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Among flowers and thorns: birds associated with *Encholirium spectabile*, a keystone bromeliad in a Brazilian semi-arid region

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Abstract

Birds are common visitors ofbromeliads, despite the scarcity of studies on the association of these plants with bird communities, especially for terrestrial and rupicolous species. In the present study we first address the association of a bird community with rupicolous bromeliads (*Encholirium spectabile*) in rocky outcrops of the Brazilian semi-arid region. The observations were made monthly between 2014 and 2018. The species of birds which used bromeliads were recorded, as well as the abundance of individuals and the interaction (guilds) between bird species and bromeliads. We also test the possible effects of seasonality on the richness and composition of bird species recorded between the dry and rainy seasons. Twenty-one species in 12 families that used bromeliads regularly were recorded and this number rises to 31 species in 16 families when considering the opportunistic records. Birds used bromeliads as a feeding site for either nectar or small animals, and as a place for nesting or resting. There were no significant differences as to the richness or abundance of bird species between seasons, but the species composition changed between them. The study shows that *E. spectabile* is an important kind of bromeliad for the bird community, as it plays a key role in inhabiting their surroundings. Therefore, the conservation of these bromeliads directly impacts the conservation of birds that use them. We suggest the clumps of *E. spectabile* as a place for bird watching in the semi-arid region of Brazil.

Keywords Animal-plant interaction · Caatinga · Macambiras · Rocky outcrops

Introduction

Bromeliads create internal microclimates which minimize the effects of external temperature and humidity (Benzing 2000; Kitching 2000; Romero et al. 2010). Such effects are even more exacerbated in environments with water and thermal stress, especially in seasonally dry environments (Silva et al. 2011; Rocha 2022). The effects of temperature and humidity variation in the semi-arid region of Brazil is high throughout the day and throughout the year (Ab'saber 1974; Velloso et al. 2002), and the bromeliads help to mitigate such effects to the animal species which use them (Jorge et al. 2020).

Bromeliads can promote entire communities of organisms in their leaf structures providing shelter (Lounibos and Frank 2009), food resource for floral visitors (Queiroz et al. 2016; Jorge et al. 2018) and herbivores that feed on the bromeliad tissues (Canela and Sazima 2003; Fischer et al. 2003, 2008; Schmid et al. 2010). In addition, bromeliads also serve as a foraging area for predators, as a thermoregulation site and breeding site for several animal taxa (Benzing 2000;

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Ramalho et al. 2004; Santos et al. 2009; Jorge et al. 2021a, b), elevating them to the status of keystone species and ecosystem engineers (Jones et al. 1994). By supporting these communities in their structures and presenting great replicability and easy isolation, bromeliads are considered excellent models for ecological studies (Srivastava et al. 2004).

The Bromeliaceae family currently has about 3731 described species, with 39.5% of these occurring in Brazil (Butcher and Gouda 2017; Ulloa et al. 2017; Gouda et al. 2018), while about 81% of the species in this family are under threat of extinction (Zizka et al. 2020). Due to these threats to bromeliads, the diversity of other species that depend on these plants can be reduced (Ladino et al. 2019). Therefore, knowing organisms which depend on bromeliads is necessary to reduce their damage, as well as the importance that such species present for bromeliads (Rocha et al. 2004).

Invertebrates comprise the most studied group in bromeliads, given that they show a higher richness and abundance in these plants (Kitchen 2000; Rocha et al. 2004; Leroy et al. 2013; Rogy et al. 2017). Amphibians are among the most studied vertebrates due to their relationships with bromeliads, especially in terms of reproduction (Benzing 2000), as there is a total dependence relationship in bromeligenous species (Sabagh et al. 2017). However, other groups also use bromeliads, such as lizards (Jorge et al. 2021c), birds and mammals, which are still little studied (Benzing 2000).

Birds constitute a very diverse group in species, especially regarding the neotropical region (Develey 2021). However, studies are focused on relationship with birds and the epiphyte species (Cruz-Angon and Greenberg 2005; Cestari and Pizo 2008). A variety of birds seek food resources in inflorescences of bromeliads, such as nectar and insects (Sick 1997; Rocha 2022). Bromeliads can also provide microhabitats, shelters, nest materials, and water, thus acting as "wildlife restaurants" (Rocha 2022), mainly due to the large abundance of prey in these plants (Sillett et al. 1997; Cestari and Pizo 2008; Machado and Semir 2009; Ladino et al. 2019; Rocha 2022).

Despite the importance of these plants for birds and the diversity of bromeliads and birds in the tropics (Cestari and Pizo 2008), many basic aspects of interactions between birds and bromeliads remain unknown in arid and semi-arid regions. More specifically, what species use bromeliads and what is the role of bromeliads in structuring bird communities in these regions (Santana and Machado 2010). Most studies have been concentrated in the brazilian Atlantic Forest region due to the richness of bromeliad species (Sillett et al. 1997; Cestari and Pizo 2008; Ladino et al. 2019). Very little is known about birds and bromeliads in other regions such as arid regions, as well as the semi-arid region of Brazil.

Studies regarding the subfamilies which compose the Bromeliaceae family are focused on the importance of floral visitors and potential pollinators of Bromelioideae and Tillandioideae subfamilies (Sazima et al. 1999; Rocha 2022), and the use of structures in Puyoideae (Rees and Roe 1980). Few studies on associated birds are available to the subfamily Pitcairnioideae, such as for pollinators of *Encholirium spectabile* in the semi-arid region of Brazil (Queiroz et al. 2016; Jorge et al. 2018).

In semi-arid zones of Brazil, there is a conspicuous presence of *Encholirium* bromeliads, locally known as "arrow-macambiras" which create a microclimate that softens the effects of external temperature and increased internal humidity (Jorge et al. 2020, 2021b). The softening effects that these bromeliads have are important in environments with a striking seasonal variation, such as in the semi-arid region, especially in view of the effects of climate change, where these species are expected to play an even more important role (Romero et al. 2010, 2022; Rocha 2022).

Encholirium spectabile Mart.ex Schult. and Schult. F. (Pitcairnioideae) are plants which characterize the landscapes of the Caatinga biome (Jorge et al. 2021a). It is an endemic bromeliad in Brazil, with distribution restricted to rocky outcrops in the semi-arid region and border areas with the coastline (Ramalho et al. 2004). It is considered a keystone species for regional biodiversity, as it establishes association with various organisms (Jorge et al. 2014, 2018, 2020, 2021b; Sales et al. 2015), including birds, although these associations are rarely reported.

The present study aimed to know which species of birds use the clumps of the rupicolous bromeliads (*Encholirium spectabile*); which types of resources are exploited by bird species, and how the interactions between both groups are maintained throughout the seasons in the semi-arid region.

Methods

Study area

This study was conducted at the Fazenda Tanques (5.853º S; 35.701º W; datum WGS84, 137 m elev.), in the municipality of Santa Maria in Rio Grande do Norte state, Brazil (Fig. 1), region included in the "Depressão Sertaneja Setentrional" ecoregion of the Caatinga (Velloso et al. 2002). This ecoregion is characterized by irregular rainfall and a dry season from July to December. The climate is semi-arid, hot and dry, with an average annual precipitation of 500–800 mm/year (Velloso et al. 2002). The municipality of Santa Maria is located in the "Agreste" region, a transition zone between the Caatinga and the Atlantic Forest, with characteristics of both environments (Rizzini 1997). The rainy season in the

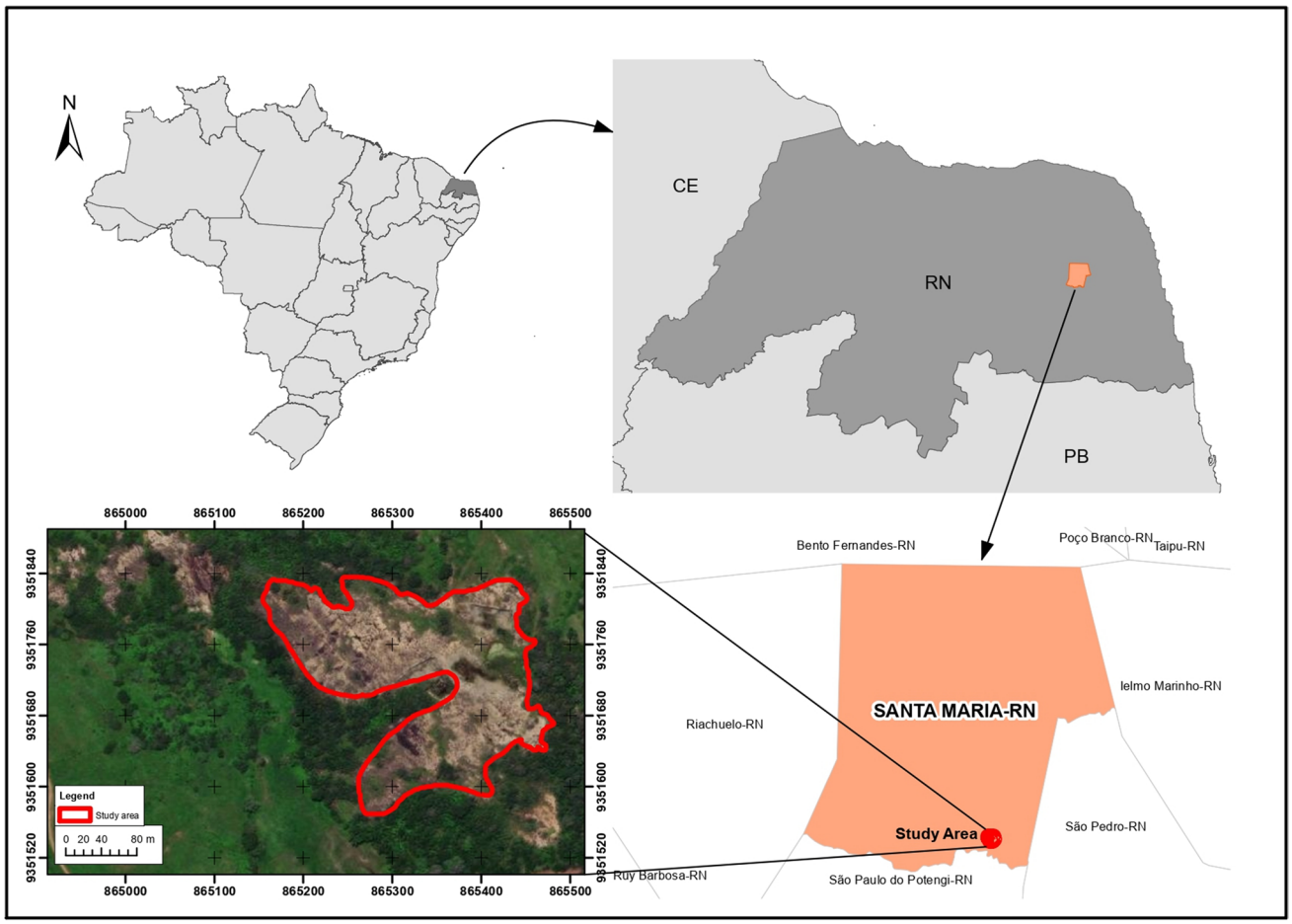

Fig. 1 Location of the rocky outcrop where this study was conducted in the Brazil country, highlighting the Rio Grande do Norte state and the study area (Tanques Farm) in Santa Maria municipality

"Agreste" usually extends from January–June (Velloso et al. 2002). The minimum monthly temperatures in Santa Maria range from 22–24ºC, and the maximum monthly temperatures range from 28–32ºC, with an average annual rainfall of 781 mm (Jorge et al. 2015) (Fig. 2). There is a common presence of rocky outcrops with a large abundance of *E. spectabile* bromeliads in the study area.

The fieldwork was carried out in a large granite rocky outcrop (5.855º S; 35.702º W; datum WGS84, 137 m elev.) in an area of around 5.8 ha (Fig. 1). The surroundings of the study area are covered by arboreal-shrubby vegetation, with the occurrence of Caatinga trees such as "juremas" (*Mimosa* spp.), "imburanas" (*Commiphora leptophloeos* (Mart.) J.B. Gillett), "cajueiros" (*Anacardium occidentale* L.) and "barrigudas" (*Ceiba glaziovii* (Kuntze) K.Schum.). *Encholirium spectabile* patches in this rock outcrop occupy a large part of its extension. Aside from the bromeliads in the rocky outcrop, the presence of "xique-xique" cactus (*Pilosocereus gounellei*) is also common (Jorge et al. 2020).

Data collection and analysis

We carried out observation of birds visiting bromeliads from 2014 through 2018. This study is part of a project which

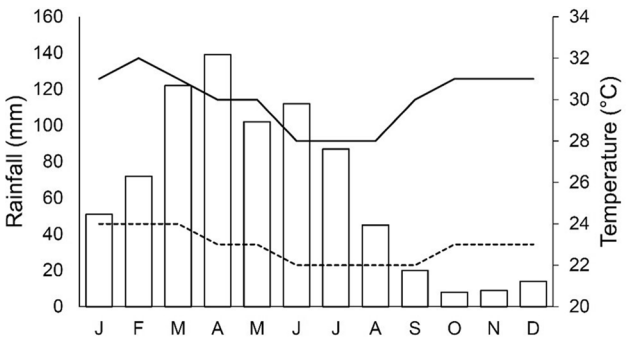

Fig. 2 Rainfall (bars) and average maximum (solid line) and minimum (dotted line) monthly temperatures in Santa Maria Municipality in Rio Grande do Norte in northeastern Brazil, adapted from Jorge et al. (2015). Values are averages of a series of 30 years. Source: www.climatempo.com.br

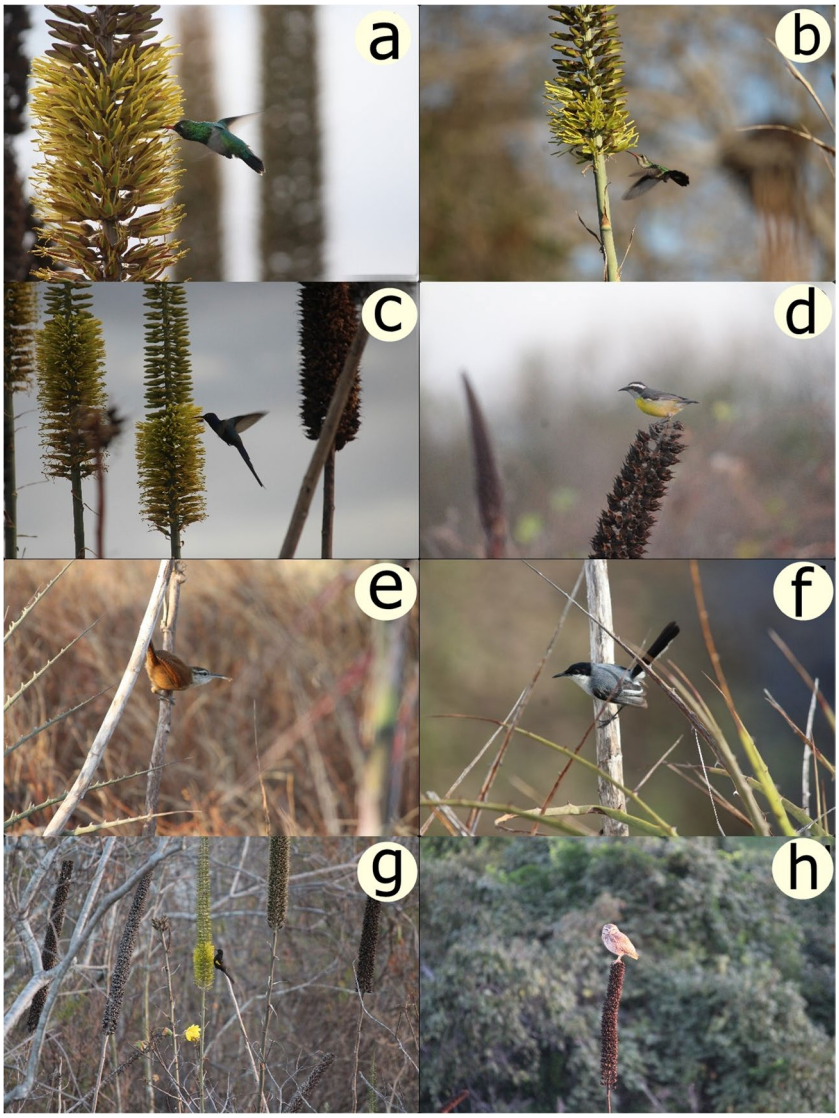

Fig. 3 Birds recorded in *Encholirium spectabile* clumps at the *Fazenda Tanques*, municipality of Santa Maria, Rio Grande do Norte state, Brazil. **a**) male of *Clorostilbun lucidus*; **b**) female of *Clorostilbun lucidus*; **c**) *Eupetomena macroura*; **d**) *Coereba flaveola*; **e**) *Cantorchilus longirostris*; **f**) *Polioptila atricapilla*; **g**) *Icterus pyrrhopterus*; **h**) *Athene cunicularia*

surveyed the fauna associated with clumps of *Encholirium spectabile* in the brazilian semi-arid region, totaling approximately 5500 h of sampling effort (Jorge et al. 2020, 2021a). Search and data collection occurred throughout three parallel transects of 12 m width and about 1500 m length, situated on the north border, the center and on the south border of the outcrop. All three transects were explored once per day during three consecutive days in each month by a single observer (JSJ) in the morning, afternoon, and night. Thus, each transect was surveyed once during each time of the day each month. All bromeliad clumps along the transect were inspected by visual active search, with the observer registering all specimens of birds occupying the bromeliads in a field notebook. Each survey in the transects lasted about two hours. The absolute frequencies of each species were registered according to the number of specimens sighted. The fieldwork comprised at least 12 h of observation during the day and four hours at night during the years in which the study was conducted. Daytime observations started at 7:00 am and continued until 6:00 pm; observations at nighttime resumed at 7:00 pm and continued until 11:59 pm. Each sighting was recorded in a notebook and specimens were photographed for later identification by specialists.

Each taxon observed in association with *E. spectabile* was assigned to a trophic guild category based on their feeding habits reported in the literature (Blondel 2003). Observations were made using binoculars and a digital camera with a 75 X 300 mm lens. Each individual was photographed for confirmation at the species level. Bird observations were authorized by the Biodiversity Information and Authorization System of Chico Mendes Institute for Biodiversity Conservation (SISBIO – ICMBio, Authorization No. 71469–1).

Table 1 Bird species associated to *Encholirium spectabile* during the years 2014–2018, at Fazenda Tanques, municipality of Santa Maria, Rio Grande do Norte, Brazil. Nec: Nectarivores; Pre: Predators; She: Shelter; Nes: Nest Builders; Top: Top Predators. * = Represent species with opportunistic records; *N* = Number of records

Family	Species	*N*	Use
Accipitridae	*Geranoaetus melanoleucus* (Vieillot, 1817)*	1	-
	Geranospiza caerulescens (Vieillot, 1817)*	1	-
Caprimulgidae	*Hydropsalis torquata* (Gmelin, 1789)	12	Pre, Nes, She
	Nyctidromus hirundinaceus (Spix, 1825)	26	Pre, Nes, She
Columbidae	*Columbina minuta* (Linnaeus, 1766)	87	Nes, She
	Columbina picui (Temminck, 1813)	113	Nes, She
Falconidae	*Falco sparverius* (Linnaeus, 1758)*	1	-
Fringilidae	*Euphonia chlorotica* (Linnaeus, 1766)*	1	-
Furnariidae	*Pseudoseisura cristata* (Spix, 1824)	9	Pre
	Synallaxis hellmayri (Reiser, 1905)*	1	-
Icteridae	*Icterus jamacaii* (Gmelin, 1788)	23	Nec, Pre
	Icterus pyrrhopterus (Vieillot, 1819)	17	Nec, Pre
Mimidae	*Mimus saturninus* (Lichtenstein, 1823)	43	Pre
Passerellidae	*Zonotrichia capensis* (Statius Muller, 1776)	4	Pre, She
Picidae	*Veniliornis passerinus* (Linnaeus, 1766)*	1	-
Polioptidae	*Polioptila atricapilla* (Swainson, 1831)	143	Pre
Strigidae	*Athene cunicularia* (Molina, 1782)	17	Top, Pre
	Glaucidium brasilianum (Gmelin, 1788)	7	Top, Pre
Thaupidae	*Coereba flaveola* (Linnaeus, 1758)	124	Nec, Pre, Nes
	Euscarthumus meloryphus (Wied, 1831)*	1	-
Trochilidae	*Chlorostilbon lucidus* (Shaw, 1812)	112	Nec
	Chrysolampis mosquitus (Linnaeus, 1758)	9	Nec
	Chrysuronia leucogaster (Gmelin, 1788)	36	Nec, Pre
	Eupetomena macroura (Gmelin, 1788)	134	Nec, Pre
	Heliomaster squamosus (Temminck, 1823)	13	Nec
Troglodytidae	*Cantorchilus longirostris* (Vieillot, 1819)	32	Pre, She
	Tachyphonus rufus (Boddaert, 1783)	16	Pre
	Troglodytes musculus (Naumann, 1823)*	1	-
Tyrannidae	*Phaeomyias murina* (Spix, 1825)*	1	-
	Pitangus sulphuratus (Linnaeus, 1766)	29	Pre
	Tyrannus melancholicus (Vieillot, 1819)*	1	-
Total		1016	

We constructed rarefaction curves to test the effects of seasonality on the bird composition associated with *E. spectabile*, i.e., a general curve using all records and another curve for each season of the year (wet and dry). The seasons were divided according to the rainy and dry periods defined in the literature, with the rainy period being considered from January to June, and the dry period from August to December (Fig. 2) (Ab'saber 1974; Velloso et al. 2002). Next, we conducted a non-metric multidimensional scaling (NMDS) using the Bray–Curtis index as a measure of distance (calculated based on the frequencies of each species) and an analysis of similarities (ANOSIM) using the Past Programs (Hammer et al. 2001). An independent sample t-test was performed to compare the averages of individuals recorded by season as well as species richness (dry season versus wet season).

Occasional records in other areas of the Caatinga were considered whenever possible to identify the species and the type of use they made of *E. spectabile*. Such information was not used in the statistical analyses. The taxonomic classification of bird species follows that adopted by the Brazilian Committee of Ornithological Records (Pacheco et al. 2021).

Results

We accounted 1006 records of 21 bird species from 12 families visiting *E. spectabile* (Fig. 3, Table 1). We also observed another 10 species in opportunistic records, thus totaling 31 species and 16 families in our study area. The most frequent bird species was the white-bellied gnatcatcher (*Polioptila atricapilla* (Swainson, 1831)) (*N* = 143), followed by the swallow-tailed hummingbird (*Eupetomena macroura*

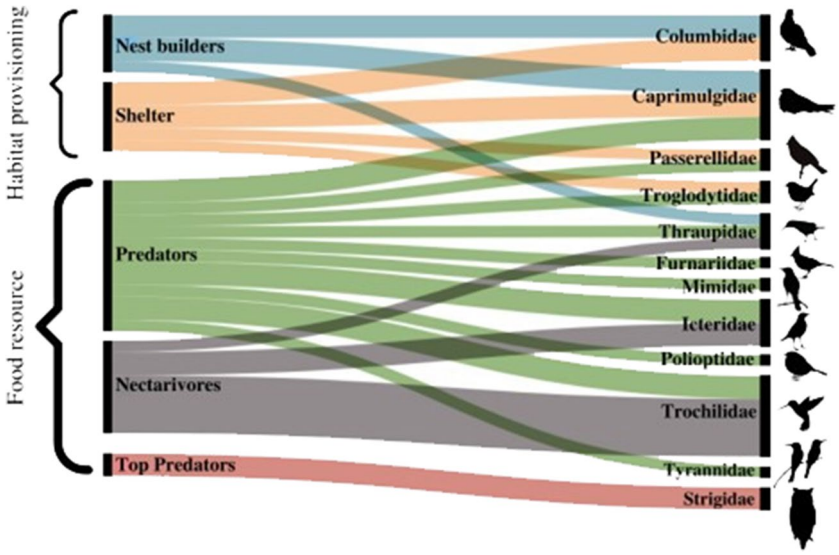

Fig. 4 Alluvial diagram summarizing the use categories (guilds) for each bird species associated to *Encholirium spectabile*. The set of species contained in each taxonomic group is shown on the right side; on the left, the division into the two major use categories: habitat provisioning and food resource. The width of the bar corresponds to the number of species registered in each usage category

(Gmelin, 1788)) ($N=134$), and the bananaquit (*Coereba flaveola* (Linnaeus, 1758)) ($N=124$) (Fig. 4, Table 1). Trochilidae was the species-richest group with five species.

The majority of bird species used bromeliads for food (70.26%), while 29.72% did it for structural purposes. Most species were classified as predators ($N=16$, 43.24%), followed by nectarivores ($N=8$, 21.62%). We also observed six species using bromeliads for shelter (16.21%). In general, trophic use was more common than habitat one (Fig. 4, Table 1).

The differences between seasons on the richness of bird species associated to *E. spectabile* was not positive, as shown by the rarefaction curves (Fig. 5), and corroborated by the t-test ($t=$-1.425, $gl=20$, $P>0.05$), but species composition of birds differed between seasons (ANOSIM; $R=0.1371$, $P=0.0002$, Fig. 6). The most recorded species in the rainy season was picui ground-dove (*Columbina picui* (Temminck, 1813)) ($N=88$), followed by white-bellied gnatcatcher (*Polioptila atricapilla*) ($N=72$) and plain-breasted ground-dove (*Columbina minuta* (Linnaeus, 1766)) ($N=56$). The most common species in the dry season was *E. macroura* ($N=115$), followed by *C. flaveola* ($N=111$) and glittering-bellied emerald (*Chlorostilbon lucidus* (Shaw, 1812)) ($N=97$) (Fig. 6, Table 1).

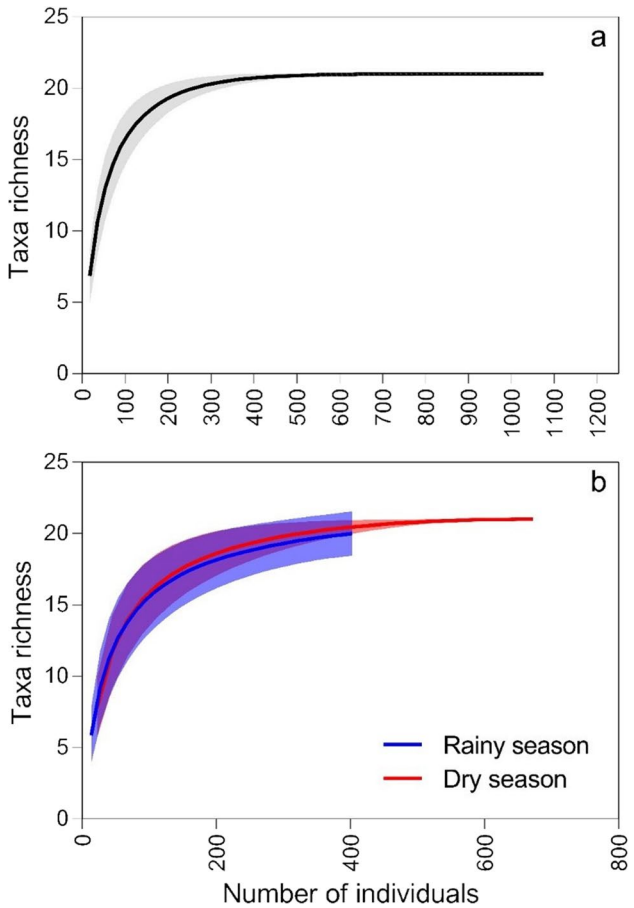

Fig. 5 Rarefaction curves for the richness of birds recorded in association with *Encholirium spectabile* during the sampling period, 2014–2018, at Fazenda Tanques, Santa Maria municipality, Brazil. **a**) curve with the total number of records; **b**) curve between seasons, comparing the rainy season "blue line" with the dry season "red line"

Discussion

The results found in the present study demonstrate the importance of clumps of *E. spectabile* for the bird fauna of the semi-arid region of Brazil, as shown in other studies with birds in bromeliads epiphytes in the Brazilian Atlantic Forest (Sillett et al. 1997; Cestari and Pizo 2008; Cestari 2009). *Encholirium spectabile* proved to be an important source of resources for birds in the semi-arid region, providing food

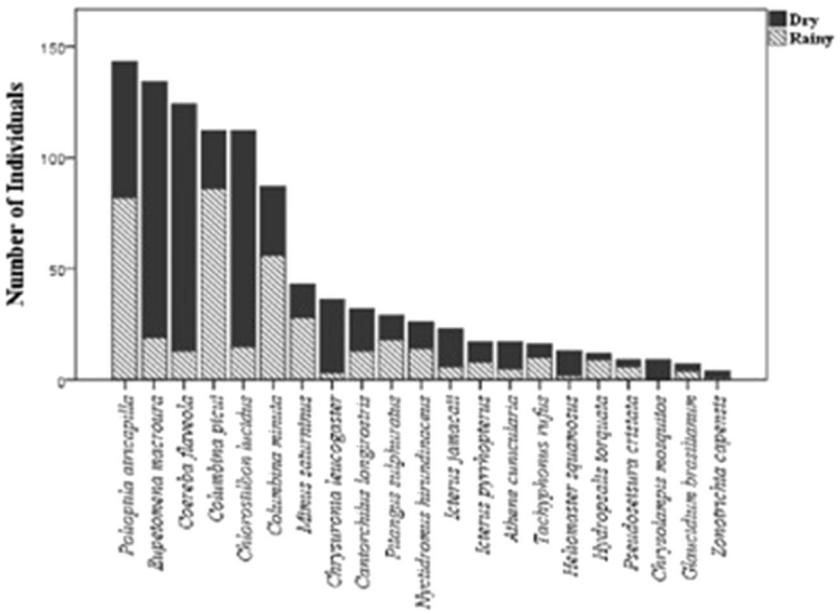

Fig. 6 Number of records per season of each species recorded in association with *Encholirium spectabile* during the sampling period, 2014–2018, at Fazenda Tanques, Santa Maria municipality, Brazil. Black bars: "Dry Season"; Bars with lines: "Rainy season"

and structural components for the species that shelter or nest among the clumps.

Studies with bird communities in terrestrial bromeliads are scarce and focus mainly on epiphytic bromeliads (Cestari and Pizo 2008; Cestari 2009; Boechat et al. 2019; Rocha 2022), and there are no studies on rupicolous bromeliads in semi-arid regions. Therefore, this is a pioneer study with a community of birds associated with non-phytotelmata bromeliads for Brazil, as well as for the Caatinga Biome (Cestari 2009).

The Trochilidae family (hummingbirds) is often reported as the bird group which use bromeliads most frequently (Cestari and Pizo 2008; Cestari 2009; Boechat et al. 2019; Leal et al. 2020; Rocha 2022). The Trochilidae family is composed of hummingbirds, being among the most frequent birds in bromeliads (Cestari and Pizo 2008; Cestari 2009; Boechat et al. 2019; Leal et al. 2020; Rocha 2022), mainly as floral visitors (Sazima et al. 1996; Krömer et al. 2006). Hummingbirds are recurrent floral visitors of *E. spectabile* in the study area (Jorge et al. 2018), being one of the main groups of pollinators of these plants (Queiroz et al. 2016; Jorge et al. 2018), as well as other bromeliads (Sazima et al. 1995, 1996; Benzing 2000). Some hummingbird species, such as the swallow-tailed hummingbird (*Eupetomena macroura*) and the plain-bellied emerald (*Chrysuronia leucogaster*) which visit *E. spectabile* not only seek nectar, but are also predators of small invertebrates that take shelter in bromeliads.

Moreover, 43.24% of the bird species recorded in the present study prey on invertebrates or small vertebrates, which demonstrates the importance of these bromeliads in structuring food webs in the region where they occur, although further studies are needed to better understand these interactions. Invertebrates are the most abundant group among the clumps of *E. spectabile* (Jorge et al. 2021a), and end up attracting their predators, including birds.

About 21.62% of the birds recorded are nectarivores species, meaning that *E. spectabile* is an important source of food for Trochilidae species, especially in the dry season. *E. spectabile* blooms can open throughout the year, but mainly bloom in the dry season (Queiroz et al. 2016; Jorge et al. 2018), when food scarcity is a limiting factor in this region, sometimes being the only source of food nearby. These bromeliads serve as "wildlife restaurants" (Rocha 2022), for fauna in periods of scarcity (Santana and Machado 2010).

Encholirium spectabile clumps grow in a circular shape, in clusters with a high density of individuals, creating a strongly imbricated environment with thorns on the edges. This type of environment creates a protected fortress that can retain more humidity and a milder temperature than the external environment, being an appropriate place for species reproduction (Jorge et al. 2020, 2021a). Columbids (*C. minuta* and *C. picui*) and Thraupid (*C. flaveola*) nest frequently in the middle of the leaves (Fig. 7). Many bird species use bromeliads as a nesting site (Bodrati and Cockle 2017; Zima et al. 2019), as they are an appropriate environment for reproduction, both because of the mitigation of abiotic conditions and the physical imbrication structure of the leaves.

The availability of food (nectar) during the dry season (Jorge et al. 2018), and shelter, nesting site and food (small prey) in the rainy season (Jorge et al. 2021a, b, c), are the factors that explain the non-significant difference in richness, however, significant for the species composition between

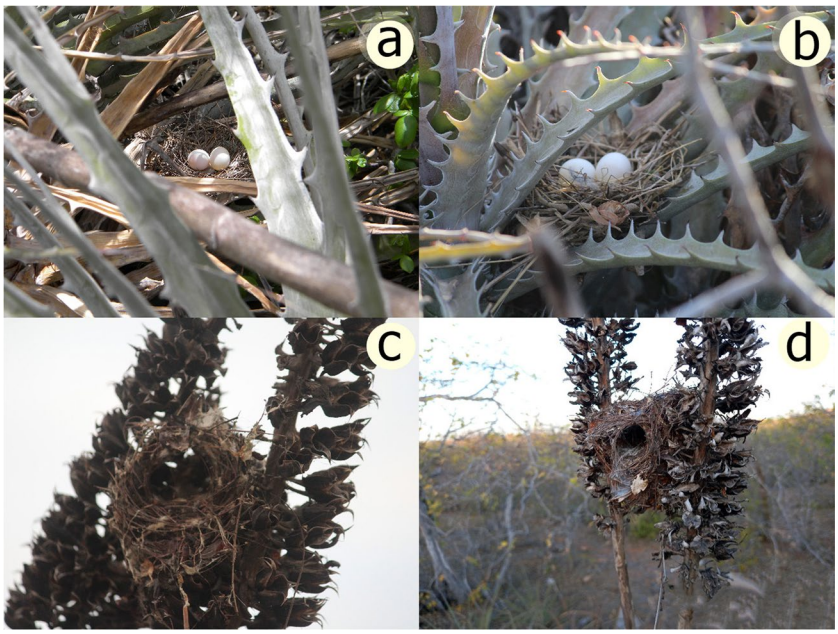

Fig. 7 Nests of some species among *Encholirium spectabile* clumps at the *Fazenda Tanques*, municipality of Santa Maria, Rio Grande do Norte state, Brazil. **a**) nest of plain-breasted ground-dove (*Columbina minuta*) among leaves; **b**) nest of a picui ground-dove (*Columbina picui*); **c**) nest of a bananaquit (*Coereba flaveola*) in stems; **d**) nest of a bananaquit (*Coereba flaveola*) among stems

seasons. These factors mitigate the abiotic influences during periods of drought, playing a crucial role for the birds in the semi-arid region, and manage to maintain these species in the region throughout the year.

As shown, *E. spectabile* is an important habitat for the bird community that inhabits rocky outcrops in the Brazilian semi-arid region. Thinking in conservationist terms, these associations imply important strategies for the in situ maintenance of both groups involved. Conserving rupicolous bromeliads directly implies in the conservation of the birds that use them, especially those that nest among the clumps, following the same proposal for other groups, such as amphibians and reptiles (Jorge et al. 2018, 2020, 2021a). *Encholirium spectabile* is a keystone species for a whole diversity of organisms that use them, being considered an amplifier of regional biodiversity, stabilizing abiotic conditions, and structuring biotic interactions.

Therefore, the present study shows the importance of rupicolous bromeliads (*Encholirium spectabile*) for the ornithofauna of the Brazilian semi-arid region, serving as a place for feeding, providing food resources in drought periods, and as an important nesting site. Policies aimed at these interactions need to be consider the conservation of both groups involved (birds and bromeliads), the benefits to these interactions and the ecosystem services involved, especially those from pollinating birds and insect pest controllers (Whelan et al. 2015; Machado and Semir 2009), allied to the services provided by the rupicolous bromeliads themselves, such as climate regulation, supply, and support (Millennium Ecosystem Assessment 2005).

We also suggest the clumps of rupicolous bromeliads as a place for bird watching in the semi-arid region of Brazil, which is based on the method used in interpretive trails. Combining bird watching and the conservation of rupicolous bromeliads and consequently all their associated fauna, can become an important point of connection between environmental education and regional biodiversity conservation.

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Declarations

Conflict of interest On behalf of all authors, the corresponding author states that there is no conflict of interest.

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