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ORIGINAL RESEARCH

Land use intensification has extensive effects on the functional and phylogenetic diversity of neotropical ant communities

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Abstract

The effects of land-use change on biodiversity can be idiosyncratic, varying not only across taxa and land-use type, but also between different levels and dimensions of diversity. Using a species-level phylogeny and morphological traits to build a functional dendrogram, we compared the phylogenetic and functional diversity and the trait composition of ant communities in five habitats (Forest, Savanna, Tree plantations, Pastures, and Soy fields), representing a gradient of land-use intensity in Brazil´s Cerrado. Results shown that ant communities in the most intensive land-use type (soy fields) presented the most distinct morphological trait composition. Furthermore, communities in the soy fields presented significantly lower levels of functional and phylogenetic alpha diversity as compared to the forest and savanna communities. There was evidence of functional and phylogenetic clustering in the soy field communities and of functional clustering in the pasture communities, whereas those in the remaining land uses presented a random functional and phylogenetic structure. In addition, we found evidence of biotic homogenization in the soy field communities, as the dissimilarity in the functional and phylogenetic composition between soy field sites was significantly smaller than the dissimilarity between forest or savanna sites. These results suggest that intensification of land use in the Cerrado affects multiple dimensions of ant diversity. The species found in the soy fields represented a nested subset of those found in most of the remaining land uses, and this has potential implications for the delivery of ant services to soybean farmers.

Keywords Biotic homogenization · Cerrado · Conservation · Habitat structure · Land-use change

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Introduction

Land-use change is one of the major causes of species extinctions worldwide (Newbold et al. 2015; Powers and Jetz 2019). The conversion of natural habitats for agriculture, ranching, or other anthropogenic land uses reduces the amount of suitable habitat for many native species, negatively affecting the size and spatial distribution of their populations (Feeley and Silman 2010; Machado et al. 2023). In addition, land-use change can lead to a process known as biotic homogenization, whereby native species extinctions and replacements (by exotics or habitat generalists) increase community similarity over space and time (McKinney and Lockwood 1999; Gossner et al. 2016). As a result of these processes, the ecosystem services provided and the resilience of communities to further environmental disturbances may be reduced (Foley et al. 2005).

Nonetheless, there is strong evidence that the nature and magnitude of the effects of land-use change on biodiversity can be idiosyncratic, varying not only across taxa and type of land-use change (Graham et al. 2019; Carvalho et al. 2022), but also between different levels and dimensions (facets) of diversity (Rabello et al. 2021; Rurangwa et al. 2021). Yet, most assessments of the effects of land-use change on biological communities have focused merely on taxonomic diversity, therefore neglecting the evolutionary histories, the ecological niches, and the functional roles played by the species lost or gained with the conversion of natural habitats into other land uses. Land- use change can produce non-random changes in the phylogenetic and functional diversity of communities (Newbold et al. 2012; Graham et al. 2019) and affect disproportionally species that may provide unique ecosystem functions and services (Cadotte et al. 2012). As such, some authors have argued that functional and phylogenetic diversity may be more useful indicators of the effects of land-use change on biodiversity than taxonomic diversity (Cadotte et al. 2008; Newbold et al. 2012).

Functional diversity, defined as the diversity of traits in a community, provides an explicit link to ecological niches and the functional roles that species play in ecosystems (Petchey and Gaston 2006). On the other hand, phylogenetic diversity (the diversity of lineages in a community) provides information about the amount of evolutionary history and the level of divergence between the component species of a community (Cavender-Bares et al. 2009). Land-use change can affect functional and phylogenetic diversity, at both the alpha and beta levels, by selecting against or favoring species with certain traits (e.g., Newbold et al. 2012) and/or from specific lineages (Kusuma et al. 2018). Consequently, local communities may become functionally and phylogenetically more clustered and more homogeneous across space and time (Weideman et al. 2019).

The Brazilian savanna biome – known as Cerrado – has witnessed very rapid transformation over the past few decades, losing over 50% of its original vegetation (Parente et al. 2021). Moreover, a process of agricultural intensification has taken place within the region due to the expansion of land devoted to production of agricultural commodities, notably soybean (Rausch et al. 2019). Studies about the effects of land-use change on the Cerrado´s biota indicate that the conversion of natural habitats can strongly affect the taxonomic diversity of biological communities, especially where land use intensification is high (Laste et al. 2019; Carvalho et al. 2022). However, much less is known about the extent to which changes in taxonomic diversity and composition results in concomitant changes in the functional and phylogenetic diversity and structure of Cerrado communities (but see Rabello et al. 2021; Carvalho et al. 2022; Maciel et al. 2023). In fact, a recent study has documented

that the spatial patterns of avian taxonomic, functional, and phylogenetic diversity within the Cerrado domain are not necessarily congruent (Borges et al. 2021), implying that taxonomic losses due to land-use change and intensification may or may not affect the evolutionary history and/or the ecosystem services provided by the biological communities (see also Maciel et al. 2023).

Here we compared ant communities across five habitats (Forest, Savanna, Tree plantations, Pastures, and Soy fields), representing a gradient of land-use intensity, from both a functional and phylogenetic perspective. Ants are ecologically dominant and highly diverse in tropical savannas (Andersen and Vasconcelos 2022), where they are involved in several ecosystem services (Del Toro et al. 2012; Parr et al. 2016). Our analyses are based on a species-level phylogeny and on morphological traits commonly used in studies of ant functional diversity (Parr et al. 2017; Martello et al. 2018; Neves et al. 2023). Specifically, we evaluated the differences between communities in different habitats (hereafter land-use types) in relation to (a) their morphological trait composition, (b) functional and phylogenetic diversity, and (c) functional and phylogenetic structure. Following the stress-dominance hypothesis (Coyle et al. 2014), we expected that changes in habitat structure caused by land-use intensification would increase the importance of environmental filtering as a mechanism of community assembly. By filtering for species with certain traits and/or from certain lineages, land-use intensification could also result in the impoverishment and homogenization of the ant fauna both functionally and phylogenetically. Finally, since several morphological ant traits can be sensitive to variation in habitat structure (Yates and Andrew 2010; Gibb and Parr 2013; Salas-Lopez et al. 2017), we expected to detect differences in morphological trait composition among different land-use types.

Materials and methods

Study area and sampling

The study was conducted in Uberlândia, Minas Gerais, in southeastern Brazil (19° 10’ S, 48° 23’ W). The region has a tropical climate, characterized by a dry winter and a rainy summer. The mean annual temperature is 22 °C and the mean annual precipitation is around 1,600 mm. The original, dominant vegetation in this region is tropical savanna, with interspersed patches of forest. This mosaic of vegetation types is determined by variation in the physical and chemical characteristics of the soil and in the frequency of fires (Oliveira-Filho and Ratter 2002). Over the past few decades, however, most of the native vegetation has been converted into anthropogenic land uses (Prado-Júnior et al. 2020).

The present study is based on previous sampling of the ground-dwelling ant fauna in the five major land-use types in the region. These were: (a) Semideciduous forest, which is a type of seasonal forest with a high diversity of trees, occurring predominantly on nutrient-rich soils (Oliveira-Filho and Ratter 2002), (b) Woodland savannas (locally known as cerrado *sensu stricto*), which is the dominant vegetation physiognomy in our study region, characterized by two distinct layers: an open woody layer composed of large shrubs and trees up to 8 m in height, and a ground layer composed of small shrubs, herbs and grasses (Oliveira-Filho and Ratter 2002), (c) Eucalypt tree plantations of approximately five to six years of age, and trees between 15 and 17 m in height, (d) Cattle pastures planted with

introduced African grasses (*Urochloa decumbens*), in which there was the presence of scattered trees (ca. 5 trees per ha), (e) Soy fields (~one month old), where soil tillage was not performed prior planting. These three anthropogenic land uses represent a spectrum of agricultural intensification within the region.

The ant sampling took place in November and December (early wet season) of 2017. Ants were sampled in a total of 40 sites, eight per land-use type. We a kept a minimum distance of 2 km between any two sampling sites and there was a good spatial interspersion between sites from different land-use types (Supplementary Material Fig. 1). In each site, a 100×100 m plot was established. Pitfall traps were installed at the corners and at the mid-points of the sides of the plot, totaling eight traps per site. The pitfall traps, consisted of plastic containers (19 cm diam, 11 cm height and filled with 150 ml of a saline solution and detergent), buried at ground level and left in the field for 48 h. Using this protocol, we were able to collect ca. 80% or more of the ant species expected to be found in each land-use type (Carvalho et al. 2022).

Functional traits

For each species we measured eight morphological traits (eye length, eye position, femur length, mandible length, number of spines, pilosity, scape length, and Weber's length) which are thought to reflect interspecific differences in foraging strategies, diet, and habitat use (Gibb et al. 2015; Parr et al. 2017). Whenever possible, measurements were made on five specimens from each species. When fewer than five specimens were available, we measured all specimens. A detailed account of the hypothesized functions of each trait can be found in Parr et al. (2017) but briefly, (1) Weber's length is a measure of body size, which correlates with metabolic characteristics, (2) eye length is indicative of food searching behavior and activity times, (3) eye position is related to hunting method or the component of habitat occupied, (4) femur length is indicative of locomotory abilities and food searching behavior, (5) mandible length is indicative of the ant's diet, 6) scape length is indicative of sensory abilities, 7) pilosity, which may increase tolerance to dehydration, and 8) spinosity (number of spines) which may act as defense mechanism.

To remove the correlation with body size, we relativized each trait measure (except pilosity, number of spines, and Weber's length) by dividing the value of the trait by the Weber´s length. All trait measures were then standardized to zero mean and unit variance. The eight morphological traits were used to calculate the Gower distance between pairs of species. The matrix of distances between species was then employed to build a functional dendrogram through Unweighted Pair Group Method with Arithmetic Mean (UPGMA). Functional distance was calculated using the 'Daisy' function implemented by the "cluster" package (Maechler et al. 2022).

Phylogenetic tree

For phylogenetic analysis, we obtained DNA sequences of ultraconserved elements (UCEs) for 357 ant 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 (Supplementary Material Fig. 2), with IQTREE v.1.6.12 (Nguyen et al. 2015), to reflect phylogenetic relatedness. Prior to the analysis, the phylogenetic tree was pruned, using the "drop.

tip" function incorporated in the "ape" package (Paradis and Schliep 2019), to include only the 181 ant species found in the present study.

Functional and phylogenetic alpha and beta diversity

We used the topology of the functional dendrogram for analyses of functional diversity, and the topology of the phylogenetic tree for the phylogenetic diversity analyses. To compare patterns of functional and phylogenetic alpha diversity between land-use types we considered two different diversity metrics. As a measure of phylogenetic richness in each sampling site, we calculated Faith´s phylogenetic diversity index (hereafter PD) that sums branch lengths connecting species within a community (Faith 1992). As a measure of divergence, we used the mean pairwise phylogenetic distance (MPD; Tucker et al. 2017) among all species from each community. Additionally, we considered the average distance between a species and the most closely related species (i.e., the mean nearest taxon distance; $MNTD_{phy}$). Similarly, we determined the total branch length in the functional dendrogram to determine the functional richness of each community (hereafter FD) and the functional equivalents of MPD (hereafter MFD) and $MNTD_{phy}$ (hereafter $MNTD_{fun}$) as measures of functional divergence.

To evaluate if land-use change could result in the functional or phylogenetic homogenization of ant communities, we compared patterns of beta diversity between sites of the same land-use type. For this, we determined, for each land-use type separately, the dissimilarity (functional or phylogenetic) between all pairs of sampling sites. We used the "betapart" package to calculate the overall dissimilarity (as based on the Sørensen index) and to partition this dissimilarity into its turnover (as based on the Simpson index) and nestedness components (Baselga 2010).

All the statistical analyses were based on the standard effect sizes (SES) of the above-described (alpha and beta) diversity metrics, given standardized metrics are less sensitive to differences in species richness between the sampled communities and allow the test of hypotheses regarding the functional and phylogenetic structure of communities (Webb 2000). We generated null communities by randomizing (999 randomizations) the community data matrix using the "independent swap" algorithm, which maintains the row and column totals of the original matrix. Then, we determined the difference between the observed diversity value and the mean of the null values and divided this difference by the standard deviation of the null values. These analyses were performed using the package "picante" (Kembel et al. 2010).

Statistical analyses

We used one-way ANOVAs to compare the metrics of functional/phylogenetic diversity between land-use types, at the alpha and beta levels. Separate analyses were performed for each metric and diversity level. A posteriori multiple comparison tests were conducted based on the Tukey method. We made statistical inferences about the functional/phylogenetic structure of ant communities in different land-use types by testing if the mean standardized effect size of the diversity metrics were significantly different from zero (Agavekar et al. 2019). Mean values of ses.FD /ses.PD above zero are indicative that functional/phylogenetic richness is greater than expected given the species richness of the sampled community,

whereas values below zero represented the opposite trend. Mean values of the standardized metrics of functional/phylogenetic divergence (ses.MFD/ses.MPD and ses.$MNTD_{fun}$ / ses.$MNTD_{phy}$) above zero were indicative of functional/phylogenetic dispersion, whereas values below zero indicative of functional/phylogenetic clustering (Webb 2000). The same approach was used to determine whether the observed values of overall dissimilarity, turnover and/or nestedness between sites of the same land-use type were significantly higher or lower than the null expectation.

To illustrate the differences in morphological trait composition between communities in different land-use types, we performed a Principal Component Analysis (PCA). PCA reduces the dimensionality of the data set and creates orthogonal axes that summarizes the information contained in the original data matrix. Our data matrix was built using the community-weighted mean (CWM) of each morphological trait in each of the 40 sampling sites. Although CWM can produce inflated Type I errors under some circumstances (Lepš and de Bello 2023), it was used here merely for descriptive purposes. According to Lepš and de Bello (2023), Type I errors in CWM analyses occur under one of the following scenarios: (a) when all species are everywhere, except for one or a few species whose abundances increases linearly along the studied gradient (in our case the land-use intensity gradient), or (b) when there is strong species co-occurrences, so that different species are in different parts of the gradient. However, we believe none of these scenarios apply to our data. This is because contrary to scenario "b" several species were found in all land-use types (see Fig. 1). Similarly, scenario "a" also does not apply to our data since only some (and not most) of the ant species we sampled were everywhere. In addition, we did not collate abundance data as required in scenario "a" but rather incidence data, which ranged from zero (meaning that the species was absent for a given land-use type) to eight (meaning that the species was present in all sites of that land-use type).

We used the R package "FD" (Laliberté et al. 2014) to compute the CWMs of morphological traits, whereas the PCA analysis was performed in PcOrd 7.08 using the software default settings (McCune and Mefford 2018).

Results

In total we recorded 181 species of ants from seven different subfamilies and 47 genera (Fig. 1). Savannas and forests were the habitats with the highest diversity of species (114 and 97 species, respectively), whereas the soy fields presented the lowest diversity (34 species in total). The tree plantations and the pastures presented a total of 64 and 78 species, respectively. Members of several ant clades were not found or were very rare in the soy fields, including notably members of the tribe Attini (especially *Cephalotes* and most of the lower-attines), Camponotini, Ectatommini (especially *Ectatomma*), and Ponerini (see box in Fig. 1). Typical arboreal ants, such as those from the genus *Camponotus* and *Cephalotes*, were also relatively rare in the pastures (Fig. 1).

Morphological trait composition

The first two axes of the PCA explained 65.4% of the variation in morphological trait composition between ant communities in different land-use types (Fig. 2). Axis 1 summarized

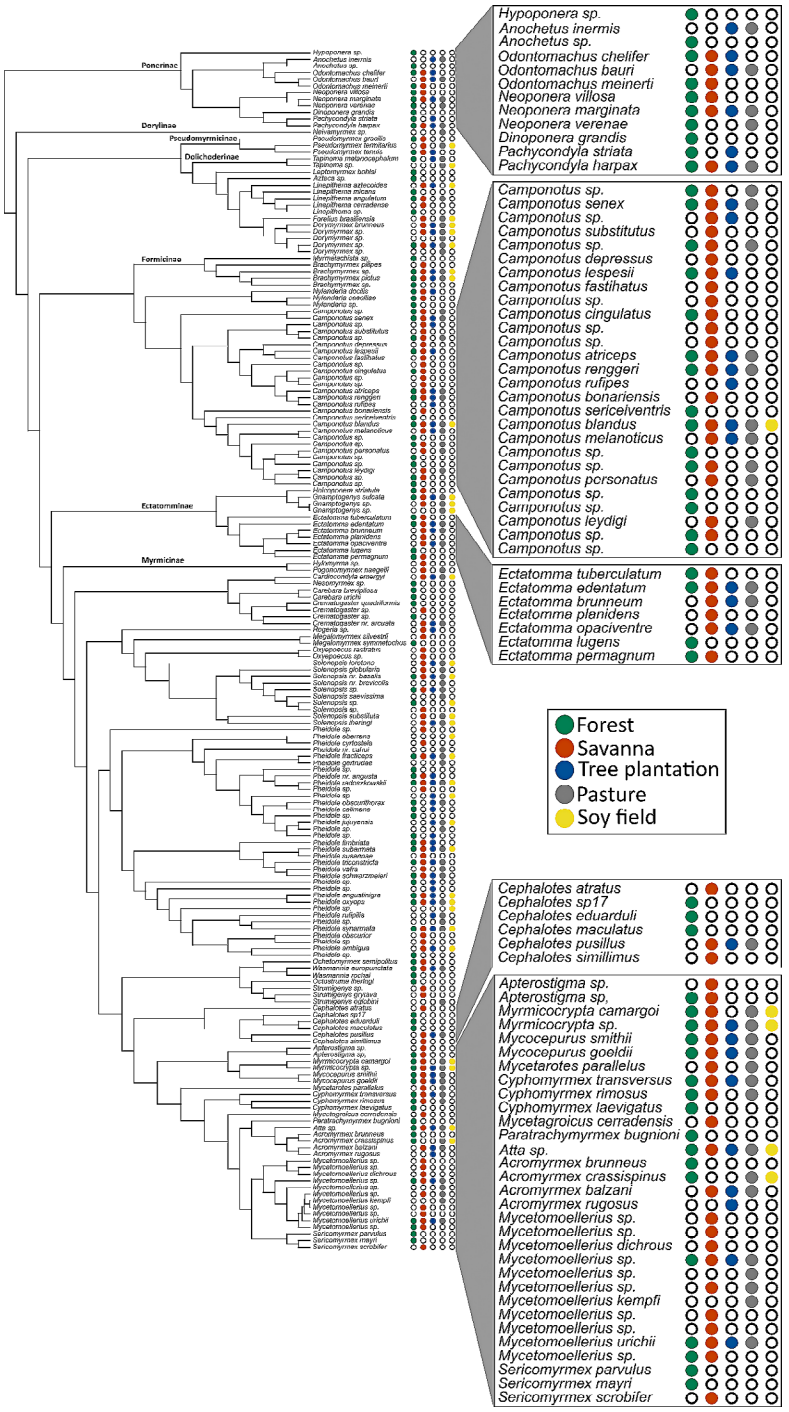


Fig. 1 Phylogenetic tree of the ant species found in different land-use types as based on ultra-conserved elements (UCE), evidencing the taxa not recorded in the most intensive land-use type (soy fields). Filled symbols represent the presence of the species, whereas empty symbols indicate its absence

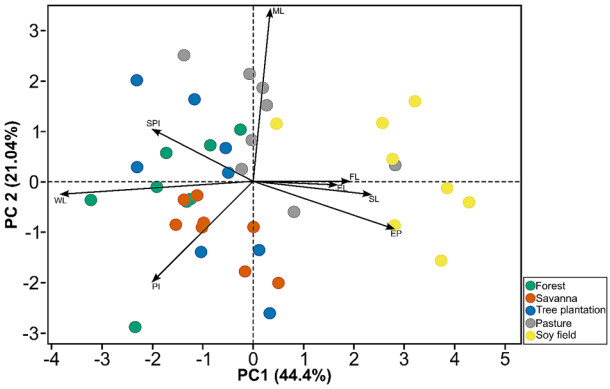


Fig. 2 Biplot of the Principal Component Analysis (PCA) describing the differences in the community-weighted means (CWM) of functional traits for ant communities in forests, savannas, tree plantations, pastures, and soy fields. EL=relative eye length; EP=relative eye-position; FL=relative femur length; ML=relative mandible length; PI=pilosity; SPI=spinescence; WL=Weber´s length

most of the variation (44.4%) and was negatively correlated with the CWM for Weber´s length (correlation coefficient = -0.90), pilosity (-0.65), and number of spines (-0.65). Furthermore, Axis 1 was positively correlated with the CWMs for eye position (0.77), relative scape length (0.70), relative femur length (0.63), and relative eye length (0.58). This axis clearly discriminated the soy field communities from those in the less intensive land-uses (tree plantation and pastures) or in the natural habitats (forest and savanna) (as also seen looking at the individual traits; Supplementary Material Fig. 3). Axes 2 (21.0% of the variation), which was positively correlated with the CWM for mandible length (0.85) and negatively related to pilosity (-0.65), discriminated the pasture from the savanna communities (Fig. 2).

Functional and phylogenetic alpha diversity and structure

We found significant differences between land-use types for all the three metrics of functional alpha diversity analyzed (Fig. 3a-c). The mean functional richness (ses.FD), and the mean functional divergence among community members (ses.MFD) were significantly higher in the forest and savanna than in the soy field communities. Meanwhile, the mean functional distance to the nearest taxon (ses.$MNTD_{fun}$) was higher in the forest than in the soy field communities.

In the forest, savanna, and tree plantations, the observed standardized effect size of the alpha functional diversity metrics did not deviate significantly from the null expectation (Fig. 3a-c). Conversely, in the pasture communities both mean ses.FD and mean ses.$MNTD_{fun}$ were smaller than zero, whereas in the soy field communities this was the case for all the three functional diversity metrics (Fig. 3a-c).

We did not find any significant difference in phylogenetic richness (ses.PD) or in mean phylogenetic divergence (ses.MPD) between land-uses types (Fig. 3d, e). However, the mean phylogenetic distance to the nearest taxon (ses.$MNTD_{phy}$) was significantly smaller in the soy field than in the savanna communities (Fig. 3f). In most land-use types, the mean standardized effect size of the phylogenetic alpha diversity metrics was not significantly different from zero (Fig. 3d-f). The soy field communities were an exception by presenting lower than expected values of ses.PD and ses.$MNTD_{phy}$ (Fig. 3d, f).

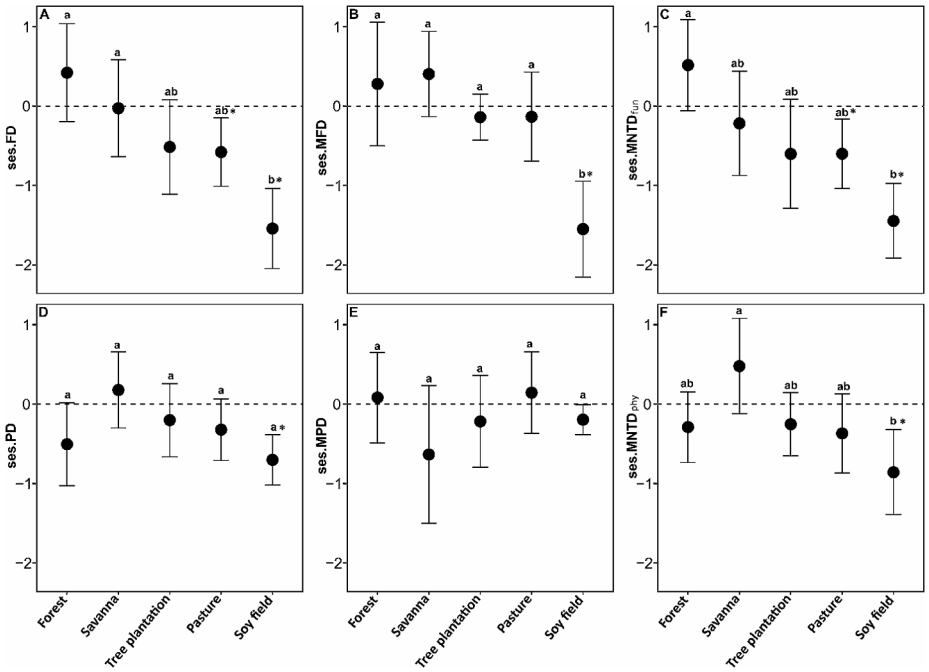


Fig. 3 Differences in the functional (**a-c**) and phylogenetic (**d-f**) alpha diversity between ant communities in different land-use types. Mean values and 95% confidence intervals for the standardized effect size (SES) of functional and phylogenetic richness (ses.FD, ses.PD), mean functional/phylogenetic divergence among community members (ses.MFD, ses.MPD), and mean functional/phylogenetic distance to the nearest taxon (ses.MNTD$_{fun}$, ses.MNTD$_{phy}$) are shown. Means with different letters are significantly different from each other. An asterisk denotes the mean SES values whose 95% CI are above or below the dashed line and thus are significantly different from the null expectation

Functional and phylogenetic beta diversity

Comparing the functional dissimilarity between sites of the same land-use type, we found that the overall dissimilarity between the forest sites was significantly greater than the dissimilarity between the soy field sites (Fig. 4a). Similarly, functional turnover was greater between the forest or the savanna sites than between the soy field sites (Fig. 4b), whereas functional nestedness was significantly smaller in the savanna or forest sites than in the soy field sites (Fig. 4c). Both the overall phylogenetic dissimilarity and the phylogenetic turnover were greater between the forest, savanna, or tree plantation sites than between the soy fields (Fig. 4d, e). Dissimilarity due to phylogenetic nestedness did not differ significantly between land-use types (Fig. 4f).

The functional and the phylogenetic dissimilarity between sites of the same land-use type was significantly smaller than zero in all land-use types and this was true when looking at the overall dissimilarity and the dissimilarity due to turnover (Fig. 4a, b,d, e). Functional dissimilarity due to nestedness was significantly higher than the null expectation in communities from the tree plantations, pastures, and soy fields, and significantly lower than expected in the savanna communities (Fig. 4c). Phylogenetic nestedness was significantly

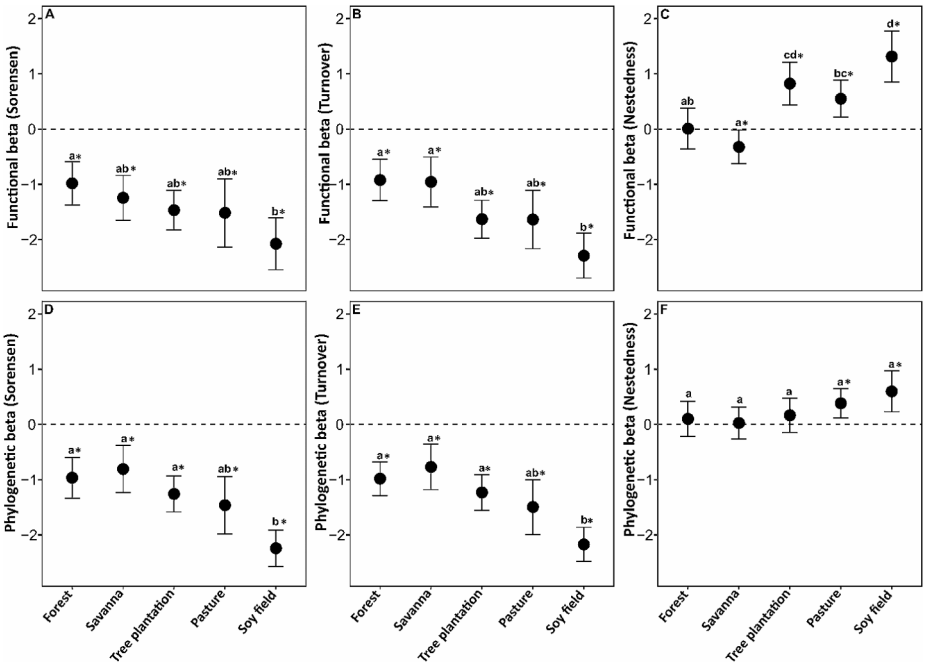


Fig. 4 Functional (**a**-**c**) and phylogenetic (**d**-**f**) dissimilarity between sites of the same land-use type. Shown is the overall dissimilarity (Sørensen index), the dissimilarity due to turnover (Simpson index), and the dissimilarity due to nestedness. Different letters indicate significant differences between mean values. An asterisk denotes the mean SES values whose 95% CI are above or below the dashed line and thus are significantly different from the null expectation

higher than expected in the soy fields and pastures, whereas in the remaining land-use types mean phylogenetic nestedness did not differ from zero (Fig. 4f).

Discussion

We evaluated the extent to which land-use change in the Brazilian Cerrado affects ant communities both from a functional and a phylogenetic perspective. The Cerrado biome has witnessed large and rapid transformations over the past few decades, with the conversion of its natural vegetation for agriculture, cattle ranching, or forestry. Furthermore, a process of land-use intensification is ongoing, as land used to produce soybeans is rapidly expanding into natural areas and areas previously devoted to other land uses (Rausch et al. 2019; Song et al. 2021). Overall, our results suggest that the conversion of natural habitats (forest and savanna) into soy fields is more detrimental for the Cerrado ant fauna than is the conversion of these habitats into pastures or tree plantations. Several lines of evidence give support to this contention.

Firstly, when looking at the morphological trait composition of the ant communities, we found that the soy field communities were more distinct from the forest and savanna communities than were those in pastures or tree plantations. Secondly, we found that, regardless of the metric analyzed, functional alpha diversity (as based on morphological traits) was

smaller in the soy field communities than in those from the natural habitats (forest and savanna). Similarly, phylogenetic alpha diversity was smaller in the soy field than in the savanna communities when looking at the mean distance to the nearest taxon (ses.MNTD-$_{phy}$). In contrast, levels of functional and phylogenetic alpha diversity in the pastures and tree plantations did not differ from those observed in the forest and savannas.

Thirdly, we found evidence that habitat filtering plays a comparatively greater role in structuring ant communities in the most intensive (and thus more stressful) land-use types, similarly as predicted by the stress-dominance hypothesis (Coyle et al. 2014). This is because ant communities in the soy fields presented a clustered functional and phylogenetic structure, whereas in the pastures only functional clustering was detected. In the tree plantations, like in the natural habitats, the functional and phylogenetic structure did not differ from the null expectation.

Finally, we found that the soy field communities, in contrast to those in pastures or in tree plantations, were significantly more homogeneous across space (i.e., from site to site) than were the forest or savanna communities. Although a similar trend was detected in the pasture and tree plantation communities, the difference in functional and phylogenetic dissimilarity (beta diversity) between these communities and those in the natural habitats was not statistically significant. However, it is important to mention that functional nestedness among the pasture or the tree plantation sites (similarly as found in the soy fields) was higher than among the savanna or forest sites and higher than expected by the null model. In this sense, and at least from a functional point of view, the pasture and tree plantation communities can also be regarded as spatially more homogeneous than the forest and savanna communities, since more nestedness implies in less turnover. Interestingly, a previous analysis did not find evidence of functional homogenization of the ant communities as a result of land-use changes in the Cerrado (Carvalho et al. 2022). However, this previous analysis involved only three qualitative traits, while here eight continuous traits were used, reinforcing the view that functional diversity analyses can be sensitive to the number and types of functional traits involved (Gaëlle et al. 2020).

We suggest that the lower functional and phylogenetic diversity found in the soy fields is in part the result of the absence of some key structural elements (cf. Tews et al. 2004) for ant nesting in this habitat. In particular, there was no trees in the soy fields, as opposed to all remaining habitats we sampled, including the pastures. Not surprisingly thus, most arboreal or predominantly arboreal clades, such as *Cephalotes* and most of the Camponotini, were not found in the soy fields. Similarly, the absence of tree logs and the lack of a permanent litter layer, substrates where many Ponerinae and lower-attines usually nest (Brown 2000), probably explains why these ants were so rare in the soy fields we surveyed. Nevertheless, several of the ant species that were not found in the soy fields (e.g., those from the genus *Ectatomma* as well as several attines and Ponerinae) nest underground (Brown 2000). For these species, the unsuitability of the soy fields as a nesting habitat is perhaps associated with the frequent use of agrochemicals (De la Mora et al. 2015), and/or with the low primary productivity during the dry season, when soy is not cultivated, and the fields are abandoned.

Regardless of the exact factors involved, our data indicate that by disproportionally affecting species from certain clades and with certain traits, land-use intensification affects the morphological trait composition of ant communities. As these changes are probably mediate by changes in the structure of the habitat, our findings give support to the idea that ant morphological traits (commonly used in studies of functional ant diversity) can

be sensitive to variation in habitat structure (Yates and Andrew 2010; Gibb and Parr 2013; Salas-Lopez et al. 2017). As evidenced by the PCA analysis, ants in the structurally simplest habitat (i.e., the soy fields) tend to have relatively longer scapes, longer legs, and more dorsally positioned eyes than ants in the remaining land-use types (see also Supplementary Material Fig. 3). Ants with more dorsally positioned eyes, such as those in the genus *Dorymyrmex* (one of the most prevalent genera in the soy fields), can see far ahead than those with eyes that are positioned laterally, which may be advantageous for ants foraging on bare ground as opposed to those foraging in the leaf-litter (Gibb and Parr 2013). Similarly, relatively longer legs may be of advantage for ants in more open and warmer habitats, such as the soy fields, as the relative size of the leg affects the foraging speed and the thermoregulatory strategy of ants (Parr et al. 2017). However, although pilosity is thought to increase resistance to dehydration (Parr et al. 2017), we found that ants in both the soy fields and pastures presented comparatively less hairs than those in the remaining land uses. Likewise, although body size is expected to be negatively related to the complexity of the ground surface (Parr et al. 2017), ants in the soy fields tended to be smaller than those in forests, savannas, and tree plantations. The comparatively small size of ants in the soy fields is probably associated with the scarcity of nesting substrates for ants that have large body sizes, such as some of the arboreal ants (Almeida et al. 2023) and most of the Ponerinae. Likewise, although spines are thought to work as anti-predatory mechanism in ants (Parr et al. 2017), the lower incidence of ants with spines in the soy fields may be best explained by the relatively unsuitability of the soy field habitat for spinescent ants such as those in the genus *Cephalotes* and the lower attines.

In short, we have shown that the effects of land-use change and agricultural intensification on Cerrado´s ant communities go beyond merely altering their taxonomic diversity (Laste et al. 2019). Rather, we found that the functional and phylogenetic diversity and structure of these communities are also affected, notably when land is converted for soybean production, reinforcing the view that land-use intensification can have extensive effects on multiple dimensions of diversity (Chapman et al. 2018; Kusuma et al. 2018; Weideman et al. 2019; Monge et al. 2022).

We suggest that future studies should evaluate the extent to which land-use intensification affects the delivery of ant-mediated services (e.g., pest control) (Del Toro et al. 2012; De la Mora et al. 2015). We have shown that the morphological trait composition of the ant communities is severely altered by land-use intensification, and that some ant clades are more adversely affected than others. In this respect, it is interesting to note that previous studies indicate that certain ant species or groups seem to have a disproportionate influence on predation rates. For instance, differences in below-ground ant predation rates between soy fields and adjacent savanna areas were not related to differences in overall ant abundance or in species richness, but rather with differences in the abundance of ants from one particular clade (Dorylinae) (Pacheco et al. 2017). Similarly, a study in the Amazon showed that land-use type differences in ant predation rates were not associated with differences in taxonomic richness, but rather with the abundance of a large-sized predatory species (*Ectatomma brunneum*) (Wilker et al. 2023).

Although we acknowledge that the production of agricultural commodities is key for the Brazilian economy, there are alternatives that can minimize the impact of the conversion of Cerrado´s vegetation for large-scale intensive agriculture. This includes, for instance, the maintenance of arboreal elements within the agricultural lands (Frizzo and Vasconcelos

2013; Prevedello et al. 2018), or increasing the amount of natural habitat in the surrounding landscape (Pacheco et al. 2013; Przybyszewski et al. 2022; Harmange et al. 2023). Such management recommendations could largely be achieved simply through compliance with the existing environmental legislation, given that several Cerrado trees are protected by law and cannot be cut by farmers without previous authorization from the environmental agency (Portaria IBAMA no. 113, artigo 16, January 9, 1996). Similarly, although it is mandatory that landowners keep 20 to 35% of their properties with Cerrado vegetation (as "legal reserves" or "areas of permanent preservation"), cases where the law is not being followed are, unfortunately, not uncommon (Rausch et al. 2019).

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Data availability The data that support the findings of this study are openly available in Zenodo at https://doi.org/10.5281/zenodo.1103400. DNA sequences, in FASTQ format, are deposited in the NCBI Sequence Read Archive (BioProject ID: PRJNA927311).

Declarations

Competing interests The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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