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ECOLOGY, BEHAVIOR AND BIONOMICS

Semi-arid's Unsung Heroes: Hymenoptera and the Vital Ecosystem Services Enabled by *Encholirium spectabile*, a Rupicolous Bromeliad in the Brazilian Semi-arid Region

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Abstract
The concept of Ecosystem Services (ES) recognizes the importance of natural ecosystems in supporting human well-being. Hymenoptera, a diverse group of insects including ants, bees, and wasps, play crucial roles in providing ESs. Despite their significance, the provision of ESs by Hymenoptera is often undervalued, leading to ecosystem degradation and loss of important services. This study focuses on the association between Hymenoptera and a rupicolous bromeliad species (*Encholirium spectabile*) and explores the ESs promoted directly and indirectly by these insects. The study area is located in the Caatinga region of Brazil, characterized by irregular rainfall and a dry season. The results show that Hymenoptera, particularly bees, ants, and wasps, provide a range of ESs including pollination, honey production, pest control, cultural symbolism, and educational value. These services are vital for plant reproduction, food production, and ecosystem functioning in both seasons; there are no differences in species richness between seasons, but rather in species composition. Understanding the importance of Hymenoptera for ESs is crucial for informing conservation and management practices to ensure the sustainability of natural ecosystems. The study highlights the need for conservation actions to protect the intricate ecological relationships between Hymenoptera and bromeliads, which indirectly support ESs by providing habitat and resources, especially during droughts when resources are scarce in the region. By recognizing the importance of bromeliads in supporting Hymenopteran communities, conservation efforts can focus on preserving these critical ecological interactions and maintaining ES provision.

Keywords Animal-plant interaction · Caatinga biome · Keystone species

Introduction

The concept of Ecosystem Services (ES) has gained increasing recognition in recent years as a way to highlight the importance of natural ecosystems to human well-being. ESs are provided by a wide range of species and ecological processes, from the pollination of crops by bees to the regulation of climate by forests (Millennium Ecosystem Assessment 2005; IPBES 2016). However, the provision of ESs is often undervalued and overlooked in decision-making processes, leading to the degradation of ecosystems and the loss of important services (Iverson et al. 2014; Mortimer et al. 2018). Insects, and in particular Hymenoptera, play important roles in promoting ESs such as pollination, biological control, and nutrient cycling (Brock et al. 2021).

Hymenoptera are a diverse group of insects that includes bees, wasps, and ants. They are among the most important pollinators, accounting for over 80% of all insect-mediated pollination and are critical to produce many crops and wild plants (Klein et al. 2006; IPBES 2016). Hymenoptera are also important biological control agents, controlling pest populations and reducing the need for chemical pesticides (Grissell 2010). In addition, they contribute to nutrient cycling and soil health through their role as decomposers and soil engineers (Wilson et al. 2009; Brock et al. 2021).

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The role of Hymenoptera in providing ESs has gained increasing attention in recent years due to their important contributions to providing them (Noriega et al. 2018; Brock et al. 2021). Hymenoptera are among the most diverse and abundant groups of insects and play crucial roles in maintaining the health and functioning of ecosystems (Elizalde et al. 2020). Understanding the ways in which Hymenoptera contribute to ESs is important for informing conservation and management practices that promote the sustainability of natural ecosystems and the conservation of these taxa (Brock et al. 2021; van Klink et al. 2020).

Ecosystem Services refer to the benefits that humans derive from natural ecosystems. These benefits can be divided into four categories: provisioning, regulating, supporting, and cultural (Millennium Ecosystem Assessment 2005; BPBES 2019). Provisioning services are the tangible products that humans obtain from ecosystems, such as food, water, timber, and medicine. These resources are essential for our survival and well-being, and they form the basis of many economic activities. Regulating services are the natural processes that regulate the environment and provide benefits to human society, such as climate regulation, water purification, erosion control, and pollination. These services help to maintain the balance of ecosystems and ensure their long-term sustainability. Supporting services refer to the fundamental processes that enable ecosystems to provide other services, such as nutrient cycling and soil formation. These services are essential for the maintenance of biodiversity and the functioning of ecosystems. Finally, Cultural services refer to the non-material benefits that humans derive from ecosystems, such as spiritual and recreational values. These services are essential for our cultural identity, mental health, and overall well-being (Millennium Ecosystem Assessment 2005; BPBES 2019).

One of the most well-known ES provided by Hymenoptera is pollination (Brock et al. 2021). Bees are important pollinators for many flowering plants, including crops such as apples, almonds, and blueberries (Klein et al. 2006; Winfree et al. 2007). Without these insects, many plants would not be able to reproduce, leading to a decline in plant populations and potentially affecting entire ecosystems (Klein et al. 2006). In addition to pollination, Hymenoptera also contribute to pest control (Southon et al. 2019). Many wasps and some species of ants are natural predators of other insects, including those that are considered pests (Grissell 2010). By controlling the populations of these pests, Hymenoptera help to maintain the balance of the ecosystem and prevent crop damage.

Hymenoptera also play a role in nutrient cycling. Ants, for example, are known for their ability to move soil and debris, which can help to aerate the soil and promote the growth of healthy plants (Klein et al. 2006; Winfree et al. 2007). Some species of bees and wasps also contribute to nutrient cycling by decomposing organic matter and aiding in the breakdown of dead plant material (Brock et al. 2021). Hymenopterans (ants, bees, and wasps) provide services like pollination, honey production, cultural symbolism, traditional practices, biological control, and educational value (Klein et al. 2006; Winfree et al. 2007; Noriega et al. 2018; Sumner et al. 2018; Brock et al. 2021). They are vital for plant reproduction, have culinary and symbolic significance (Jones 2019), are used in rituals, control pests naturally (Southon et al. 2019), and offer insights into social organization and ecology (Brock et al. 2021). These services emphasize their ecological importance and impact on human societies.

Despite their importance, many Hymenoptera species are facing declines due to habitat loss, pesticide use, and climate change (Wagner et al. 2021). These declines have significant implications for the provision of ESs (van Klink et al. 2020; Brock et al. 2021), and understanding the role of Hymenoptera in promoting ESs is crucial for informing conservation and management practices that promote the sustainability of natural ecosystems.

Bromeliads are recognized for being important habitats for a range of animal species, mainly invertebrates (Kitching 2000). By creating suitable places for local fauna, bromeliads begin to fulfill the role of fauna keepers and keystone species for the conservation of these groups (Jorge et al. 2021a). Among the groups of invertebrates that most use bromeliads are the Hymenoptera, mainly ants and the intricated relationship (Benzing et al. 2000). Bromeliads play a crucial role in supporting ESs indirectly through their interactions with Hymenopteran species. By providing habitat, resources, and protection, bromeliads foster the survival, reproduction, and genetic diversity of these beneficial insects. Recognizing the importance of bromeliads in supporting Hymenopteran communities is essential for the conservation and management of these intricate ecological relationships.

In this paper, we list the species of Hymenoptera associated with a rupicolous bromeliad (*Encholirium spectabile*) and their ESs promoted directly and indirectly. We also explore the significance of this association and its relevance to conserving the species involved and ecosystem services (ESs). Our aim is to provide a comprehensive understanding of the importance of Hymenoptera associated with bromeliads, specifically the macambiras, and the ESs they provide, while highlighting the need for conservation plans for all actors involved (animals and plants), to ensure the continuous provision of these crucial services.

Methods

Study area

This study was conducted at the Fazenda Tanques (5.853°S; 35.701°W; datum WGS84, 137 m elev.), in the municipality of Santa Maria in Rio Grande do Norte state, Brazi, 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 "Agreste" usually extends from January–June (Velloso et al. 2002). The minimum monthly temperatures in Santa Maria range from 22 to 24 °C, and the maximum monthly temperatures range from 28 to 32 °C, with an average annual rainfall of 781 mm (Jorge et al. 2020). There is a common presence of rocky outcrops with a large abundance of *E. spectabile* bromeliads in the study area.

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, 2023).

Methodological procedures

Species record

This study is part of a project which 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, 2021b). The methodology was based in the methodology used by Jorge et al. (2020, 2023), were the principal 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, the transects were sampled monthly between 2011 and 2018. 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 arthropods occupying the bromeliads in a field notebook. Each survey in the transects lasted about 2 h. 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 4 h 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. Individuals of each taxon were collected, identified following Baccaro (2006) for ants, Silveira et al. (2002) for bees and Elisei (2017), and (Somavilla et al. 2021) for wasps and subsequently deposited in the invertebrate collection from UFRN. The list of observed species followed the same references, which record these species for the States of Rio Grande do Norte and Paraíba.

Observations and complementary collections take place in the municipalities of Lajes, Pedro Avelino, Angicos, Serra de São Bento, Mossoró, Areia Branca, Serra do Mel, São Bento do Norte and João Câmara, state of Rio Grande do Norte; and in the state of Paraíba, in the municipalities of Santa Luzia, Pocinhos, Araruna, and Juazeirinho. In these additional municipalities, observations occurred varying between 5 and 10 consecutive days in different months between the years 2021 and 2023.

Each taxon observed in association with *E. spectabile* was assigned to usage categories based on their habits according to Blondel (2003). Arthropod observations were authorized by the Biodiversity Information and Authorization System of Chico Mendes Institute for Biodiversity Conservation (SISBIO – ICMBio, Authorization No. 71469–1). An observation time (focal animal) of 20 to 30 min was established to understand what type of interaction each taxon performed in the bromeliads. The recorded observations were compared with the relationships already recorded in the literature, so that we could assign which type of usage categories each taxon established.

Ecosystem Services Survey

To survey the ESs provided by hymenoptera associated with "macambira-de-flecha" (*E. spectabile*), field observations were conducted to study the ecology and biology of the recorded taxa. Additionally, interviews were conducted with residents living around the study area to gather their knowledge on the importance of ants, bees, and wasps to both themselves and the environment. These interviews were conducted alongside the administration of questionnaires for another survey on ES promoted by macambiras in the region (see Jorge et al. 2023). The categories of ES

were based on the four categories established in Millennium Ecosystem Assessment (2005) and BPBES (2019), provisioning, regulating, supporting, and cultural. We conducted a detailed literature search for published articles addressing the topic ES in Hymenoptera species phylogenetically close to those recorded in the present study (Table 2). We outlined a cross-approach between previously recorded ES instances and field observations, as well as reports from residents of the region.

Furthermore, an extensive bibliographical research was conducted on ESs promoted by hymenoptera, including ants, bees, and wasps worldwide (Online Resource 1). We use the definition of ESs provided by Brock et al., (2021). This research enabled us to establish a connection between the previously documented ESs and those observed in the field and reported by residents.

Data analyses

A mixed-effects model of analysis of variance (ANOVA) was made to test the effects of seasonality (dry and rainy seasons) on the species richness patterns of Hymenoptera associated with *E. spectabile* clumps. To control for potential inter-annual variations, we considered the sampled years (2011 to 2018) as a random factor and the seasonality as a fixed factor in the analyses, with the rainy period being considered from January to June, and the dry period from July to December (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). A significance level of alpha = 0.05 was considered in all analyses. The statistical analyses were performed using STATISTICA software, version 10 (StatSoft Inc 2001).

Results

During the sampling period, nine families and about 32 species of ants, bees, and wasps grouped in the order Hymenoptera were recorded (Table 1). These groups were responsible for providing the four known categories of Ecosystem Services (Table 2, Fig. 1, 3).

Bees were the most abundant group, with 17,319 records, followed by ants with 6748 records, and lastly, wasps with 3811 records. The group with the highest number of registered species was wasps, with 20 species distributed among eight families. Bees had eight species in one family, and ants had four species in one family. The most abundant group was the Meliponinae sub-family (9214 records), followed by the Apidae family (8085 records), and the Formicidae family (6748 records) (Table 1). The most abundant species were *Trigona spinipes* (Fabricius) (8,026 records), *Apis mellifera* L. (7661 records), followed by *Crematogaster* sp. (2350 records) (Table 1, Fig. 2).

Regarding the ESs promoted by Hymenoptera (ants, bees, and wasps), all four categories of services were recorded, with Support and Regulation services being the most frequent, and Provisioning being the least frequent (Table 1, 2, Fig. 3, Online Resource 1). Wasps were primarily responsible for Supporting and Regulating services, while bees played a significant role in Provisioning services. Additionally, ants played an important role in providing Cultural services (Figs. 2, 3, 6).

The Uses Categories that the species make of rupicolous bromeliads, five categories were identified. Most use them to forage, mainly as Predators. Other species use them to feed on nectar (Nectarivores), parasitize other species (Parasitoids), or feed on organic matter provided by bromeliads (Detritivores). Some species also use them as nesting sites, building their nests among the protected leaves of bromeliads (Nest builders) (Fig. 2).

According to the results of the mixed-effects model analysis of variance, the local species richness of Hymenopterans associated with *E. spectabile* clumps did not differ significantly between the rainy and dry seasons, while controlling for sampled years (Table 3; Fig. 4). Regarding species composition, it differed significantly between seasons (ANOSIM; $R = 0{,}111$, $p = 0.0001$, stress = 0,2371, Fig. 5).

Discussion

The study presents new findings regarding the Ecosystem Services promoted by hymenopterans in association with a plant species, where all four categories of ES were documented in the study area (Millennium Ecosystem Assessment 2005; IPBES 2016). Rupicolous bromeliads (*E. spectabile*) were found to be significant for the maintenance of ESs promoted by Hymenoptera in the semi-arid region of Brazil, owing to the high species richness observed in association with these plants and the services they provide. By making resources available to Hymenoptera, such as shelter, a place to build nests, and food, rupicolous bromeliads help indirectly promote the ESs made available by these groups.

Information collected in the field, along with insights from the literature, highlights the significance of interactions between hymenopterans and rupicolous bromeliads (*E. spectabile*) in the semi-arid region of Brazil. All groups comprising the Hymenoptera order (ants, bees, and wasps) were documented in association with rupicolous bromeliads within the sampled areas, emphasizing the importance of their ESs (Fig. 6).

Table 1 Taxa registered in association with the rupicolous bromeliad (*Encholirium spectabile*), in the semi-arid region of Brazil, pointing out the uses they make of bromeliads (guilds) and the total abundance and between the different seasons, rainy and dry

Order/family	Species	Dry season	Rainy season	Total	Guild	ES
Hymenoptera						
Apidae	*Apis mellifera* Linnaeus, 1758	3386	4275	7661	Nec	All
	Centris sp.	87	337	424	Nec	
Meliponinae	*Melipona mandacaia* Smith, 1854	358	102	460	Nec	All
	Melipona subnitida Ducke, 1910	520	-	520	Nec	All
	Plebeia flavocincta Friese, 1911	-	208	208	Nid	All
	Trigona spinipes (Fabricius, 1793)	3227	4799	8026	Nec	All
Xylocopinae	*Xylocopa abbreviata* Lepeletier, 1836	4	15	19	Nec, Nid	II, III
	Xylocopa macambirae Ducke, 1910	1	-	1	Nid	II, III
Vespidae	*Apoica flavissima* (Fabricius, 1804)	103	-	103	Nid, Pre	II, III
	Agelaia pallipes (Olivier, 1791)	87	92	179	Nid, Pre	II, III
	Brachygastra lecheguana (Latreille, 1824)	49	57	106	Nid, Pre	II, III
	Polistes canadensis (Linnaeus, 1758)	785	1175	1960	Nec, Pre	All
	Polistes versicolor (Olivier, 1791)	175	128	303	Nid, Pre	All
	Polybia occidentalis (Olivier, 1791)	70	180	250	Nec, Pe	All
	Polybia chrysothorax (Fabricius, 1793)	35	60	95	Nid, Pre	II, III
	Polybia ignobilis (Haliday, 1836)	88	93	181	Nec, Pre	II, III
	Polybia rejecta (Fabricius, 1793)	17	22	39	Nec, Pre	II, III
	Polybia ruficeps (Schrottky, 1909)	23	31	54	Nec, Nid	II, III
	Polybia sericea (Olivier, 1791)	173	-	173	Nec, Pre	II, III
	Protopolybia exigua (de Saussure, 1854)	75	139	214	Nid, Nec	II, III
	Synoeca surinama (Linnaeus, 1767)	13	18	31	Nec, Pre	II, III
Sphecidae	*Sceliphron* sp.	8	28	35	Nid, Ref	II, III
Eumeninae	*Zeta argillaceum* Linnaeus, 1758	6	5	11	Nid, Pre	II, III
Braconidae	-	12	8	20	Par	II, III
Chalcididae	-	4	5	9	Par	II, III
Evaniidae	-	5	12	17	Par	II, III
Ichneumonidae	-	5	17	22	Par, Pre	II, III
Pompilidae	*Pepsis sp.*	2	6	8	Pre	II, III, IV
Formicidae	*Crematogaster* sp.	950	1400	2350	Nid, Nec	II, III
	Camponotus sp. 1	600	912	1512	Nid, Det	II, III
	Camponotus sp. 2	405	1455	1860	Nec, Nid, Det	II, III
	Atta sp.	306	720	1026	Det	All
Total	-	**21.671**	**13.140**	**34.811**	**-**	

Det detritivores, *Nec* nectarivores, *Nid* Neste builders, *Pre* predator, *Par* parasitoid, *ES* ecosystem service provided, I provisioning service, II supporting service, III regulating service, IV cultural service, All all services

Table 2 Hymenoptera associated to the rupicolous bromeliads (*Encholirium spectabile*) and the ecosystem services in the semi-arid region of Brazil

Ecosystem service	General taxa	Local use	Reference
I. Provisioning services			
(1) Pharmaceuticals and medicine	Bees, wasp	Medicinal syrup, steep, honey, royal jelly, propolis, bee wax	Chen and Akre (1994); Krell (1996); Duplantier et al. (1998); Castaldo and Capasso (2002) Brown et al. (2003); Brown *et* al. (2004); Yamada et al. (2005); Kroiss et al. (2010); Rastogi (2011); Reddy et al. (2011); Santos et al. (2011); Mendes et al. (2013); Moreno et al. (2014); Silva et al. (2015); Das Neves et al. (2016); Liu et al. (2018); Aryal et al. (2020)
(2) Food	Ants, bees, wasps	Honey, royal jelly; larvae of wasps, queen of *Atta sp.* (Tanajuras)	Ramos Elorduy and Rodríguez (1977); Chen and Akre (1994); Krell (1996); DeFoliart (1997, 1999); Puwastien and Attig (1997); Carreck and Williams (1998); Hunt et al. (1998); Cortopassi-Laurino et al. (2006); Sribandit *et* al. (2008); Nonaka (2010); Raksakantong *et* al. (2010); Acuña et al. (2011); Rastogi (2011); Santos et al. (2011); Aryal et al. (2020); Brock et al. (2021)
(3) Other products (silk, wax, and others)	Ants, Bees		Krell (1996); Carreck and Williams (1998); Cortopassi-Laurino et al. (2006); Siri and Maensiri (2010)
II. Regulating services			
(1) Pollination	Ants, bees, wasps	Crop and native pollination	Peakall (1989); Southwick and Southwick (1992); Carreck and Williams (1998); Corlett (2001); Mant et al. (2002, 2005); Slaa et al. (2006); Klein et al. (2006) Fateryga (2010); Mello et al. (2011); Rostás and Tautz (2011); Perez-Balam et al. (2012); Hallett et al. (2017); Aryal et al. (2020)
(2) Biological control	Ants, wasps	Pest insect control by predation and Parasitism by parasitoid wasps	Majer (1976); Gould and Jeanne (1984); Harris (1991); Adana de la Torre et al. (2000); Sears et al. (2001); Van Mele and Cuc (2001); Philpott and Armbrecht (2006); Van Mele (2008); Vandermeer et al. (2010); Bommarco et al. (2011); Drummond and Choat (2011); Vega and Gómez (2014); Wielgoss et al. (2014); Gonthier et al. (2015); Prezoto et al. (2019); Southon et al. (2019); Brock et al. (2021)
(3) Seed dispersal	Ants, wasps	Native seed dispersal	Wolff and Debussche (1999); Ness et al. (2004, 2009); Wallace et al. (2008); Lengyel et al. (2010); Chen et al. (2017)
III. Supporting services			
(1) Bioturbation	Ants	Soil aeration in nesting construction	Cammeraat and Risch (2008); Dauber et al. (2008); Frouz and Jilková (2008); Cerdà et al. (2009); Vlasakova et al. (2009); Vele et al. (2010); Del Toro et al. (2015)

Table 2 (continued)

Ecosystem service	General taxa	Local use	Reference
(2) Nutrient and carbon cycling and decomposition	Ants, wasps	Decomposition of organic matter via degradation and accumulation of organic matter in anthills nests of social wasps	Lavelle et al. (2006); Wagner and Jones (2006); Cammeraat and Risch (2008); Frouz and Jilkova (2008); Ginzburg et al. (2008); Paris et al. (2008); Kaspari and Yanoviak (2009); Wilson et al. (2009); Kaspari et al. (2010); Del Toro et al. (2015); Farji-Brener and Werenkraut (2017); King et al. (2018)
(3) Energy flow	Ants, bees, wasps	As potential prey for other taxa	Hölldobler and Wilson (1990); Levin et al. (2009); Redford and Dorea (2009); Griffiths et al. (2018)
IV. Cultural services			
(1) Bioindicators	Bees, wasps	Rare species sensitive to environmental changes (native bees and some wasps)	Majer (1983); Andersen (1997); Lobry de Bruyn (1999); Porrini et al. (2002); Celli and Maccagnami (2003); Andersen and Majer (2004); Parr et al. (2004); Urbini et al. (2006); de Souza et al. (2010); Del Toro et al. (2010); Vieira et al. (2011); Skaldina et al. (2018)
(2) Cultural traditions & religion	Ants, bees, wasps	Use of some species in cultural rituals such as the collection of *Atta* sp. (tanajuras) during the flight The flight of "tanajuras" also signals the beginning of the rains, according to local traditional knowledge, marking the start of the planting period for annual crops Children use the soldiers of *Atta sp.* for "batalha de soldados" (soldier battles)	Sleigh (2003); Sleigh (2004); Mariño-Pérez (2006); Preston (2006); Botelho and Weigel (2011); Sumner et al. (2018); Aryal et al. (2020)
(3) Literature & arts	Ants, bees, wasps	Use of popular images and names in local businesses and cordel literature	Sleigh (2004); Preston (2006); Jones (2019); Elizalde et al. (2020)

We examine the involved taxa and services within the four categories of ecosystem services (ESs) established in the literature. Emphasizing both the services available in the study areas and those previously documented in the literature

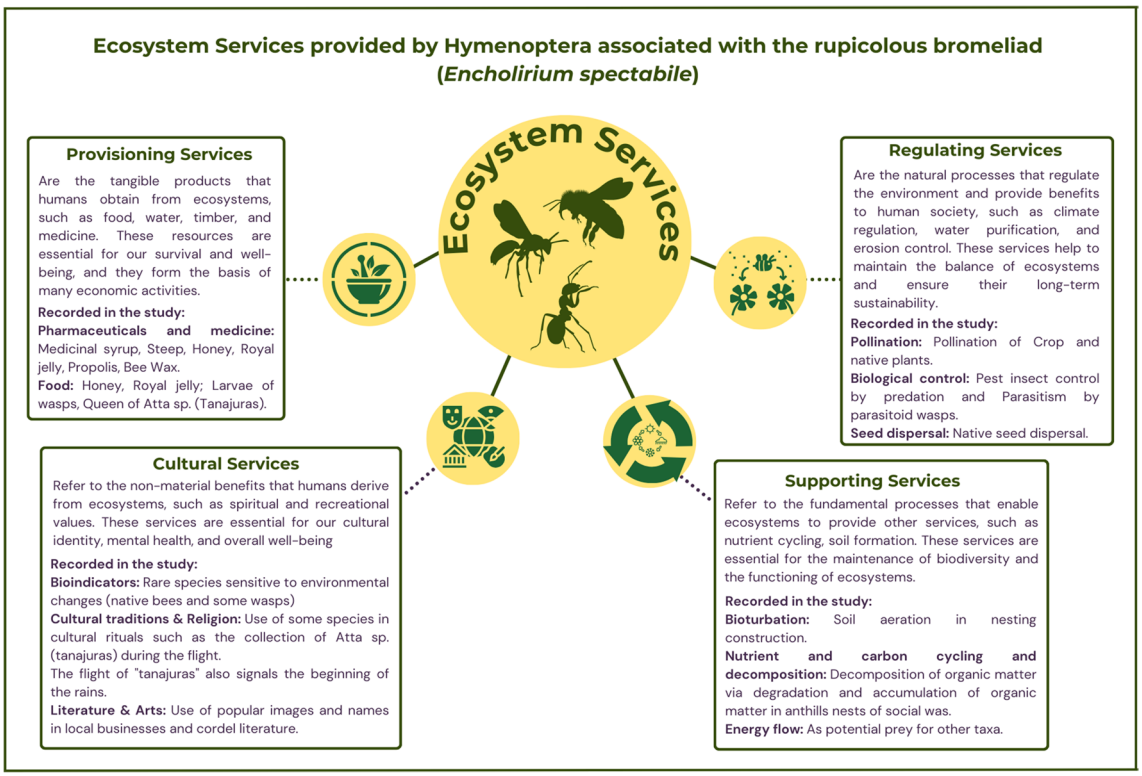

Fig. 1 Infographic synthesizing the four categories of Ecosystem Services provided by registered Hymenoptera associated with the rupicolous bromeliad (*Encholirium spectabile*) in the semi-arid region of Brazil

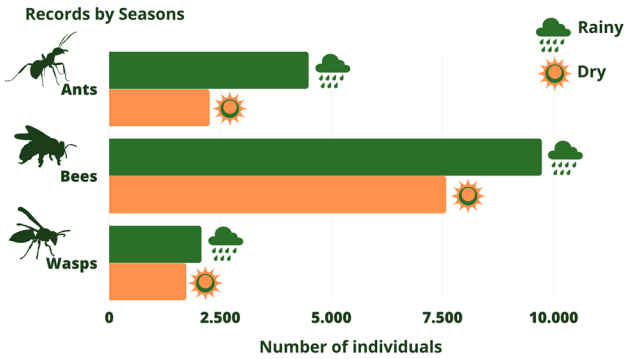

Fig. 2 Number of records per season (dry and rainy) of major taxonomic groups in the order Hymenoptera, associated with the rupicolous bromeliad species *Encholirium spectabile* in a semi-arid region of Rio Grande do Norte state, Brazil. Green bar: rainy season; orange bar: dry season

The documented diversity of hymenopteran species, including ants, bees, and wasps, during the sampling period emphasizes the ecological significance of rupicolous bromeliads for these taxa in the studied ecosystem. The comprehensive survey recorded nine families and approximately 32 species within the order Hymenoptera, collectively contributing to the provision of the four recognized categories of Ecosystem Services. Notably, bees were the most abundant group, with a substantial 17,319 records, highlighting their ecological prominence. Ants followed with 6748 records, and wasps with 3811 records. The diversity within these groups was further underscored by the identification of 20 wasp species distributed among eight families, eight bee species in one family, and four ant species in one family. The Meliponinae sub-family, Apidae family, and Formicidae family emerged as the most abundant groups, significantly contributing to the overall hymenopteran diversity in the sampled area. This study is the first to document such results at the family and genus levels, serving as a pioneer in elucidating the relationship between species promoting ecosystem services and their association with facilitating bromeliads.

Results from the mixed-effects model analysis of variance provided additional insights into the temporal dynamics of hymenopteran communities associated with *E. spectabile* clumps. Interestingly, local species richness did not show significant differences between the rainy and dry seasons, even when accounting for the years sampled, as expected for the semi-arid region (Vasconcellos et al. 2010). However, the analysis revealed a significant disparity in species composition between these seasons. This finding suggests that, although overall diversity remains relatively stable across

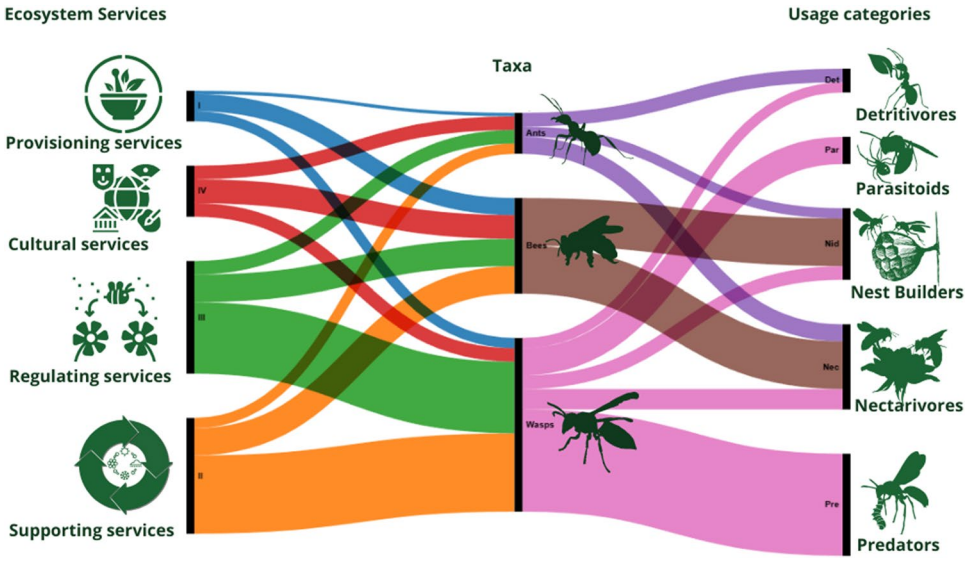

Fig. 3 Alluvial diagram displaying the proportion of ecosystem services (ESs) provided and the Usage Categories utilized by Hymenoptera associated with the rupicolous bromeliad (*Encholirium spectabile*) in a semi-arid region of Rio Grande do Norte, Brazil. The left side represents categories of ESs promoted by Hymenoptera, the right side represents guilds (use of bromeliads), and the center represents groups of Hymenoptera. The width of the bands represents the proportion of taxa utilizing a specific guild or providing a particular ES

Table 3 Summary of the mixed-effects model analysis of variance (ANOVA) for the effects of season (fixed effect) and year (random effect) on the Hymenopterans-associated fauna of *Encholirium spectabile* clumps in the years 2011 to 2018

Factor	df	MS	*F*	*P*
Season (fixed)	1	5.85	1.09	0,29
Year (random)	7	9.13	1.71	0,10
Error	471	5.33		

df degrees of freedom, *MS* mean of squares. Bold *p* values indicate significant statistical effects ($p < 0.05$)

seasons, there are noticeable changes in the specific species that contribute to the Hymenoptera community during different climatic conditions. This variation is likely mediated by bromeliads. In other words, the effects of seasonality are minimized by the clumps, which provide shelter and food during the dry season, as was found for other groups such as birds (Jorge et al. 2023).

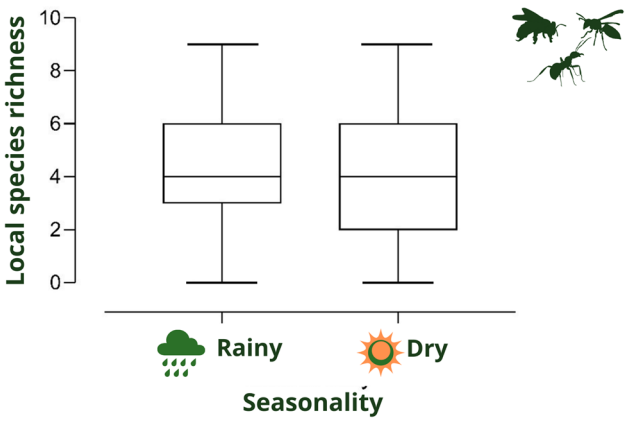

Fig. 4 Box plot depicting the effects of seasonality (rainy and dry seasons) on the average local species richness of Hymenopterans associated with *Encholirium spectabile* clumps, considering all sampled years. The whiskers represent the maximum and minimum values, while the central horizontal lines represent the median

This temporal variation in species composition may indicate the adaptive strategies employed by Hymenoptera to deal with the different challenges imposed by the rainy and dry seasons in the study area, highlighting the role that bromeliads play in this environment. They function as an oasis for these species, especially during the dry period, like other tank bromeliads (Islair et al. 2014) and food made available by the carcasses of animals killed during the dry period (Santos et al. 2014). The results found indicate differences in species composition, which may have significant consequences for the availability of ecosystem services promoted by these taxa. By offering shelter and primarily providing pollen and nectar during periods of scarcity, bromeliads indirectly enhance the availability of ecosystem services, thereby facilitating the persistence of these taxa in the region and, consequently, the ecosystem services they promote.

Ants

Ants associated with *E. spectabile* play crucial roles in providing ESs in the study area, especially support and regulating services. Ants are important components in the processes of seed dispersal, nutrient cycling, biological control, and soil aeration (Del Toro et al. 2012; Perfecto and Philpott 2023). Ants, renowned for their ecosystem engineering abilities, contribute to nutrient cycling and soil health; additionally, ants are efficient decomposers, aiding in the breakdown of organic matter and nutrient cycling (Eldridge et al. 2011; Perfecto and Philpott 2023). These findings highlight the

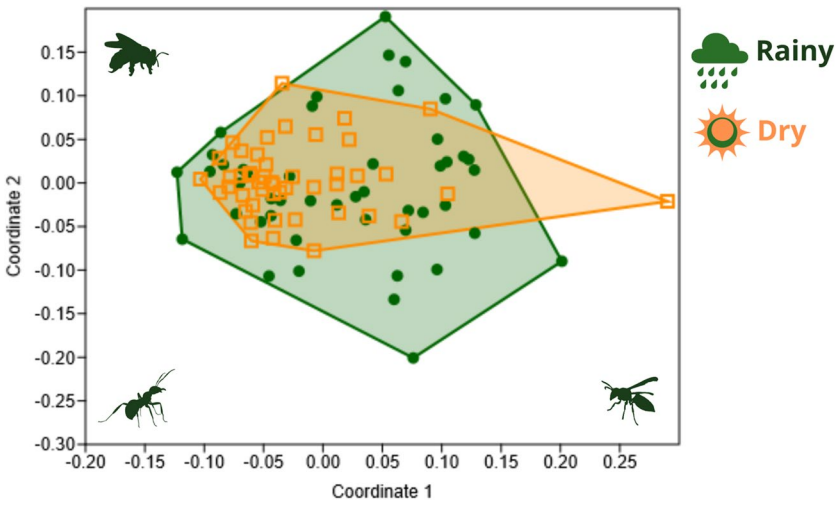

Fig. 5 Results of non-metric multidimensional scaling (NMDS) showing the differences in species composition between seasons in association on *Encholirium spectabile* in Santa Maria, Rio Grande do Norte, Brazil (2011–2018). Blue dots: species recorded in the rainy season; green squares: species recorded in the dry season

Fig. 6 Species associated with rupicolous bromeliads (Encholirium spectabile) in the semi-arid region of Rio Grande do Norte, Brazil, and their activities contributing to available Ecosystem Services: a A bumble bee (*Xylocopa sp.*) visiting a flower. b European bee (*Apis mellifera*) and paper wasp (*Polybia occidentalis*) visiting native tree flowers. c Braconidae wasp, a parasitoid of beetles. d Paper wasps (*Polybia sp.*) collecting organic matter (dried flowering stem of E. spectabile) for nest building. e Species of wasps (*Polystes canadenses* and *Polybia sp.*) and bees (*Apis mellifera* and *Trigona spinipes*) visiting coconut palm flowers (*Atta sp.*). f Ant nests (Atta sp.)

positive impact of ants on nutrient cycling and soil health. This is even more significant when one considers the rocky environment in which these bromeliads develop, which is poor in organic nutrients and demands an external supply of nutrients.

Ants also play a crucial role in seed dispersal, collecting and dispersing seeds, aiding in the dispersion and germination of various plant species (Lengyel et al. 2010; Penn and Crist 2018). This dispersal mechanism is especially important for the survival and distribution of certain plant populations (Perfecto and Philpott 2023). The clumps of *E. spectabile* create an environment conducive to seed germination of native species, given the ability of these plants to form tussocks, combined with the internal humidity that they maintain within the clumps (Jorge et al. 2020). As ants build their nests, aerate the soil, and carry seeds to these sites, they contribute to the seed dispersal and germination of native species.

These insects also provide provisioning and cultural services, such as serving as food and having cultural significance. In the semi-arid region, during their flight, the queens of *Atta* sp. are collected and consumed as food, the flight coinciding with the onset of the rainy season in region (JSJ personal observation). The flight of "tanajuras" also signals the beginning of the rains, according to local traditional knowledge, marking the start of the planting period for annual crops. Additionally, children use the soldiers of *Atta* sp. for soldier battles due to their powerful jaws, engaging in fights until one soldier prevails.

Ants that utilize rupicolous bromeliads are also important in structuring trophic webs in these environments, serving as the basis of the diet for many organisms, including amphibians, lizards, and birds (Jorge et al. 2020, 2023). Ants also establish a proto-cooperative relationship with other species, such as butterfly caterpillars (Lycaenidae), aphids, and leafhoppers (Homoptera), creating an interaction cycle (Jorge et al. 2021b).

Bees

In the study area, bees make up the most abundant group in numbers of individuals, being also the most frequent group during the flowering period of the rupicolous bromeliads (*E. spectabile*). Native bees and European bees are the most abundant group in the dry season, and the flowering period of the rupicolous bromeliads in dry season, supports these groups by producing honey and derivatives (provisioning services) in periods of scarcity in the region (Jorge et al. 2018).

Bees are indeed renowned for their essential role as pollinators (Klatt et al. 2014). They transfer pollen from male to female flower parts, facilitating fertilization and fruit production. This service is crucial for the reproduction of countless flowering plant species, including many crops that rely on bee pollination for successful yields (Klatt et al. 2014; Kevan and Silva-Nunes 2021), as in the field of the present study. Besides pollination, bees contribute to maintaining biodiversity. By visiting various flowers in search of nectar and pollen, they inadvertently aid in cross-pollination between plant species (Aryal et al. 2020; Ghosh et al. 2020). This intermixing of genetic material contributes to the genetic diversity of plants, which is vital for their long-term survival and adaptability to changing environmental conditions.

Bees also produce honey, a valuable food source for humans and other animals (Ajibola et al. 2012). Beekeeping not only supports the livelihoods of beekeepers but also plays a significant role in local economies (Aryal et al. 2020). Moreover, beeswax, another bee product, has multiple applications in various industries, including cosmetics and candle making (Krell 1996). In the period from 2002 to 2020, honey production in Brazil increased from 24,028 tons to 51,507 tons, according to IBGE data for 2022 (IBGE 2023), showing the importance that bees play for the population that uses honey. Brazilian native bees, specifically meliponines, play a crucial role in honey production in the semi-arid region (Barbiéri and Francoy 2020), producing a honey rich in medicinal properties, widely used in traditional medicine.

These bees are of utmost importance due to their unique characteristics; they are adapted well to the challenging environmental conditions of the region, making them resilient honey producers (Barbiéri and Francoy 2020; Matias et al. 2017). Moreover, they contribute to the pollination of native flora, aiding in the preservation of biodiversity (Villas-Bôas 2018). With their efficiency in honey production and their ecological role as pollinators, these native bees are essential for sustaining the honey industry and maintaining a healthy ecosystem in the semi-arid region (Barbiéri and Francoy 2020), and the rupicolous bromeliads (*Encholirium*) play a significant role in the maintenance of these native bees, serving as a food source and a place for their nest construction.

Wasps

Wasps often get a bad reputation, but do they offer any ESs in the region? Despite their negative image, wasps indeed provide important ES, and the richness of species in association with *E. spectabile* play an important role in these ES promoted. Wasps, often misunderstood and feared, play a crucial role in our ecosystems by providing various ecosystem services (Brock et al. 2021). One of the primary ecosystem services provided by wasps is pest control (Polidori et al. 2010). Many wasp species are skilled predators, preying on a wide range of insects, including crop pests and garden nuisances such as caterpillars, flies, and aphids (Gaston and Lawton 1988; Grissell 2010).

Around the study area, there are many small plantations, where residents keep their crops during the rainy season, and according to them, pests are common, mainly caterpillars of butterflies and moths and wasps usually feed on these caterpillars. By hunting and feeding on these pests, wasps help regulate their populations, preventing potential damage to agricultural crops and supporting overall plant health (Sumner et al. 2018). Many wasp species are natural predators, preying on a wide range of insect pests, including many species of caterpillars (Akre and Myhre 1994; Greeney et al. 2012). By controlling pest populations, wasps help maintain the balance of ecosystems and can even be beneficial to agriculture in the region.

Wasps act as pollinators as well as bees and ants in the study site. While bees are commonly associated with pollination, wasps also play a role in this vital process, certain wasp species visit flowers to feed on nectar, inadvertently

transferring pollen from one flower to another as they move around (Brock et al. 2021). In the study area, many species of wasps are floral visitors of native and cultivated species, playing the role of pollinators of these plants. The sociable species, such as *Polistes* and *Polybia*, are the most numerous and common to be observed (Jorge et al. 2021a, b). This facilitates the reproduction and genetic diversity of flowering plants, contributing to the overall biodiversity of ecosystems (Shuttleworth and Johnson 2012).

Wasps also serve as a food source for other organisms in the ecosystems (Brock et al. 2021). Birds, reptiles, amphibians, and mammals, including some insectivorous bats, rely on wasps as a part of their diet, not being different in the study area, where these species are part of the diet of several other groups (Jorge et al. 2021a, b; 2023). The presence of wasps in the food chain supports the survival and diversity of these predator species, contributing to the overall ecological balance. It is important to note that not all wasp species provide the same ecosystem services, and some can be pests themselves in certain situations. However, understanding and appreciating the valuable contributions of wasps to our ecosystems can help foster a better understanding of their ecological importance and encourage their conservation. Despite their negative reputation, wasps play a vital role in maintaining the balance of ecosystems. From pest control and pollination to providing a food source for other animals, these remarkable insects offer crucial ESs that contribute to the functioning and resilience of our natural world.

Conservation of actors involved

The rupicolous bromeliad, *E. spectabile*, holds great importance for Hymenopterans and the ESs they provide in the semi-arid region of Brazil as show in the text. Hymenopterans, such as ants, bees, and wasps, depend on this bromeliad for various reasons, were the bromeliads serves as a vital habitat, offering shelter and nesting sites for Hymenopterans and offering food resources. It provides a refuge from harsh environmental conditions, enabling their survival and population growth in the semi-arid region.

Moreover, the rupicolous bromeliad contributes to essential ESs provided by Hymenopterans. Conserving Hymenopterans and their habitat, including the rupicolous bromeliad, is of utmost importance. These species contribute to the overall ecological balance and functioning of the semi-arid region's ecosystem (Jorge et al. 2021a). Their conservation helps to safeguard biodiversity, maintain the services, and promote the resilience of the ecosystem in the face of challenging climatic conditions. Efforts to conserve Hymenopterans involve preserving their habitat, implementing sustainable land management practices, and raising awareness about their ecological significance. Protecting the rupicolous bromeliad and the Hymenopteran species that depend on it is vital for maintaining the health and sustainability of the semi-arid region's ecosystem.

Seasonal variations significantly influence the composition of Hymenopterans associated with *E. spectabile* but have a non-significant impact on species richness across different seasons. This aligns with prior studies on invertebrates in the semi-arid region of Brazil, all reporting similar positive effects on species richness and composition (Vasconcellos et al. 2010; Bento et al. 2016). The concentrated rainfall in this region during specific periods profoundly affects the biology and ecology of various taxa, particularly invertebrates, ultimately impacting the entire food chain (Sales et al. 2011; Ribeiro and Freire 2011).

During the dry season, *E. spectabile* bromeliads bloom (Queiroz et al. 2016; Jorge et al. 2018), providing essential resources like nectar, pollen, and flower tissues to a diverse range of organisms, including ants, bees, and wasps (Jorge et al. 2018). This resource availability enables these bromeliads to attract and sustain these taxa even when resources are scarce. Research on the invertebrate assemblage associated with *Aechmea bromeliifolia* in the semi-arid region (Islair et al. 2014) found differences in abundance but not in species richness between seasons, attributed to the presence of phytotelmata, acting as water reservoirs and resource sources during the dry season. *Encholirium spectabile*, by offering sustenance and refuge to its associated fauna throughout both dry and rainy seasons, helps bridge the disparities between these distinct periods of the year.

Non-phytotelmata bromeliads, exemplified by *E. spectabile* in the semi-arid region of Northeast Brazil, emerge as crucial allies in sustaining species of bees, wasps, and ants year-round. These findings underscore their significance as a vital resource for these hymenopteran insects, especially during the challenging dry periods that characterize the region. *Encholirium spectabile*, during its bloom in the dry season, offers a lifeline to these pollinators and predators, providing them with a consistent source of nectar, pollen, and shelter. This resource stability is pivotal in maintaining the populations of these insects, as they play essential roles in the region's ecosystem.

The implications of these non-phytotelmata bromeliads extend far beyond the survival of individual species. They contribute significantly to ecosystem services in the semi-arid region, particularly during the dry season. The stability of hymenopteran populations supported by these bromeliads ensures consistent and effective pollination services for plants, including those of economic importance. Furthermore, the presence of these insects acts as a natural form of pest control in agriculture, reducing the reliance on harmful pesticides. Therefore, preserving and managing habitats that sustain non-phytotelmata bromeliads becomes paramount for the region's ecological balance and

agricultural productivity, particularly during the challenging dry periods that can make or break local ecosystems and communities.

Conclusions

In conclusion, we listed for the first time the main ESs promoted by Hymenoptera associated with rupicolous bromeliads (*E. spectabile*) in rocky outcrops in the semi-arid region of Brazil. These bromeliads are important maintainers of faunal diversity in the Brazilian semi-arid region (Jorge et al. 2021a), including the Hymenoptera, and with them, their promoted ESs. Bees excel in pollination services, supporting agricultural productivity and wild plant communities. Ants contribute significantly to nutrient cycling and soil health through their roles in decomposition and soil engineering. Wasps play a vital role in natural pest control and pollination. Furthermore, interactions among these insect groups may have synergistic effects on ESs. These scientific findings highlight the importance of conserving and protecting ants, bees, and wasps to ensure the long-term sustainability of ecosystems and human well-being.

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Data Availability Data availability can be accessed by requesting the corresponding author.

Declarations

Conflict of interest The authors declare no competing interests.

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