Journal of Vegetation Science

Journal of Vegetation Science IAVS

SPECIAL ISSUE: ISLAND PLANT COMMUNITIES OPEN ACCESS

Islanded Islands: Dual Isolation Drive Distinctive and Threatened Floras of Neotropical Maritime Inselbergs

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Received: 1 April 2025 | **Revised:** 1 April 2025 | **Accepted:** 24 April 2025

Co-ordinating Editor: Jorge Capelo

Funding: Financial support for this work was provided by the Fundação de Amparo à Pesquisa do Estado de São Paulo (FAPESP; grant no. 2022/02667-1) and CBioClima (Processo FAPESP 2021/10639-5). Additional funds were provided by grants from FAEPEX (FUNCAMP) to F.P. and fellowships to G.P.S. (FAPESP; grant no. 2023/02443-9 and 2024/20342-8), V.A.K. (FAPESP; grant no. 2022/09041-0 and 2024/17825-7), and F.P. (Conselho Nacional de Desenvolvimento Científico e Tecnológico, CNPq produtivity grant no. 302849/2021-1). I.K. thanks the Conselho Nacional de Desenvolvimento Científico e Tecnológico, CNPq productivity (grant no. 315048/2021-2). G.M.M. thanks FAPERJ (E-26/205.680/2022) for the research grants awarded. This study was also financed in part by the CAPES—Finance Code 001.

Keywords: conservation | extinction | geodiversity | inselberg | island environment | macroecology | phylogenetic composition | rock outcrops | rupicolous plant community

ABSTRACT

Questions: Inselbergs, isolated rock outcrops, support unique plant communities. Maritime inselbergs (MIs) experience transient isolation due to maritime fluctuations, creating harsh survival conditions. This study is the first to investigate the plant communities' patterns on MIs, comparing them with those on continental inselbergs (CIs). We explore how oceanic filtering and climatic factors shape species and phylogenetic diversity, the threatened statuses of the species, and the impact of extinction scenarios on phylogenetic diversity and structure.

Location: MIs and CIs in the Atlantic Forest of Southeast Brazil.

Methods: We analyzed species and phylogenetic patterns across 15 inselbergs (nine CIs and six MIs), including new data from Alcatrazes Island. Floristic dissimilarities were assessed using ward's clustering, and species and phylogenetic relationships were explored through NMDS ordination and phylogenetic PCA. Oceanic filtering and climatic factors were evaluated using convex hulls and bioclimatic variable fits. Phylogenetic diversity (PD) and structure, measured as mean pairwise distance (MPD), were assessed, along with species threat status based on the Brazilian Red List. Simulated extinction scenarios, randomly removing 5%–90% of species, were modeled to evaluate effects on phylogenetic metrics.

Results: MI species and phylogenetic composition differed significantly from CIs, influenced by oceanic isolation, isothermally, and precipitation seasonality. We found no significant difference in PD between CIs and MIs. Only 11% of the 753 species were shared, with 10% classified as threatened. PD decreased with increasing extinction rates ($p < 0.01$, $R^2 > 0.7$) across all

This article is a part of the Special Issue "Island plant communities: natural experiments at the intersection of biogeography, conservation and global change ecology", edited by Alessandro Chiarucci, Jorge Capelo and Julian Schrader.

communities. MIs exhibited clustered phylogenetic structures, while CIs showed random structures. Random extinction sharply reduced PD, and phylogenetic structures were disrupted in all communities at 25% extinction.

Conclusions: We introduce the concept of MIs, demonstrating that their flora differs significantly from CIs due to oceanic isolation and climatic factors. Although historically connected, geomorphological conditions, subsequent isolation, and environmental filtering by the sea have led to a unique maritime species and phylogenetic composition. Extinction scenarios show significant declines in PD, highlighting these ecosystems' vulnerability. The distinct flora and loss of PD emphasize the need for targeted conservation efforts.

1 | Introduction

Isolated habitats offer valuable models for understanding biodiversity patterns and the ecological processes and mechanisms shaping community assembly (Barthlott and Porembski 2000a; Vanschoenwinkel et al. 2024). Geological phenomena, encompassing both terrestrial and maritime processes, create topographic variations that isolate natural populations, thereby forming dispersal barriers and leading to spatially restricted resources and habitat conditions (Vieira et al. 2018; Pinheiro et al. 2021). Inselbergs, ancient continental rock outcrops geographically isolated and scattered across diverse biomes, are often compared to oceanic islands due to their distinct ecological and climatic contrasts with surrounding landscapes (Azevedo et al. 2024; Pinto-Junior et al. 2024; Vanschoenwinkel et al. 2024). These formations are recognized as biodiversity hotspots characterized by elevated levels of endemism (Meirelles et al. 1999; Barthlott et al. 2005). Neotropical inselbergs are primarily composed of ancient granitic and gneissic rocks that have been shaped by geological processes over millions of years (Twidale 1982; Porembski et al. 1997). This geological stability contributes to the development of distinct microhabitats that promote evolutionary divergence among plant species (Porembski et al. 2000). Besides its geology, it holds singular assemblages of flora (Azevedo et al. 2024).

During glacial periods, continental shields become exposed, connecting landmasses that currently are immersed or scattered emersed as maritime islands (Leite et al. 2016). When inselbergs become true islands due to isolation caused by sea level rise, the newly formed stressful habitat imposes additional challenges on species establishment and survival (Scarano 2002; Neves et al. 2017). This intensifies their isolation through strong environmental filtering (hereafter referred to as dual isolation) and selective pressures that speed up local adaptation and the development of specialized and endemic species (e.g., Coelho and Catharino 2008; Leme and Kollmann 2013; Sabino et al. 2023, 2024). Although there are some descriptive studies on the vascular flora of inselbergs that have become true islands (e.g., Meirelles et al. 1999; Bovini et al. 2014; Kurtz et al. 2017), no ecological study has tested or formally defined this type of Neotropical inselberg, leaving a significant knowledge gap. Here, we propose the term "maritime inselbergs" (MIs) for such situations where inselbergs are true maritime islands, particularly in the context of their biogeography, as well as the species and phylogenetic diversity (PD) associated with their unique environmental challenges.

Despite the typically harsh environmental conditions, such as drought, high solar radiation, nutrient scarcity, limited or absent soil, and, near the sea, high salinity (Barthlott and Porembski 2000b; Scarano 2002; Neves et al. 2017), there is a remarkable floristic diversity in Brazil evidenced by documenting 576 species in the inselbergs of the Atlantic Forest (Azevedo et al. 2024). However, a quick database search reveals an even greater diversity nationwide, with over 1600 species (CRIA 2024), which reinforces the inselbergs of eastern Brazil as one of the richest in the world (Porembski 2005). The flora of these ecosystems includes significant representatives such as bromeliads, orchids, aroids, cacti, and ferns adapted to xeric conditions by being either poikilohydric or geophytic (Barthlott and Porembski 2000b). Species assemblages on CIs differ markedly from those in the surrounding landscape (Vanschoenwinkel et al. 2024). Recent research suggests that inselbergs comprise a combination of generalist species that are also present in the matrix and unique endemics that are exclusive to these formations (Porembski and Barthlott 2000; Kulkarni et al. 2023).

The dissimilarity in floristic composition among Neotropical CIs of different biomes suggests that distinct evolutionary histories have shaped the current plant communities (Pinto-Junior et al. 2024); for example, inselbergs of each biome present a unique flora, with the Atlantic Forest and Caatinga exhibiting closer phylogenetic ties compared to their counterparts in the Amazon (Siqueira Filho et al. 2006; Barbosa-Silva et al. 2022). Floristic differences among inselbergs highlight the significant compositional heterogeneity of rupicolous flora in eastern South America (Fernandes et al. 2020; De Paula et al. 2021), characterized by high phylogenetic turnover among sites (Pinto-Junior et al. 2024). Distinctive assemblages indicate that nearly 70% of species of CIs are restricted to a single biome (Barbosa-Silva et al. 2022). Although the MIs located on the continental shield established transitory connections during the period of the sea fluctuations caused by glaciations (Lambeck et al. 2014), the posterior isolation that presumably led to dual isolation has not been explored in terms of its species and phylogenetic composition in Neotropical MIs.

Inselbergs act as refugia for threatened species (Saunders and Norton 2001; Tulloch et al. 2023) but face growing threats from climate change and human activities such as mining, urban expansion, and tourism, which drive habitat fragmentation and biodiversity loss (Carlucci et al. 2015; Porembski et al. 2016; Tulloch et al. 2023). The isolation of inselbergs facilitates allopatric speciation, where populations become genetically distinct due to geographical separation (Silveira et al. 2020). Research indicates that inselbergs in the Neotropics exhibit profound genetic differentiation among plant species due to limited seed-restricted gene flow and genetic drift, both of which are intensified by their isolation (Palma-Silva et al. 2011; Pinheiro et al. 2014; Mota et al. 2020).

The substantial genetic diversity and structure within inselberg species and populations underscore their role as centers of endemism and species diversity in tropical ecosystems (Palma-Silva et al. 2011; Mota et al. 2020). Although some distant inselbergs exhibit phylogenetic convergence (de Paula et al. 2020), Neotropical inselbergs generally maintain high phylogenetic turnover, reinforcing their role in supporting distinct evolutionary lineages (Pinto-Junior et al. 2024). An open question remains regarding whether dual isolation will contribute significantly to this phylogenetic turnover.

Here, we investigated the influence of environmental filtering driven by geographic isolation imposed by the ocean—encompassing dual isolation, which includes both the isolation of inselberg environments and geographic separation—along with climatic factors on MIs versus CIs, with a focus on how these elements shape species and PD and composition. Additionally, we explored the threat statuses of the species and how the phylogenetic structure and diversity of these inselbergs might respond under random hypothetical extinction scenarios. Specifically, we address three key questions: (1) how oceanic geographic isolation and climatic factors influence the species and PD and composition of inselberg flora, (2) what the threatened statuses of the species are and (3) how increasing extinction scenarios impact the phylogenetic structure and diversity of CIs and MIs. We hypothesize that, besides the past transitory connections by the continental shield exposure during glaciation periods (Leite et al. 2016), the oceanic filtering combined with the current climatic factors of MIs results in a distinct flora with high levels of endemic species compared to their CIs counterparts (Kier et al. 2009; Whittaker et al. 2017) and promotes significant phylogenetic divergence due to restricted gene flow and adaptive pressures (Pinto-Junior et al. 2024). The dual isolation of MIs, coupled with the high levels of endemic species (Whittaker et al. 2017), likely results in a high number of threatened species compared to those found in the continent. Finally, under increasing extinction scenarios, we predict that MIs will experience greater PD loss than CIs, as their communities exhibit lower PD and more clustered structures, potentially leading to disruptions in their phylogenetic structures (Eiserhardt et al. 2015; Nic Lughadha et al. 2020).

2 | Methods

2.1 | Study Area and Sampling Design

We compiled a dataset of vascular plant communities from eight studies conducted across 15 inselberg sites in four states in southeastern Brazil (latitudes ranging from 17° to 24° and longitudes from 40° to 46°), including new data for Alcatrazes

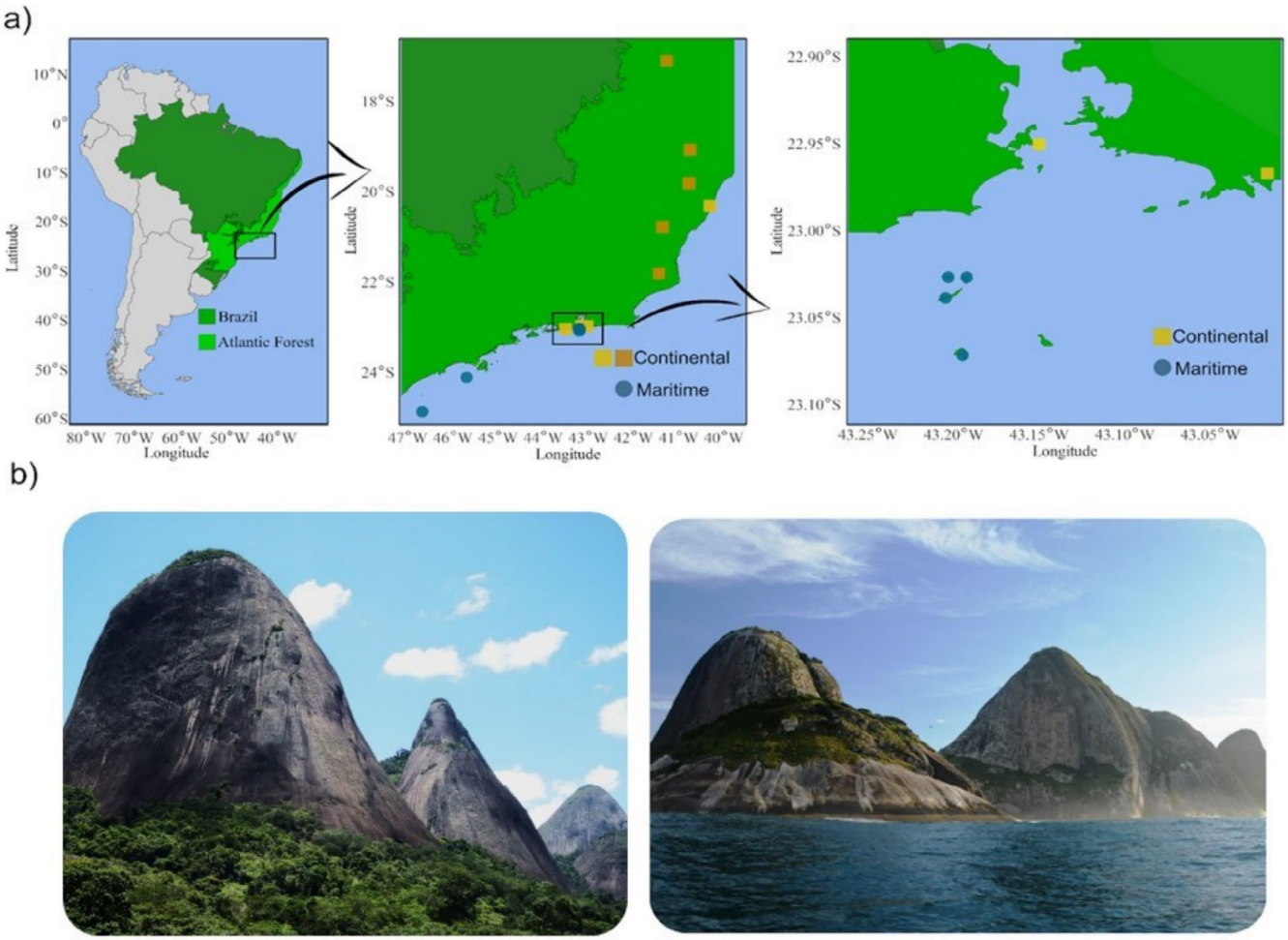

FIGURE 1 | (a) Study area and distribution of 15 inselbergs investigated along the Atlantic Forest, southeastern Brazil; Inland continental inselbergs are shown in brown, while coastal continental inselbergs are represented in yellow. (b) Studied inselbergs along Atlantic Forest, Brazil. A continental inselberg located in Pancas, Espírito Santo State (left) and a maritime inselberg on Alcatrazes Island, São Paulo State (right).

Island (Appendix S1). Six of these sites are MIs, while nine are CIs. Among the CI communities, five are located inland (20 km or more from the coast), while four are located on the coast (Figure 1a,b). Only vascular plant surveys conducted within inselbergs in the Atlantic Forest biome were selected, and we included only taxa identified at the species level. Studies sampling multiple inselbergs were subdivided into independent lists (e.g., Bovini et al. 2014; Mauad 2013). For the survey on Alcatrazes Island, we conducted 14 field expeditions from March 2022 to September 2024, collecting reproductive specimens using the walking survey method (Filgueiras et al. 1994). Taxonomic classification followed the APG IV system (2016) for angiosperms and the PPG I system (2016) for ferns or lycophytes. Nomenclature and synonymizations were updated according to the Flora e Funga do Brasil (2020).

The MIs became true continental islands after sea level rise (Lambeck et al. 2014) and are now completely surrounded by the Atlantic Ocean (Figure 2). Their landscapes primarily consist of granitic rocky outcrops scattered with patches of forest and shrub vegetation. Vegetation on the MIs varies depending on factors such as substrate type, slope, and light exposure, ranging from rupicolous vegetation growing directly on the rocks to forested areas, particularly in valleys where soil accumulates (Bovini et al. 2014; Kurtz et al. 2017; Sabino et al. 2023). These islands also serve as important nesting sites for marine birds (Bovini et al. 2014; Muscat et al. 2014) and as critical nurseries for aquatic organisms (Hoff et al. 2023). In contrast, the CIs maintain connectivity with the continental landmass along at least one section of the outcrops. They also support a range of vegetation types, microhabitats, and associated biota, some of which may be rare or absent in the surrounding landscape matrix (Vanschoenwinkel et al. 2024). Both MIs and CIs share similar granite/gneiss outcrops (Azevedo et al. 2024), dating back tens of millions of years (Vanschoenwinkel et al. 2024).

2.2 | Environmental Parameters and Phylogenetic Tree Construction

To correlate each locality (inselberg) with climatic variables, we obtained the WorldClim v 2.1 GeoTIFF map layers (worldclim.org), which provide high-resolution (30 arc sec, approximately 1 km^2) gridded climate data interpolated from a comprehensive network of weather stations (Fick and Hijmans 2017). We selected maps reflecting 19 bioclimatic variables, including mean annual temperature (MAT), mean annual precipitation (MAP), and various seasonality metrics (Appendix S2).

The phylogenetic tree was constructed for all sampled species (Appendix S3), based on the hypothetical supertree, using a mega-tree approach in the "V.PhyloMaker" R package (Jin and Qian 2019). We generated the phylogenetic tree employing the "phylo.maker" function, applying the phylogenetic hypotheses outlined in scenario "S3" (Appendix S4a). In this scenario, tips representing new genera or species not included in the mega-tree are anchored to the midpoint of the corresponding family or genus branch, effectively illustrating the connection between the family and genus root nodes and their basal nodes (Jin and Qian 2019). By linking the family and genus root nodes to their basal nodes, scenario "S3" provides a calibrated phylogeny with approximate divergence times. This approach enhances the biological relevance of phylogenetic distance-based metrics, ensuring more accurate comparisons across taxa (Jin and Qian 2019).

2.3 | Data Analysis

To address the first question, we began by examining the number of shared and exclusive species on CIs and MIs and then focused specifically on the inselbergs within each group. Floristic similarity among sites was assessed using Ward's hierarchical cluster analysis based on square root–transformed Bray–Curtis distances (Borcard et al. 2018). Ward's method was chosen as it minimizes within-group dispersion at each binary fusion using the classic sum-of-squares criterion (Murtagh and Legendre 2014). The primary floristic groups of inselbergs were identified by applying a level cut of 1.2 to the dissimilarity index in the clustering dendrogram (Figure 4c). Variations in species composition across the identified floristic groups were tested using analysis of similarities (ANOSIM) with 999 permutations (Anderson and Walsh 2013).

To further explore the first question, we analyzed the relationships between floristic patterns and climatic variables plus inselberg areas, evaluating floristic variation using non-metric multidimensional scaling (NMDS; McCune and Grace 2002) based on Simpson dissimilarity. Singletons (species occurring at only one site) were excluded in NMDS as recommended by Lepš and Šmilauer (2003), and the binary presence/absence data were Hellinger-transformed to reduce the influence of double zeros and improve the ecological interpretability of distances (Legendre and Gallagher 2001). Convex hulls were calculated for the inselberg

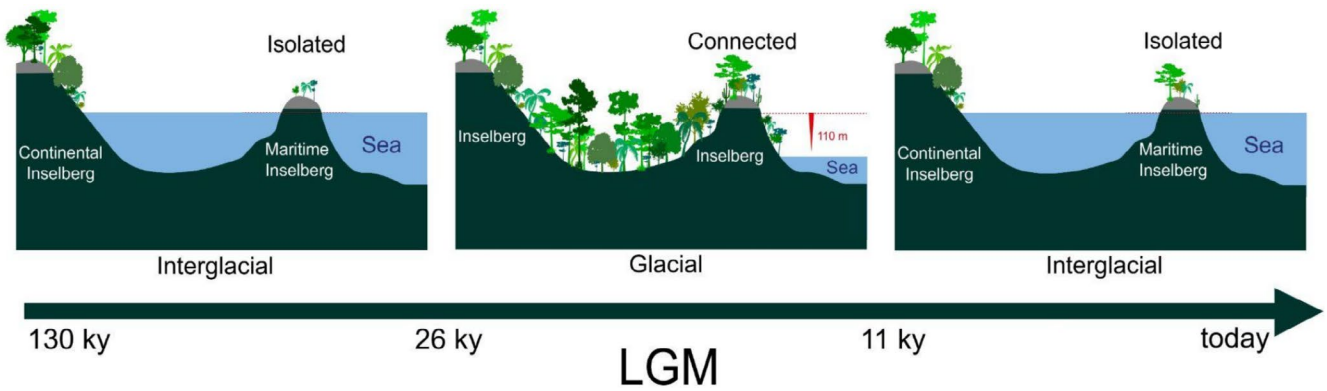

FIGURE 2 | Isolation and connectivity of maritime inselbergs between glacial and interglacial periods. LGM: last glacial maximum.

groups (CI and MI) to assess overlaps and divergence, providing insights into oceanic filtering. We then performed multiple ordinary least squares (OLS; Quinn and Keough 2002) to investigate the relationships between floristic composition and inselbergs area and bioclimatic variables. The NMDS axes were included in the OLS models, excluding bioclimatic variables that were either not statistically significant ($p > 0.05$) or weakly correlated with the axes ($r < 0.3$) (Appendix S2). Relationships between phylogenetic composition and climatic variables were examined using evolutionary principal component analysis (evoPCA) based on a phylogenetic tree constructed with Hellinger distance, implemented via the "evopcahellinger" function from the "advi" R package (Pavoine 2020). Additionally, group overlaps were further evaluated using convex hulls, while associations between phylogenetic composition and bioclimatic variables were analyzed using the same multiple linear regression approach.

To assess the number of threatened species, second question, we classified plant species based on their conservation status using the Official Brazilian Red List (MMA 2022). Species were categorized according to the IUCN's threat levels (IUCN 2022), including endangered, vulnerable, and critically endangered, as well as the corresponding threat categories in the Brazilian Red List.

To address Question 3, we investigated the differences in current values of PD (measured in millions of years; Faith 1992) and the standardized effect size of mean pairwise distance (MPD; Webb et al. 2008) between MI and CI plant communities, and the effects of random species extinction on PD and MPD of these communities. We compared the mean PD values between the two groups of inselbergs, MI and CI, using the ANOVA model. Given the strong separation between these communities observed in cluster and ordination analyses, we conducted the extinction simulations separately for each group (MI and CI). Extinction rates were simulated from 0% (current PD and MPD) to 90% in 5% increments, with 1000 iterations per rate. For each scenario, community data were standardized, filtered, and species names aligned for consistency. For each group of inselbergs, phylogeny trees of all species (Appendix S4b,c) as well as the remaining species were generated for each simulation using the "V.PhyloMaker" function (Jin and Qian 2019), enabling the calculation of PD and MPD at each extinction level. PD was determined by summing branch lengths within each community's phylogeny, while MPD was calculated using the independent swap model with 999 permutations to evaluate the effects of community structure on phylogenetic dispersion. Linear models were used to evaluate trends in PD and MPD across extinction rates, with p-values and adjusted R-squared values serving as indicators of model fit. To determine whether MIs experience greater PD loss compared to CIs, we compared the average slopes of the linear models using a Mann–Whitney U test.

3 | Results

We recorded 753 species across all communities (Appendix S3). Species richness varied across inselbergs, with continental sites ranging from 27 to 124 species and maritime sites from 21 to 207 species (Table 1). MIs showed greater variability, including both the lowest and highest richness values observed. Of these, 456 were registered on CIs, 383 on MIs, and 86 species were shared between the two inselberg types (Appendix S6). A total of 39% of the species were exclusive to MIs, while 49% were restricted to CIs (Figure 3a,b, Appendix S6). The richest plant families across all communities were Orchidaceae, with 64 species, followed by Bromeliaceae (61), Asteraceae (51), and Fabaceae (47) (Appendix S3). Together, these families accounted for 30% of the registered species. On MIs, the richest families were Fabaceae, with 28 species, followed by Poaceae (21), Asteraceae and Bromeliaceae (19 each). In contrast, for CIs, Orchidaceae and Bromeliaceae were the most diverse, each with 51 species, followed by Asteraceae (37) and Fabaceae (23).

High species turnover was observed across all communities, with no species found in every community and 541 species (72% of the total) being exclusive (Figure 3, Appendix S6). Only 10 species (1%) occurred in eight or more sampled communities. The species with the widest distributions, found in 10 communities, were *Coleocephalocereus fluminensis* (Cactaceae) and *Cyrtocymura scorpioides* (Asteraceae). *Maranta divaricata* (Marantaceae), *Megathyrsus maximus* (Poaceae), *Pereskia aculeata* (Cactaceae), and *Talinum paniculatum* (Talinaceae) were recorded in nine communities. For MIs, 70% of the species were restricted to a single community. Only *T. paniculatum* (Talinaceae) was registered in all sampled communities, while eight species—*Guapira opposita* (Nyctaginaceae), *Syagrus romanzoffiana* (Arecaceae), *M. divaricata* (Marantaceae), *Passiflora mucronata* (Passifloraceae), *Tarenaya aculeata* (Cleomaceae), *Eleusine indica* and *M. maximus* (Poaceae), and *Lantana camara* (Verbenaceae)—occurred in five out of six sampled communities. For CIs, 73% of the species were restricted to a single community. No species occurred in all sampled communities, and only six species—*Doryopteris collina* (Pteridaceae), *C. fluminensis* (Cactaceae), *C. scorpioides* (Asteraceae), *Trilepis lhotzkiana* (Cyperaceae), *Paliavana prasinata* (Gesneriaceae), and *Tillandsia stricta* (Bromeliaceae)—were found in seven or eight out of nine sampled communities.

Cluster analysis identified two main floristic groups (Figure 4a) corresponded by the MIs and the CIs communities. A high cophenetic correlation coefficient (0.79) and NMDS low stress (0.03) were observed, and the two main floristic groups presented significant differences in their species composition, which was confirmed by the ANOSIM ($R = 0.73$, $p < 0.01$), indicating that, in general, floristic dissimilarities tended to increase with greater distances between areas within the same group (Figure 4a). Nevertheless, within the group of continental communities, there is an additional separation between coastal communities (Con3, Con7, Con8, Con9, Appendix S1) and inland communities (Con1, Con2, Con4, Con5, Con6, Appendix S1), regardless of the geographical distance among them, also confirmed by the ANOSIM ($R = 0.41$, $p < 0.05$).

The NMDS ordination revealed clear separation between CIs and MIs, with distinct floristic groups and no convex hulls overlapping, indicating significant differences in species composition (Figure 4b). The ordination showed strong and significant correlations with three bioclimatic variables (Appendix S2). The first axis mainly distinguished CIs from MIs, with the annual temperature range (Bio_7) and isothermality (Bio_03) positively correlated with this axis (Figure 4b). The second axis further divided the CIs into two groups—coastal and inland

TABLE 1 | Species richness, phylogenetic diversity (PD), and standardized effect size of mean pairwise distance (MPD) for nine continental and six maritime inselbergs in the Atlantic Forest, Brazil.

	Richness	Current PD	Mean adjusted R^2/mean p	Current MPD/p	Mean adjusted R^2/mean p
Continental inselbergs					
Continental_1	*82*	5690	**0.86/$p < 0.001$**	1.66/$p > 0.05$	0.01/$p > 0.05$
Continental_2	*100*	6529	**0.86/$p < 0.001$**	0.50/$p > 0.05$	0.01/$p > 0.05$
Continental_3	*27*	2265	**0.73/$p < 0.001$**	**−1.79/$p < 0.01$**	0.01/$p > 0.05$
Continental_4	*106*	6507	**0.87/$p < 0.001$**	0.98/$p > 0.05$	0.02/$p > 0.05$
Continental_5	*124*	6556	**0.91/$p < 0.001$**	−0.22/$p > 0.05$	0.01/$p > 0.05$
Continental_6	*69*	5023	**0.83/$p < 0.001$**	−0.86/$p > 0.05$	**0.30/$p < 0.01$**
Continental_7	*65*	4644	**0.69/$p < 0.001$**	−1.34/$p > 0.05$	0.01/$p > 0.05$
Continental_8	*66*	4702	**0.81/$p < 0.001$**	**−2.53/$p < 0.001$**	**0.53/$p < 0.001$**
Continental_9	*73*	5555	**0.79/$p < 0.001$**	**1.986/$p > 0.95$**	**0.22/$p < 0.01$**
Maritime inselbergs					
Maritime_1	*21*	2273	**0.69/$p < 0.001$**	**−1.05/$p < 0.01$**	**0.52/$p < 0.01$**
Maritime_2	*96*	6779	**0.85/$p < 0.001$**	0.88/$p > 0.05$	0.01/$p > 0.05$
Maritime_3	*71*	5586	**0.82/$p < 0.001$**	**−1.21/$p < 0.01$**	**0.23/$p < 0.01$**
Maritime_4	*59*	4897	**0.83/$p < 0.001$**	**−1.44/$p < 0.01$**	0.06/$p > 0.05$
Maritime_5	*124*	7475	**0.90/$p < 0.001$**	**−2.04/$p < 0.001$**	**0.55/$p < 0.001$**
Maritime_6	*207*	11,744	**0.93/$p < 0.001$**	**3.10/$p > 0.999$**	**0.51/$p < 0.001$**

Note: Summary of the mean adjusted R^2 and p-values from linear models evaluating trends under simulated extinction scenarios. Current PD reflects the observed PD at zero extinction rates, while MPD represents the phylogenetic structure of each community. Significant p-values ($p < 0.05$ and $p > 0.95$) are highlighted in bold font, with results presented separately for continental and maritime inselbergs.

communities—regardless of geographical distance, while the MIs were split into two groups, with MI5 and MI6 (the southernmost MIs) clustering together and the remaining MI communities forming a separate group. This axis was strongly associated with the mean temperature of the warmest quarter (Bio_10) and isothermality.

The evoPCA also highlighted significant differences in phylogenetic composition between CIs and MIs, with no overlap in convex hulls (Figure 4c). The first axis has similarly separated CIs from MIs, with the annual temperature range, precipitation seasonality (Bio_15), and isothermality positively correlated with this axis (Figure 4c). However, in contrast to the species ordination, the second axis predominantly distinguished inselbergs with the highest PD, separating the most diverse CIs and MIs (Figure 4b,c) from the others. The mean temperature of the warmest quarter and isothermality were again strongly associated with the second axis.

We identified 70 species classified as threatened according to the Official Brazilian Red List (MMA 2022). Of these, 41 are categorized as endangered, 19 as vulnerable, and 10 as critically endangered (Appendix S7). Additionally, 89% of the recorded species lack a threat assessment. The families with the highest number of threatened species were Bromeliaceae (19 species), Orchidaceae (12), and Begoniaceae (6). Notably, seven species are endemic to Alcatrazes Island (MI6), the only MI of our study known to harbor endemic species.

We found no significant differences in PD between CIs and MIs ($p > 0.05$), although Alcatrazes Island exhibited nearly twice the PD of the other inselbergs studied. Similarly, the effects of simulated extinction scenarios on PD were comparable between continental and maritime communities (Figure 5a,b), with both types of inselbergs experiencing a consistent decline in PD and no substantial variation in the rate of loss (Table 1), and no significant differences in average estimated slope between them ($W = 24$, $p > 0.05$). Regarding the MPD, most CIs displayed communities with random phylogenetic structures, whereas most MIs showed communities with clustered structures (Table 1).

Higher PD did not result in overdispersed phylogenetic structures ($p > 0.95$), nor did low PD lead to clustered structures ($p > 0.05$) in either type of inselberg. Patterns of MPD variation under simulated extinction scenarios revealed similar trends between the two inselberg types (Appendix S8), with no significant difference in average estimated slope ($W = 32$, $p > 0.05$) and with all communities either maintaining or shifting toward random phylogenetic structures.

4 | Discussion

Here we present and discuss the concept of MIs for a set of unique maritime islands in southeastern Brazil that matches

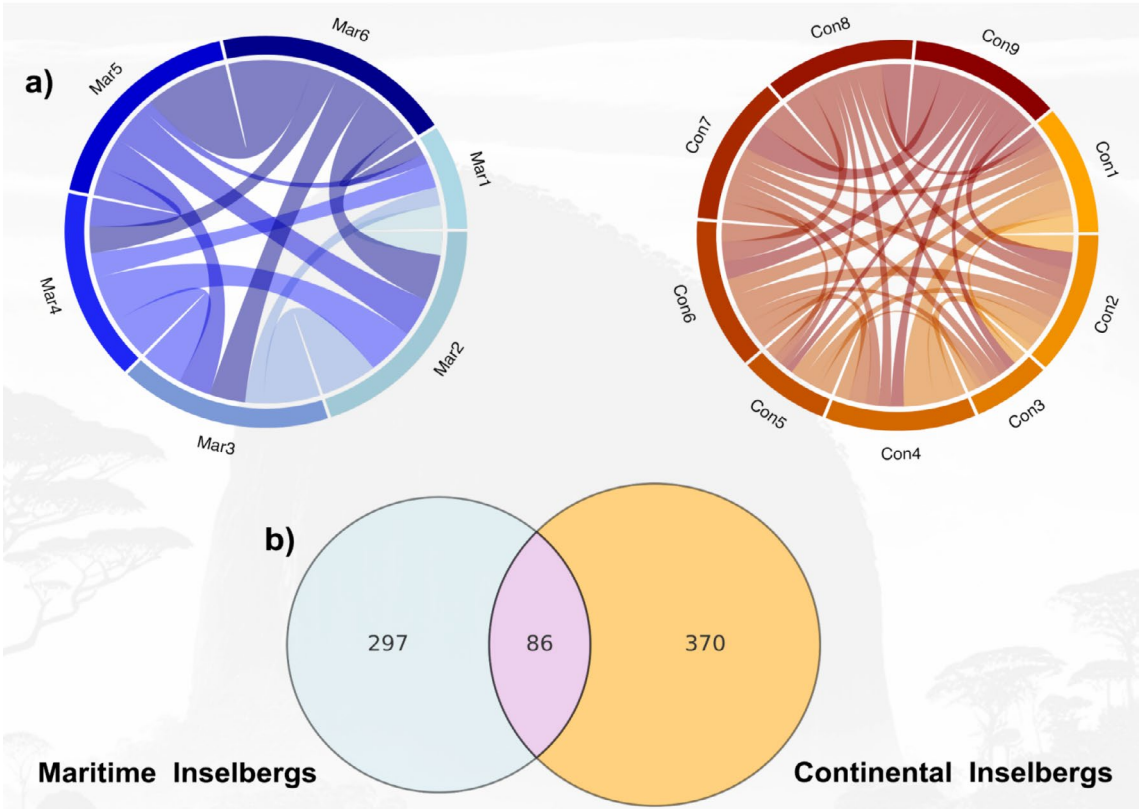

FIGURE 3 | Chord diagram (a) depicting shared (nonunique) species among maritime and continental inselbergs in the Atlantic Forest, Brazil. The width of the edges connecting pairs of inselbergs represents the proportion of shared species between them. Venn diagram (b) illustrating exclusive and shared species between maritime and continental inselbergs.

geomorphologically and ecologically with the continental inselbergs (CIs). However, the particular history that each one experienced resulted in great distinction of the flora among these inselbergs. The species and phylogenetic compositions of MIs were associated with lower precipitation seasonality and reduced temperature variation, suggesting that distinctions can be explained by the current climatic factors plus environmental filtering from oceanic geographic isolation associated with harsh maritime environmental conditions, characteristic of shoreline, like high exposure to wind and salt, playing a key role in shaping their unique flora. Additionally, we observed a phylogenetic distinction between MIs and CIs and high species turnover across the studied plant communities, indicating that the species pool is closely linked to the specific environment in which the community occurs. Our study also identified numerous threatened and even endemic species, a result of the intrinsic isolation of inselbergs. Finally, random modeled extinction scenarios revealed a consistent decline in PD across both inselberg types, underscoring the vulnerability of these communities to biodiversity loss. These findings align with other inselberg studies and provide a strong foundation for conservation efforts aimed at preserving the biodiversity of these unique and fragile environments.

4.1 | Dual Isolation Shapes the Distinctive Flora of Maritime Inselbergs: Species and Phylogenetic Clustering

Inselbergs are characterized by microhabitats and associated biota that may be rare or absent in the surrounding landscape matrix (Vanschoenwinkel et al. 2024), configuring a barrier for colonization and leading to the isolation of these scattered ecosystems (Palma-Silva et al. 2011; Pinheiro et al. 2014; Mota et al. 2020). The matrix permeability is intrinsically linked not only to species' dispersal ability but also to the texture of the matrix and how compatible its environmental conditions are with the species' climatic envelope (Barbosa-Silva et al. 2022; Vanschoenwinkel et al. 2024). In this context, during drier periods, a xeric species from a CI may be more likely to disperse through a dryland matrix via stepping stones than through the maritime matrix present in MIs.

Although there were putative connections between MIs and the continent during glacial periods (Figure 2), the surrounding sea creates a second, even greater barrier to colonization as it limits the dispersal of propagules by fauna (Schupp et al. 2010). Similarly, pollen transport by pollinators (Araújo et al. 2004; Borges et al. 2020) and seed dispersal (Pinheiro et al. 2021) between the continent and MIs communities is also limited, restricting gene flow between plant populations. This limitation is particularly evident in MIs located farther from the continent, such as Queimada Grande Island (MI5) and Alcatrazes Island (MI6), which are over 32 km offshore. Thus, historical vicariance in vascular plants on MIs may have played a crucial role in shaping plant community assembly, much like its influence on other types of continental islands (Queiroz 2005; Médail 2022).

Maritime ecosystems impose a wide array of adverse environmental conditions, such as constant wind, nutrient scarcity, and high salinity, subjecting plant communities to harsh conditions

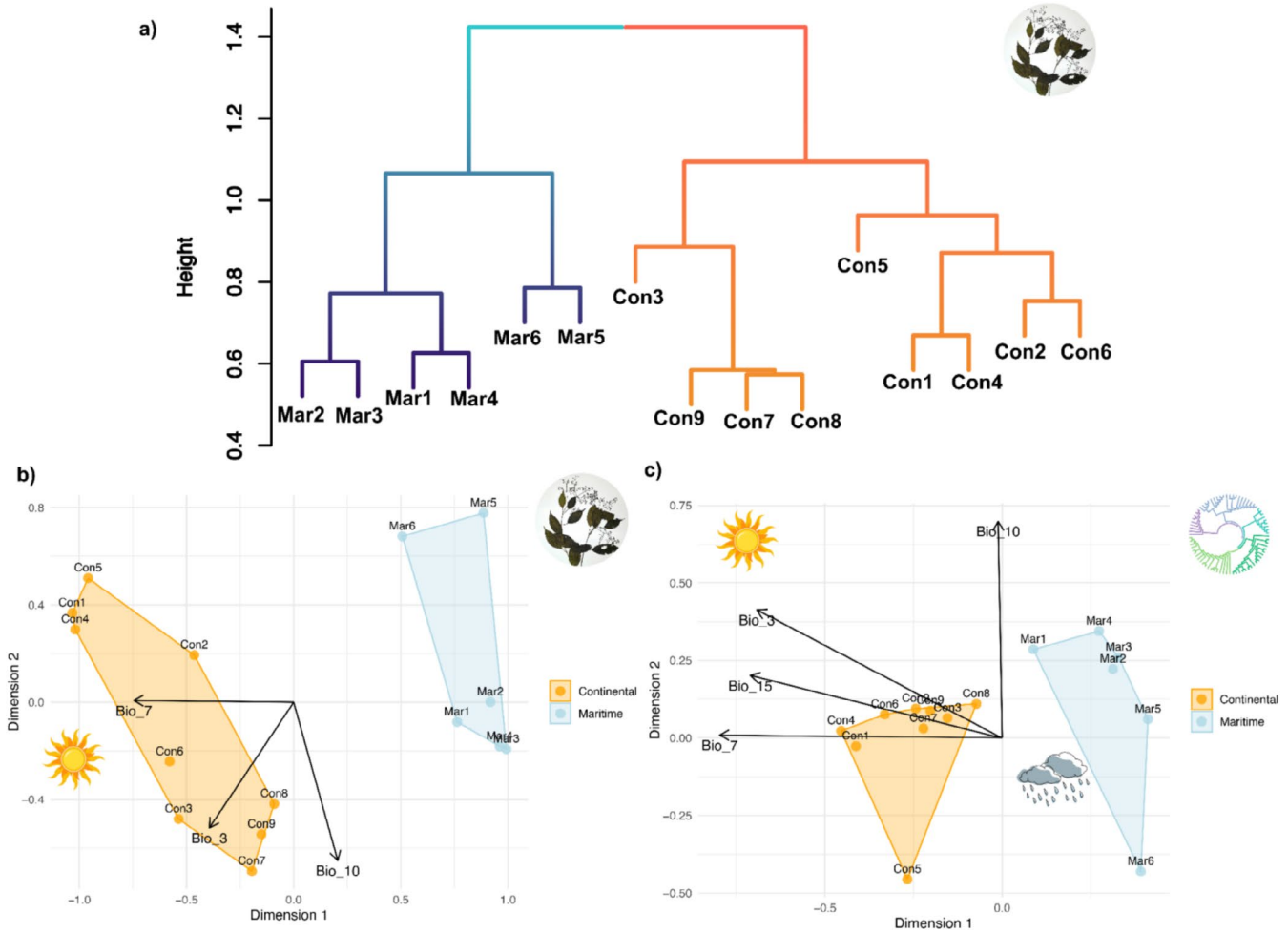

FIGURE 4 | Ward's hierarchical clustering dendrogram (a) highlights two distinct clusters (colored). The dendrogram height represents the Euclidean distance between clusters, and the horizontal endpoints correspond to the 15 plant communities from maritime and continental inselbergs in the Atlantic Forest, Brazil. Panels (b) and (c) show species and phylogenetic ordination analyses, respectively. Arrows indicate significant environmental vectors, while polygons delineate groups of inselbergs (continental or maritime). Bio_3, isothermality; Bio_7, temperature annual range; Bio_10, mean temperature of warmest quarter; and Bio_15, precipitation seasonality.

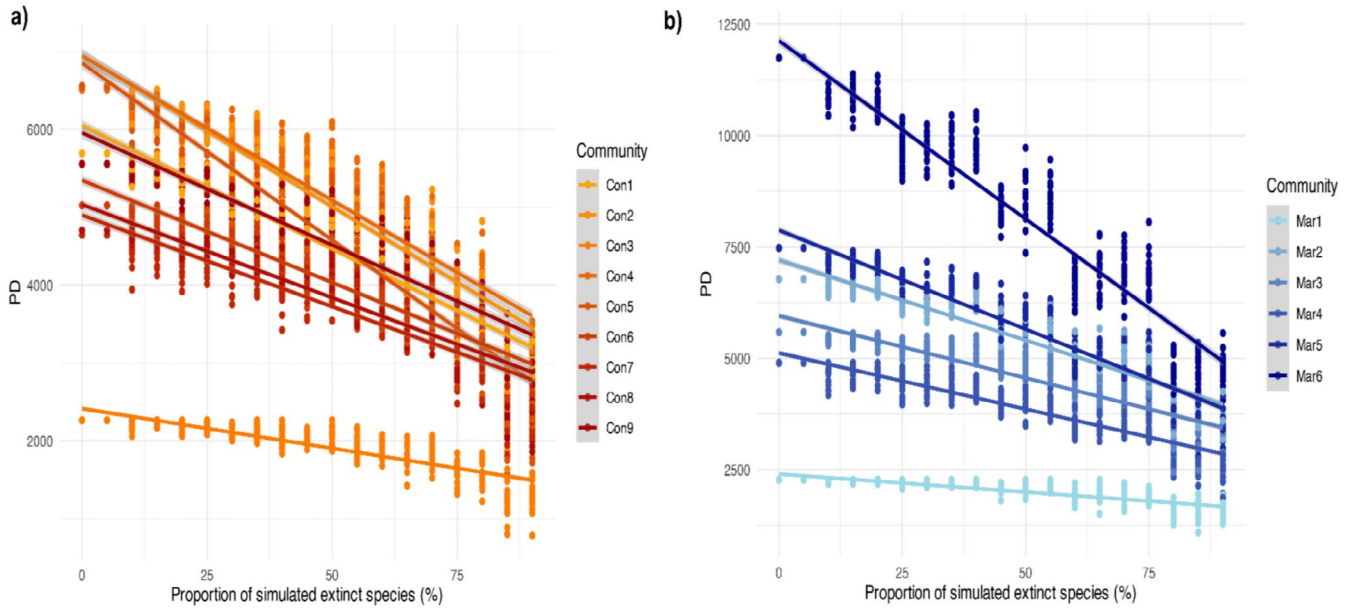

FIGURE 5 | Current phylogenetic diversity (PD) (0% of extinction) and the relationships between random species extinction and PD for continental (a) and maritime (b) inselbergs in the Brazilian Atlantic Forest.

(Scarano 2002; Neves et al. 2017). These challenges, combined with the rocky substrate of inselbergs—characterized by shallow or absent soils, large temperature fluctuations, high irradiance, and limited water availability—further restrict the plant species that can establish and thrive (Barthlott and Porembski 2000b; Scarano 2002; Neves et al. 2017). In MIs, the limited terrestrial habitat further increases competition among species, suggesting that extinctions and flora homogenization are likely frequent. Nevertheless, it is surprising to find a high diversity of plant species and lineages thriving in these environments. In fact, the high levels of species diversity are also reflected in commonly high levels of genetic diversity found in inselberg populations (Palma-Silva et al. 2011; Pinheiro et al. 2014, 2021), suggesting high effective population sizes and long periods of stability.

As expected, we found a strong floristic and phylogenetic distinction between the CIs and MIs communities, suggesting distinct evolutionary histories that have driven the differentiation of their floristic composition. Furthermore, we identified additional clustering within the CI communities, with coastal communities (those near the shoreline) grouping together and inland communities (those farther from the shore) forming separate clusters, regardless of the geographical distance between them. This pattern may be attributed to the strong influence of the regional species pool and the high species turnover in the assembly of plant communities on inselbergs (Pinto-Junior et al. 2024; Azevedo et al. 2024). The climatic distinction among the coastal and inland, as revealed by the cluster, reflects a gradient of seasonality of the temperature and precipitation, with higher values of isothermality and precipitation seasonality in CIs, with the inland communities subjected to longer dry periods than the coastal and strong temperature range (Figure 4). In comparison with the CIs, the MIs present lower seasonality and temperature range, suggesting a lower harsh condition due to its filters but, on the other hand, are exposed to more winds and salinity coming from the ocean, which can constrain the biota on MIs, reflecting in the observed pattern.

Currently, the MIs are surrounded by the sea and are located on the southernmost portion of the CI communities (Figure 1). Even among the MIs, the Queimada Grande (MI5) and Alcatrazes (MI6) grouped together in the cluster, reflecting the most southern position of both, which are more exposed to lower temperatures (Figure 4). On the other hand, the Cagarras Islands are grouped in the same cluster of the MI, even close to the shore. Although geographically distant, the MIs sites putatively established historical connections during the climatic fluctuations of the Quaternary, when transitory connections were established by the decreases in sea level caused by glaciation, exposing the continental shelf (Leite et al. 2016; Buso Junior et al. 2019; Ledru and Araújo 2023). Although currently submerged by the sea, they once formed extensive coastal plains, with a transitory period of immersion, allowing the establishment of the terrestrial vegetation—perhaps representing analogous to the current locally known as "restingas" during the Last Glacial Maximum (Leite et al. 2016; Buso Junior et al. 2019; Ledru and Araújo 2023), and consequently biota connections (Figure 2). Part of the floristic composition found in MIs may reflect what was once present in these "restingas," which could explain the clustering of these communities. Indeed, several species thriving in the exposed rocks of Alcatrazes Island (MI6) are found growing in the sand dune vegetation of "restingas," rocky shores, or as epiphytes in the coastal plain (Sabino unpubl. results). Nonetheless, further structural studies are needed to better understand these species' role in inselbergs' plant communities.

We found typical inselberg species from southeastern Brazil in many of the studied communities, including *C. fluminensis* (Cactaceae), *D. collina* (Pteridaceae), and *T. lhotzkiana* (Cyperaceae) (e.g., Mauad 2013; Bovini et al. 2014; Kurtz et al. 2017; de Paula et al. 2017; Arantes et al. 2024). Conversely, we also identified many generalist species, with broad distribution across various vegetation types and habitats throughout the country, such as *C. scorpioides* (Asteraceae) (Picanço et al. 2024), *T. paniculatum* (Talinaceae) (Hassemer 2024), and *P. aculeata* (Cactaceae) (Zappi and Taylor 2024). The presence of both specialist and generalist species in a significant number of communities suggests that a combination of environmental filters shapes community assemblies, enabling both specialist and generalist species adapted to these habitats to thrive (Safford and Martinelli 2000; Kulkarni et al. 2023). The harsh conditions of inselberg habitats favor the establishment of species with traits, typically associated with specialist species, such as poikilohydry, geophytism, or tolerance for low nutrient availability (Barthlott and Porembski 2000b). On the other hand, inselbergs allow the establishment of generalist species that could have a competitive advantage over specialist species.

4.2 | Threatened Species, Endemism, and Risks to Maritime Inselberg Flora

We found that more than 9% of the species in the studied communities are under threat, particularly within the families Bromeliaceae, Orchidaceae, and Begoniaceae (MMA 2022). Contrary to our hypothesis, MIs exhibited a lower proportion of threatened species compared to CIs (Appendix S7). However, it is important to note that over 90% of the registered species lack conservation assessments. Nationally, only 13.1% of Brazilian plant species have been evaluated for conservation status (CNCFlora 2024), with the highest number of threatened species found in the Atlantic Forest (IBGE 2022). As more detailed studies on species threats are conducted, the number of threatened species is likely to increase, especially in environments like inselbergs, where species often have locally restricted distributions—an important factor in threat classification (Porembski 2007; Pinto-Junior et al. 2020).

The plant endemism found on Alcatrazes Island (MI6) comprises species from Bromeliaceae (Leme and Kollmann 2013; Sabino et al. 2023, 2024), Begoniaceae (Smith and Wasshausen 1983), and Arecaceae (Coelho and Catharino 2008) (Appendix S7), reinforcing the significant role these families play in the plant communities of inselbergs. In fact, the number of endemic species in such environments may be largely underestimated due to cryptic speciation, where morphological similarities between island and mainland populations may hide already strong genetic differences and almost complete levels of reproductive isolation (Pinheiro et al. 2021). Endemism on Alcatrazes Island is not restricted to plants but extends to animals as well (Lutz 1973; Marques et al. 2002). Although no endemic plant species have yet been described on Queimada Grande Island (MI5), one snake

species, *Bothrops insularis*, is known to be endemic to the island (Duarte et al. 1995). Endemic organisms not only play a crucial role in the local ecosystem but also represent unique elements essential for maintaining the ecological integrity of the insular environment. Thus, the extinction of plant species within MIs communities would not only result in the definitive loss of the species but could also trigger local ecosystem imbalances (Burns and Neufeld 2009).

In contrast to the absence of endemic plant species in CIs, we identified eight micro-endemic and critically endangered species, including *Rhipsalis cereoides* (Cactaceae) and *Orthophytum zanoni* (Bromeliaceae), confined to few and specific outcrops (Mauad 2013; Arantes et al. 2024). This restricted distribution can be associated with the nature of inselberg specialist plants, which are closely tied to unique microhabitats of these outcrops and have limited dispersal, with the surrounding matrix acting as a strong barrier to their spread (Vanschoenwinkel et al. 2024). The threats facing inselberg floras, particularly MIs, are exacerbated by factors such as rising sea levels, wildfires—often ignited by human activities like ballooning—and the invasion of exotic species (Kurtz et al. 2017; Pfadenhauer et al. 2024; Possley et al. 2024). Notably, *M. maximus* and *Melinis minutiflora* (Poaceae), both invasive and highly competitive species, are present in 60% and 40% of the studied MI communities, respectively. These species contribute to the accumulation of dry biomass, facilitating fire spread (Gorgone-Barbosa et al. 2020), and outcompete native species that have more specific ecological requirements (Pivello et al. 1999; Zenni et al. 2019; Instituto Hórus 2024). Inselbergs, characterized by high levels of localized endemism and restricted species distributions, are particularly vulnerable to these threats. For instance, decades of human-driven fires aimed at eliminating the endemic snake *B. insularis* and expanding banana cultivation (Duarte et al. 1995) have been the primary drivers of vegetation loss on Queimada Grande Island, increasing the number of invasive plant species (Kurtz et al. 2017). Therefore, a conservation action plan to preserve inselberg flora is essential, as the extinction of plant species in these habitats could trigger cascading ecological imbalances, negatively impacting not only species richness but also the overall integrity of these unique ecosystems (Burns and Neufeld 2009; Vanschoenwinkel et al. 2024).

4.3 | Phylogenetic Diversity and Structure: Current Patterns and Responses to Extinction Scenarios

Our study provides significant insights into the PD and structure (MPD) of CIs and MIs. Contrary to our expectations, we found no significant differences in PD between CIs and MIs, and our results confirm the extensive range of PD in inselbergs (Pinto-Junior et al. 2024), with CIs exhibiting values from 2265 to 6556 million years (my) and MIs displaying a broader range from 2273 to 11,222 my, notably with Alcatrazes Island showing nearly double the PD of other inselbergs (Table 1). This variation in PD could be influenced by differences in species richness, as inselbergs with higher richness may host species from multiple evolutionary lineages, while species-poor inselbergs may be dominated by a few closely related taxa, potentially reflecting distinct colonization histories, ecological filters, and biogeographic constraints (Pinto-Junior et al. 2024; Vanschoenwinkel et al. 2024). Although we found no significant differences in PD between CIs and MIs, the pronounced variation in their phylogenetic composition highlights the role of distinct ecological conditions and evolutionary histories in shaping these systems, elevating some inselbergs to biodiversity hotspots (Tietje et al. 2023). Environmental filtering typically reduces PD (Neves et al. 2020; Kamimura et al. 2022) by favoring species with adaptations for survival in harsh environments (Cadotte and Tucker 2017). However, filtering can also promote PD by promoting coexistence among diverse lineages, as inselbergs often act as refugia that foster local adaptation (Vanschoenwinkel et al. 2024). Also, two types of species differences determine competitive exclusion with opposing effects on relatedness patterns, where competition typically eliminates closely related taxa, but can sometimes eliminate more different and less related taxa, even when the traits underlying the relevant species differences are phylogenetically conserved (Mayfield and Levine 2010; Cadotte and Tucker 2017). In both CI and MI, the coexistence of specialists and generalists suggests that harsh conditions act as strong filters, while competition shapes communities without necessarily reducing PD (Porembski and Barthlott 2000; Kulkarni et al. 2023). For MI, additional transitory connections to the continent likely facilitated species colonization, while dual isolation—encompassing both inselberg-like environmental conditions and geographic oceanic barriers—has likely driven speciation. These processes may promote phylogenetic overdispersion and lineage diversification, potentially explaining the higher PD observed in these systems (Leite et al. 2016; Buso Junior et al. 2019; Ledru and Araújo 2023). Moreover, the elevated PD in certain MIs, such as Alcatrazes Island, may also be attributed to their designation as strictly protected national areas, where reduced human disturbances have helped preserve biodiversity (Bovini et al. 2014; Kurtz et al. 2017; ICMBio—Instituto Chico Mendes de Conservação da Biodiversidade 2017).

Both CIs and MIs exhibited phylogenetic structures ranging from overdispersed and random to clustered structure. CIs predominantly displayed random structures, and despite the high species turnover observed across plant communities (Figure 3a,b), the phylogenetic compositions of CIs were generally similar, except for elevated CI (>1000 m.a.s.l.), where higher altitudes favored the presence of species from distantly related clades (Bergamin et al. 2021; Kamimura et al. 2022). The ecological and evolutionary dynamics of inselbergs, embedded within a terrestrial matrix, lead to significant interactions between inselbergs and surrounding populations. These interactions can drive phylogenetic convergence among clades in CI located within the Atlantic Forest domain (de Paula et al. 2020), with different species from the same clades occurring in CIs, resulting in randomly structured phylogenetic patterns (Mayfield and Levine 2010). On the other hand, MIs were characterized by a notable prevalence of clustered structures. The dual isolation and harsh environmental conditions of MIs—characterized by high irradiance, strong winds, and limited resources—enhance environmental filtering and may intensify interspecific competition (Hopper et al. 2021), also often leading to phylogenetically clustered assemblages (Mayfield and Levine 2010; Cadotte and Tucker 2017). Nevertheless, the disharmony typical of island systems, where some clades are overrepresented

and others underrepresented compared to continental sources (Gillespie et al. 2012; Roeble et al. 2024), likely accounts for the phylogenetic overdispersion, such as observed on Alcatrazes Island. These patterns highlight the complexity of ecological and evolutionary processes shaping inselbergs, particularly in MIs, where unique conditions foster distinctive phylogenetic assemblages. The preservation of inselbergs is therefore essential for safeguarding their unique biodiversity, as their isolation and reduced human impact provide critical refugia for specialized and endemic lineages (Vanschoenwinkel et al. 2024).

The inherent isolation of inselbergs, coupled with small population sizes and limited genetic flow, further heightens the vulnerability of their flora, amplifying extinction risks (Porembski et al. 1997; Pinheiro et al. 2014, 2021; Mota et al. 2020). Together with no differences in PD, we found no significant differences in slopes of PD loss between CIs and MIs under increasing random extinction scenarios (Figure 5a,b). The consistent decline in PD under simulated extinction scenarios for both types of inselbergs underscores their shared vulnerability to biodiversity loss and highlights the uniqueness of these ecosystems (Tietje et al. 2023; Vanschoenwinkel et al. 2024), where both slopes and coefficients of determination were strongly elevated ($R^2 > 0.69$). Also, both inselberg plant communities exhibited disruptions in their phylogenetic structure, consistent with patterns observed in tree communities (e.g., Eiserhardt et al. 2015). The random extinction affects both types of inselbergs in the same way, where both clustered and overdispersed communities became random at 25% extinction rates. The loss of taxa reduces diversity and disrupts the evolutionary balance among closely and distantly related species, particularly concerning, given that only 9% of species are shared between CI and MI, illustrating that loss of biodiversity can exclude endemic species of one type of inselberg or even a specific inselberg. Thus, our findings underscore the need to integrate phylogenetic and species diversity into conservation strategies to protect these unique ecosystems (Mace 2004; Winter et al. 2013), which are vital for maintaining regional biodiversity and enhancing resilience to environmental changes (Violle et al. 2014; Oliver et al. 2015).

5 | Conclusion

In conclusion, our study demonstrates that MIs possess a unique flora shaped by a combination of continental isolation and the harsh maritime environment. This dual isolation has resulted in distinct floristic and phylogenetic compositions compared to CIs, with high levels of species turnover and a significant proportion of threatened and endemic species. While both inselberg types exhibit similar vulnerability to biodiversity loss under simulated extinction scenarios, their distinct phylogenetic structures highlight the importance of conserving both species and PD within these unique ecosystems. The findings underscore the need for comprehensive conservation strategies that address the specific threats facing these isolated habitats, such as invasive species, habitat degradation, and climate change. Current studies have quantified differences in species composition, but differences among populations within species are still scarce. Future studies should focus on population-level differences among inselbergs and between mainland and island populations, aiming to uncover potential differences in genetic structure (Hmeljevski et al. 2017; Pinheiro et al. 2021) and functional traits (Schrader et al. 2021). Such studies will provide valuable data to quantify the contribution of neutral and adaptive forces in shaping inselbergs' flora.

Author Contributions

G.P.S., V.A.K., G.M.M., and F.P. conceived the research idea. G.P.S., V.A.K., G.M.M., M.M.T., and I.M.C. led the field sampling. G.P.S. made the compilation. V.A.K., J.S.C., and G.P.S. conducted data analysis and interpretation. G.P.S. and V.A.K. wrote the manuscript, which was subsequently critically revised by all the authors.

Acknowledgments

We are grateful to "Instituto Chico Mendes de Conservação da Biodiversidade" (ICMBio) of the Alcatrazes Wildlife Refuge and Tupinambás Ecological Station. The Article Processing Charge for the publication of this research was funded by the Coordenação de Aperfeiçoamento de Pessoal de Nível Superior - Brasil (CAPES) (ROR identifier: 00x0ma614).

Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

The data that supports the findings of this study are available in the Supporting Information of this article.

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Supporting Information

Additional supporting information can be found online in the Supporting Information section.