



Earth mounds with the presence of palms have high evolutionary history in the Cerrado–Caatinga ecotone

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Abstract The presence of palms on earth mounds may increase community phylogenetic diversity (PD) by promoting facilitation and acting as natural perches that enhance species recruitment. We investigated whether palm presence and mound size affect the phylogenetic diversity (alpha and beta) and structure of woody vegetation. We selected 42 earth mounds in an ecotone between the Cerrado

and Caatinga biomes: 15 with *Copernicia prunifera* (Mill.) H.E. Moore, 12 with *Astrocaryum vulgare* Mart., and 15 without palms. We sampled the woody vegetation, measured the area of mounds and collected the geographic coordinates in order to construct a distance matrix. We then built a phylogenetic tree and calculated the standardised effect sizes of phylogenetic diversity (ses.PD) and phylogenetic distances (ses.MPD and ses.MNTD), in order to control for species richness. We partitioned phylogenetic beta diversity into its turnover and nestedness components. Earth mounds with *Astrocaryum vulgare* exhibited higher ses.PD and phylogenetic overdispersion (ses.MPD=0.76; ses.MNTD=0.88; $p < 0.05$). By contrast, mounds with *Copernicia prunifera* displayed a random phylogenetic structure (ses.MPD=0.02; ses.MNTD=−0.21; $p > 0.05$), whereas mounds without palms exhibited lower ses.PD and phylogenetic clustering based on ses.MPD (−0.70; $p < 0.05$). The dissimilarities between mounds were driven by species turnover rather than geographic distance. Additionally, larger mounds exhibited higher PD. Our study highlights the potential of palms, particularly *Astrocaryum vulgare*, to promote the phylogenetic diversity of woody plant lineages on earth mounds, suggesting that their use is an effective strategy for ecological restoration in challenging environments.

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Introduction

The importance of biological interactions, such as facilitation, for plant community diversity under limiting conditions has received increasing attention in ecological research (Bertness and Callaway 1994; Brooker et al. 2008; Bertness et al. 2024). Facilitator plant species can alter their environment in a way that favours the survival, reproduction and colonisation of other species (Brooker et al. 2008; Navarro-Cano et al. 2015). These species promote niche diversification and increase the richness of plant communities, making them particularly important in environments with adverse conditions (Navarro-Cano et al. 2015; Soliveres et al. 2015; Bertness et al. 2024).

Facilitation promotes the coexistence of species that tend to conserve their phylogenetic history over evolutionary time (Valiente-Banuet et al. 2006; Valiente-Banuet and Verdú, 2007). Specifically, the facilitation promotes phylogenetic overdispersion in communities by bringing together species that are far apart in the phylogenetic tree, favouring the complementarity of vacant niches (Valiente-Banuet and Verdú, 2013; Navarro-Cano et al. 2016; Carrión et al. 2017). Facilitation enables closely related species to coexist, even when they exhibit similar ecological characteristics, because positive interspecific interactions tend to increase community richness (Soliveres et al. 2012; Valiente-Banuet and Verdú, 2013). Therefore, taking into account the evolutionary history of species can help to identify areas in which ecological interactions shape communities in environments with limited resources (Cavender-Bares et al. 2009; Soliveres et al. 2012; Oviedo et al. 2014).

Notable formations of earth mounds known as “murundus”, “covais” or termite savannas are scattered across flooded plains in Brazil (Oliveira-Filho 1992a; Jancoski et al. 2019; Guilherme et al. 2022; Campos et al. 2023). These mounds are similar to the termite mounds found in North America and in the savannas of South Africa (Burnham and Johnson 2012). In the state of Piauí, in north-eastern Brazil, mounds are found in periodically flooded plains, functioning as islands for woody vegetation, free from seasonal flooding and soil water saturation (Araújo-Neto et al. 1986; Morais et al. 2022c). These seasonal floods act as environmental filters, shaping the composition and structure of the vegetation on the mounds (Cianciaruso et al. 2005; Silva and Batalha

2006). Despite their high concentration of endemic fauna and flora (Bassani et al. 2025), these ecosystems are overlooked in Brazilian legislation (Law No. 12,651/2010), planning policies and scientific research (Rosolen et al. 2015; Durigan et al. 2022). This neglect makes research conducted in these ecosystems particularly important for conservation and management policies, as they help us to understand the factors that determine the structure and diversity of the vegetation.

Previous studies conducted in the mounds of the north-eastern region have highlighted the potential of *Copernicia prunifera* (Mill.) H.E. Moore and *Astrocaryum vulgare* Mart. to facilitate the seed rain and the formation of seed banks, and therefore, the composition of the woody communities (Morais et al. 2022c, 2022a, 2022b). These palm species act as natural perches, attracting dispersal agents that transport diaspores across the flooded plain, promoting the colonisation of the mounds and increasing local diversity (González-García et al. 2022; Morais et al. 2022b). Palms can also generate a “nurse” effect (sensu Niering and Whittaker 1963) by depositing dead fronds, which regulate light and soil moisture around the base of the stipe (Kinhil and Parthasarathy 2010; Hernández-Salmerón et al. 2023). This facilitates the germination and colonisation of species, thereby enhancing the biodiversity of the community (Bertness and Callaway 1994; Bruno et al. 2003; Shemesh 2025). In addition to the presence of palms, it is predicted that, in accordance with the well-known premises of the theory of island biogeography, diversity will increase with the size of the mounds (MacArthur and Wilson 1963; Cararo et al. 2026).

Studies of earth mounds have traditionally focused on measures such as changes in species richness and composition (Oliveira-Filho 1992a; Marimon et al. 2015; Jancoski et al. 2019; Guilherme et al. 2022; Morais et al. 2022c). However, isolated taxonomic measures can obscure significant biodiversity patterns as they assume that all species are equivalent in terms of their ecological and evolutionary information (Cianciaruso et al. 2009; Tucker and Cadotte 2013; Tucker et al. 2017). Conversely, analysing the phylogenetic component of diversity (PD) enables the evolutionary dimension of biodiversity present in earth mounds to be captured, as well as the ecological processes responsible for its maintenance (Faith 1992; Tucker and Cadotte 2013). Not only does PD preserve

species diversity, it also preserves the unique genetic and functional characteristics that have evolved over time (Pontara et al. 2018; Rezende et al. 2020; Farias et al. 2025). Therefore, PD prioritises conservation and is increasingly recognised as an important global component of biodiversity that can contribute to the conservation of mound fields (Forest et al. 2007; Pollock et al. 2015, 2017; Muvengwi et al. 2022).

Measuring phylogenetic beta diversity helps us to understand how lineages are distributed among the mounds (Leprieur et al. 2012; Dvorak et al. 2025). Its partitioning clarifies whether variability in the composition of these sites is due to lineage turnover or nestedness (Baselga 2010; Leprieur et al. 2012). The high contribution of lineage turnover among earth mounds may be associated with the presence of palms. Due to the combined effects of “nurse” and “perch”, earth mounds with palms may exhibit a distinct lineage composition compared to those without (Bertness and Callaway 1994; Garrote et al. 2019; Spadeto et al. 2024; Lima et al. 2025). Conversely, the geographical distance between the mounds may not be a relevant factor in determining their composition, since the colonisation of these earth mounds depends on long-distance dispersal processes involving fauna (MacArthur and Wilson 1963; Campos et al. 2023). Therefore, it can be expected that the presence of palms, rather than the distance between the mounds, will influence the composition of the woody vegetation.

In this study, we evaluated the diversity and phylogenetic structure of mounds containing the palms *Copernicia prunifera* and *Astrocaryum vulgare*, as well as mounds without palms. Specifically, we tested the following hypotheses: (i) higher PD will be found in mounds with palms since they act as natural perches that recruit diaspores and improve environmental conditions for colonisation by species with distant phylogenetic lineages; (ii) the phylogenetic structure of mounds with palms will be overdispersed as facilitation influences community organisation by recruiting species from distinct phylogenetic lineages; (iii) Mounds with palms will harbor different lineages compared to mounds without palms, and this difference will be better explained by lineage turnover than by the distance between the mounds. This is expected because, in addition to providing favourable conditions for species establishment, palms can recruit sets of species with distinct lineages. (iv) Larger mounds

will support higher phylogenetic diversity (PD), with no effect of the interaction between mound size and the presence of palms.

Material and methods

Study area

The study was conducted in a legal reserve area on private property (04° 51' 10" S, 42° 12' 07" W) in the municipality of Campo Maior in the state of Piauí in north-eastern Brazil (see Fig. 1). According to the Köppen classification, the regional climate is of type As (tropical with a dry summer), with average temperatures ranging from 28 °C to 35 °C and annual precipitation of around 1,300 mm (Medeiros et al. 2020). The regional vegetation, known as the “Campo Maior Complex”, is one of the most important ecological transition zones between the Cerrado and Caatinga domains in the mid-northern region of the state (Farias and Castro 2004; Castro et al. 2009). This region features transition zones between the Cerrado and Caatinga domains in terms of edaphoclimatic conditions, as well as distinct soil types that vary over short distances (Barros and Castro 2006). These factors result in a complex arrangement of different vegetation types, ranging from grasslands to various Cerrado phytophysiognomies and Caatinga, Carrasco and semideciduous forests (Farias and Castro 2004). In this region, our focus was on the cerrado parkland and campo cerrado areas, which are characterised by continuous grassy layers and a strong presence of *Copernicia prunifera* (Castro et al. 2009; Morais et al. 2022c). In these areas, earth mounds occur as islands of woody vegetation, which are continuously colonised from the surrounding landscape. The study site is frequently flooded due to a shallow water table. The hydromorphic soils are prone to erosion and have low base saturation and clay content (Barros and Castro 2006).

Vegetation sampling

We randomly selected 42 earth mounds, distributed into three distinct and mutually exclusive categories. There were 15 mounds containing *Copernicia prunifera* (PC), 12 containing *Astrocaryum*

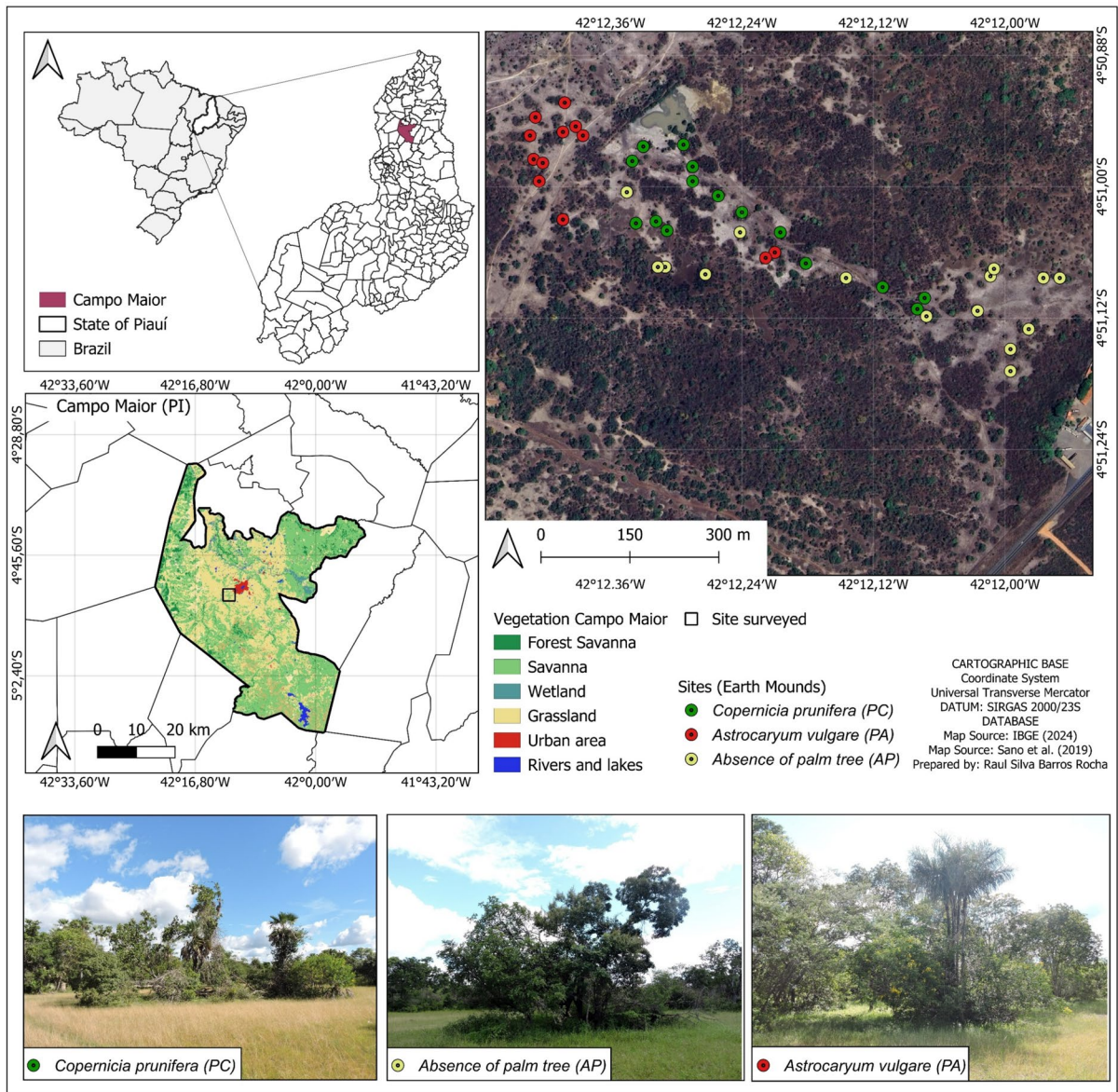


Fig. 1 Location of the study area and the mounds studied in the municipality of Campo Maior, Piauí, Brazil

vulgare (PA), and 15 without palms (AP; Fig. 1). These palms occur associated with earth mounds on seasonally flooded plains (Farias and Castro 2004; Morais et al. 2022c), but they can also be found scattered across vast, open grasslands characterised by herbaceous vegetation and sparse trees. These palms are able to withstand seasonally dry climates, but also develop in waterlogged soils with a shallow water table (Barros and Castro 2006). According

to the owner's report, the studied mounds were not subjected to any human activities or sporadic fires.

We sampled all trees and shrubs with a ground-level perimeter (GLP) of at least 10 cm present in each mound. The collection and herbarium methods were carried out according to Fidalgo and Bononi (1984). We measured the length (the largest dimension of each mound) and width of each mound using a measuring tape, and calculated its area in m² using

the formula in Oliveira-Filho (1992b). All mounds were georeferenced (UTM) using a GPS. Identification was carried out by consulting specialised bibliographies and comparing specimens with exsiccatae in the TEPB Herbarium at the Federal University of Piauí. The taxonomic classification followed APG IV, and species synonymy and distribution were verified using Flora e Funga do Brasil (2026).

Data analysis

For tree construction, we compiled a species list with their respective genera and families following APG IV (2016). This species list was used to generate a phylogenetic tree by pruning the ultrametric supertree “GBOTB.extended.TPL.tre”, available in the R package V.PhyloMaker2 (Jin and Qian 2022). This supertree synthesises seed plant phylogenies from Smith and Brown (2018) and vascular plant phylogenies from Zanne et al. (2014). The supertree is dated in millions of years based on fossil records, molecular data from GenBank and phylogenetic information from the Open Tree of Life (Jin and Qian 2022). It contains calibrated data for 74,529 vascular plant species, including age estimates for all botanical families, all of which are monophyletic (Jin and Qian 2022). All species sampled in this study are present in the supertree.

To test our hypotheses, we first generated presence–absence matrices to calculate phylogenetic indices. To address the first hypothesis, which aimed to assess whether mounds with the presence of palms exhibit higher phylogenetic diversity, we calculated Faith’s phylogenetic diversity (PD), defined as the total sum of branch lengths connecting species in the phylogenetic tree (Faith 1992). As this index is strongly correlated with species richness, which can potentially obscure variation in lineages among sites (Tucker et al. 2017; Xavier et al. 2019), we calculated a standardised effect size (SES) to control for this bias (Kembel et al. 2010; Tucker et al. 2017). The SES of PD (ses.PD) was calculated using 5,000 randomisations of species identities across samples, while keeping species richness constant (Kembel et al. 2010). Positive values of ses.PD indicate a higher PD than would be expected under the null model, whereas negative values indicate a lower PD than would be expected. The “pd” and “ses.pd” functions from the R

picante package were used to calculate phylogenetic diversity and its standardised equivalent, respectively (Kembel et al. 2010; R Core Team 2024).

To address the second hypothesis, which investigated whether the phylogenetic structure of mounds containing palms would exhibit phylogenetic overdispersion, we constructed a cophenetic distance matrix and calculated the standardised effect size (SES) of the mean pairwise phylogenetic distance (SES.MPD) and the mean nearest taxon distance (ses.MNTD) (Webb et al. 2002; Kembel et al. 2010). While ses.MPD detects phylogenetic structure in more basal portions of the phylogeny, ses.MNTD does the same in shallower portions of the phylogeny (Webb et al. 2002). The ses.MPD and ses.MNTD values were calculated using the R functions “ses.mpd” and “ses.mntd”, generating 5,000 randomisations with the “independentswap” algorithm from the picante package (Kembel et al. 2010; R Core Team 2024). This null model shuffles the occurrence of species across all plots while maintaining both species richness and the number of locations in which species occur (Hardy 2008). The model assumes that species can disperse freely between locations, and that the probability of colonisation is proportional to the frequency of occurrence of the species (Gotelli and Entsminger 2001; Hardy 2008; Gastauer et al. 2017). In the context of our research, these assumptions are reasonable, given the occurrence of the sampled mounds within the same geographical landscape. Positive values for the ses.MPD and ses.MNTD indices are indicative of phylogenetic overdispersion, whilst negative values are suggestive of phylogenetic clustering (Webb et al. 2002).

To verify whether PD, ses.PD and ses.MNTD differ between mound categories, we applied a Welch ANOVA, followed by a Games-Howell post hoc test. The Welch ANOVA was used because the data were normally distributed, but the assumption of homogeneity of variances was violated. The differences in ses.MPD were verified using a Kruskal–Wallis test followed by Dunn’s post hoc test. To test whether standardized effect size values differed from zero, we used a one-sample Wilcoxon signed-rank test for the ses.MPD index (non-parametric data) and a one-sample t-test for the ses.MNTD index (parametric data) (Castro et al. 2022). Welch ANOVA and Games–Howell post hoc tests were conducted by using the functions “oneway.test” from the R package

stats and “oneway” from the R package userfriendlyscience (Peters 2018; R Core Team 2024). The Kruskal–Wallis test and Dunn’s post hoc test were performed using the “kruskal.test” function from the R package stats and the “dunnTest” function from the R package FSA (Ogle et al. 2025; R Core Team 2024), respectively. The Wilcoxon signed-rank test was performed using “wilcox.test” function, and the t-test using “t.test” function (R Core Team 2024).

To test the third hypothesis, which examined whether lineage turnover could better explain dissimilarities between sites, we first created a phylogenetic distance matrix using the phylogenetic Sørensen similarity index (Phylosor; Bryant et al. 2008). Phylosor quantifies the total branch length shared between pairs of communities (Bryant et al. 2008). Following Baselga (2010) and Leprieur et al. (2012), we then partitioned Phylosor into components of phylogenetic turnover (i.e. when two communities exhibit distinct sets of lineages) and nestedness (i.e. when the phylogenetic branches of one community are subsets of those of another). Phylosor was calculated using the “phylosor” function and partitioned using the “phylo.beta.pair” function, both of which are implemented in the R package picante (Kembel et al. 2010; R Core Team 2024).

We constructed a Venn diagram using the “venn.diagram” function from the R package VennDiagram (Chen and Boutros 2011) to assess the number of exclusive and shared species among earth mound categories. We evaluated the effect of geographic distance on phylogenetic dissimilarity by generating 999 permutations using a Mantel test. To this end, we created two matrices: a Euclidean distance matrix based on UTM coordinates and a phylogenetic dissimilarity matrix based on Phylosor ($1 - \text{Phylosor}$). Finally, to test our fourth hypothesis that PD increases with mound area, we fitted simple linear regression models with mound area (in m²) as the predictor variable and PD as the response variable, including its interaction with the different earth mound categories.

Results

In the 42 mounds, we found 49 species belonging to 43 genera and 23 families (Fig. 2). Of these, 40 species occurred in mounds with *C. prunifera* (PC), 33 in mounds without palms (AP) and 32 in

mounds with *A. vulgare* (PA). The richest families were Fabaceae (13 species), Bignoniaceae (5), and Rubiaceae (5). The complete floristic list of species recorded in each earth mound is provided in Table S1 (online resource).

We found no differences in PD between the mound categories ($F_{\text{Welch}} = 2.78$; $p = 0.08$; Fig. 3a). However, when we removed the effect of species richness by using the standardised equivalent ses.PD, we found that PA had a greater evolutionary history and differed from AP ($F_{\text{Welch}} = 12.65$; $p\text{-holm-adj} < 0.001$; Fig. 3b).

Mounds with *A. vulgare* exhibited a more overdispersed phylogenetic structure than mounds without palms (Fig. 4). The ses.MPD detected a clustered phylogenetic pattern in AP (ses.MPD = -0.70 ; $V = 19$; $p = 0.03$), a random pattern in PC (ses.MPD = -0.02 ; $V = 72$; $p = 0.56$) and a overdispersed pattern in PA (ses.MPD = 0.76 ; $V = 77$; $p = 0.02$; Fig. 4a). We found differences in phylogenetic structure between AP and PA (Kruskal–Wallis $X^2 = 10$; $p\text{-bonferroni-adj} < 0.001$), while PC did not differ significantly from the other categories (PC–AP: $p\text{-bonferroni-adj} = 0.06$; PC–PA: $p\text{-bonferroni-adj} = 0.42$; Fig. 4a). Conversely, the ses.MNTD values detected phylogenetic overdispersion for PA (ses.MNTD = 0.88 ; $V = 73$; $p = 0.04$; Fig. 4b), while the other mound categories exhibited a random pattern ($p > 0.05$; Fig. 4b). We found no differences in ses.MNTD between the mound categories ($F_{\text{Welch}} = 2.13$; $p = 0.14$).

We found a positive relationship between PD and mound area ($F = 37.36$; $R^2 = 0.49$; $p < 0.01$; Fig. 5). However, we found no interaction effect with mound categories ($F = 0.64$; $p = 0.53$; See Fig. S1 in the online resource for additional information).

We found that the contribution of turnover was predominant over nestedness across all mound categories (Fig. 6a). The highest levels of turnover occurred between PC and AP, and between PA and PC. We recorded 16 species that were exclusive to mounds with palms, 12 of which occurred only in PC (Fig. 6b; See Table S1 in the online resource for additional information). By contrast, 23 species were found across all mound categories, with greater sharing between PA and AP (Fig. 6b). Furthermore, we found that the distance between mounds does not explain differences in lineage composition (Mantel: $r = -0.13$; $p = 0.93$).

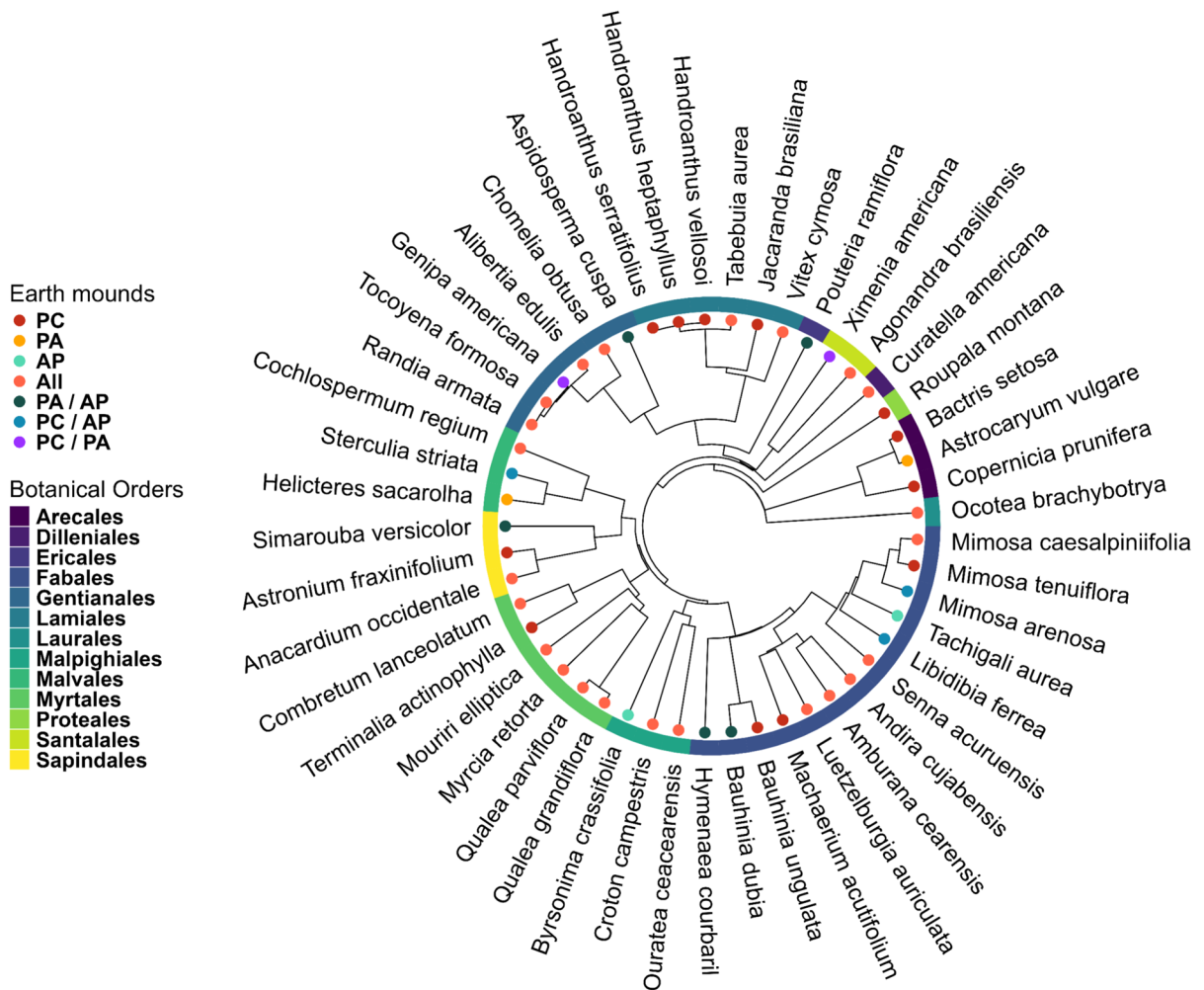


Fig. 2 Phylogenetic tree showing the species sampled in 42 mounds (PA: presence of *A. vulgare*; PC: presence of *C. prunifera*; AP: absence of palms; All: present in all earth mounds)

Discussion

We demonstrate that the woody vegetation of earth mounds with palms, particularly those with *A. vulgare*, is more diverse and phylogenetically distinct than that of mounds without palms. Specifically, we show that mounds containing *A. vulgare* exhibit higher standardised phylogenetic diversity (ses. PD) and an overdispersed phylogenetic structure. In contrast, mounds with *C. prunifera* exhibited a predominantly random phylogenetic structure, whilst mounds without palms showed phylogenetic clustering and lower standardised phylogenetic diversity (ses. PD). Furthermore, we found that phylogenetic

diversity increases with the area of the mounds and that phylogenetic composition is mainly determined by the replacement of lineages between mound categories, rather than by the distance between them. These results are consistent with the idea that the presence of nurse plants and their role as natural perches may be associated with the occurrence of phylogenetically distinct species, with greater niche complementarity within the community (Valiente-Banuet and Verdú, 2013; Navarro-Cano et al. 2016; Carrión et al. 2017). This interpretation is also consistent with the stress gradient hypothesis, which predicts that facilitative interactions tend to become more important under severe environmental

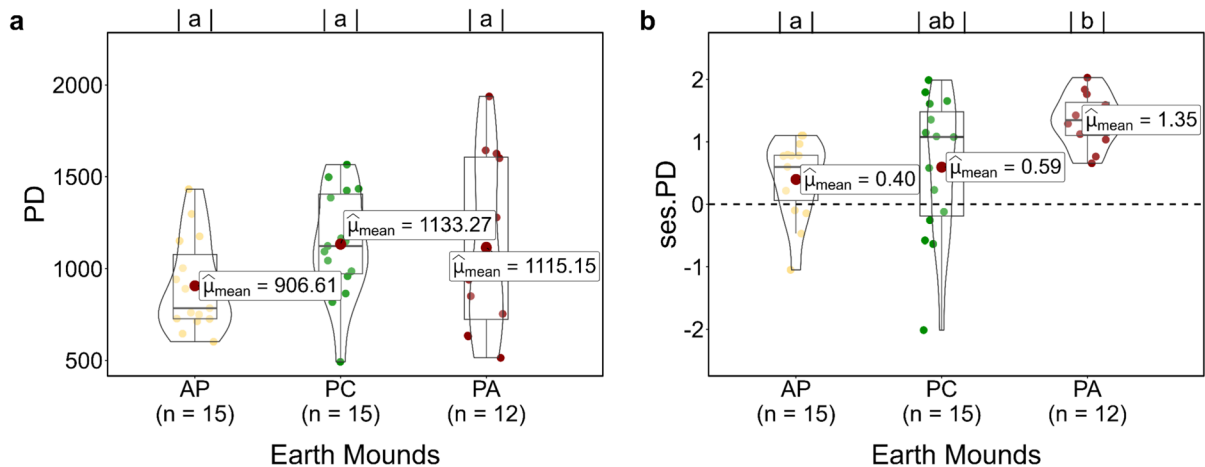


Fig. 3 Comparison of phylogenetic diversity (PD, Fig. a) and standardised effect size of phylogenetic diversity (ses.PD, Fig. b) between mounds without palms (AP); mounds with the presence of *C. prunifera* (PC) and mounds with the presence of

A. vulgare (PA). The mean is represented by the red dot. Different letters indicate significant differences between the means ($p < 0.05$)

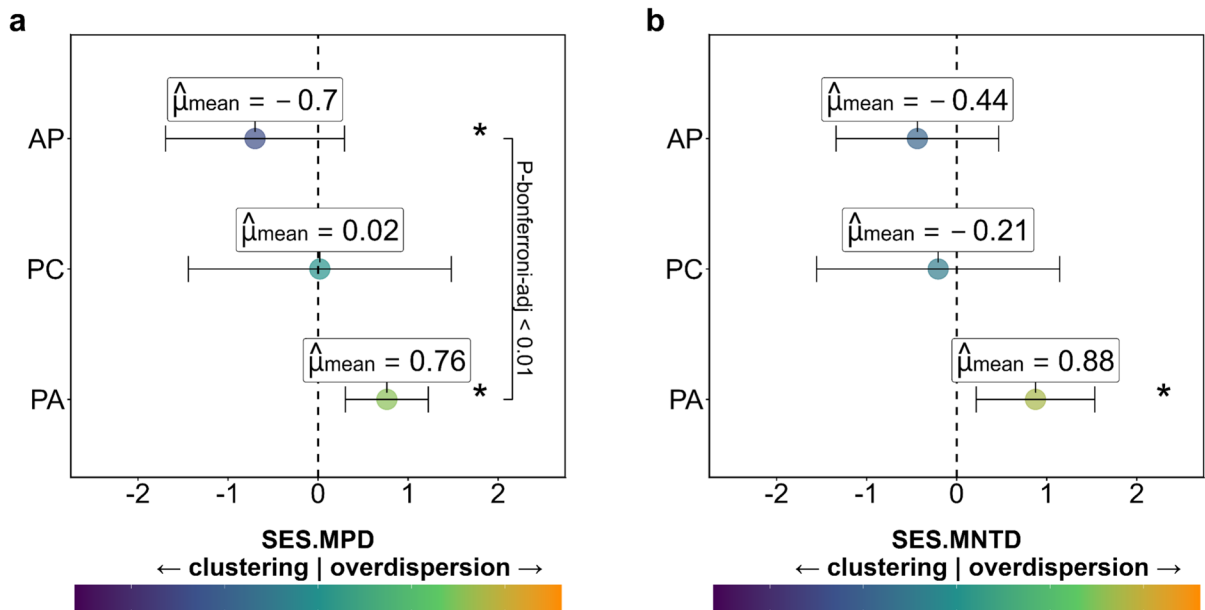


Fig. 4 Comparison was made of the standardised effect size of the pairwise mean phylogenetic distance (ses.MPD, Fig. a) and the phylogenetic distance to the nearest taxon (ses.MNTD, Fig. b) between mounds without palms (AP); mounds with the presence of *C. prunifera* (PC) and mounds with the presence of

A. vulgare (PA). Asterisks (*) indicate means that differ from the null model. Square brackets represent differences between mound categories according to the post hoc test (Dunn test, $p < 0.05$)

conditions, such as seasonal flooding (Maestre et al. 2009).

We believe that the high standardised phylogenetic diversity (ses.PD) observed in mounds containing *A.*

vulgare, as well as the shift from a clustered pattern in mounds without palms to a random pattern in mounds containing *C. prunifera*, and an overdispersed pattern in mounds containing *A. vulgare*, may be related

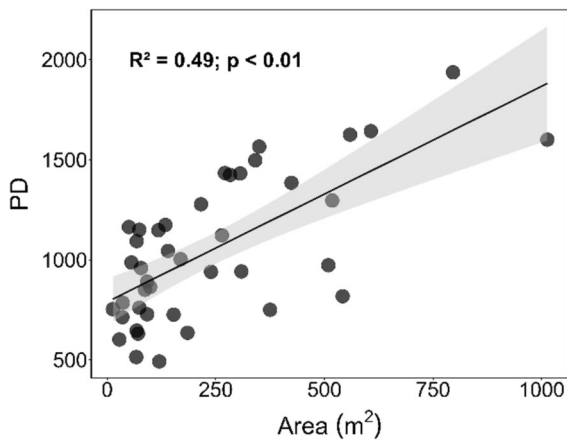


Fig. 5 Association between phylogenetic diversity (PD) and mound area in the Campo Maior vegetation complex, Piauí, Brazil

to two factors associated with the presence of these palms. Firstly, these palm trees can act as “perches” (*sensu* Debussche et al. 1982), which helps to attract dispersers and promote nucleation. The second factor may be linked to the nurse plant effect (Niering and Whittaker 1963), which improves environmental conditions and facilitates the establishment of species. Previous studies conducted in these mounds

corroborate the “perch” effect of these palms, demonstrating greater seed richness and density in mounds with palms (Morais et al. 2022c, 2022b, 2022a). More specifically, seed dispersal is greater in mounds containing *C. prunifera*, with zoochory being the dominant dispersal syndrome (Morais et al. 2022a, 2022b).

The short-term alternation between periods of drought and flooding creates instability for the woody vegetation in mound fields (Cianciaruso et al. 2005, 2009). Seasonal flooding thus acts as an environmental filter, limiting the dispersal of woody species and reducing species richness in the mounds (Oliveira-Filho 1992a; Cianciaruso et al. 2005). Conversely, during periods of drought, the shallow depth of the water table in the floodplain can also act as an important environmental filter, limiting the survival and establishment of woody species (Xavier et al. 2019). However, the nutritious fruit that palm trees provide, as well as the shelter they offer for nesting, may attract many fruit-eating birds (Batista et al. 2016; Fernandes et al. 2019; Tella et al. 2020; Glória and Tozetti 2021; Martins et al. 2024). Consequently, these palm trees may be preferred by birds as perches, shelters and foraging areas, resulting in defecation and regurgitation of many viable seeds (Batista et al. 2016; Garrote et al. 2019; González-García et al. 2022). We also recognise the importance of other

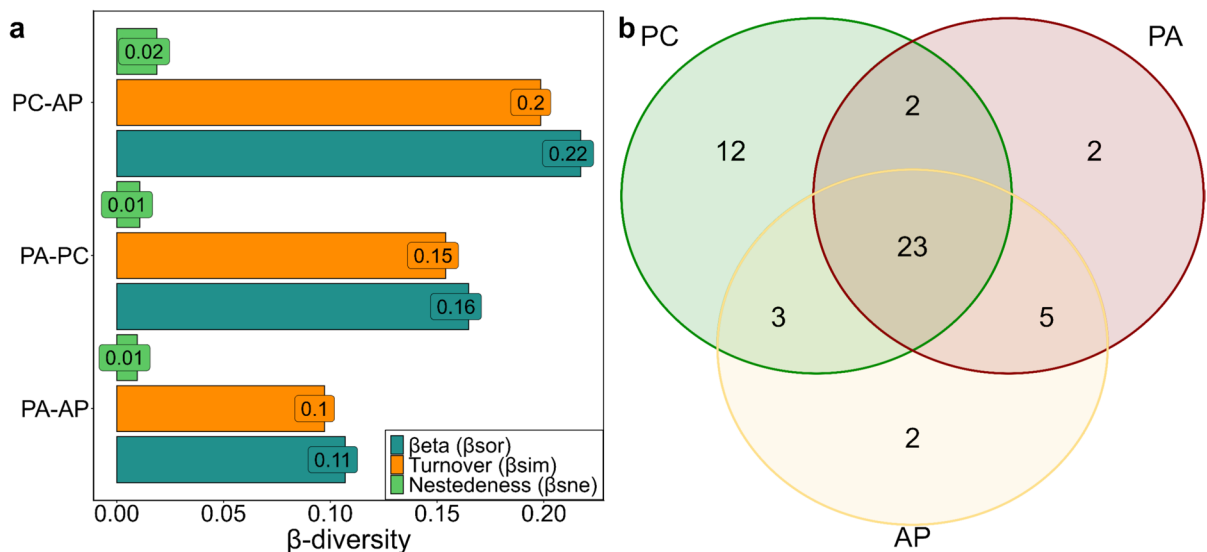


Fig. 6 **a** Pairwise contribution of turnover and nestedness components of phylogenetic beta (β) diversity (Phylosor), and **b** a Venn diagram of shared species among mounds without

palms (AP), mounds with the presence of *C. prunifera* (PC), and mounds with the presence of *A. vulgare* (PA)

vertebrates in dispersing seeds to these mounds, given that rodents and primates are major consumers of palm fruits (Fernandes et al. 2019). Frequent visits by seed-dispersing fauna to these palms, particularly those containing *A. vulgare*, may therefore increase the arrival of seeds and trigger nucleation processes. This would increase the amount of evolutionary history present in the mounds (Valiente-Banuet and Verdú, 2013; Garrote et al. 2019, 2022; González-García et al. 2022; Morais et al. 2022b).

It is also important to note that palm trees can facilitate the establishment of other species by improving the environment through the “nurse plant” effect. The temperature, humidity and light conditions beneath the palm canopy may be more favourable (Kinhil and Parthasarathy 2010; Lima et al. 2025), and the area beneath the trunk may offer greater protection from herbivores (Garrote et al. 2019). Furthermore, the soil around palm trunks tends to be richer in nutrients due to litter accumulation (Reis et al. 2000; Leite et al. 2013; Hernández-Salmerón et al. 2023). Thus, by improving the environment in areas adjacent to their trunks, palm trees can expand the regeneration niches of species and form functionally and phylogenetically distinct communities (Bruno et al. 2003; Valiente-Banuet and Verdú, 2007; Navarro-Cano et al. 2016; Carrión et al. 2017).

Therefore, the combined effects of nurse plants and perches may increase the recruitment of phylogenetically unrelated plants with distinct ecological niches, at least during the regeneration phase (Cavender-Bares et al. 2009; Butterfield et al. 2013; Valiente-Banuet and Verdú, 2013; Navarro-Cano et al. 2016). This could lead to greater phylogenetic diversity and generate phylogenetic superdispersion within the woody community, which aligns with the outcomes of our research, particularly for stands containing *A. vulgare*. For *C. prunifera* stands, however, such patterns were more subtle, as the phylogenetic structure was predominantly random. The arrival of seeds triggered by the perching effect is highly likely to have resulted in the coexistence of closely and distantly related species within the community, contributing to the randomness observed in the phylogenetic structure (Cavender-Bares et al. 2009; Navarro-Cano et al. 2016). Despite this, the results for earth mounds with *C. prunifera* should not be overlooked, as they harbor greater lineage diversity compared with mounds

without palms, where patterns of phylogenetic clustering were detected in one of the indices analyzed.

Phylogenetic turnover provided a better explanation for the compositional differences between the mounds than nestedness. This is probably because palm trees attract different dispersal agents that introduce different sets of diaspores and seeds to the mounds than those that colonise open areas. The colonisation of mounds by woody species present in the surrounding landscape depends on long-distance dispersal processes, as these are the main means by which seeds reach these isolated environments (Campos et al. 2023). This occurs due to flooding around the mounds at certain times of the year (Furley 1986; Marimon et al. 2015). In this regard, the nucleation processes triggered by birds visiting palm trees may result in increased seed dispersal. This could lead to distinct plant communities forming between mounds with and without palm trees (Yarranton and Morrison 1974; Schöb et al. 2013; Garrote et al. 2019; Morais et al. 2022c).

We demonstrate that mounds containing *A. vulgare* and *C. prunifera* harbour distinct lineages. Morphological differences between these species of palm may affect the availability of nesting sites and result in different types of seeds (Martins et al. 2024; Batista et al. 2016; Fernandes et al. 2019). *Copernicia prunifera* has a globose crown and a solitary, thornless trunk. In contrast, *A. vulgare* may have a solitary or tufted stem covered in long thorns, which provide greater protection against predators (Martins et al. 2024). Both species produce fruit with a fleshy mesocarp that attracts dispersing fauna (Martins et al. 2024; Silva et al. 2025). Furthermore, although mounds with *C. prunifera* exhibit greater species richness and a higher number of endemic species, these species are distributed across both closely and distantly related clades, resulting in a random phylogenetic structure. In contrast, mounds with *A. vulgare* harbour fewer species, which are distributed across more distantly related clades, leading to higher values of ses.PD, ses.MPD and ses.MNTD. This pattern suggests that *A. vulgare* does not necessarily increase species richness, but it may encourage the arrival of phylogenetically distinct lineages. This could be achieved by acting as a dispersal hub and creating microhabitats that facilitate the establishment of species with different ecological strategies (Butterfield

et al. 2013; Navarro-Cano et al. 2016; Spadeto et al. 2024).

The distance between the mounds did not affect the composition of the communities, probably because these environments are susceptible to colonisation by long-distance dispersal agents, such as birds that disperse seeds. It is well established that the distance of the “islands” (mounds) from their source area (the surrounding vegetation matrix) can influence community composition (MacArthur and Wilson 1963). However, the distance between mounds does not appear to affect the composition of the area, as both nearby and distant mounds have a similar chance of receiving seeds through long-distance dispersal processes (MacArthur and Wilson 1963; Campos et al. 2023). Conversely, phylogenetic diversity increases with mound size, presumably because larger mounds provide more space for woody vegetation to grow and become established. Smaller mounds provide a limited area that is not flooded, which restricts many woody species (Oliveira-Filho 1992a, b). This result is consistent with the well-established assumptions of island biogeography theory (MacArthur and Wilson 1963; Cararo et al. 2026) and with results from other studies conducted on these mounds and on mounds in different regions (Morais et al. 2014, 2022c; Silva et al. 2016).

We recognize that the observational approach used to test the hypotheses is a limiting factor of the study; however, this does not diminish the value of our results. By highlighting a longer evolutionary history in mounds with palms, especially those with *A. vulgare*, we suggest that perch and nurse plant effects likely guide the establishment and survival of new species in these environments. These synergistic effects likely favour both a greater arrival of seeds and greater survival of changes in these locations, resulting in the coexistence of distinct and ecologically diverse lineages. Palm species in other regions of the globe have demonstrated high potential for restoration. More specifically, the palm *Chamaerops humilis* L., present in Mediterranean grasslands, exhibits positive spatial associations with woody plants, in addition to greater seed transport via faecal deposition by dispersing birds (Garrote et al. 2019; González-García et al. 2022). On the other hand, in dry forests, palm species of the genus *Sabal* have demonstrated facilitating potential, mitigating the effects of seasonal drought by increasing soil moisture in their

surroundings (Hernández-Salmerón et al. 2023). We believe that the palms present in the mounds assessed here can also act as regeneration nuclei, facilitating the establishment of other species. These species may be particularly promising for the restoration not only of humid environments, but also of dry environments, given their high resistance to aridity (Martins et al. 2024; Silva et al. 2025). Thus, we believe that areas of the Caatinga undergoing management and desertification processes can benefit from the potential of these species in restoration projects.

Earth mounds are ancient ecosystems of great conservation value (Martin et al. 2018; Bassani et al. 2025), as they can provide various ecosystem services and exhibit a distinctive floristic composition due to the adaptation of their flora to flood-prone environments (Cianciaruso et al. 2005; Verona et al. 2026). However, protection of this Brazilian ecosystem remains fragile and specific federal legislation for mound fields is still lacking. Law No. 12,651/2012 (the Native Vegetation Protection Law) legally protects mound fields as they are classified as “diffuse water springs” (olhos d’água difusos, in Portuguese) due to natural groundwater outcrops. Nevertheless, this law is often misapplied, primarily because these sites are not recognised as wetlands formed by “diffuse water springs” by scientists, environmental managers or public agencies (Bassani et al. 2025). In our study, we demonstrate that these sites merit greater attention for conservation, particularly the larger mounds that host palm species. These mounds host a higher concentration of phylogenetic lineages, which may reflect greater genetic variability and specific ecological strategies related to the provision of ecosystem services (Forest et al. 2007; Muvengwi et al. 2022; Farias et al. 2025). Our results are particularly relevant as they were obtained in the context of the Cerrado–Caatinga ecotone, which is characterised by environmental heterogeneity and high floristic dynamics between distinct domains (Ibiapina et al. 2026). Small environmental variations in these regions, such as the alternation between periods of flooding and drought, can disproportionately affect community composition. Furthermore, structurally dominant species, such as palms, can facilitate the recruitment of new species (Morais et al. 2022c). Therefore, our findings help to explain how positive interactions influence the maintenance of diversity in ecotone regions, where the boundaries between

biomes are dynamic and sensitive to climate change (Navarro et al. 2024).

Conclusions

Our study highlights the importance of palms, particularly *Astrocaryum vulgare* in the recruitment and diversification of phylogenetic lineages within woody vegetation on earth mounds. Earth mounds with the presence of *Astrocaryum vulgare* exhibited higher standardized phylogenetic diversity and an overdispersed phylogenetic structure. In contrast, mounds with *Copernicia prunifera* showed a predominantly random phylogenetic structure, whereas mounds without palms displayed phylogenetic clustering and lower standardized phylogenetic diversity. We suggest that the use of these palms, especially *Astrocaryum vulgare*, may represent a promising strategy for ecological restoration in limiting environments.

By emphasising the role of *Astrocaryum vulgare* and *Copernicia prunifera* in maintaining phylogenetic diversity, this study indicates that the protection of these palms and their associated earth mounds should be prioritised in areas under anthropogenic pressure. Furthermore, the preservation of larger earth mounds may contribute to the maintenance of environmental heterogeneity and evolutionary diversity in fragmented landscapes. This reinforces the importance of public policies that recognize these environments as key units for the conservation of the Cerrado and Caatinga domains. Additionally, the patterns observed here suggest that analogous topographic structures and other palm species may play similar roles in structuring phylogenetic diversity, highlighting the potential generalization of these mechanisms to other ecological systems.

We recommend that future studies adopt an experimental approach to directly assess the facilitative potential and the role as natural perches of *Astrocaryum vulgare* and *Copernicia prunifera* in their immediate surroundings. This would provide a clearer understanding of the potential of these species in shaping ecological communities, while also assisting environmental managers in considering these species in restoration projects of degraded areas.

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Author contributions RSBR and RFM conceived the ideas and designed the methodology; RFM, LCSJ, RAI, MTSM, NSR and FMS collected the data; RSBR, RFM and EBS analysed the data; RSBR prepared the original draft of the manuscript; RSBR, NSR, FMS, LCSJ, RAI, MTSM, EBS and RFM reviewed and edited the manuscript. All authors contributed critically to the drafts and approved the final version for publication.

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Data availability No datasets were generated or analysed during the current study.

Declarations

Conflict of interest The authors declare no competing interests.

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