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Spatial patterns of evolutionary diversity in Cactaceae show low ecological representation within protected areas



Danilo Trabuco Amaral^{a, b, d, *}, Isabel A.S. Bonatelli^c, Monique Romeiro-Brito^a, Evandro Marsola Moraes^a, Fernando Faria Franco^a

^a Departamento de Biologia, Centro de Ciências Humanas e Biológicas, Universidade Federal de São Carlos (UFSCar), Sorocaba, Brazil

^b Programa de Pós Graduação em Biologia Comparada, Faculdade de Filosofia, Ciências e Letras de Ribeirão Preto, Universidade de São Paulo (USP), Ribeirão Preto,

^c Departamento de Ecologia e Biologia Evolutiva, Universidade Federal de São Paulo (UNIFESP), Diadema, São Paulo, Brazil

^d Universidade Federal do ABC (UFABC), Centro de Ciências Naturais e Humanas (CCNH), Santo André, São Paulo, Brazil

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ABSTRACT

Mapping biodiversity patterns across taxa and environments is crucial to address the evolutionary and ecological dimensions of species distribution, suggesting areas of particular importance for conservation purposes. Within Cactaceae, spatial diversity patterns are poorly explored, as are the abiotic factors that may predict these patterns. We gathered geographic and genetic data from 921 cactus species by exploring both the occurrence and genetic databases, which are tightly associated with drylands, to evaluate diversity patterns, such as phylogenetic diversity and endemism, paleo-, neo-, and superendemism, and the environmental predictor variables of such patterns in a global analysis. Hotspot areas of cacti diversity are scattered along the Neotropical and Nearctic regions, mainly in the desertic portion of Mesoamerica, Caribbean Island, and the dry diagonal of South America. The geomorphological features of these regions may create a complexity of areas that work as locally buffered zones over time, which triggers local events of diversification and speciation. Desert and dryland/dry forest areas comprise paleo- and superendemism and may act as both museums and cradles of species, displaying great importance for conservation. Past climates, topography, soil features, and solar irradiance seem to be the main predictors of distinct endemism types. The hotspot areas that encompass a major part of the endemism cells are outside or poorly covered by formal protection units. The current legally protected areas are not able to conserve the evolutionary diversity of cacti. Given the rapid anthropogenic disturbance, efforts must be reinforced to monitor biodiversity and the environment and to define/plan current and new protected areas.

1. Introduction

A meaningful observation regarding biodiversity is that organisms have uneven distribution across the globe, which can reveal how speciation, extinction, and dispersal events may have impacted species distribution (Lomolino et al., 2009). Naturalists have long been interested in explaining why some regions are biologically richer than others as a way to minimize the Wallacean shortfall of biodiversity knowledge. Mapping biodiversity patterns across taxa and environmental conditions is crucial to address the evolutionary and ecological dimensions of species distribution, such as endemism patterns that emerge in regions with significant concentrations of organisms with little representation elsewhere. Areas such as these are particularly meaningful for conservation purposes (Willig et al., 2003; Graham and Fine, 2008; Swenson et al., 2012; Rosauer and Jetz, 2015).

Endemism has multiple spatial and temporal dimensions that can be related to different taxonomic levels, from families to subspecies (Morrone, 2008). Species-rich areas tend to have high endemism, which is usually correlated with contemporary and historical climate regimes and topography (Sandel et al., 2011; Daru et al., 2015; Barratt et al., 2017; Fenker et al., 2020). The metrics used to estimate endemism (see appendix A in Supplementary material) are influenced by the defined spatial scale, which can range from large (e.g., continent) to small areas (mountain tops). On a temporal scale, endemism can be described as a result of recent speciation with no dispersion out of the ancestral area (neoendemism) or as the persistence of lineages extinct elsewhere

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Brazil

^{*} Corresponding author at: Rodovia João Leme dos Santos, Km 110, SP 264, 18052-780 Sorocaba, Brazil. *E-mail address:* danilo.trabuco@ufabc.edu.br (D.T. Amaral).

(paleoendemism) (Stebbins and Major, 1965). Such patterns could also be associated with the concepts of cradles (neoendemism) and museums of biodiversity (paleoendemism), and they are not mutually exclusive in geographical space (mixed-endemism; Mittelbach et al., 2007).

While traditional approaches to capture endemism rely on taxonomic diversity measures such as the number of endemic or rangerestricted taxa in a region (Kier et al., 2009), approaches using phylogenetic endemism (PE) are more inclusive by accounting for the evolutionary history underlying endemism inferences (Mishler et al., 2014; Sandel et al., 2020). To integrate the biological diversity and phylogenetic singularity, the PE metric weights the branch lengths of each lineage by their respective geographic ranges (Rosauer et al., 2009). For example, the observation of long branches restricted to a small geographic area is interpreted as high PE. Under this approach, endemism is not focused exclusively at the species level, as clades at all levels can also be endemic, encompassing intra- to interspecific scales (Mishler et al., 2014). As a consequence, PE patterns can be better related to evolutionary processes and biogeographic events responsible for the changes in speciation and extinction rates (Davies and Buckley, 2011: Schluter and Pennell, 2017).

Areas with historical climatic instability tend to harbor fewer endemic species, often represented by phylogenetically derived species (neoendemics) (Jansson, 2003; Sandel et al., 2011). Conversely, historical stable areas may have allowed the survival of ancient lineages, which have been extinct elsewhere (paleoendemics) (Fjeldså et al., 1999). As a result, paleoendemisms and neoendemisms have different effects on PE inferences. The local extinction of paleoendemic lineages, for instance, increases patterns of PE (Daru et al., 2020). However, the loss of neoendemic lineages would strongly impact the PE only if the entire clade disappeared. Dispersal rates also have important influences on PE. While higher dispersal rates reduce the concentration of endemic species, poor dispersal ability increases endemism (Daru et al., 2017).

Contrasting biodiversity patterns based on phylogenetic information is of special interest in systems in which taxonomy is in flux and may not reflect true lineage diversity, such as the Cactaceae family. These plants have an endemic distribution covering the Americas (except for Rhipsalis baccifera) and are associated with a myriad of xeric environments, soil textures, solar irradiance, and altitude (Parker, 1988; Taylor and Zappi, 2004). Cactaceae is a charismatic group of plants and a bona fide example of recent radiation (Arakaki et al., 2011), harboring remarkable diversity in growth forms (Hunt et al., 2006). Additional reasons to assess the endemic levels within the family are to evaluate the levels of endemism, the number of species with disjunct and small range sizes, the threatened IUCN criteria for many species, and the insufficiently protected areas for the group (Barthlott et al., 2015; Goettsch et al., 2019; Pillet et al., 2022). Moreover, the low level of protected areas may cover just a small portion of the cactus occurrence, which needs to be evaluated and formally recognized in semiarid and arid lands in the Neotropics (Barthlott et al., 2015).

Here, we explored geographic and genetic data from cactus species to evaluate the diversity pattern for this plant family. We addressed three main goals: (1) to compare spatial patterns of species distribution, (2) to identify putative drivers of the spatial patterns of endemism, and (3) to evaluate gaps for species protection based on the distribution of protected areas of cacti species. We hypothesize that long-term stable areas such as historical refugia concentrate cactus evolutionary diversity and show high levels of PE. In addition, based on the taxon requirements, we hypothesize that the main abiotic factors driving the diversity patterns in the family are climate conditions (temperature and precipitation) and environmental heterogeneity which affects species persistence and dispersal along with geographic space (see appendix B in supplementary material for more details about the hypotheses tested).

2. Methods

2.1. Species distribution data

In this study, we used geographic information on Cactaceae species found in the Nearctic and Neotropical regions, extending from southern Canada to southern South America. The species *R. baccifera*, the only species naturally present in and outside of the American border, was subsampled to the Americas. We used three geographic databases to recover species occurrences, the GBIF (Global Biodiversity Information Facility), iNat (iNaturalist), and iDigBio (Integrated Digitized Biocollections), using the *spocc* package in R (Chamberlain et al., 2021; R Core Team, 2019) between March 10th and 12th, 2021. The Caryophyll ales.org checklist (Korotkova et al., 2021) was checked to remove any taxa with incorrect names or misspellings. Points with spatial uncertainty, inappropriate localization, or inaccurate localization were removed using the *CoordinateCleaner* package in R (Zizka et al., 2019).

2.2. Molecular data and phylogenetic analysis

The genetic data were recovered using the phytotaR package in R (Bennett et al., 2018) and the script available at the phylotaR GitHub page (https://github.com/ropensci/phylotaR/). The genes were aligned using MAFFT v.7.31 (Katoh et al., 2002) and concatenated to generate a supergene using the program catfastat2phyml.pl (available at: htt ps://github.com/nylander/catfasta2phyml). The topology reconstruction was carried out in IQTree v.2.1 software (Nguyen et al., 2015) using 10,000 ultrafast bootstrap replicates, and constraints on the main clades of subfamily Cactoideae: core Cactoideae (I and II) and tribe Cacteae. We included five outgroups: Portulaca grandiflora, Portulaca oleracea, Talinella dauphinensis (Portulacaceae), Anacampseros filamentosa (Anacampserotaceae), and Trigastrotheca stricta (Molluginaceae). Branches with <50 % bootstrap support values were contracted using the iTOL v.6.4.2 online web server (Letunic and Bork, 2006; available at https://it ol.embl.de/). Considering the potential bias on datasets, phylogenetic reconstruction of the Cactaceae tree was performed using three datasets with distinct amounts of missing data (MD; 40 %, 60 %, and 80 %; Fig. S1). We compared the phylogenetic topologies with the symmetric Robinson-Foulds (RF) pairwise distance (Robinson and Foulds, 1981) in the R package phytools (Revell, 2012) and performed a principal coordinate analysis (PCoA) in the R package PCAmixdata (Chavent et al., 2017). We also conducted experimental pilots using the three MD datasets and observed a similar diversity pattern, except for the 40 % MD dataset, which was an outlier in PCA, showed shorter branches, and displayed the highest level of PD. Thus, we used the tree topology generated with the dataset containing 80 % missing data (Fig. S2). After phylogenetic reconstruction, we crossed the information among species with geographical coordinates and the species with genetic information, summarizing the final dataset to 921 cacti species (~53 % of all accepted species according to Korotkova et al., 2021) from 130 genera (~92 % of all accepted genera, according to Korotkova et al., 2021). This dataset was used in the downstream analyses.

2.3. Calculation of diversity metrics

The geographic coordinates and the phylogeny recovered in this study were imported into Biodiverse v.3.1 (Laffan et al., 2010) using the Biodiverse pipeline in R (https://github.com/NunzioKnerr/biodiverse _pipeline). We defined 100×100 km grids ($1^{\circ} \times 1^{\circ}$), which generated 1963 grid cells covering the Nearctic and Neotropical regions. We matched our occurrence dataset to the mapped grid cells and incorporated our phylogenetic relationship and branch lengths into the analysis. The metrics calculated were: taxon richness (TR), weighted endemism (WE), phylogenetic diversity, relative phylogenetic diversity (RPD), phylogenetic endemism (PE), and relative phylogenetic endemism (RPE; for more details see appendix A in the supplementary material). The

statistical significance of the PD, PE, RPD, and RPE of each grid cell was estimated using a null model that randomly reassigns the species to each grid cell. The randomizations were run 999 times, and the grid cells were classified as significantly high or low (values higher than 97.5 % or lower than 2.5 %, respectively).

We also performed endemism categorization using CANAPE (Categorical Analysis of Neo- and Paleo- Endemism) and evaluated statistical significance using randomization-based tests in Biodiverse software. We estimated endemism based on WE, PD, RP, WPE, and RPE. To determine the areas of high diversity patterns within formally protected areas per country, we also overlapped the endemism, PD, and PE maps with the compiled of shapes of formal and publicly available protected areas in the Neotropical and Nearctic regions (UNEP-WCMC and IUCN, 2022), using QGIS 2.18 software (QGIS Development Team, 2009). Briefly, this database is an up to date source for world protected areas updated monthly with submissions from governments, nongovernmental organizations, landowners and communities.

2.4. Abiotic correlates of diversity pattern

To assess the correlation among spatial patterns of endemism, PD, PE, paleo-, neo-, mixed, and super endemism obtained in this study with abiotic features, we compiled 49 environmental variables, including current and past climatic, topographic, solar irradiation, and soil features from public databases (see Table S1 for more details). Due to uniformity resolution among variable rasters, we resampled all of them to 50 km resolution using the function resample present in the R package raster (Hijmans, 2019). We also removed the collinear variables using the variance inflation factor (VIF), present in the R package usdm (Naimi, 2017). In this analysis, we used a threshold of 10, which reduced from 49 to 17 abiotic variables: present and past precipitation (wc_Bio15, wc_Bio18, and wc_Bio19; lig_Bio14, lig_Bio15, lig_Bio18, and lig_Bio19), past temperature (lig_Bio2, lig_Bio3, lig_Bio8, and lig_Bio9), topography (terrain roughness index, current_tri; wetness index, current_topoWet), soil features (nutrient availability, sq1; oxygen viability to the root, sq4; and texture and phase, sq7), and solar irradiance (direct normal irradiation, dni; see more details in Table S1). To identify possible abiotic variables that may predict the spatial pattern of diversity, we ran, trained, and ensembled the prediction of the correlative model obtained from four machine learning algorithms (random forest, neural network, support-vector machine, and generalized linear model) implemented in the Caret package in R (Kuhn et al., 2020; R Core Team, 2019) using a modified version of the script described by Paz et al. (2021).

3. Results

The spatial distribution and phylogenetic datasets were applied to investigate the diversity pattern associated with the geographical distribution of the Cactaceae family. The tree topology (Fig. S2) recovered the main major Cactaceae clades (Guerrero et al., 2019). The relationships between the minor Cactaceae clades were also similar to the topology reported by Guerrero et al. (2019), with exceptions made for relationships of the tribe Rhipsalideae and the *Incertae sedis* genera *Frailea* and *Copiapoa* within the core Cactoideae clade. It is worth noting that the recovered position of tribe Rhipsalideae and the genus *Copiapoa* are in agreement with recent phylogenomic studies (Acha and Majure, 2022; Romeiro-Brito et al., 2022).

3.1. Geographic estimate patterns

Cactaceae has a distribution predominantly associated with open and xeric formations that usually display distinct annual temperatures, solar irradiation, and precipitation levels (Bonatelli et al., 2014; Lavor et al., 2020; Sarmiento, 2021). Furthermore, the diversity pattern is unevenly distributed among these areas (Fig. 1). Here, we observed

three main cores of high endemism (from north to south): i.) the Chihuahuan Desert and Sierra Madre Oriental (southwest of the United States and Mexico); ii.) Dry Chaco (or Chacoan Dominion; sensu Morrone, 2014; Argentina, Bolivia, Paraguay, and Brazil) and the Sechura Desert/Atacama Desert/Chilean Matorral (Peru and Chile) and iii.) the southern Brazilian Atlantic Forest and part of the Espinhaço Range (eastern Brazil), the second largest mountain chain of South America. Small hotspot areas were also found in savanna patches from southern Florida (United States), Guatemala to Panama, and in the Espinhaço Range. (Fig. 1b). The high PE areas also coincided with the regions of weighted endemism, while the estimated areas of phylogenetic diversity (PD) were more striking than the endemism and PE cell grid (Fig. 1c-d). High PD areas comprised a large portion of central-northern Mexico (desert and xeric shrubland areas in North America), the Dry Chaco, from the southern part of the Brazilian Atlantic Forest to Pampas, and the northern portion of the Espinhaço Range and southern Andean steppes, both areas of remarkable species richness.

There were spatial discrepancies between the PD and relative phylogenetic diversity (RPD), PE, and relative phylogenetic endemism (RPE) patterns (Fig. 1e-h), which were mainly correlated with significantly lower PD values along the Brazilian Atlantic coast. The central portion of Mexico and the Andes/Dry Chaco cells recovered with the highest PE, RPE, and RPD values. Areas with significantly low PD were more common than areas with significantly high PD, recovering only a small portion of the family distribution. These areas were also recovered in both Neotropical and Nearctic realms, mainly along the borders of the Sonoran and Chihuahuan Deserts, Atacama Desert, and Caatinga plus Brazilian Atlantic coast. However, the highly significant PD areas involved part of the Argentina and Bolivia, Caribbean islands, and the northeastern portion of the Pacific coast in Peru and Ecuador. Areas of significantly low and high RPD, PE, and RPE (Fig. 1f-h) showed a similar pattern; three main areas of significantly high values in central Mexico, the Andes plus Dry Chaco (Chile, Argentina, Bolivia, Paraguay, and Brazil), and southern Brazil, while significantly low values were observed in a large portion of the United States and the northeastern portion of the Brazilian Atlantic Forest.

3.2. Paleo-, neo-, and superendemism spatial patterns

We identified five areas of paleoendemism, which included centraleastern Mexico, the northern Andes in Peru, western Cuba, central Bolivia (intersection between Dry Chaco and Chiquitania), Chile, Paraguay, and southern Brazil (Fig. 2). Seven areas of expanded neoendemism were identified across the Americas, occurring in the savannas of the eastern United States, south of Baja California (United States), Caribbean islands, southern Florida, southern Mexico, northern South America (Venezuela and Guyana), Atacama Desert, Dry Chaco, and southern portion of Espinhaço Range. The expanded mixed endemism, which involved part of Baja California and Mexico, Caribbean islands, eastern Brazil, most of the Andean region and Dry Chaco, and southeastern Argentina, recovered most of the grid cells classified as significantly high PE by CANAPE (Fig. 2). Four main portions of superendemism were identified: in the California Chaparral (United States), the Chihuahuan Desert plus Sierra Madre in Mexico, centraleastern Peru, Atacama Desert (Chile), Dry Chaco (Argentina, Bolivia, Paraguay, and Brazil), and southern Espinhaço Range (details in Fig. 2). Expanded areas of mixed and super endemism were commonly detected across the Chihuahuan Desert (southwestern United States and Mexico), Atacama Desert, and Andean regions. It is worth noting that only the southwestern portion of the Dry Diagonal of South America, which comprises the Dry Chaco, displayed significant levels of endemism of any kind, with a low contribution of Brazilian savanna and Caatinga (Fig. 2c).





(caption on next page)

Fig. 1. Spatial phylogenetics of the 921 cacti species showed four cores of high diversity in the Neotropical region. (a) Taxon richness, (b) weighted endemism (WE), (c) phylogenetic diversity (PD), (d) phylogenetic endemism (PE), (e and f) distribution of phylogenetic diversity (PD), and relative phylogenetic diversity (RPD), and (g–h) similar plots of phylogenetic endemism (PE) and relative phylogenetic endemism (RPE) for Neotropical cacti. Blue and red cells show areas with significantly high (>0.975) and significantly low (<0.025) randomized values. Roman numbers represent the four cores of the diversity pattern: I.) the Chihuahuan desert + the Sierra Madre Oriental (southwest of the United States and Mexico); II.) Dry Chaco (Argentina, Bolivia, Paraguay, and Brazil) + the Sechura Desert/Atacama Desert/ Chilean Matorral (Chile), III.) southern Brazilian Atlantic Forest and part of the Espinhaço range (eastern Brazil), and IV.) the Caribbean islands. The biogeographic regions used here followed the classification proposed by Morrone (2014). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)



Fig. 2. Spatial phylogenetics of Cactaceae showed areas of paleo-, neo-, and superendemism scattered in the Neotropical region. Red and blue cells show concentrations of significant neoendemism and paleoendemism, respectively; purple areas indicate concentrations of mixed endemism (both short and long branches present); dark purple indicates superendemism; beige cells show nonsignificant endemism areas. Scatter plots show the correlation between PD and PE. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

3.3. Correlates of spatial diversity patterns

Past climatic, topography, and solar irradiance seem to highly contribute to the predictions of endemism, PD, and PE, while the soil features also displayed high contributions to the prediction of paleo-, neo-, mixed, and superendemism into the Cactaceae family (Fig. 3). The overall results of the four machine learning approaches used in this study show that the most influential factor on endemism and PE was isothermality during the Last Interglacial period (14.7 % and 16.6 %, respectively; LIG), followed by terrain roughness (11.7 % and 8.8 %, respectively; Fig. 3a). The factor most predicting PD was direct normal irradiation (15.1 %), followed by the mean temperature of the driest quarter of the past (11.1 %; Fig. 3b). The soil texture and soil phases (15.9 %) contributed highly to predicting paleoendemism, followed by past isothermality (10.4 %); to neoendemism, the mean diurnal range (11.5 %) and direct normal irradiation (11.2 %) were the highly contributing predictors; to mixed endemism, past isothermality (16.4 %), direct normal irradiation (12.1 %), and terrain roughness (11.5 %);

and to superendemism, the highly contributing predictors were direct normal irradiation (12.4 %), soil texture and soil phases (8.4 %), and past isothermality (8.3 %). Thus, the multimodel selection suggested a role of past temperature, soil, and solar irradiation as the main correlates of all kinds of endemism.

3.4. Protected areas associated with cacti diversity pattern hotspots

Here, we overlapped the grid cells of endemism, PD, PE, paleo-, neo-, and superendemism of cactus species with the legally protected areas present in the Nearctic and Neotropical regions (Fig. 4a–d). We showed that few cells associated with high diversity patterns were within legally protected areas (endemism cells: 17.2 %; PD cells: 3.2 %; PE cells: 1.12 %). Areas of neo- (52 %) and paleo- (9.5 %) seem to be better covered by these protected areas than areas of superendemism (28.8 %). Most of them are located in the United States, Mexico, and Central America. In South America, the few legally protected areas in Chile, which comprise a great part of the cactus endemism (including an area of super



Fig. 3. The relative importance (in percentage) of predictors of diversity for Cactaceae species. Panel (a) corresponds to predictor variables of the patterns of endemism, phylogenetic diversity (PD), and phylogenetic endemism, while in panel (b), we observed the predictors of the pattern of endemism diversity (see Table S1 for more details about variable description). * Last Interglacial layers.

endemism; Fig. 4d), mainly in the Atacama Desert/Chilean Matorral, are evident. The Andes and the Campos Rupestres (Brazil) from Espinhaço Range were also poorly protected, even though both contained an enormity of endemic and microendemic species (Särkinen et al., 2012; Rapini et al., 2021). Thus, the analyses showed that only a small part of the cactus evolutionary history is legally protected (Goettsch et al., 2019; UNEP-WCMC and IUCN, 2022).

We better explore the diversity metric patterns per country (Table 1), evaluating the contribution of political boundaries to the protection of Neotropical biodiversity. It is possible to observe that the sum of protected units in both South and North America comprises, on average, >30 % of the total protected area. However, countries such as Barbados, Colombia, Uruguay, and Peru (important centers of PD and PE for Cactaceae, Fig. 1) displayed fewer units and areas responsible for protecting and covering a great part of the endemism of cactus species (Fig. 4; Table 1), at least considering the database used in this study. Moreover, with the exception of Mexico and Guatemala, the protected units poorly covered the areas with high endemism, PD, and PE for cactus (Fig. 4), certainly imposing challenges for the management and conservation of Cactaceae.

4. Discussion

In this study, we integrated phylogenetic and spatial approaches to determine levels of diversity and endemism across the distribution of the family Cactaceae. Hotspots of cactus diversity were previously described (e.g., Rzedowski, 1993; Taylor, 1997; Barthlott et al., 2015; Noroozi et al., 2018; Sosa et al., 2018, 2020; Nanni et al., 2019; Lavor et al., 2020), including deserts (Chihuahuan and Sonoran, southwest portion of the United States and Mexico, and Atacama, in Chile) and montane dry tropical forests (e.g., the Sierra Madre Oriental, Mexico). These analyses were able to identify similar areas previously described by Taylor (1997) and Barthlott et al. (2015) using patterns of species richness and endemism, respectively. According to both studies, and here using PD and PE metrics, it is clear the importance of the diversity centers in the southern United States and Mexico, the south and the central Andes, and portions of the Brazilian Caatinga and Atlantic Forest, all of which have similar xeric conditions but distinct topographic, soil, and ecological features. By adding empirical data based on new endemism metrics, we also highlighted the importance of cactus diversity in the Atacama Desert, montane dry sub- and tropical forests

(Chiquitania, Bolivian Montane Dry Forest, Chilean Matorral, Dry Chaco, etc.), patches of xeric vegetation within the Brazilian Atlantic Forest, and portions of the Espinhaço Range. We also identified the importance of endemism and PD patterns associated with several Central American countries, such as Guatemala, Honduras, El Salvador, Nicaragua, and Costa Rica, which were undervalued in previous studies. It is worth noting that many of these areas are climatically stable (Hartley et al., 2005; Mucina and Wardell-Johnson, 2011; Werneck et al., 2012; Costa et al., 2018; Pie et al., 2018) and thought of as museums and cradles for drought-adapted plants (Murphy et al., 2015). Our results suggest that the Neogene orogenic processes giving rise to the Gulf of California, the Mexican and Central American mountain systems, the central Andes, and the Espinhaco Range (which extend to the Cretaceous) might be important determinants of PE areas. The profound changes in physiography, climate, and drainage caused by these orogenic events (Saadi, 1995; Morán-Zenteno et al., 1999; De-Nova et al., 2018; Rech et al., 2019) triggered local events of diversification and speciation in many plant and animal taxa (Steinbauer et al., 2016; Rull, 2020) and may have impacted cactus diversification and distribution.

The significantly high PD in some areas, such as the Chihuahuan Desert, Peru, and Ecuador Pacific coasts, the Andes, and the central portion of Dry Chaco, suggests that these areas might be associated with historical refugia and centers of diversification to the family. The significantly low values of PD recovered in areas of high endemism, such as the Sonoran (southwest portion of the United States) and Atacama deserts (Chile) and a great part of the Caatinga and Brazilian Atlantic Forest (Brazil), may suggest strong lineage clustering (neoendemism). These areas present examples of rapid and recent diversification of Cactaceae, such as the genera Cereus (Bombonato et al., 2020; Amaral et al., 2021b.) and Pilosocereus (Bonatelli et al., 2014; Lavor et al., 2019) and the Mammilloid clade (Breslin et al., 2021), favored the prevalence of closely related taxa. This result is in line with the prevalence of recent in situ diversification and recurrent habitat specialization in the diversification and historical assembly of the Caatinga flowering plants (Fernandes et al., 2022).

Most of the high PE areas comprise both ancient and recent diversity (mixed endemism). However, areas of paleoendemism (museums) are encrusted within mixed-endemism cells (Fig. 2), suggesting a complex pattern of spatial endemism compartmentalization in some regions. These areas include the northern and central Andes and Atacama



Fig. 4. Endemism hotspot of Cactaceae with the legally protected areas of the Americas in green (UNEP-WCMC and IUCN, 2022). The map shows the low level of cells containing high (a) endemism, (b) phylogenetic diversity (PD), and (c) phylogenetic endemism (PE), and the possible areas of neo-, paleo-, and superendemism overlapped for the current formally protected areas. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Desert/Matorral in Chile. At the same time, we observed neoendemism cells (possible cradles) in the peripheral regions with significantly high PE values (Fig. 3), which may indicate new centers of diversity.

Based on our diversity pattern results, deserts and drylands/dry forests may have acted as both museums and cradles of cactus lineages. This likely holds for other plants and animal groups in these landscapes (Sosa et al., 2018, 2020; Dick and Pennington, 2019; Candela et al., 2021). In the Neotropics, mainly in the Campos Rupestres from the Espinhaço Range, a major effort is underway to understand the environmental and evolutionary forces driving the increased rates of species richness and endemism in the old, climatically buffered, infertile landscapes (OCBILs; Hopper et al., 2021). Here, we found that the Campos Rupestres in the northern Espinhaço Range present a high level of endemism and richness for Cactaceae (Fig. 1a–b). Indeed, similar results were reported for other species groups in this region (Colli-Silva et al., 2019; Assunção-Silva and Assis, 2021). We stress the Campos Rupestres from the Espinhaço Range as a center of superendemism to the South American cacti, being a remarkable hotspot of biodiversity and focus of conservation strategies.

4.1. Predictor variables of Cactaceae endemism

The association between long-term climate stability and endemism is widely discussed in biogeographic and ecologic studies (Barratt et al., 2017; Feng et al., 2019; Zuloaga et al., 2019). However, specific abiotic features may be more meaningful than others in explaining differences in diversity patterns among species and/or bioregions (Barratt et al., 2017; Costa et al., 2018; Paz et al., 2021). Our results suggested that abiotic variables associated with temperature, terrain roughness (topography), soil texture/phase, and solar irradiation are important factors that may explain the diversity pattern in Cactaceae.

The role of temperature and precipitation as drivers of diversification

Table 1

Estimates of high endemism, phylogenetic diversity, and phylogenetic endemism areas of cactus species per country and within protected units (shapefile used: UNEP-WCMC and IUCN, 2022).

Country	Country area (km ²)	Protected unit area per country		Area of endemism		Endemism areas within protected unit		Areas of phylogenetic diversity		Phylogenetic diversity areas within protected unit		Areas of phylogenetic endemism		Phylogenetic endemism areas within protected unit	
		km ²	%	km ²	%	km ²	%	km ²	%	km ²	%	km ²	%	km ²	%
Antigua and Barbuda	565.39	232.11	41.05	-	_	-	_	-	_	-	_	_		_	_
Argentina	3,448,767.73	2,450,699.82	71.06	364,103.38	10.56	55,816.81	15.33	117,059.23	3.39	17,838.45	15.23	67,773.8	1.96	19,797.16	29.21
Bahamas	13,371.7	5161.2	38.60	-	-	-	-	-	-	-	-	-	-	-	-
Barbados	461.13	10.96	2.38	-	-	-	-	-	-	-	-	-	-	-	-
Belize	23,196.02	9065.53	39.08	-	-	-	-	-	-	-	-	-	-	-	-
Bolivia	1,142,329.73	315,656.72	27.63	319,333.65	27.95	20,585.34	6.44	159,165.42	13.93	30,852.56	19.38	181,772.94	15.91	36,874.76	20.28
Brazil	8,761,755.48	2,940,014.09	33.56	266,564.68	03.04	29,345.88	11.01	64,966.07	0.74	22,605.87	34.79	34,243.31	0.39	1329.58	3.88
Chile	962,724.11	382,102.51	39.69	127,223.97	13.21	11,982.2	9.42	-	-	-	-	48,710.93	05.05	4175.32	8.57
Colombia	1,147,188.1	226,017.04	19.70	24,164.66	2.11	6726.03	27.83	-	-	-	-	-	-	-	-
Costa Rica	52,165.7	48,379.45	92.74	43,113.17	82.65	39,797.76	92.31	-	-	-	-	-	-	-	-
Cuba	118,047.6	49,147.44	41.63	8925.05	7.56	3520.35	39.44	-	-	-	-	-	-	-	-
Dominica	797.46	246.86	30.96	-	-	-	-	-	-	-	-	-	-	-	-
Dominican Republic	51,396.76	16,812.6	32.71	7268.87	14.14	5813.64	79.98	-	-	-	-	-	-	-	-
Ecuador	257,179.36	81,731.89	31.78	54,028.39	21.01	11,102.45	20.54	-	-	-	-	-	-	-	-
El Salvador	21,302.34	4774.04	22.41	6184.31	29.03	2351.27	38.02	62.91	0.30	0.00	0.00	-	-	-	-
French Guiana	84,359.65	46,568.27	55.20	-	-	-	-	-	-	-	-	-	-	-	-
Grenada	356.31	84.93	23.84	-	-	-	-	-	-	-	-	-	-	-	-
Guatemala	113,898.33	41,801.24	36.70	32,371.59	28.42	4530.76	13.99	23,975.31	21.05	22,605.87	94.28	-	-	-	-
Guyana	212,835.76	18,658.09	8.77	-	-	-	-	-	-	-	-	-	-	-	-
Haiti	28,860.57	2353.1	8.15	-	-	-	-	-	-	-	-	-	-	-	-
Honduras	116,745.33	46,827.01	40.11	2514.97	2.15	595.64	23.68	-	-	-	-	-	-	-	-
Jamaica	11,672.57	3670.18	31.44	-	-	-	-	-	-	-	-	-	-	-	-
Mexico	2,157,665.94	487,621.24	22.60	1,307,497.94	60.60	255,109.69	19.52	1,318,132.77	61.09	215,751.36	16.36	555,122.88	25.72	72,365.47	13.03
Nicaragua	132,208.05	72,868.53	55.12	5793.27	4.38	5117.19	88.23	-	-	-	-	-	-	-	-
Panama	75,381.15	40,241.94	53.38	-	-	-	-	-	-	-	-	-	-	-	-
Paraguay	436,307.71	132,353.83	30.33	-	-	-	-	-	-	-	-	-	-	-	-
Peru	1,319,758.28	309,307.78	23.44	167,866.11	12.72	9074.52	5.4	-	-	-	-	34,243.31	2.59	1102.77	3.22
St. Kitts and Nevis	206.03	107.77	52.31	-	-	-	-	-	-	-	-	-	-	-	-
St. Lucia	658.33	326.63	49.61	-	-	-	-	-	-	-	-	-	-	-	-
St. Vincent and the Grenadines	353.73	182.34	51.55	-	-	-	-	-	-	-	-	-	-	-	-
Suriname	146,355.06	35,299.12	24.12	-	-	-	-	-	-	-	-	-	-	-	-
Trinidad and Tobago	5127.24	1526.2	29.77	-	-	-	-	-	-	-	-	-	-	-	-
United States	13,837,809.73	3,518,060.12	25.42	249,903.1	1.81	39,537.81	15.82	427,853.88	03.09	85,081.42	19.89	_	-	-	-
Uruguay	212,228.95	22,326.28	10.52	-	-	-	-	13,367.81	6.30	318.66	2.38	-	-	-	-
Venezuela	924,793.55	840,734.56	90.91	-	-	-	-	-	-	-	-	-	-	-	-
Total	35,818,830.88	12,150,971.42	33.92	2,986,857.11	8.33	514,073.12	17.21	2,124,583.4	17.48	395,054.19	18.59	921,867.17	7.58	135,645.06	14.71

-: the metric was not observed in the country.

and bioregionalization has long been recognized (e.g., Antonelli, 2017). For Cactaceae, temperature seems to be the most important factor for predicting the species diversity in the Neotropics, which was also demonstrated for specific genera of cactus and other groups of species distributed in xeric landscapes (Gottlieb et al., 2019; Mosco, 2019; Aquino et al., 2021). The isothermality (diurnal range of temperatures per temperature seasonality) in arid and semiarid regions, including desertic areas, displays low oscillations between day and night, which seems to favor CAM photosynthetic metabolism and the reduction in evapotranspiration of Cactaceae (stomata remaining closed during the daytime; Mosco, 2019). Thus, arid areas may work as locally buffered zones over time, which might also have increased the diversity pattern in Cactaceae (Short et al., 2017).

Landscape metrics, such as topographic roughness, revealed some endemism patterns in South America (Moeslund et al., 2013; Paz et al., 2021). We found that topography (terrain roughness) may act as a good predictor of endemism patterns in the Cactaceae family. The topographic heterogeneity associated with areas of highest PE values in our analysis, such as the Chihuahuan and Atacama deserts and Andes, may produce a direct effect on cactus diversification. Guerrero et al. (2011) showed a complex pattern of diversification in the Atacama Desert, in which the topography offers several distinct habitats, also acting as a buffered area against climatic changes (Moeslund et al., 2013). Local soil patterns (e.g., soil pH and salinity) and texture are also important features directly affected by topography and act as predictors of species richness (Cingolani et al., 2010), which might represent an important influence on plant diversity, including desert plants (Moeslund et al., 2013; Muenchow et al., 2013). In Cactaceae, the soil texture, such as that found in limestone outcrops, was demonstrated to be important to species persistence and, consequently, to diversification (Ruedas et al., 2006; Bárcenas-Argüello et al., 2010). For instance, Flores et al. (2019) showed that the rock landform surface, which is a common substrate for many cactus species, is associated with species richness in arid environments. Thus, topographic roughness and soil texture may be proxies for habitat heterogeneity and diversification in arid and xeric regions. It is likely that other soil characteristics, such as pH and salinity, might be important predictors of diversity. Recently, Aquino et al. (2021) used a detailed Mexican soil database to highlight the relevance of soil pH in explaining patterns of distribution of the cactus genus Epithelantha.

As already demonstrated, cactus species are well adapted to grow and persist in environments with extremely high temperatures and solar radiation (Mauseth, 1999; Aliscioni et al., 2021), displaying particular morphological and physiological features to explore these habitats (Albanese et al., 2019). Spines, cladode structure and shape, number of columns, and growth orientation are important features for minimizing the absorption of solar radiation (Zavala-Hurtado et al., 1998; Menezes et al., 2015; Aliscioni et al., 2021), reducing damage processes associated with excess heat and light and balancing the amount of daily quanta absorbed into the photosynthetic system (Albanese et al., 2019). Recently, Amaral et al. (2021a) uncovered positive selection signatures in genes associated with the photosynthetic system in Cereus fernambucensis (Cereeae), which reinforces the importance of solar irradiance within Cactaceae. Furthermore, irradiance seems to influence flowering and fruiting evolution since seasonal variations in irradiance limits alter reproductive phenologies and seed development (Zimmerman et al., 2007). The importance of solar irradiance to cactus species may explain the function of this predictor in diversification and endemism in the family.

4.2. Conservation phylogenetics

Here, we highlighted regions with elevated levels of phylogenetic diversity and endemism for the Cactaceae family, including those of broad interest to conservation. Approximately 30 % of Cactaceae species are currently at some risk of extinction (Goettsch et al., 2015, 2019). Threatened cactus species are of heightened concern due to their

meaningful scientific value and their significant social and economic role (Pedrosa et al., 2020; Tremlett et al., 2021). We identified that a substantial part of the cactus cell grids that comprise areas with high levels of PD, PE, paleo-, neo-, and superendemism are still out from legally protected areas (Fig. 4). Some of these regions were recognized as relevant for cactus diversity by Goettsch et al. (2015, 2019), Taylor (1997), and Barthlott et al. (2015) using traditional diversity metrics, such as species richness and endemism. Our results were important to reveal that several areas with high PD and PE lack conservation efforts and are covered by fewer protective units.

Despite the United States, Mexico, and Central American countries (Guatemala, Costa Rica, and Nicaragua) displaying several protected areas that include arid and semiarid lands (Fig. 4), the number of protected areas in South America is still insufficient to preserve cactus diversity. Countries such as Brazil, Chile, and Peru that comprise a substantial part of the PD and PE of cactus species are protecting < 10 %of the cactus biodiversity within their borders (Table 1). These findings are extremely concerning, indicating that proposals for conservation areas in these regions have neglected the diversity found in the speciesrich cactus family. More meaningful is the fact that pen formations, such as dry forests and xeric lands, are exposed to a variety of different threats, many times being more threatened than rain tropical forests, based on area extension and biodiversity richness (Janzen, 1988; Miles et al., 2006; Fremout et al., 2020). The high level of anthropogenic activity, such as overexploitation and overgrazing, and its association with the fewer areas of formal protective units demonstrate the priority of conservation efforts for these remaining environments (Portillo-Quintero and Sánchez-Azofeifa, 2010; DRYFLOR et al., 2016; Carvalho et al., 2022; Meiado and Almeida, 2022). Thus, studies such as this are important to illustrate to stakeholders how conservation management in South America still needs to be further developed and that limited decisions have been made in the last few decades by neglecting many open formations.

The use of nontraditional metrics to estimate diversity patterns seems to provide new and additional information about biodiversity aspects, including evolutionary history associated with distinct geographic areas. This approach may help to improve conservation decisions. For instance, high-diversity cells that suggest rapid radiation events seem to be common among Cactaceae and may carry genetic variation potentially able to respond to future climate changes (Xu et al., 2019). Thus, cells that comprise paleo-, neo-, and superendemism areas display high importance to the planning and management of strict protective units. Overall, <50 % of the areas that we recovered in the analysis as of high conservation interest are unprotected. We also reaffirm the importance of species richness and endemic metrics, instead of disagreement in relation to their use. We proposed, similar to many other authors (Lee and Mishler, 2014; Laity et al., 2015; Xu et al., 2019), the incorporation of these metrics to improve the monitoring and planning of conservation areas.

Given the rapid anthropogenic disturbance, mainly in the past three decades, most of the areas outside and even inside the legally protected units have been lost due to predatory agriculture and cattle ranching and criminous fires, such as those observed in Brazil in recent years (Pivello et al., 2021). Based on our results, distinct efforts may be made to plan protection areas, mitigate resource exploration, and manage threatened species in semiarid and arid lands. We propose to reinforce the conservative efforts to maintain the already existing protected areas, mainly those that may recognize PE areas, not only for Cactaceae but also for all fauna and flora diversity. Investment in a better system/model to monitor biodiversity and the environment, rigorous and straightforward legal governmental politicians, and prioritization of regions of high biodiversity are fundamental for this purpose. Furthermore, the planning and establishment of new protected units, mainly in South America, using diversity metrics may improve and upgrade the preservation of the management board.

4.3. Caveats

Here, we propose a first attempt to cover the general diversity patterns related to the cactus species richness distributed in the Neotropical xeric landscapes. We recovered both molecular and occurrence data for >50 % of accepted species of the Cactaceae family, comprising 92 % of the genera. These percentages are similar to or even higher than those in other studies with the same purposes (e.g., Schmidt-Lebuhn et al., 2015; Paz et al., 2021; Albassatneh et al., 2021). In this family, the species generally have a narrow range compared with the genus distribution, which decreases biases associated with species underrepresentation of the phylogenetic tips (Rodrigues et al., 2005; Pollock et al., 2015; McCulloch et al., 2022). However, even here, poor sampling may lead to overestimation of richness and endemism metrics based on the totally explored genus (Baldwin et al., 2017). Thus, we were conservative in our discussion by emphasizing areas of high PD and PE, which may display even higher metric values than indicated by our data. Furthermore, we are still facing a lack of genetic data for some cactus groups, resulting in an unbalanced number of species and publication data related to some overlooked countries/regions (Franco et al., 2022). It is expected that by using high-throughput sequencing technologies, more complete datasets might be available in the future (including new taxa), optimizing the branch length estimates and, consequently, the metrics reported here. New and improved public databases that include specific variables with an increased resolution (e.g., soil pH) may also promote more detailed cell grids with diverse endemic patterns. Thus, we seek to standardize the metrics of analyses and genetic and occurrence sampling to minimize these caveats, conscious of the barriers and biases associated with this approach. Despite this, we were able to define areas of ecological importance to the maintenance and diversification of the family, displaying the main areas deserving conservatism efforts and describing the importance of protective unit planning to the Neotropics.

CRediT authorship contribution statement

DTA, IASB, and FFF conceived the idea. DTA, IASB, and MRB performed data collection and analyses. DTA led writing. IASB, MMR, EMM, and FFF all contributed with many conceptions and writing. All authors contributed to the intellectual development of the paper, made multiple revisions and approved the final draft.

Data accessibility statement

The dataset supermatrices of 40 %, 60 %, and 80 % missing data, as well as the tree topology obtained for the three datasets, were deposited on FigShare (https://doi.org/10.6084/m9.figshare.17057816).

Declaration of competing interest

The authors declare no conflict of interest.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.biocon.2022.109677.

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