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RESEARCH ARTICLE

Closing the Scottian shortfall in the Brazilian Caatinga seasonally dry forests: conservation status of endemic bat-pollinated angiosperms and their main threats

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Abstract

Background and aims – Bats are the third most important animal pollinators in the Brazilian Caatinga seasonally dry forest, but little is known about the conservation status of the chiropterophilous plant species in this domain, and their main threats. The Scottian shortfall relates to deficits in assessments of IUCN conservation statuses. We aimed to evaluate the current conservation status of chiropterophilous species in the Caatinga, investigate the main changes in land use and land cover in the last years and their impacts on conservation of these species.
Material and methods – We compiled a dataset and evaluated the extinction risk of 16 species following the IUCN Red List categories and criteria using the geographic range criterion. Analyses of reductions of natural vegetation were carried out using data from the project MapBiomas.
Key results – Our results show that approximately 80% of the assessed species saw their conditions worsen in the last years. We verified that *Dyckia viridiflora* and *Ipomoea vespertilia* are categorized as Endangered and *Stigmatodon limae* is considered Vulnerable. The main sources of disturbances impacting these species according to land use are pastures and mosaics of land uses, but we highlight that urbanization is the second or third most important threat for all species. The three main threats affected the species differently. Although half of the species is assessed as Least Concern, all species had their suitable areas impacted by human activities.

Keywords

conservation, chiropterophilous angiosperms, land cover, land use, Red List Categories, threatened species

INTRODUCTION

Changes induced by human action on land cover has been one of the main factors contributing to drastically modify ecosystem structure, thus affecting biodiversity patterns (Western 2001). Nature conservation policies are essential to preserve natural resources and the species that inhabit ecosystems. However, conservation policies need to be planned by assessing the conservation status of species and their habitats (Lopes-Lima et al. 2021). The lack of adequate ecological knowledge can affect conservation methods, funding, and policies (Lopes-Lima et al. 2021; Marrone et al. 2022). This deficit of conservation status information has been called the Ostromian shortfall,

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named after the North American economist, Elinor Ostrom (1933–2012), who developed work on resource governance and their impact in biodiversity management and policies (Lopes-Lima et al. 2021). A recent conceptual advancement by Haelewaters et al. (2024) introduced the Scottian shortfall, named in honour of Peter Markham Scott (1909–1989), the founder of the IUCN Red List. This shortfall quantifies the disparity between the number of described species and those that have received formal IUCN Red List assessments. In contrast to the Ostromian shortfall, the Scottian shortfall offers a more readily quantifiable metric, as it compares two concrete numbers: the total number of described species versus the total number of assessed species. The Ostromian shortfall, while equally important, remains vague.

One of the Brazilian phytogeographic domains that suffers the most from the Scottian shortfall is the Caatinga, the largest Seasonally Dry Tropical Forest (SDTF) in South America (Pennington et al. 2000). The vegetation in the Caatinga is mostly deciduous during the dry season and is marked by spiny and succulent species (Mooney et al. 1995). Approximately 30% of the plant species in this domain are classified in an extinction risk category, but this number can be even higher due to the poor knowledge on the Caatinga biodiversity, as this is the least studied Brazilian domain (Leal et al. 2003). Despite being the world's most species rich SDTF, it is still a low priority for conservation investment (Tabarelli et al. 2018), being the least protected Brazilian phytogeographic domain, with less than 2% of its area contained in Protected Areas (Leal et al. 2003; CNUC/MMA 2015). Its main anthropic disturbances are linked to land cover changes, such as the construction of roads and water reservoirs, agriculture, overexploitation of native vegetation for firewood production, and free-ranging livestock grazing (Singh 1998; Ribeiro et al. 2015; Silva et al. 2017).

These disturbances affect the persistence of native species, which are integral to maintaining the natural biodiversity, and ecosystem productivity and services (Isbell et al. 2011). One ecosystem service that can be altered by anthropic disturbances in the SDTFs is pollination (Quesada et al. 2011; Del-Claro and Torezan-Silingard 2021). Caatinga-inhabiting angiosperm species show an elevated degree of dependence on animals for pollination, including vertebrates (Machado and Lopes 2004; Leal et al. 2017). Bats are the third most important animal pollinators in this phytogeographic domain, accounting for approximately 13% of pollination relationships (Machado and Lopes 2004). At least 38 interactions between plants and nectivore bats are known for the Caatinga so far (Machado and Vogel 2004; Rocha et al. 2007; Forzza and Leme 2015; Queiroz et al. 2016; Monteiro et al. 2018; Aguilar-Rodríguez et al. 2019; Costa-Lima and Chagas 2019; Domingos-Melo et al. 2020, 2023; Rocha et al. 2020; Cordero-Schmidt et al. 2021; Albuquerque-Lima et al. 2023).

To attract relatively large and energetically expensive pollinators, during their evolutionary history, chiropterophilous angiosperms have developed flowers with specific features, such as large and resistant flowers with white or greenish coloration, campanulate or brush-like shapes, fermented odour, and production of large amounts of nectar (van der Pijl 1961; Helversen and Winter 2003; Fleming et al. 2009; Willmer 2011; Rech et al. 2014; Winter and Helversen 2019; Domingos-Melo et al. 2020). These features are widespread across flowering plant clades (van der Pijl 1961; Fleming et al. 2009; Kunz et al. 2011; Geiselman and Sarah 2020). The Caatinga houses at least 90 bat species (Carvalho-Neto et al. 2017) and 11 of which feed on nectar, either as specialists or opportunists (Domingos-Melo et al. 2023), including three endemic species, *Lonchophylla mordax* Thomas, 1903, *Lonchophylla inexpectata* Moratelli & Dias, 2015, and *Xeronycteris vieirai* Gregorin & Ditchfield, 2005. *Xeronycteris vieirai* is considered Vulnerable (VU) (ICMBio/MMA 2016, although DD in IUCN Red List) and feeds on pollen and nectar of plant species from several families (Cordero-Schmidt et al. 2017; Gomes et al. 2018; Domingos-Melo et al. 2023).

Considering that the diet of these Caatinga bat species mostly consists of nectar and pollen (Solmsen 1998; Tschapka and Dressler 2002), preserving chiropterophilous plant species is indispensable; however, little is known about the conservation status and the main threats of these angiosperms. Thus, there is an urgency for conservation efforts for chiropterophilous angiosperms and hence assessing the conservation status of chiropterophilous plants will provide important information for the scientific community, governmental bodies, non-governmental organizations, and society as a whole, helping in conservation decision-making. The Caatinga represents a distinctive semi-arid domain characterized by pronounced seasonal drought cycles, remarkable floristic endemism, and intricate ecological adaptations that maintain its biological diversity (Leal et al. 2003; Tabarelli et al. 2018). A particularly vital component of this ecosystem involves the specialized mutualisms between chiropterophilous plant species and nectarivorous bats. These plant-pollinator interactions constitute fundamental ecological processes that enhance ecosystem resilience and maintain structural stability within this unique biome (Machado and Vogel 2004; Rocha et al. 2007; Forzza and Leme 2015; Queiroz et al. 2016; Monteiro et al. 2018; Aguilar-Rodríguez et al. 2019; Costa-Lima and Chagas 2019; Domingos-Melo et al. 2020, 2023; Rocha et al. 2020; Cordero-Schmidt et al. 2021; Albuquerque-Lima et al. 2023).

Therefore, following recent attempts to reduce the Scottian shortfall via defining conservation status, we establish in this study the following questions: 1) What is the current conservation status of chiropterophilous species in the Caatinga? 2) What are the main changes in land use and land cover in the distribution of these species in the last 36 years? We expect that our study will represent an important advancement in reducing the

Scottian shortfall in the Caatinga, one of the least studied neotropical ecosystems.

MATERIAL AND METHODS

Study area

The Brazilian Caatinga phytogeographic domain covers 10.1% of the country, totalling an area of 862,818 km^2 (Fig. 1). It is contained almost exclusively in the Northeast region, except for areas in the north of the state Minas Gerais in the Southeastern region (IBGE 2019). The Caatinga has approximately 70% of its area in crystalline basement (Proterozoic) and 30% in sedimentary basins (Paleozoic and Mesozoic) (Cole 1986; Sampaio 1995). The climate is semi-arid, and the mean temperature is constant throughout the year, varying from 25 to 30°C. Annual precipitation, on the other hand, has a large temporal-spatial variation, with a dry season that varies from seven to ten months per year, and a wet season with precipitation between 600 and 1,200 mm/month (Silva et al. 2017). The name Caatinga comes from the Tupi Indigenous language and means "white forest", referring to the loss of the leaves during the long drought period (Prado 2003). The dominant vegetation is Seasonally Dry Tropical Forest (SDTF) (Pennington et al. 2009), but savanna-like formations, enclaves of rain forests, and rock outcrops are also present, the Caatinga being generally characterized by spiny caducifolious species (Mooney et al. 1995; de Queiroz et al. 2017; IBGE 2019).

The Caatinga is the most populous semi-arid region in the world, with more than 28 million inhabitants (14.5% of the Brazilian population) and 10.4 inhabitants/km^2 distributed in thousands of small rural dwellings (Silva et al. 2017). Most of the economy of the Caatinga is supported by an extractive agropastoral system, mostly based on family cultivation of beans, maize, and cassava, besides raising goats and cattle (Sampaio 1995; Silva et al. 2017;

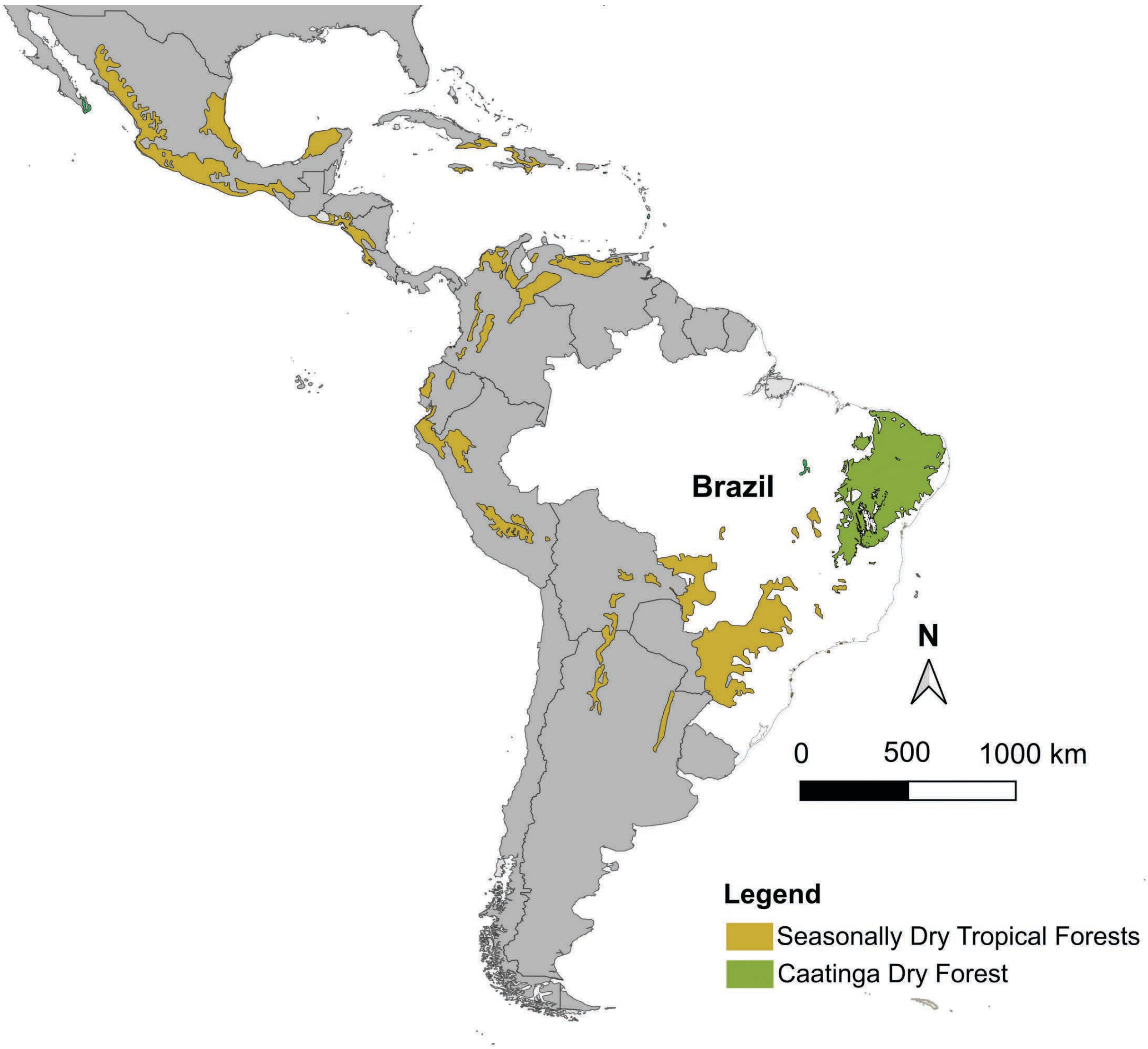

Figure 1. Map showing the Seasonally Dry Tropical Forests (yellow) of the neotropical region with emphasis on the Caatinga (green). Map created using QGIS v.2.18.12. (QGIS Development Team 2020).

Tabarelli et al. 2018). Large landholdings are concentrated in the irrigated areas around the São Francisco River, supporting a system of fruit orchards and vineyards. Due to pressure from agriculture, animal grazing, and continuous extraction of forest products, the Caatinga domain has been suffering intense modification that has resulted in desertification processes and suppression of forest vegetation (Tabarelli et al. 2017).

Study group

We used the list of chiropterophilous Caatinga species available in Domingos-Melo et al. (2023). We verified that the 38 chiropterophilous species occur in this ecosystem (Machado and Vogel 2004; Rocha et al. 2007; Forzza and Leme 2015; Queiroz et al. 2016; Monteiro et al. 2018; Aguilar-Rodríguez et al. 2019; Costa-Lima and Chagas

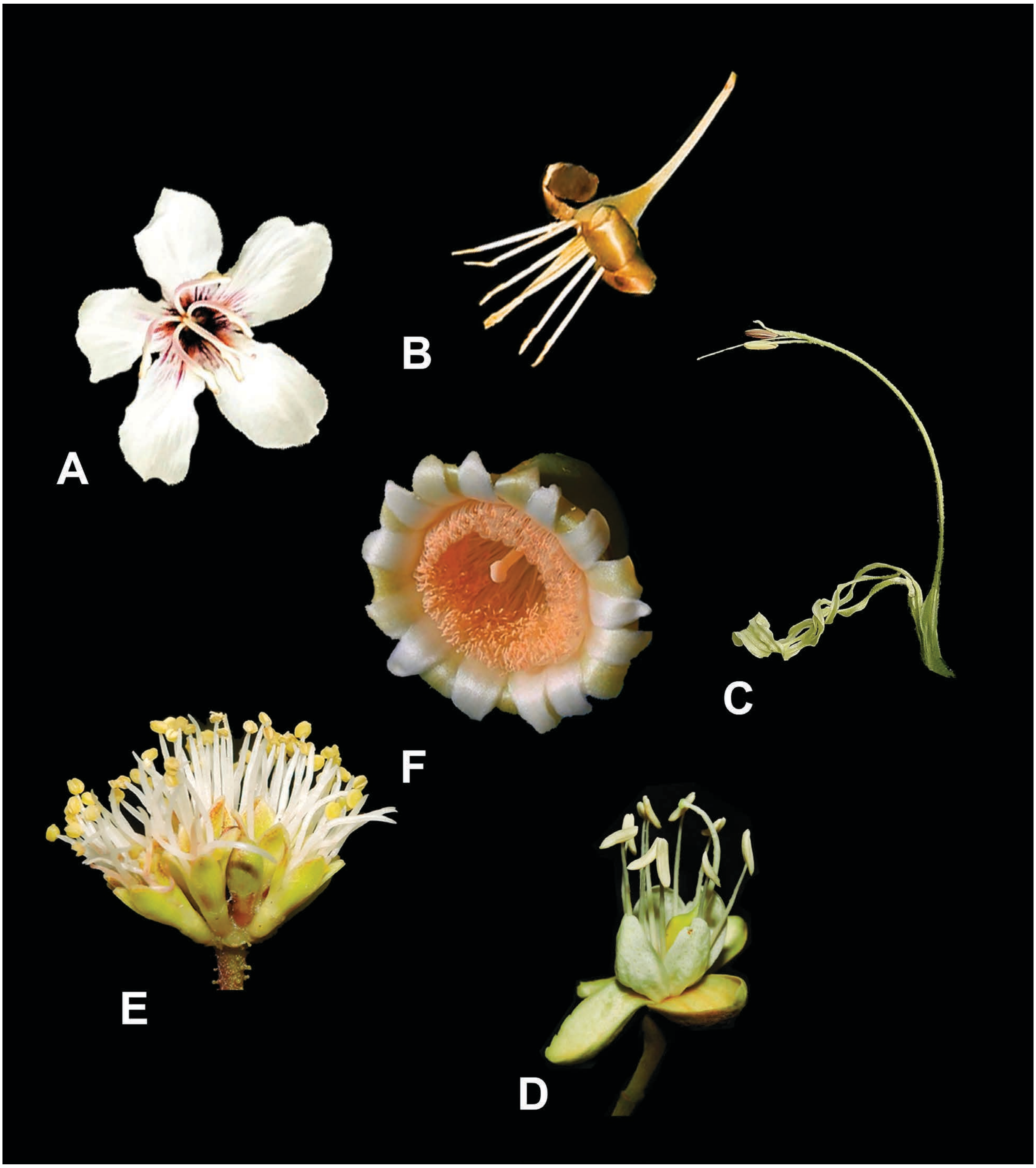

Figure 2. Flowers of chiropterophilous species occurring in the Caatinga. **A**. *Ceiba glaziovii*. **B**. *Dyckia viridiflora*. **C**. *Harpochilus neesianus*. **D**. *Hymenaea cangaceira*. **E**. *Mimosa lewisii*. **F**. *Pilosocereus catingicola*. Photos: A–B, D–F by Rubens Queiroz; C by Camila Alcantara.

2019; Domingos-Melo et al. 2020, 2023; Rocha et al. 2020; Cordero-Schmidt et al. 2021). We then selected the species endemic to Brazil from that initial list, as this allows us to more completely access the available collections and more closely verify their identity. Only specimens identified by experts were included. Some species were excluded due to insufficient occurrence data, including the ones that are rare and/or known only from type specimens. We included only species with at least seven herbarium specimens with confirmed occurrence locality. Species with less than seven confirmed occurrences were not assessed due to data limitation, and therefore considered Not Evaluated (NE).

After the described procedure, we ended up with 16 angiosperm species in this study (42% of the total: 38 species): *Harpochilus neesianus* Mart. ex Nees; *Harpochilus paraibanus* F.K.S.Monteiro, J.I.M.Melo & E.M.P.Fernando (Acanthaceae); *Dasyphyllum donianum* (Gardner) Cabrera (Asteraceae); *Adenocalymma dichilum* A.H.Gentry (Bignoniaceae); *Dyckia viridiflora* Forzza; *Stigmatodon limae* (L.B.Sm.) D.R.Couto & A.F.Costa (Bromeliaceae); *Pilosocereus catingicola* (Gürke) Byles & Rowley; *Pilosocereus chrysostele* (Vaupel) Byles & G.D.Rowley; *Pilosocereus piauhyensis* (Gürke) Byles & G.D.Rowley (Cactaceae); *Ipomoea marcellia* Meisn.; *Ipomoea vespertilia* D.Santos, G.C.Delgado-Junior & Buril (Convolvulaceae); *Calliandra aeschynomenoides* Benth.; *Hymenaea cangaceira* R.B.Pinto, Mansano & A.M.G.Azevedo; *Mimosa lewisii* Barneby (Fabaceae); *Sinningia brasiliensis* (Regel & Schmidt) Wiehler & Chautems (Gesneriaceae); and *Ceiba glaziovii* (Kuntze) K.Schum. (Malvaceae) (Fig. 2). Nine species had been previously assessed (Pôrto et al. 2004; CNCFlora 2012; Forzza and Leme 2015; Amaro and Messina 2016; Monteiro et al. 2018; Costa-Lima and Chagas 2019; Santos et al. 2019) for their conservation status, but we carried out an updated re-assessment, and the other seven species were assessed for the first time.

Data compiling

We collected data for the 16 chiropterophilous species occurring in the Caatinga and endemic to Brazil. Collection locality information (geographical coordinates) was extracted from the databases GBIF (https://www.gbif.org/), Reflora (https://floradobrasil.jbrj.gov.br/reflora), and speciesLink (https://specieslink.net/) (Supplementary material 1). We avoided citizen science databases, such as iNaturalist (included in GBIF), because of the high taxonomic inconsistencies. Instead, we only used specimens deposited in collections. The searches included the accepted name of the studied species, as well as homotypic and heterotypic synonyms for each species (when applicable). We only included specimens identified by experts, because smaller better curated biological databases are more accurate than larger poorly curated ones (Goodwin et al. 2015; Cardoso et al. 2017). Herbarium specimen data, when carefully analysed, is essential to confidently assess conservation status (Nic Lughadha et al. 2018; Pessoa and Alves 2019; Cintra et al. 2023). The data was cleaned using the R package scrubr v.0.4.0 (Chamberlain 2021), to remove coordinates that had impossible or unlikely latitude/longitude values or were incomplete (lacking latitude, longitude, or information that allow georeferencing). Then, we used the R package CoordinateCleaner v.2.0-1 (Zizka et al. 2019) with the clean_coordinates function applying default options to exclude coordinates in the sea, coordinates containing only zeros, coordinates assigned to country and province centroids, coordinates within urban areas, and coordinates assigned to biodiversity institutions. For localities without coordinates, those were obtained using available gazetteers in the GeoLoc tool on speciesLink. Maps with the distribution of the analysed species are available in Supplementary material 2. We are aware that there is uncertainty in herbarium records that may reduce the accuracy of the data, but it is the most powerful source of information for conservation studies on plants.

We selected a total of 2,425 records of the 16 chiropterophilous angiosperms. The number of records per species varied from 7 to 551 (7–15 = three species, 16–100 = six species, 101–554 = seven species). The three species with the highest number of records were *Dasyphyllum donianum* (551 records), *Ceiba glaziovii* (329 records) and *Harpochilus neesianus* (284 records), and the three species with the lowest number of records were *Ipomoea vespertilia* (7 records), *Dyckia viridiflora* (10 records), and *Stigmatodon limae* (11 records) (Supplementary material 1). The presence of the species in the protected areas of the municipalities where they occur has been verified using the Painel Unidades de Conservação Brasileiras (Ministério do Meio Ambiente 2021), the ICMBio platform, and the Centro Nordestino de Informações sobre Plantas (CNIP 2023). A literature review was conducted to verify plant-bat interactions. Seven species have pollination data available (Machado and Vogel 2004; Queiroz et al. 2016; Domingos-Melo et al. 2020, 2023; Rocha et al. 2020). The main pollinators of *A. dichilum*, *D. viridiflora*, *Harpochilus neesianus*, *Hymenaea cangaceira*, *M. lewisii*, *P. catingicola*, and *S. brasiliensis* were compiled based on the available literature (Locatelli et al. 1997; Machado and Vogel 2004; Vogel et al. 2004, 2005; Sanmartin-Gajardo and Sazima 2005; Gomes et al. 2018; Domingos-Melo et al. 2020; Albuquerque-Lima et al. 2023).

Conservation status

The conservation status of the species was assessed based on the IUCN Red List categories and criteria (IUCN Standards and Petitions Committee 2024). The list has nine categories: Extinct (EX), Extinct in the Wild (EW), Critically Endangered (CR), Endangered (EN), Vulnerable (VU), Near Threatened (NT), Least Concern (LC), Not Evaluated (NE), and Data Deficient (DD). IUCN also establishes five quantitative criteria (IUCN Standards and

Table 1. Summary of the criterion B used to assess the conservation status of the taxa. Based on IUCN Standards and Petitions Committee (2024) and Stroh et al. (2014).

	CR	EN	VU	NT	LC
B1. Extent of occurrence (EOO)	< 100 km²	< 5,000 km²	< 20,000 km²	< 20,000 km²	> 20,000 km²
B2. Area of occupancy (AOO)	< 10 km²	< 500 km²	< 2,000 km²	< 2,000 km²	> 2,000 km²
(a) Number of locations	= 1	≤ 5	≤ 10	11–30	> 30
(b) Continuing decline observed in any of: (i) extent of occurrence; (ii) area of occupancy; (iii) area, extent and/or quality of habitat	Data obtained from collection 7 of "Uso e Cobertura da Terra do Brasil" (Land Use and Coverage in Brazil) by MapBiomas (2023)				

Petitions Committee 2024) from which we used criterion B to estimate the conservation status of chiropterophilous species, following Nic Lughadha et al. (2018) who highlighted that herbarium specimens are sufficient to distinguish between threatened and non-threatened species. Criterion B is based on geographic distribution and identifies species with severely fragmented populations or occurring in few locations, or in locations with declining quality of habitat, or showing extreme fluctuations in the area they occupy. This criterion is the most widely applied in the assessment of plants, as the type of data required for other criteria, such as populational estimates, is usually sparse in this biological group (Golding 2004; Rivers et al. 2011; Nic Lughadha et al. 2018; Rocchetti et al. 2021).

To use criterion B, we first needed to verify if the general distribution threshold was met for one of the risk categories, either in extent of occurrence (EOO) or area of occupancy (AOO). The species needs to fulfil at least two of the three listed conditions for criterion B: (a) severely fragmented or number of locations, (b) continuing decline, or (c) extreme fluctuations. We used the species occurrence database we compiled (Supplementary material 1) to calculate the EOO using the area of the minimal convex polygon containing all occurrence records. The AOO was calculated by summing the area of occupied cells in a 2 × 2 km grid system (IUCN Standards and Petitions Committee 2024). We used the GeoCAT tool (Bachman et al. 2011) to calculate the EOO and AOO.

Species extinction risk was categorized based on the EOO and AOO values. Based on the IUCN recommendations and considering the precautionary principle, we granted the higher risk category to a species when its EOO results were different from the AOO. According to Rivers et al. (2011), the precautionary principle is the conception that the highest risk category should be attributed when conservation evaluation parameters result in different conservation categories. To use the Near Threatened (NT) category, we followed the recommendation by Stroh et al. (2014) that species should reach the AOO and/or EOO limits but occur in 11–30 localities (Table 1).

To fulfil the conditions of criterion B, besides the information about the number of locations (condition a), we estimated the decline in habitat quality in the species distribution area (condition b) (IUCN Standards and Petitions Committee 2024). Analyses of absolute reductions in distribution areas of the species by vegetation suppression (conditions of decline b(i), b(ii), and b(iii); IUCN Standards and Petitions Committee 2024) recorded in the last 36 years were carried out with collection 7 of "Uso e Cobertura da Terra do Brasil" (Land Use and Coverage in Brazil) by MapBiomas (2023). MapBiomas has annual land cover maps based on satellite imagery since 1985. We downloaded images in GEOTIFF format from the MapBiomas collection 7 for the period 1985–2021, using the toolkit prepared in the Google Earth Engine (GEE) data asset, aiming to verify significant change in land use and land cover in the EOO and AOO of the species in this 36-year period. GEE is a geospatial processing service hosted on an online platform that allows to process and download satellite images or derived products by using Java script and by using a cloud space, reducing the processing time and disk space on a desktop pc. We uploaded to this platform the shapefile (.shp) of the locations of the selected species and we then cropped the MAPBIOMAS raster available in the GEE database by selecting an area of 2 km² from the geographical coordinate from each sample (AOO) or by creating a polygon that take each geographical coordinate as a vertex (EOO). The image dataset from MapBiomas collection 7 is produced through Landsat Thematic Mapper (TM), Enhanced Thematic Mapper Plus (ETM+), and Operational Land Imager and Thermal Infrared Sensor (OLI-TIRS) sensors.

We calculated the coverage data for the EOO and AOO of the 16 analysed species from the 30-meter pixel resolution Landsat mosaics. For each image, the area in km² of each land use and land cover class (following collection seven class codes) was calculated from counting the pixels for each class by the pixel area in the EOO and AOO (1 pixel = 30 × 30 m = 0.0009 km²). For each species, we calculated the percentage increase or decrease in distribution area for each class in the period 1985–2021, focusing on the reduction of natural vegetation (forest or non-forest) and anthropic use classes, such as pastures, agriculture, urban infrastructure, etc. (Supplementary material 3).

Table 2. Conservation assessment of chiropterophilous species endemic to the Caatinga. Based on IUCN Standards and Petitions Committee (2024).

	EOO (km²)	AOO (km²)	Number of locations	Criterion	Category
Acanthaceae					
Harpochilus neesianus	559,871	620	47	B2b(i,ii)	LC
Harpochilus paraibanus	143,756	44	27	B2b(i,ii)	NT
Asteraceae					
Dasyphyllum donianum	947,516	344	208	B2b(i,ii)	LC
Bignoniaceae					
Adenocalymma dichilum	218,207	148	27	B2b(i,ii)	NT
Bromeliaceae					
Dyckia viridiflora	6,364	20	5	B1ab(i)+2ab(ii)	EN
Stigmatodon limae	7,696	24	7	B1ab(i)+2a	VU
Cactaceae					
Pilosocereus catingicola	997,077	724	124	B2b(i,ii)	LC
Pilosocereus chrysostele	141,789	208	57	B2b(i,ii)	LC
Pilosocereus piauhyensis	244,964	96	20	B2b(ii)	NT
Convolvulaceae					
Ipomoea marcellia	690,403	396	68	B2(i,ii)	LC
Ipomoea vespertilia	10,611	16	6	B1ab(i)+2ab(ii)	EN
Fabaceae					
Calliandra aeschynomenoides	210,457	224	19	B2b(i,ii)	NT
Hymenaea cangaceira	271,951	96	19	B2b(i,ii)	NT
Mimosa lewisii	243,410	592	38	B2b(i,ii)	LC
Gesneriaceae					
Sinningia brasiliensis	483,761	440	62	B2b(ii)	LC
Malvaceae					
Ceiba glaziovii	767,158	672	146	B2b(i,ii)	LC

RESULTS

Our study addresses the Scottian shortfall, the critical gap in conservation status assessments, by evaluating 16 species. Furthermore, we integrate essential land cover change data, providing a robust foundation for developing targeted conservation policies. The results revealed that among the assessed species, two were categorized as EN and one as VU, totalling three species included in at risk categories. Another five species were assessed as NT and eight as LC (Table 2, Fig. 3). Regarding geographic extent, the results showed that the largest EOO is found for *P. catingicola* (997,007 km²), while *D. viridiflora* had the smallest EOO (6,364 km²) (Table 2). The largest AOO belonged to the cactus species *P. catingicola* (724 km²), while *I. vespertilia* had the smallest AOO (16 km²) (Table 2). The number of locations where the records of each species were found varied from five locations for *Dyckia viridiflora* to 208 locations for *Dasyphyllum donianum*. Regarding the presence in protected areas, the species *Dyckia viridiflora* is present in only two areas, while *Dasyphyllum donianum* is found in 84 protected areas, being the species most represented in protected areas from those evaluated.

The species that faced the largest absolute decrease in distribution areas (forested or non-forested natural vegetation classes) in the last 36 years for anthropic use classes that include economic activities were *I. vespertilia* (AOO = -18%), *Pilosocereus chrysostele* (AOO = -11%), and *Calliandra aeschynomenoides* (EOO = -11%, AOO

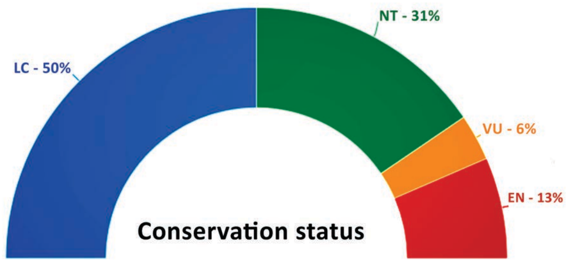

Figure 3. Results of the conservation status assessments of 16 chiropterophilous species occurring in the Caatinga and endemic to Brazil, based to the IUCN criteria and categories.

Table 3. Estimates of increase or decrease (in %) in distribution area of chiropterophilous species endemic to the Caatinga in the period 1985–2021 for Natural Vegetation and Anthropic Use classes.

Species	EOO 1985 Natural Vegetation	EOO 2021 Natural Vegetation	AOO 1985 Natural Vegetation	AOO 2021 Natural Vegetation	EOO 1985 Anthropic Use	EOO 2021 Anthropic Use)	AOO 1985 Anthropic Use	AOO 2021 Anthropic Use
Adenocalymma dichilum	67	59 (-8)	62	59 (-3)	33	41 (+8)	38	41 (+3)
Calliandra aeschynomenoides	64	53 (-11)	60	52 (-8)	36	47 (+11)	40	48 (+8)
Ceiba glaziovii	66	58 (-8)	55	48 (-7)	34	42 (+8)	45	52 (+7)
Dasyphyllum donianum	63	53 (-10)	61	57 (-4)	37	47(+10)	39	43 (+4)
Dyckia viridiflora	72	63 (-9)	62	59 (-3)	28	37(+9)	38	41 (+3)
Harpochilus neesianus	65	57 (-8)	58	54 (-4)	35	43(+8)	42	46 (+4)
Harpochilus paraibanus	69	61 (-8)	66	57 (-9)	31	39 (+8)	34	43 (+9)
Hymenaea cangaceira	63	55 (-8)	53	51 (-2)	37	45 (+8)	47	49 (+2)
Ipomoea marcellia	68	61 (-7)	60	53 (-7)	32	39 (+7)	40	47 (+7)
Ipomoea vespertilia	71	65 (-6)	71	53 (-18)	29	35 (+6)	29	47 (+18)
Mimosa lewisii	56	48 (-8)	59	57 (-2)	44	52 (+8)	41	43 (+2)
Pilosocereus catingicola	70	63 (-7)	42	35 (-7)	30	37 (+7)	58	65 (+7)
Pilosocereus chrysostele	74	66 (-8)	67	56 (-11)	26	34 (+8)	33	44 (+11)
Pilosocereus piauhyensis	69	60 (-9)	48	48 (0)	31	40 (+9)	52	52 (0)
Sinningia brasiliensis	52	48 (-4)	36	36 (0)	48	52 (+4)	64	64 (0)
Stigmatodon limae	21	17 (-4)	35	39 (+4)	79	83 (+4)	65	61 (-4)

= -8%), assessed as EN, LC, and NT respectively (Table 3). The species *Hymenaea cangaceira* and *Mimosa lewisii* showed the smallest losses (AOO = -2%). From the 16 analysed species, 13 (81.2%) had a reduction in natural vegetation classes for both EOO and AOO; two species (12.5%), *Pilosocereus piauhyensis* and *Sinningia brasiliensis*, showed reduction in EOO but maintained their AOO, and only one species (6.2%), *Stigmatodon limae*, had a reduction in EOO but an increase in its AOO (Table 3).

Although most species are not assessed as threatened, approximately 80% of the species showed a worsening of their conditions in the last 36 years. The most important threats based on land cover changes for chiropterophilous species in the Caatinga are pastures, mosaics of land uses (small properties with multiple uses), and urbanization. Twelve species (75%) had pastures as the main threat in the last 36 years, while three species (18.75%) had mosaics of land uses as the main threat, and one species (6.25%) had urbanization as the main threat. We highlight that urbanization is the second or third most important threat for all species (Fig. 4). The conservation status assessments for each species and their specifics are available in Supplementary material 4. Among the evaluated species, seven have their pollinators precisely identified (Fig. 5). The widespread *Glossophaga soricina* Pallas, 1766 and *Phyllostomus discolor* Wagner, 1843, and the Brazilian endemics *Lonchophylla mordax* and *Xeronycteris vieirai* are the most commonly cited bat pollinators among these species (Machado and Lopes 2004; Machado and Vogel 2004; Sanmartin-Gajardo and Sazima 2005; Queiroz et al. 2016; Domingos-Melo et al. 2020, 2023; Rocha et al. 2020). We highlight *Glossophaga soricina* as the most important bat pollinator among the ones present in literature, since it was mentioned for all seven species (Machado and Lopes 2004; Sanmartin-Gajardo and Sazima 2005; Queiroz et al. 2016; Domingos-Melo et al. 2020, 2023; Rocha et al. 2020) (Fig. 5).

DISCUSSION

Current conservation status of chiropterophilous species in the Caatinga

Our work has revealed new information for the conservation of chiropterophilous species occurring in the Caatinga and endemic to Brazil, addressing the Scottian shortfall to avoid extinction. This information will be important for the creation of conservation policies and strategies on chiropterophilous angiosperms, especially for decision-making. Bat-pollinated species are especially important because they are the basis of

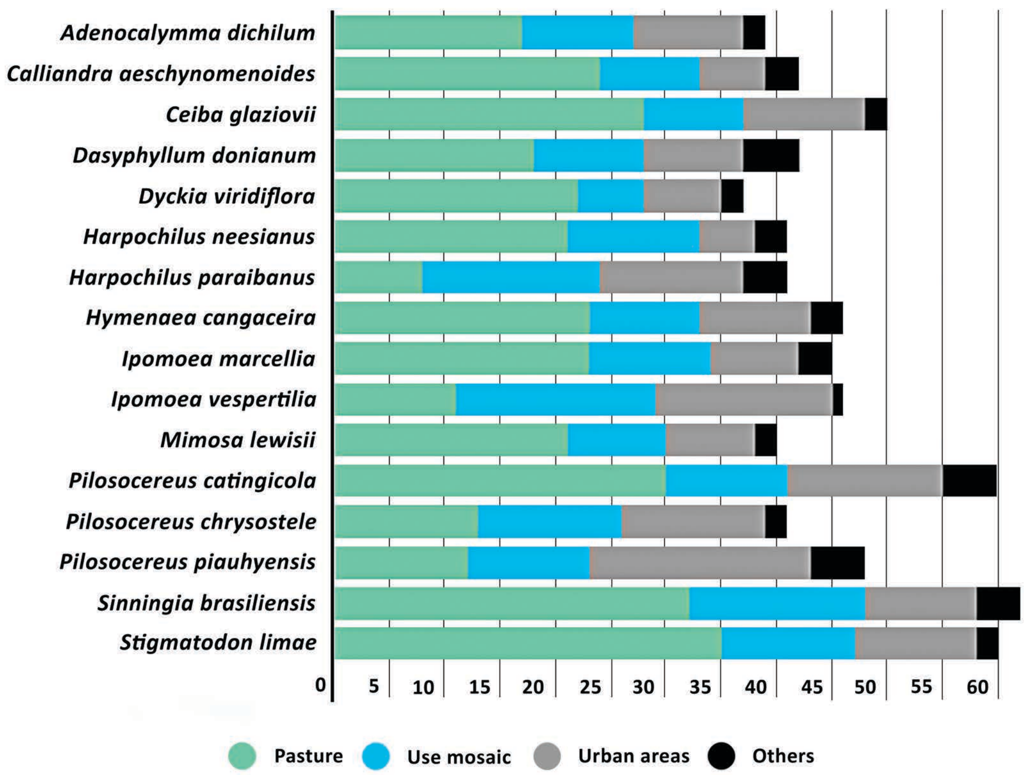

Figure 4. Most important threats to chiropterophilous species occurring in the Caatinga during the last 36 years according to AOO 2021 (in %). Pasture: goats and cattle; Mosaics of land uses: small properties with multiple uses; Urban areas: cities; Others: agriculture, aquaculture, forestry, and mining.

the diet of the Caatinga bat species that mostly rely on pollen and nectar (Solmsen 1998; Tschapka and Dressler 2002). Pollination is a fundamental process that supports several other ecosystem services (Rech et al. 2014). Plant-pollinator interruptions make tropical plants particularly vulnerable (Quesada et al. 2011). While this study primarily evaluates extinction risks for plant species, the conservation status of their associated bat pollinators warrants equal consideration. Among flower-visiting bats in the Caatinga (Domingos-Melo et al. 2023), most are currently listed as Least Concern. However, two species raise particular ecological concerns: *Lonchophylla mordax* (Near Threatened) and *Xeronycteris vieirai* (Vulnerable or Data Deficient), the latter a Caatinga-endemic species whose uncertain status poses a hidden risk. The potential decline of these two species could directly affect reproduction of the plant species that rely on their pollination services.

We identified three species under at-risk IUCN categories, besides five Near Threatened species. From the 16 assessed species, nine (*Adenocalymma dichilum*, *Ceiba glaziovii*, *Dyckia viridiflora*, *Harpochilus paraibanus*, *Ipomoea vespertilia*, *Mimosa lewisii*, *Pilosocereus piauhyensis*, *Sinningia brasiliensis*, and *Stigmatodon limae*) had already been evaluated in previous studies (CNCFlora 2012; Forzza and Leme 2015; Amaro and Messina 2016; Monteiro et al. 2018; Costa-Lima and Chagas 2019; Santos et al. 2019; Pôrto et al. 2004). However, we found that some of these species showed changes in their conservation status based on updated data.

The shrub *Harpochilus paraibanus* was first recorded in two localities in the state of Paraíba. Both populations had a reduced number of individuals, thus, it was assessed as Endangered (EN) at the time of the description (Monteiro et al. 2018). However, Costa-Lima and Chagas (2019), in a new evaluation, proposed that *H. paraibanus* should be considered Least Concern (LC), due to its wide distribution in semi-arid regions of the states of Ceará, Rio Grande do Norte, and Paraíba, being found even in areas in considerable stages of degradation. Here, we classify *H. paraibanus* as Near Threatened (NT), as it occurs in less than 30 locations (Stroh et al. 2014). According to the MapBiomas data (Supplementary material 3), this species has been losing occupancy area mainly due to mosaics of land uses and growing urbanization.

The liana *Adenocalymma dichilum* was classified as Endangered (EN) by CNCFlora (2012). However, in the last few years, new collections expanded its AOO to 148 km^2, thus being classified here as Near Threatened (NT), with the main threat being pastures (Supplementary material 3). Another species that had changes in its conservation status was the cactus *Pilosocereus piauhyensis*. According to CNCFlora (2012), the species is classified as Least Concern (LC) due to its wide distribution in the Caatinga and the stable condition of the populations. Our analysis, on the other hand, show that the species currently falls under the Near Threatened category (NT), with the main threat being urbanized areas, which have been constantly growing (Supplementary material 3).

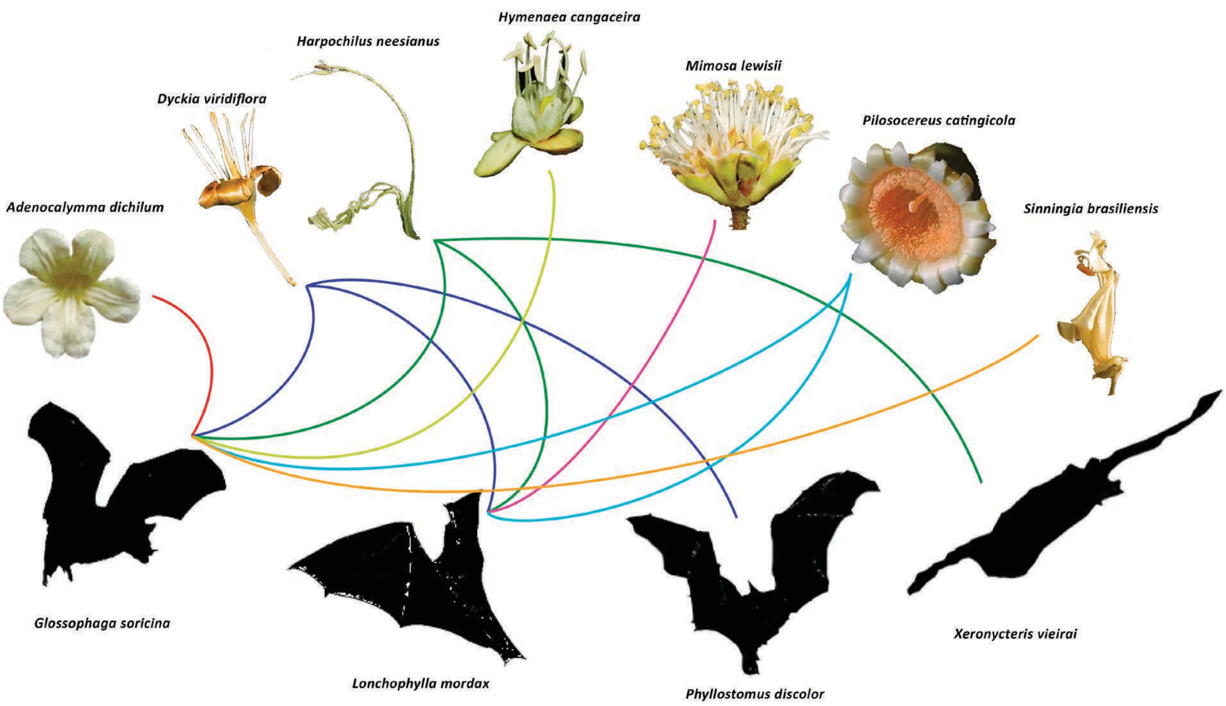

Figure 5. Main pollinators of *Adenocalymma dichilum*, *Dyckia viridiflora*, *Harpochilus neesianus*, *Hymenaea cangaceira*, *Mimosa lewisii*, *Pilosocereus catingicola*, and *Sinningia brasiliensis*. Photos of flowers: Rubens Queiroz and Camila Alcantara. Silhouettes from PhyloPic (https://www.phylopic.org).

Regarding species that had never been assessed, *Dasyphyllum donianum*, *Pilosocereus catingicola*, *Pilosocereus chrysostele*, and *Ipomoea marcellia* were classified as Least Concern (LC), although they all suffer anthropic threats such as pastures, mosaics of land uses, and urbanization (Supplementary material 3). From these, it is worth noting that *Pilosocereus chrysostele* had one of the largest habitat losses in the last 36 years (EOO = -8%, AOO = -11%). Something similar was observed for *Calliandra aeschynomenoides* (EOO = -11%, AOO = -8%), but this species was classified as NT. Even though *Hymenaea cangaceira* was also classified as NT, this species showed the smallest habitat loss in the same period (EOO = -8%, AOO = -2%).

Land cover changes and their ecological impact

We found that in the last 36 years, the area of distribution of these angiosperms in the Caatinga suffered land cover changes, being the natural vegetation replaced mainly by pastures, mosaics of land uses (small properties with multiple uses), and urban areas. The removal of native vegetation can impact not only plant-pollinator relationships but also the diet of bats (Russo and Anciollotto 2015). Although bats are omnivorous, a significant portion of their nutrition depends pollen and nectar provided by angiosperms (Barbier et al. 2023). Bats can disperse pollen over long distances and in larger amounts, as they require larger foraging areas and are larger than insects (Fleming et al. 2009; Kunz et al. 2011). Consequently, bats help to maintain the genetic diversity of chiropterophilous angiosperms (Kunz et al. 2011).

In addition to these impacts, the replacement of natural areas with pastures has been slow but constant in the Caatinga, generating loss of vegetation cover, decrease in the organic matter content in the soil, and compaction and lack of aeration of soils, reducing water infiltration capacity (Paulino et al. 2012) or increasing the recurrence of fire, which can be a threat to some species (Argibay et al. 2020). The semi-arid portion of the Northeast has a mixed model of livestock farming, with approximately 90% of properties adopting simultaneous farming of cattle, goats, and sheep (Araújo Filho 2013). This farming system is based on overgrazing, with the native Caatinga vegetation often being the only food source for herds (Araújo Filho 2013; Parente and Parente 2010). This explains why livestock farming emerges as one of the biggest threats in all analysed species. While some of the analysed species can be used as cover crops for extensive goat raising (Santo et al. 2012), others can suffer with trampling. Therefore, the need to adopt sustainable livestock farming techniques is evident, besides keeping pastures away from protected areas and areas of high ecological importance.

Most properties in the Caatinga are configured as multiple use, including agriculture, livestock farming, extractivism, and other economic activities (Tabarelli et al. 2018). In the last few years, there has been an expansion of irrigated agriculture in the subregion São Francisco valley (states of Pernambuco and Bahia) and Açú-Mossoró in the state of Rio Grande do Norte (Leão and Moutinho 2014; Tabarelli et al. 2018). The irrigated agricultural practice brings different damages to soils (Primavesi 2002); when the water management is inadequate, it can compact the soil, reducing aeration, besides increasing salinity and erosive processes (Primavesi 2002). Besides, the presence of fruit orchards can change the interactions between native plants and pollinating bats, significantly impacting pollination success (Sritongchuay et al. 2019).

In the Caatinga, the native vegetation is also removed for charcoal production, an activity that seriously impacts its biodiversity, specially of tree woody species (Albuquerque et al. 2017). Among the species assessed here, the woody *Ceiba glaziovii* and *Hymenaea cangaceira* have the highest potential for charcoal production and may suffer from extractivist practices, and both were classified as NT.

Among the semi-arid regions worldwide, the Caatinga concentrates the highest demographic density, with approximately 28 million inhabitants (IBGE 2010). The populational increase and the disorganized urban growth exert strong anthropic pressure over native forested areas, accelerating environmental degradation processes (Stanganini and Lollo 2018). Our results highlight urbanization as one of the strongest threats to the assessed species. According to Théry and Mello (2005), a higher proportion of the Caatinga population has lived in cities than in rural areas since the 1980s. The search for better conditions of work, living, and leisure are possible factors explaining urban expansion (Glaeser 2011). Urban expansion is clearly an important factor in land use change that significantly transforms the natural environments and landscapes in the Caatinga, indirectly increasing road density, which is another main variable associated to deforesting in this domain (Silva et al. 2023). It is known that some bat species are sensitive to urbanization, with some species being intolerant of anthropized environments (Russo and Anciollotto 2015), which can put plant-pollinator interaction at risk.

CONCLUSION

Our study contributes to addressing the Scottian shortfall in the Caatinga, one of the least studied phytogeographic domains of Brazil. Our updated assessments have contributed to enhancing the CNCFlora database by providing new conservation status evaluations for Brazilian plant species. The results corroborate CNCFlora's existing classifications for six taxa, while revising the status of three others. Additionally, we provide the first formal conservation assessments for seven previously unevaluated taxa. Approximately 80% of the assessed species saw their conditions worsen due to human impact on land use, with pastures, mosaics of land uses, and urbanization are the main threats. On affecting populations of chiropterophilous plant species in the phytogeographic domain, it also possibly impacted the ecology of the nectarivore bat species. Therefore, to attenuate impacts on both groups, we suggest conservation policies focusing specifically on these issues, such as: 1) creating and/or strengthening protected areas in the Caatinga focusing on priority areas for conservation in the subregions of São Francisco in the state of Pernambuco and Juazeiro in the state of Bahia, where most species classified as NT, VU, or NE are present; 2) adopting sustainable management practices in farming activities, such the use of native plants for land restoration, water conservation techniques, and the protection of ecological corridors, considering the conservation of biodiversity and natural resources, as the Caatinga is susceptible to desertification (Ministério do Meio Ambiente 2004); 3) improving urban planning focusing on maintaining native vegetation, and including native species in city landscaping; 4) developing environmental education and conscientization practices to show the impacts that predatory extraction of vegetation can cause, thus stimulating a responsible use of natural resources; and 5) limiting further land cover change with a focus on avoiding habitat loss and habitat fragmentation. We acknowledge the limitations posed by data scarcity for some species, and we also emphasize that due to the age of some collecting data, some taxa may be more threatened than currently understood. It reinforces the need for further research on taxonomy and conservation in the Caatinga to improve data availability and accuracy in future conservation efforts.

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SUPPLEMENTARY MATERIALS

Supplementary material 1

Geographical information of chiropterophilous species occurring in the Caatinga and endemic to Brazil recovered from the databases GBIF, speciesLink, and Reflora.

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Supplementary material 2

Occurrence maps of chiropterophilous species occurring in the Caatinga. **A**. *Adenocalymma dichilum*. **B**. *Calliandra aeschynomenoides*. **C**. *Ceiba glaziovii*. **D**. *Dasyphyllum donianum*. **E**. *Dyckia viridiflora*. **F**. *Harpochilus paraibanus*. **G**. *Harpochilus neesianus*. **H**. *Hymenaea cangaceira*. **I**. *Ipomoea marcellia*. **J**. *Ipomoea vespertilia*. **K**. *Mimosa lewisii*. **L**. *Pilosocereus catingicola*. **M**. *Pilosocereus chrysostele*. **N**. *Pilosocereus piauhyensis*. **O**. *Sinningia brasiliensis*. **P**. *Stigmatodon limae*.

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Supplementary material 3

Estimates of increase or decrease (in km^2 and %) in distribution area of chiropterophilous species occurring in the Caatinga for Natural Vegetation and Anthropogenic Use classes. Data obtained from collection 7 of Land Use and Coverage in Brazil by MapBiomas.

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Supplementary material 4

Conservation assessments of chiropterophilous species occurring in the Caatinga and endemic to Brazil, following IUCN criterion B (restricted geographical distribution and presenting population fragmentation, decline, or fluctuations).

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