ground-nesting species forage in trees more often at lower than at higher latitudes, whereas ground foraging by tree-nesting species shows little geographic variation (Vasconcelos et al. 2023). The trend found in the arboreal stratum towards functional/phylogenetic clustering at the colder sites (i.e. higher elevation/latitude) and overdispersion at the hotter sites, may thus be explained by the variable incidence of ground-nesting species in trees. There are strong differences in taxonomic (Wilkie et al. 2010, Vasconcelos et al. 2023) and functional trait composition (Frizzo et al. 2012, Almeida et al. 2023) between ground- and tree-nesting ants, such that the greater the incidence of ground-nesting species in trees the greater the functional and phylogenetic distinctiveness of the arboreal communities.

In conclusion, our study has revealed complex interactions between different dimensions of diversity and vertical strata. We have shown that the macroecological patterns of ant species richness that have previously been reported for Brazilian savannas (Vasconcelos et al. 2018, 2023) are not only poorly representative of other dimensions of diversity, but that such representativeness differs between ground and arboreal strata. Notably, the macroecological patterns indicate that the relative importance of competition vs environmental filtering differs between vertical strata. We have no reason to believe that such findings do not also apply to other taxa.

Acknowledgements – We thank the following agencies for granting permission to collect in protected areas of the Cerrado: Instituto Chico Mendes de Conservacão da Biodiversidade (ICMBio licença de coleta 27627-7 and 46596-1), Instituto Estadual de Florestas de Minas Gerais (licença 039/11), Fundacão Acangau, Secretaria de Estado de Meio Ambiente do Mato Grosso (SEMA/MT), and Instituto Natureza do Tocantins (Naturantis).

Funding – This research was carried out with the support from the Brazilian Council of Research and Scientific Development (CNPq grants 457407/2012-3 and 304628/2020-4 to HLV), and the U.S. National Science Foundation (NSF grants 1654829 and 1927161 to TRS).

Author contributions

Karen C. Neves: Conceptualization (equal); Data curation (equal); Formal analysis (equal); Investigation (equal); Methodology (equal); Validation (equal); Visualization (equal); Writing – original draft (equal); Writing – review and editing (equal). **Alan N. Andersen**: Conceptualization (equal); Supervision (equal); Writing – original draft (equal); Writing – review and editing (equal). **Ted R. Schultz**: Methodology (supporting); Resources (equal); Supervision (equal); Validation (equal); Writing – review and editing (supporting). **Heraldo L. Vasconcelos**: Conceptualization (equal); Data curation (equal); Formal analysis (equal); Funding acquisition (equal); Methodology (equal); Resources (equal); Supervision (equal); Validation (equal); Writing – original draft (equal); Writing – review and editing (equal).

Data availability statement

Data are available from the Zenodo Repository: https://zenodo.org/doi/10.5281/zenodo.11049815 (Neves et al. 2024).

Supporting information

The Supporting information associated with this article is available with the online version.

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