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ORIGINAL ARTICLE

The phylogenetic diversity of plant communities in response to anthropogenic disturbances in a Neotropical savanna

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• **Background and Aims** Traditional assessments of human impact on ecological communities often focus on species richness and abundance, without considering the evolutionary relationship between species. This study evaluated how anthropogenic disturbances, especially those favouring invasive species, alter the phylogenetic diversity and structure of plant communities in the Cerrado, a global biodiversity hotspot.
• **Methods** We compared α and β-phylogenetic diversity and structure (using phylogenetic richness, standardized phylogenetic richness, standardized effect size of the mean pairwise distance and standardized effect size of the mean nearest taxon distance) in plant communities from 11 roadside sites, characterized by high densities of exotic species, with ten conservation areas (reserves), where exotic species occur at much lower densities. Phylogenetic metrics were calculated using data from the entire community or from native species only.
• **Key Results** Phylogenetic richness was consistently lower in roadside communities than in reserves, reflecting reduced species richness under chronic disturbance. In contrast, standardized phylogenetic richness did not differ between habitats, indicating that roadside communities retain a broad representation of native evolutionary lineages. Differences in phylogenetic structure emerged only when exotic species were included in the analysis and, in this case, roadside communities exhibited phylogenetic clustering at both deep and terminal evolutionary levels, whereas reserve communities showed a random phylogenetic structure. Similarly, differences in phylogenetic dissimilarity between roadside and reserve communities were detected only when data from exotic species were included in the analysis. In this case, evidence of phylogenetic homogenization in roadside communities was detected, and this was probably associated with the much greater abundance of invasive grasses in these sites than in the protected habitats.
• **Conclusions** Overall, our findings indicate that chronic disturbance is associated with phylogenetic homogenization in Cerrado plant communities, particularly in habitats dominated by invasive grasses. We suggest that protected areas play a crucial role in preserving phylogenetic diversity, especially for disturbance-sensitive clades. Thus, maintaining and expanding reserves, safeguarding remnant habitats and managing biological invasions within disturbed landscapes are key strategies for conserving the evolutionary heritage and biodiversity of the Cerrado.

Key words: Biotic homogenization, Cerrado, environmental filtering, invasive grasses, *Melinis minutiflora*, roadsides, *Urochloa decumbens*.

INTRODUCTION

Anthropogenic disturbances have converted natural ecosystems into landscapes of habitat fragments embedded within a matrix of human-transformed land uses (Haddad *et al.*, 2015; Pompeu *et al.*, 2024). These changes not only reduce species richness within individual communities but also simplify species composition across communities, often leading to loss of

biodiversity and the disruption of ecosystem functioning (Socolar *et al.*, 2016; Qiu and Cardinale, 2020). Although most biodiversity assessments have focused on taxonomic patterns, growing evidence suggests that a comprehensive understanding of disturbance requires the integration of multiple dimensions of biodiversity (Kramer *et al.*, 2023).

Among these dimensions, phylogenetic diversity (PD; a metric of phylogenetic richness) provides an essential evolutionary context by quantifying the extent to which evolutionary history is represented within communities (Faith, 1992). Because PD scales directly with species richness, declines in richness driven by disturbance often translate into proportional reductions in evolutionary history (Swenson, 2009). Nevertheless, this is not always the case, and one way to address whether losses in PD are higher or lower than expected (given the taxonomic richness of the focal communities) is to compute the standardized effect sizes of PD (SES-PD) and compare them with values generated using a null model approach (Miller *et al.*, 2017). Phylogenetic divergence metrics, in contrast, describe how species are distributed across the phylogeny at different evolutionary depths. Mean pairwise distance (MPD) captures broad, deep-level structure, whereas mean nearest taxon distance (MNTD) reflects more recent divergence patterns (Webb, 2000; Webb *et al.*, 2002). Their standardized versions (SES-MPD and SES-MNTD) indicate whether assemblages are more clustered or dispersed than expected by chance, providing insights into whether disturbance favours environmental filtering of conserved traits or promotes coexistence among distantly related species (Freilich and Connolly, 2015).

Beyond local (α) diversity patterns, spatial dissimilarities in evolutionary history (phylogenetic β-diversity) provide additional insights into how disturbances reshape regional biodiversity (Graham and Fine, 2008). Phylogenetic β-diversity quantifies differences in lineage composition among sites and can reveal whether disturbance promotes phylogenetic homogenization, when unique lineages are lost and communities become increasingly similar, or phylogenetic differentiation, when distinct disturbance regimes favour different sets of lineages (Kramer *et al.*, 2023). Metrics of phylogenetic dispersion can also be extended to the β-scale (βMPD and βMNTD), enabling detection of whether species replacements in older or more recent clades drive phylogenetic dissimilarities among communities. Together, βPD, βMPD and βMNTD offer a multiscale perspective on whether disturbance restructures regional evolutionary pools by reducing deep-branch diversity, altering fine-scale relatedness, or both.

The Cerrado of central Brazil, a savanna-dominated biodiversity hotspot, provides a compelling context to investigate these processes. More than half of its original vegetation has been converted to agriculture, pasture and infrastructure (Zenni *et al.*, 2018; Pompeu *et al.*, 2024), generating chronic disturbance that triggers local extinctions and simplifies habitat structure. These altered conditions have facilitated the spread of non-native species, particularly African grasses, whose competitive dominance and tolerance to disturbance enable them to proliferate where native vegetation has been compromised (Zenni *et al.*, 2018; Mormul *et al.*, 2022). Once established, these grasses modify fire regimes and vegetation structure, reinforcing disturbance and potentially accelerating native species losses (Gorgone-Barbosa *et al.*, 2016; Damasceno *et al.*, 2018).

Roadside habitats (i.e. narrow vegetation strips along roads) represent some of the most heavily disturbed environments in the Cerrado (Altomare et al., 2025a). Chronic exposure to traffic, recurrent fires and road-maintenance management practices (van der Ree *et al.*, 2015) facilitates the expansion of exotic grasses (Vasconcelos *et al.*, 2014; Assis *et al.*, 2021). As a result, roadside plant communities often show reduced taxonomic diversity and strong dominance of African grasses relative to nearby protected areas (Vasconcelos *et al.*, 2014). That earlier study, however, focused on patterns of species richness and taxonomic composition and did not evaluate how these changes translate into differences in evolutionary relationships among species. Here, we revisit the dataset of Vasconcelos *et al.* (2014) to assess whether reductions in species richness are accompanied by shifts in phylogenetic diversity, phylogenetic structure and lineage turnover, thereby providing new insights into how disturbance reshapes the evolutionary composition of Cerrado plant communities.

Here, we compare plant communities between roadsides and nearby protected areas (reserves) with the intent of gaining a better understanding of how human-associated disturbances affect the phylogenetic diversity of Neotropical savannas, at both α- and β-scales. For this, we used: (1) α- richness metrics (PD and SES-PD) to compare evolutionary history; (2) α-divergence metrics (SES-MPD and SES-MNTD) to compare phylogenetic structure at deep and terminal branches; and (3) phylogenetic β-diversity to evaluate lineage turnover between sites of the same habitat type (roadsides or reserves). In doing so, we tested the hypothesis that the multiple disturbances associated with the roadside habitat would reduce the phylogenetic diversity and affect the phylogenetic structure of savanna plant communities. Because invasive grasses represent the most conspicuous form of disturbance along roadsides across the Cerrado (Vasconcelos *et al.*, 2014), we explored differences in the phylogenetic patterns of native savanna plant communities when exotic species were included or excluded from the analyses. Specifically, we assessed whether the differences observed between roadside and reserve communities were maintained after removal of exotic species from the dataset.

At the α-scale, we expected roadside plant communities to show reduced phylogenetic richness (i.e. lower PD and SES-PD) and a more clustered phylogenetic structure (i.e. lower SES-MPD and lower SES-MNTD) when compared with communities from nearby protected savanna areas, whereas at the β-scale we expected to find lower levels of phylogenetic dissimilarity between roadsides (and thus greater phylogenetic homogenization) than in reserve communities. Furthermore, we expected that the exclusion of exotic grasses from our analyses would be associated with changes in the magnitude of the differences between roadside and reserve plant communities. By linking these predictions to evolutionary mechanisms, our study provides a framework for better understanding human impacts on biodiversity in the Cerrado. Given that roadside vegetation represents one of the most intensely altered habitats in the region, our study might provide important insights about changes that could emerge in more preserved areas as land-use intensification in the Cerrado advances.

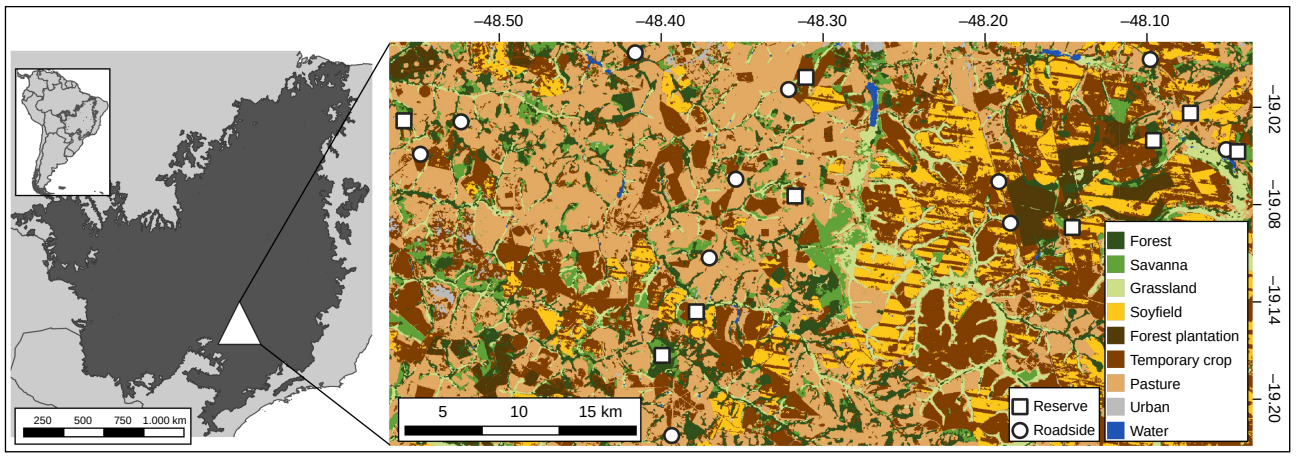

FIG. 1. Map showing the distribution of the Cerrado biome (left) and the location of the sampling sites in Minas Gerais state, Brazil (right).

MATERIALS AND METHODS

Study sites and vegetation sampling

The data used in this study derive from the study by Vasconcelos *et al.* (2014), who sampled the Cerrado plant community found in ten relatively well-preserved sites (hereafter 'reserves') and 19 roadsides located within the Triângulo Mineiro region, in Minas Gerais State, Brazil (between the coordinates −48.58538, −19.22249 and −48.04381, −18.98643; Fig. 1). The monthly average temperature in the study region is 22.8 °C; the annual average rainfall is 1600 mm, with >70 % of the precipitation occurring between November and March (Cardoso *et al.*, 2010). The dominant soils of the region are oxisols, with poor nutrient availability and moderate to strong acidity (Lopes and Cox, 1977; Haridasan and De Araújo, 1988). The vegetation in all sampled areas is the dominant type of vegetation in the Cerrado biome and known locally as cerrado *sensu stricto*. This savanna vegetation is characterized by scattered trees, shrubs, and a herbaceous layer dominated by grasses (Sano *et al.*, 2008). To minimize any possible influence of geographical distance on diversity patterns (Rosenzweig, 1995), data from 8 of the 19 roadsides sampled by Vasconcelos *et al.* (2014) were excluded from our analysis for being far away (>22 km apart) from any of the reserves. The roadside vegetation surveys were conducted in the area adjacent to the roads, where legislation prevents any activity except the expansion of the road itself (DNIT, 2013).

In each reserve or roadside, the composition and cover of species in the lower stratum were assessed using the line-intercept method (Canfield, 1941; Munhoz and Araújo, 2011). At each site, two parallel transects of 250 m each were established at a height of 1 m above the ground. Along each transect, measurements were taken at every other metre to record the length of the transect intercepted by each individual below the line. In roadside sites, transects were allocated parallel to the road, positioned 5 m from the road edge, and separated from each other by ∼10 m (Fig. S1). In protected areas, transects were placed within the interior of the fragments, away from road influence. The relative cover of each species at a given site was calculated by dividing the total intercepted length for that species by the combined length of the two transects (500 m).

Phylogenetic supertree

To obtain a phylogeny for the 271 plant species sampled by Vasconcelos *et al.* (2014) (including grasses, forbs and woody species; Supplementary Data Table S1; Fig. S2), we used the package *V.PhyloMaker* (build.nodes.1) (Jin and Qian, 2019). The package uses an updated and expanded version (i.e. GBOTB.extended.tre) of the dated megaphylogeny GBOTB for Angiosperms (Smith and Brown, 2018) and the clade in the phylogeny by Zanne *et al.* (2014) for pteridophytes. It is the largest dated mega-tree for vascular plants, including 10 587 genera and 74 533 species (Jin and Qian, 2019). V.PhyloMaker takes this mega-tree as a backbone to generate phylogenies for vascular plants. We used the 'phylo.maker' function to prune the backbone tree under Scenario 3 because this scenario is recommended for the study of community phylogenetics (Qian and Jin, 2016; Jin and Qian, 2019, 2022).

Phylogenetic diversity analyses

We assessed the phylogenetic diversity and structure of plant communities using complementary metrics at the local (α) and landscape (β) scales. All analyses were based on a site × species matrix of species cover, and metrics were calculated both for the entire community (including native and exotic species) and for native species only. This approach allows us to distinguish patterns driven by overall community composition from those reflecting the phylogenetic structure of native assemblages after removal of the contribution of exotic species. Analyses including all species capture the combined effects of disturbance and invasion, whereas analyses restricted to natives assess whether native lineages retain similar phylogenetic structure across habitats.

For α-diversity, we calculated Faith's phylogenetic diversity (PD) to quantify total evolutionary history, along with mean pairwise distance (MPD) and mean nearest taxon distance (MNTD) to capture phylogenetic relationships at deep

and terminal evolutionary scales (Webb, 2000; Webb *et al.*, 2002). Standardized effect sizes (SES-PD, SES-MPD and SES-MNTD) were computed to evaluate deviations from random expectations, such as:

$$\text{SES} = \frac{\text{Observed} - \text{Mean of null distribution}}{\text{Standard deviation of null distribution}}$$

For β-diversity, we used phylogenetic Sørensen's index (βPD), abundance-weighted pairwise distance (βMPD) and abundance-weighted nearest neighbour distance (βMNTD) (Swenson, 2011). βPD measures the fraction of branch length shared between communities (Bryant *et al.*, 2008), βMPD reflects overall dissimilarity, and βMNTD emphasizes differences among closely related species.

Null communities for both α- and β-diversity metrics were generated using the 'independent swap' algorithm with 999 randomizations, which preserves species occurrence frequencies and coverage while randomizing species associations. All analyses used the full phylogeny, including native and exotic species. Negative SES values indicate phylogenetic clustering, whereas positive values indicate overdispersion. Analyses were performed in R (Kembel *et al.*, 2010) using the *picante* package (Pavoine, 2020), with the functions 'phylosor', 'comdist' and 'comdistnt'.

Phylogenetic composition

To assess differences in phylogenetic composition among sites, we applied phylogenetic ordination techniques that capture the distribution of evolutionary lineages across communities. Specifically, we used the evolutionary principal component analysis based on the Hellinger distance (evoPCAHellinger) (Pavoine, 2016). This method effectively balances the contributions of both deep and shallow phylogenetic nodes, offering a robust framework for detecting phylogenetic patterns along environmental gradients. The analyses were performed using the *adiv* package using the 'evopcahellinger' function, in R.

Statistical analyses

To evaluate differences in phylogenetic diversity between plant communities in reserves and roadsides and to assess whether the patterns observed were maintained after the exclusion of exotic species, we fitted linear mixed-effects models for both α- and β-diversity metrics. Separate models were run for each phylogenetic index, including PD, SES-PD, SES-MPD and SES-MNTD for α-diversity, and βPD, βSES-PD, βSES-MPD and βSES-MNTD for β-diversity.

In all models, habitat (reserve vs. roadside) was included as a fixed factor. For α-diversity analyses, the random structure accounted for repeated measures of diversity derived from different community definitions within the same site (i.e. considering all species or native species only; hereafter 'community type'). For β-diversity analyses, the random structure accounted for repeated measures of phylogenetic dissimilarity calculated between pairs of sites within the same habitat type, again considering both community definitions.

To determine whether plant communities exhibited phylogenetic clustering or overdispersion, standardized effect size (SES) metrics were tested against zero using one-sample *t*-tests. All statistical analyses were conducted in R v.4.3.2 (R Core Team, 2023), using the packages *lme4* (Bates *et al.*, 2015) and *lattice* (Sarkar, 2008).

RESULTS

Vegetation structure and composition

On average, plant communities within reserves had almost twice as many native plant species as the roadside communities (reserves, 79.70 ± 13.18 species and roadsides, 40.44 ± 13.15 species; Table 1). In addition, plant communities within reserves had three times more native grass species than the roadside communities (Table 1). Of the 271 plant species found across all sampling plots, only four were exotics: *Andropogon gayanus* Kunth, *Hyparrhenia rufa* (Nees)

Table 1. Differences in the abundance and species richness of grasses, forbs and woody plants between plant communities surveyed along roadsides or within reserves (data derived from Vasconcelos *et al.*, 2014).

	Reserves			Roadsides				
	Mean		s.d.	Mean		s.d.	*t*-test	*p*-value
Species richness								
All species	81.2	±	13.9	42.36	±	14.35	6.30	<0.001
Non-native grasses	1.5	±	0.71	1.82	±	0.75	1.00	0.33
Native grasses	12.4	±	2.37	4.09	±	2.3	8.14	<0.001
Native forbs species	9.3	±	3.68	8.09	±	3.83	0.74	0.47
Native woody species	58	±	12.5	28.36	±	11.86	5.56	0.001
Plant cover (%)								
Non-native grasses	2.99	±	5	80.41	±	6	31.47	<0.001
Native grasses	34.86	±	16	4.64	±	4	5.81	<0.001
Native forbs	2.5	±	2	2.38	±	2	0.15	0.88
Native woody plants	27.04	±	13	9.87	±	5	4.02	0.002

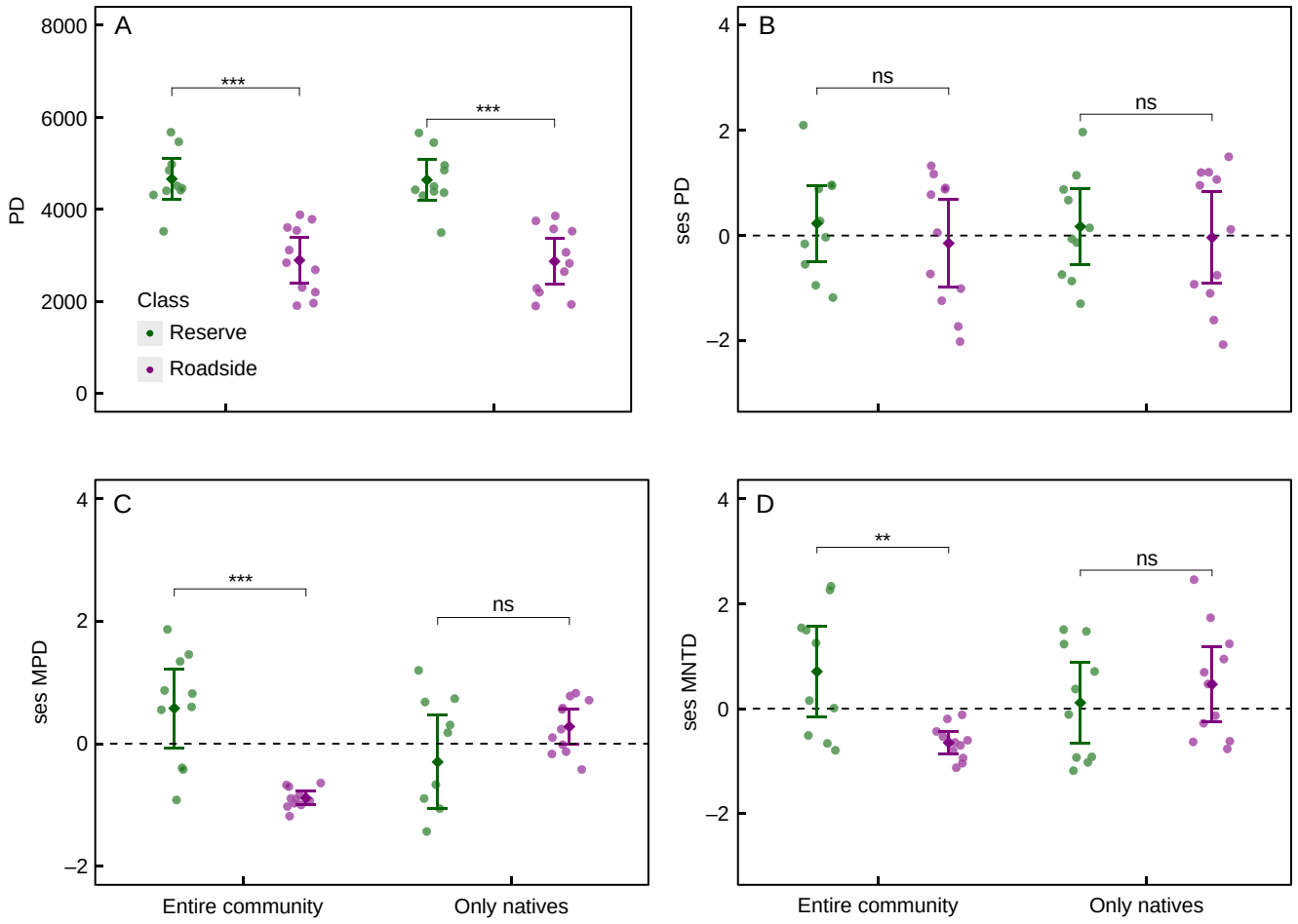

FIG. 2. Comparison of phylogenetic α-diversity between plant communities surveyed along roadsides and within reserves, calculated for datasets including all species and for datasets restricted to native species. (A) Phylogenetic diversity (PD). (B) Standardized effect size of phylogenetic diversity (SES PD). (C) Standardized effect size of the mean pairwise distance (SES MPD). (D) Standardized effect size of the mean nearest taxon distance (SES MNTD). Values represent means and 95 % confidence intervals for each metric. Dots correspond to individual plant communities. Mean values whose 95 % confidence intervals do not intersect the dotted line indicate deviation from random phylogenetic structure. *Significant difference between reserves and roadsides ($P < 0.05$); NS, non-significant differences. Differences shown reflect how phylogenetic patterns vary depending on the analytical inclusion or exclusion of exotic species.

Stapf, *Melinis minutiflora* P.Beauv. and *Urochloa decumbens* (Stapf) R.D.Webster (Supplementary Data Fig. S1). The African grass *Urochloa decumbens* was by far the most abundant species in the roadside habitat, whereas the native grasses *Echinolaena inflexa* (Poir.) Chase and *Tristachya leiostachya* Nees (all native) were the most abundant species in the reserves (Supplementary Data Fig. S2). The cover of native grasses was 7.5 times greater in the reserves than along roads, whereas the cover of exotic grasses was 27 times greater in roadsides than in reserves. The cover of forbs was similar between the two habitats, whereas that of woody species was two times greater in the reserves (Table 1).

Phylogenetic α-diversity

Phylogenetic diversity (PD) was positively correlated with species richness (Supplementary Data Fig. S3); consequently, PD was lower in roadsides than in reserves, regardless of whether exotic species were included or excluded from the analyses (habitat: PD $F_{1,19} = 35.15$, $P < 0.001$; community type (with or without exotics): PD $F_{1,19} = 23.31$, $P < 0.001$). In contrast, standardized effect sizes of PD (SES-PD) showed no significant differences between habitats, irrespective of the inclusion or exclusion of exotic species (habitat: $F_{1,19} = 0.17$, $P = 0.68$; community type: $F_{1,19} = 2.07$, $P = 0.17$). Moreover, based on SES-PD, the phylogenetic richness of plant communities in both reserves and roadsides did not differ from the random expectation, irrespective of whether the entire community or only the native species were considered (Fig. 2; Table S2).

Regarding the divergence-based metrics, mixed-effects models revealed a significant interaction between the effects of habitat and community type on both SES-MPD and SES-MNTD (habitat × community type: SES-MPD $F_{1,19} = 96.29$, $P < 0.001$; SES-MNTD $F_{1,19} = 34.06$, $P < 0.001$; Fig. 2). When all species were included in the analysis, both SES-MPD and SES-MNTD were significantly higher in reserves than in roadsides (habitat effect: SES-MPD $F_{1,19} = 28.01$, $P < 0.001$; SES-MNTD $F_{1,19} = 12.98$, $P = 0.002$). In contrast, when exotic species were excluded, no significant

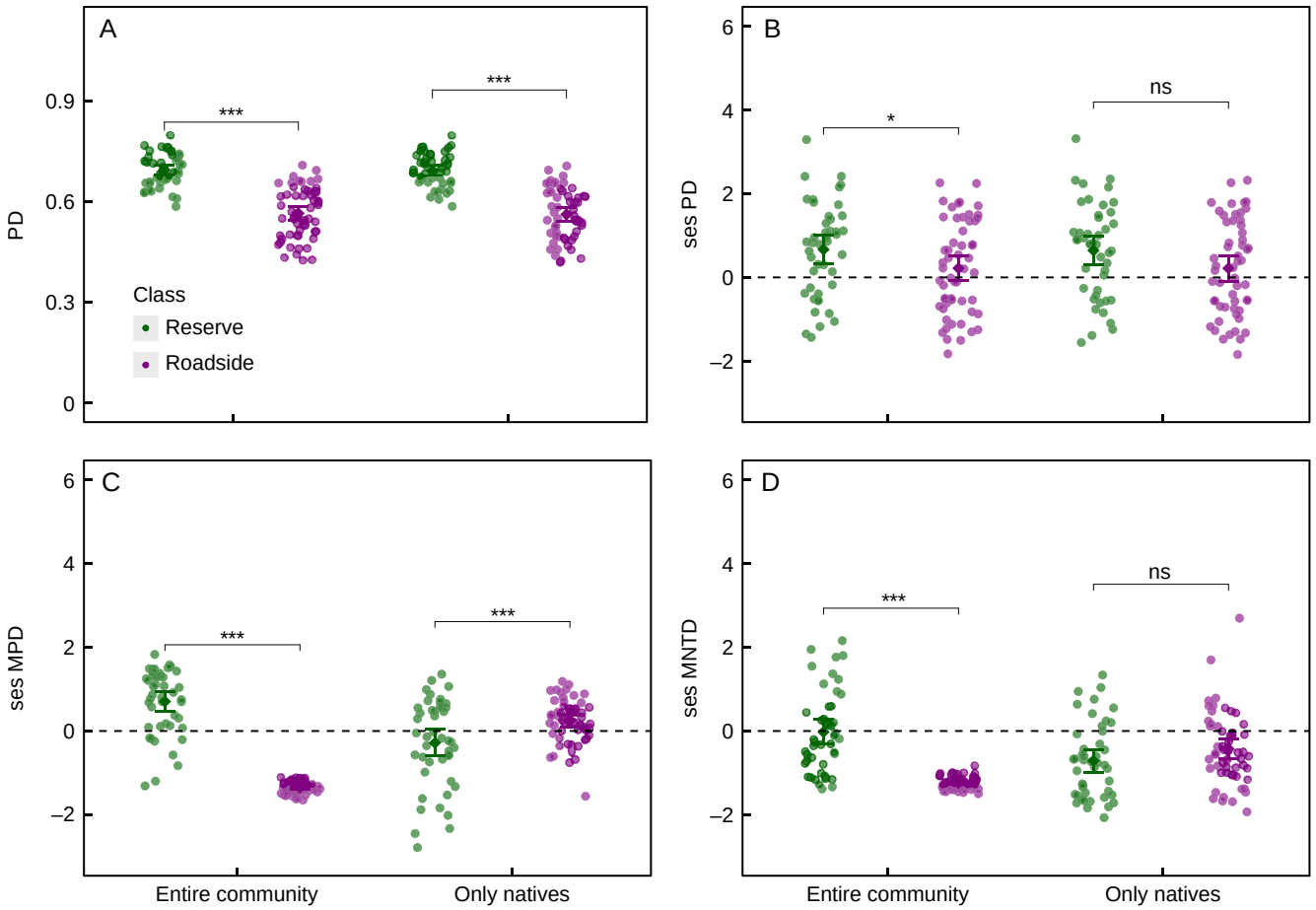

FIG. 3. Comparison of phylogenetic β-diversity between plant communities surveyed along roadsides and within reserves, calculated for datasets including all species and for datasets restricted to native species. (A) Phylogenetic β-diversity based on phylogenetic diversity (βPD). (B) Standardized effect size of phylogenetic β-diversity (SES βPD). (C) Standardized effect size of the mean pairwise distance (SES βMPD). (D) Standardized effect size of the mean nearest taxon distance (SES βMNTD). Values represent means and 95 % confidence intervals for each metric, with dots corresponding to individual pairwise comparisons between plant communities. Mean values whose 95 % confidence intervals do not intersect the dotted line indicate deviation from null expectations of phylogenetic dissimilarity. *Significant difference between reserves and roadsides ($P < 0.05$); NS, non-significant differences. Differences shown reflect how phylogenetic turnover varies depending on the analytical inclusion or exclusion of exotic species.

differences in phylogenetic divergence were detected between roadside and reserve communities (habitat effect: SES-MPD $F_{1,19} = 2.73$, $P = 0.114$; SES-MNTD $F_{1,19} = 0.55$, $P = 0.463$; Fig. 2).

Plant communities in reserves exhibited a random phylogenetic structure, regardless of whether analyses included the entire community or the native species only (entire community: one-sample *t*-test, SES-MPD: $t = 2.02$, $P = 0.07$; SES-MNTD: $t = 1.86$, $P = 0.10$; native species only: SES-MPD: $t = -0.89$, $P = 0.40$; SES-MNTD: $t = 0.33$, $P = 0.75$). In contrast, roadside plant communities displayed a clustered phylogenetic structure when considering the entire community (one-sample *t*-test, SES-MPD: $t = -17.85$, $P < 0.001$; SES-MNTD: $t = -6.66$, $P < 0.001$), but shifted to a random structure when analyses were restricted to native species (SES-MPD: $t = 2.13$, $P = 0.06$; SES-MNTD: $t = 1.45$, $P = 0.18$; Fig. 2).

Phylogenetic β-diversity

For β-diversity, we found that PD was consistently lower in roadsides than in reserves (habitat: PD $F_{1,196} = 0.41$, $P < 0.001$), regardless of whether exotic species were included or excluded from the analyses (habitat × community type: βPD $F_{1,196} = 0.001$, $P = 0.89$). However, the standardized effect size of phylogenetic β-diversity (SES-βPD) was lower in the roadside than in the reserve communities when the entire community was considered, but not when exotic species were excluded from the analysis (habitat: βPD $F_{1,196} = 4.95$, $P = 0.05$). Additionally, we detected a significant interaction between habitat and community type on β-diversity metrics based on mean pairwise distances or nearest-taxon distances (habitat × community type: SES-βMPD $F_{1,196} = 81.93$, $P < 0.001$; SES-βMNTD $F_{1,196} = 81.93$, $P < 0.001$). When all species were considered, SES-βMPD was higher in reserves than in roadsides (pairwise habitat effect: SES-MPD $t\text{-ratio}_{1,196} = 14.90$, $P < 0.001$; SES-MNTD $t\text{-ratio}_{1,196} = 7.77$, $P < 0.001$), whereas the opposite trend was found when only native species were considered (pairwise habitat effect: SES-MPD, $t\text{-ratio}_{1,196} = 3.91$, $P < 0.001$; Fig. 3). Similarly, when all species were considered, SES-βMNTD was higher in reserves than in roadsides (habitat: SES-MNTD $F_{1,196} = 36.53$, $P < 0.001$), whereas no habitat-related differences were detected when

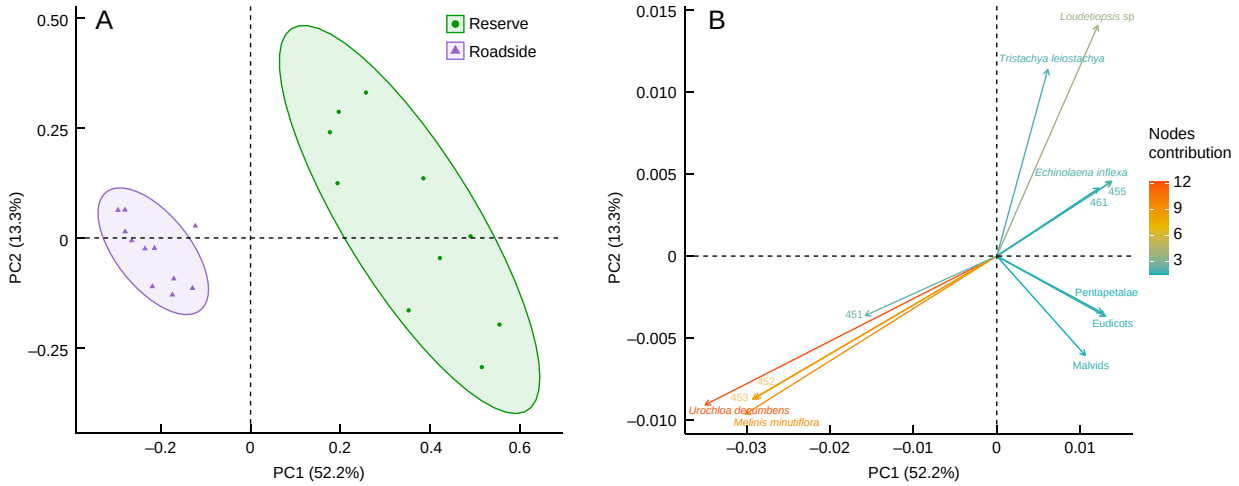

FIG. 4. (A) Ordination illustrating the differences in phylogenetic composition between plant communities in reserves or roadsides. (B) Contribution of each plant lineage to the positioning of plots in the multivariate space.

only the native species were considered (pairwise habitat effect: SES-MNTD t-ratio$_{1,196} = -1.82$, $P = 0.07$; Fig. 3; Table S3).

In all the analyses (i.e. including or excluding the exotic species), the dissimilarity in phylogenetic richness (SES-βPD) between reserve communities was significantly greater than expected (entire community: one-sample t-test, SES-PD: $t = 4.01$, $P < 0.001$; native species only: SES-βPD: $t = 3.82$, $P < 0.001$), whereas SES-βPD between roadside communities did not differ from the random expectation (entire community: one-sample t-test, SES-βPD: $t = 1.45$, $P = 0.15$; native species only: SES-βPD: $t = 1.43$, $P = 0.16$).

In reserves, analyses involving all species revealed that SES-βMPD was higher than expected (one-sample t-test: $t = 6.08$, $P < 0.001$), whereas SES-βMNTD did not deviate from randomness ($t = 0.15$, $P = 0.88$). In contrast, when analyses were restricted to native species, reserve communities exhibited a random structure for SES-βMPD ($t = 1.79$, $P = 0.08$) and a clustered structure for SES-βMNTD ($t = 5.38$, $P < 0.001$). Roadside communities presented phylogenetic clustering for SES-βMNTD, regardless of the inclusion or exclusion of exotic species ($t = 72.99$, $P < 0.001$ and $t = 3.65$, $P < 0.001$, respectively), whereas for SES-βMNTD phylogenetic clustering was detected when all species were included ($t = -63.35$, $P < 0.001$), whereas phylogenetic segregation was observed when only native species were considered ($t = 3.38$, $P = 0.001$) (Fig. 3).

Phylogenetic composition

The principal component analysis revealed that the phylogenetic composition of roadside and reserve communities was clearly distinct, with the first two principal component (PC) axes explaining 65.5 % of the total variation (PC1 = 52.2 %, PC2 = 13.3 %; Fig. 4). The first axis represented a phylogenetic gradient associated with invasive Poaceae, particularly *Urochloa decumbens* and *Melinis minutiflora* (Fig. 4B). The nodes associated with these species showed the highest contributions and longest vectors in the ordination space, clustering towards negative values of PC1. Positive values of PC1 were associated with eudicots, particularly the malvid clade. The second principal component captured additional phylogenetic differentiation within graminoid lineages as native Cerrado grasses, such as *Tristachya leiostachya* and *Echinolaena inflexa*, loaded positively on PC2 (Fig. 4B).

When exotic species were excluded from the analysis, the first two ordination axes explained a smaller proportion of the total variation (48.3 %), and phylogenetic structure was distributed across multiple nodes and clades (Supplementary Data Fig. S4). Rather than being driven by a limited set of highly influential lineages, variation in phylogenetic composition reflected broader lineage turnover involving both native graminoid species and multiple eudicot clades (Supplementary Data Fig. S4).

DISCUSSION

Our study evaluates the differences in phylogenetic diversity, structure and composition of Cerrado plant communities between habitats with contrasting levels of disturbance. At the α-scale, we hypothesized that roadside plant communities showed reduced phylogenetic richness (i.e. lower PD and SES-PD) when compared with communities from nearby protected savanna areas (reserves). Our analyses revealed that plant communities associated with roadsides have fewer species and thus lower PD than those in reserves. However, when controlling for differences in species richness between habitats (SES-PD), phylogenetic richness did not differ from the random expectation, in both the roadside and the reserve habitats. This indicates that disturbed roadside plant communities do not necessarily experience a decline of native evolutionary history despite reduced species richness.

As expected, we found a much lower degree of phylogenetic divergence between plant species in roadside than in reserve communities, and this was true for both deep and shallow nodes within the phylogenetic tree. Furthermore, plant communities associated with roadsides, in contrast to those in reserves, presented a clustered phylogenetic structure. However, this was no longer the case when exotic

species were removed from our analysis, suggesting that road-associated disturbances, particularly the invasion of non-native species, might be acting as a strong environmental filter. Although our results do not constitute direct evidence of a causal effect of exotic grasses on the phylogenetic diversity and structure of Cerrado plant communities, they are in agreement with previous studies that emphasize the prevalence of phylogenetic clustering in instances of biological invasions (Loiola *et al.*, 2018; Diniz *et al.*, 2024). Both *Urochloa decumbens* and *Melinis minutiflora*, the main invaders of the roadside habitat, were found to affect the abundance and richness of native species (Pivello *et al.*, 1999; Almeida-Neto *et al.*, 2010; Mendonça *et al.*, 2015; Damasceno *et al.*, 2018). With traits such as rapid growth, high biomass production and efficient resource acquisition, these invasive grasses can outcompete native grasses and many eudicots (Klink, 1996; Lannes *et al.*, 2016). The competitive advantages associated with these traits are likely to be exacerbated in roadside habitats, where frequent disturbances (e.g. fire, soil compaction and nutrient runoff) and higher light availability create favourable conditions for invasive grasses to spread rapidly. In contrast, native grasses, such as *Echinolaena inflexa*, are better adapted to the nutrient-poor, acidic soils typical of undisturbed Cerrado habitats (Lira-Martins *et al.*, 2025), which helps to explain their higher prevalence in reserves compared with roadsides.

At the β-scale, we predicted lower phylogenetic dissimilarity among roadside communities, thus leading to phylogenetic homogenization. Indeed, this was found to be the case only when all plant species (native and exotics) were included in the analysis. Previous studies have already emphasized the important role played by dominant invasive species, which can impose a shared phylogenetic signature across sites, in the biotic homogenization of plant communities (Li *et al.*, 2018; Petsch *et al.*, 2022; Bando et al., 2023), and our findings lend additional support to this view.

However, when exotic species were removed from the analyses, signals of phylogenetic homogenization weakened or disappeared, and in some cases, phylogenetic dissimilarity among roadside communities exceeded that observed among reserves. This unexpected pattern might indicate that environmental conditions are more homogeneous among different reserves than among different roadside sites, potentially allowing distinct native clades to establish in different roadside locations (Gutiérrez-Cánovas *et al.*, 2013). Greater environmental heterogeneity among roadsides might arise from multiple factors, including: the time since road construction, which influences successional stages and vegetation recovery; the composition of the surrounding landscape matrix, which shapes seed input and propagule pressure (Arenas *et al.*, 2017; Jakobsson *et al.*, 2018); and variation in traffic intensity and frequency, which affects disturbance regimes, pollution levels and wildlife movement (Vakhlamova *et al.*, 2016). Together, these factors can generate a mosaic of microhabitats and environmental filters among the different roadsides, potentially supporting divergent native plant assemblages across sites. Although these mechanisms are ecologically plausible, a detailed evaluation of their relative importance lies beyond the scope of the present study and represents an important direction for future research.

An alternative but not mutually exclusive interpretation is that increased phylogenetic differentiation among native roadside communities represents a transient phase preceding biotic homogenization. Under this scenario, initially distinct communities might gradually converge towards increasingly similar compositions dominated by widespread generalist taxa over time (Socolar *et al.*, 2016; Benchimol *et al.*, 2017; Rocha-Santos *et al.*, 2023). In this context, generalist species increasing in dominance can reduce both compositional and phylogenetic turnover among sites at the landscape scale. Such homogenization might constrain ecosystem functioning by narrowing the diversity of functional traits and biotic interactions within communities. Changes in trait composition and dominance structure can influence key ecological processes by altering vegetation structure, floral resource diversity, root architecture, litter inputs and biomass distribution, which, in turn, might affect pollination dynamics, soil stabilization, nutrient retention and the regulation of water fluxes, with consequences for the ecological integrity of Cerrado landscapes (Chaffin *et al.*, 2016; Damasceno *et al.*, 2018; Altomare et al., 2025b).

Our analyses of phylogenetic composition suggest that the reduced phylogenetic diversity and increased clustering observed in the roadside habitat are associated with the strong dominance of a small number of exotic grasses, rather than with exotic species richness *per se*. Although four exotic grass species were recorded across all plots, differences between roadside and reserve communities appear to have been mediated largely by the widespread dominance of *Urochloa decumbens* and *Melinis minutiflora*, which, as indicated earlier, share functional traits that allow them to outcompete native grasses and other savanna plant species (Pivello *et al.*, 1999; Mendonça *et al.*, 2015; Damasceno *et al.*, 2018).

We acknowledge that an important limitation of this study is the difficulty of disentangling the independent effects of disturbance and invasion. Plant communities along roadsides are subject to multiple types of disturbance, including highly competitive pressure from invasive grasses. Consequently, our results cannot isolate causal mechanisms and should be interpreted as describing phylogenetic patterns under combined disturbance-invasion scenarios. Future studies incorporating disturbed sites where exotic grasses are absent or rare, or sites representing early invasion stages, will be essential for separating these effects and for informing invasion prevention strategies.

Concluding remarks

Roadside habitats presented reduced α- and β-phylogenetic plant diversity relative to adjacent protected habitats. However, these differences were associated either with differences in species richness (i.e. roadsides have lower PD because these habitats have a smaller density of species) or with differences in the coverage of individual species (i.e. phylogenetic divergence was lower on roadsides but only when considering data from invasive grasses, whose coverage was much higher on roadsides). However, when differences in species richness were removed and/or when analyses were restricted to native species, habitat-related differences in phylogenetic diversity and structure disappeared, revealing that a broad

representation of native evolutionary lineages can persist in the roadside habitats despite the high levels of disturbance in such habitats.

In a biome where more than half of the original vegetation has already been lost (Pompeu *et al.*, 2024), roadside habitats provide useful model systems for anticipating how protected Cerrado areas might respond to escalating habitat disturbances and fragmentation (Altomare et al., 2025b). Although protected areas remain essential for conservation of phylogenetic diversity, especially for disturbance-sensitive clades, our findings suggest that conservation strategies should also consider the management of invasive grasses in disturbed habitats to prevent phylogenetic homogenization. In this sense, future research should integrate temporal data, functional trait information and experimental approaches to disentangle the mechanisms underlying dominance-driven phylogenetic change and assess the long-term resilience of native lineages across disturbance gradients. Such efforts will be crucial for developing conservation and management strategies that are both realistic and forward-looking in increasingly human-modified Cerrado landscapes.

SUPPLEMENTARY DATA

Supplementary data are available at *Annals of Botany* online and consist of the following. Table S1: list of plant species recorded in the study, classified by functional group (graminoids, forbs and woody species), and their occurrence across habitat types. Columns indicate whether each species was recorded in reserve sites, roadside sites or in both habitats. Table S2: differences in the phylogenetic diversity and structure (PD and ses PD), mean phylogenetic distance (ses MPD) and in mean nearest taxon distance (ses MNTD) between plant communities in reserves or along roadsides at the α-level. Comparisons include either all species in each community ('Entire community') or only the native species. The values highlighted in bold exhibit significant differences. Table S3: differences in the phylogenetic diversity and structure (PD and ses PD), mean phylogenetic distance (ses MPD) and nearest taxon distance (ses MNTD) between plant communities in reserves or along roadsides at the β-level. Comparisons include either all species in each community ('Entire community') or only the native species. The values highlighted in bold exhibit significant differences. Figure S1: schematic figure illustrating how transects were allocated across roadside areas. In reserves, the same sampling methodology was applied; however, transects were placed within the interior of habitat fragments, minimizing or excluding the influence of nearby roads. Figure S2: phylogenetic tree illustrating the evolutionary relationships among 271 Cerrado plant species. The dual-coloured bars indicate the relative abundance of each species in the reserves or along roadsides. Squares denote the functional group to which each species belongs. Red triangles represent the non-native species. Figure S3: relationships between species richness and phylogenetic diversity in plots located within reserves and along roadsides. Figure S4: (A) Ordination of plots of the native communities based on the first two axes (PC1 and PC2) of a principal component analysis using Hellinger distance on phylogenetic composition (evoPCAHellinger), illustrating the distribution of plots according to their phylogenetic similarities. (B) Same ordination showing the contribution of each lineage to the positioning of plots in the multivariate space.

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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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