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Seasonality and Generalist Plant Resource Use Drive Bee Community (Hymenoptera, Apidae) composition in herbaceous *restinga* and dune environments

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Abstract

Few bee inventories have investigated the interaction between bees and plants in the *restinga* in Santa Catarina State, a highly anthropized coastal environment, due to its value. In this context, in the southern coastal region of the State, the bee community and their foraging resources were ecologically analyzed, aiming to obtain data that support their conservation. For sampling, bees were collected over one year in herbaceous restinga and Laguna (SC) dunes, using entomological nets, trap dishes, and aromatic baits. The bees and plants were prepared, identified, and quantified. Ecological indices were calculated. Eighteen species of bees and sixteen species of associated plants were found. The collector's curve stabilized, and richness estimators indicated a possible richness of 21.57 to 26.25 species. The five subfamilies of bees occurring in Brazil were found, with Halictinae having the highest richness and Apinae having the greatest abundance. Andreninae showed only one species (*Callonychium luteimaculatum*), as abundant as *Apis mellifera*. The plants most visited in terms of bee diversity are typical of the restinga and are highly attractive to bees. The periods with the highest results were spring and summer. The variation in temperature and the increase in plant richness increased bee abundance and richness, highlighting the region's seasonality. The bee community showed a conservative generalist condition, which is favorable for species living in inhospitable conditions, providing moderate robustness. Due to the lack or absence of nesting resources, the studied bee community appears to originate from nearby adjacent areas.

Introduction

The *restinga* ecosystem is characterized by sandy soils, poor in clay and organic matter, with low capacity for retaining water and essential nutrients to maintain the biological composition; differently what happens in terrestrial environments, the primary source of nutrients, in the *restinga*, comes from sea spray and not dune soil (Araújo & Lacerda, 1987). Due to the fragility of this ecosystem (which may include areas lacking native vegetation), its plant cover plays a fundamental role in sediment stabilization, natural drainage maintenance, and preservation of its resident and migratory fauna (Falkenberg, 1999).

It is important to highlight that, in *restinga*, specific soil components (such as organic matter and litter thickness) have a greater influence on species distribution and the structural pattern of plant communities (Melo Júnior & Boeger, 2015). Due to the soil's decisive role, *restinga* vegetation is considered edaphic (Bonilha et al., 2012).

The plants in this type of environment exhibit a set of adaptations to extreme conditions of high salinity, low water availability, and intense solar radiation, with about 80% being melittophilous (Scarano et al., 2001; Viana et al., 2006).

About 87.5% of known angiosperms rely on animal pollinators at some point, indicating that these groups have evolved together, this association dating back to the Cretaceous

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period, more than 100 million years ago (Roubik, 1989; Ollerton et al., 2011). For bees, plants serve as a source of food (pollen and nectar), and for plants, the foraging activities of bees result in fertilization. Thus, without pollinators, many plants may not reproduce or produce seeds. Consequently, populations of bees dependent on these plants also decline (Garófalo et al., 2012; Kleinert et al., 2012; Imperatriz-Fonseca et al., 2012).

Since the 1970s, various surveys on bee fauna and their relationships with flora have been conducted in different ecosystems, and the results indicate that studying these communities is an appropriate method to perceive the synecology of these insects (Truylio & Harter-Marques, 2007). In addition to helping understand changes caused by humans or natural processes, biological inventories are also an essential tool for understanding the biodiversity of a specific area. It is worth noting that bees can be considered bioindicators of the preservation status of environments (Kevan, 1999; Lewinsohn et al., 2001).

In the coastal zone of Brazil, the subfamilies of bees tend to vary in the number of species. For example, in the southern region, there are more Andreninae species than in the northern region, and there is also a lower number of Apinae species than in other regions (Viana & Alves dos Santos, 2002). However, these data are pretty dated, and several inventories have been conducted since (Madeira-da-Silva & Martins, 2003; Viana & Kleinert, 2005; Steiner et al., 2006; Albuquerque et al., 2007; Gimenes et al., 2007; Oliveira et al., 2010; Kamke et al., 2011; Rêgo et al., 2012; Patrico et al., 2014; Mouga et al., 2015; Mouga & Nogueira-Neto, 2015; Silva et al., 2015; Gostinski et al., 2016; Lima, 2016; Mouga et al., 2018; Silva et al., 2022). Nevertheless, no specific studies mention the bees of the *restinga*, encompassing the coastal part as a whole, in Brazil.

On the other hand, on the coast of Santa Catarina State, several surveys have been conducted on the bee fauna (Steiner et al., 2006; Steiner et al., 2010; Kamke et al., 2011; Patricio et al., 2014; Mouga et al., 2015; Lima, 2016; Mouga et al., 2018; Silva et al., 2022). However, no studies have been conducted in the municipality of Laguna in the southern part of the State, specifically in herbaceous *restinga* and dune areas. Therefore, this study aimed to inventory and analyze the bee community in the mentioned environment, located at a meridional latitude, which includes many dunes, has a particular vegetation cover and is heavily influenced by the wind.

In general, municipalities in Santa Catarina State have been losing coastal natural environments (specifically, *restingas*) to make way for buildings and highways (Korte et al., 2013). Considering the loss of these habitats, bee inventories conducted in relatively well-preserved *restinga* areas become essential as they document species that may disappear in the future, providing basic data to develop monitoring protocols for these threatened and sensitive environments.

Material and Methods

Study area

The study took place in the municipality of Laguna (Santa Catarina State, Brazil), at Praia do Cardoso, the environment and location of the work described in Tietz et al. (2023). This area is characterized mainly by vegetated and non-vegetated dunes (Horn Filho et al., 2017) and persistent and intense winds (Pires et al., 2020). Near the study site is the Santa Marta Lighthouse, noted as a promontory with the presence of rocky shores, cliffs, and intense erosion, extending nearly 700 meters into the ocean (Guerra, 2009; Ab Razak, 2015; Google Earth, 2024).

Collection, dates, methods

With monthly collections, bee sampling took place over a year, from June 2021 to May 2022. Bees were collected on flowers using an entomological net (Sakagami et al., 1967) and prepared according to Michener et al. (1994). Colored trap dishes were also deployed, with the colors blue, green, pink, purple, red, yellow, and white (Moericke, 1955). Additionally, aromatic baits were used in 600 ml PET bottles (Dec & Mouga, 2014), using one bait for each compound: eugenol, cineole, vanillin, benzyl acetate, methyl cinnamate, and methyl salicylate.

The sampled individuals were assigned field numbers stored in Eppendorf tubes (5 ml). In the laboratory, they were entomologically mounted (Michener et al., 1994) and preserved in the CRABEU collection (Coleção de Referência de Abelhas da Univille), Laboratorio de Abelhas from Universidade da Regiao de Joinville (LABEL – UNIVILLE).

The plants associated with bees were photographed and collected, later preserved through the process of herborization for subsequent identification (Fidalgo & Bonomi, 1989). The plants are deposited in the JOI herbarium (Joinvillea Herbarium) and were described in Tietz et al. (2023).

The abiotic factors temperature (°C), relative air humidity (%), and wind speed (m/s) were recorded every hour during the sampling period, with the aid of a thermohygrometer (Gaeirt) and an anemometer (Staright).

Identification

For bee identification, the works of Silveira et al. (2002), Gonçalves & Melo (2006), Almeida (2008), Nemésio (2009), Roig-Alsina (2013), and Celis and Cure (2017) were utilized. The bee classification used is that of Melo and Gonçalves (2005) and the one available in Moure et al. (2024).

Specific literature was consulted for plant identification (Bianfé & Falkenberg, 2016).

For additional identification, specialists were consulted, that is, for bees: Enderlei Dec, Beatriz W. T. Coelho, and Gabriel A. R. Melo; and for plants: Rafael Voltz.

Data analysis

The Excel program generated graphs (species accumulation curve, abundance, richness, richness estimators, and number of interactions). The Venn diagram was manually generated using the PowerPoint program.

With the assistance of the Past 4.13 program (Hammer et al., 2001), the ecological indices Shannon-Wiener (H') and Pielou (J) were calculated. Still, using the program mentioned above, the data related to the mean temperature, relative air humidity, wind, bee and plant richness (across months and seasons), and bee abundance (across months and seasons) were subjected to normality tests (Shapiro-Wilk)

The means of temperature, relative air humidity, and bee richness over the months, and the average plant richness, bee richness, bee abundance, wind speed, temperature, and relative air humidity in each season showed a normal distribution (>0.05, Shapiro-Wilk) and, therefore, were treated with Pearson (Obilor & Amadi, 2018; Schober et al., 2018). However, the data for wind speed, plant richness (over the months), and bee abundance (over the months) did not follow a normal distribution, so these data were treated with Spearman correlation (Mukaka, 2012).

The metrics of connectance, NODF (*Nestedness Metric Based on Overlap and Decreasing Fill*), specialization (H_2'), robustness, ISA (asymmetry of dependence in the entire network), and push-pull (index that reflects the influence of the species one over the others), and the generation of the interaction graph between the bee community and the flora were obtained using the R program through the bipartite package (Dorman et al., 2008; Dorman et al., 2009), following the guide described by Mello et al. (2016).

The NODF metric indicates the nestedness of the interaction network, and its values range from 0 to 100, increasing as nestedness increases, meaning there is a total overlap of rows from top to bottom and columns from left to right (Almeida-Neto et al., 2008). The specialization index varies from 0 (generalist) to 1 (very specialist) (Mello et al., 2016). The network robustness values were obtained for the bee and botanical communities (which interact); this value ranges from 0 to 1, with values closer to 0 indicating a higher likelihood of extinction and those closer to 1 indicating less susceptibility to extinction, hence more robust communities. Regarding ISA values, positive values indicate greater dependence on the pollinator group and serve as a measure of specialization at both trophic levels (Dormann et al., 2017). A value of 0 indicates a highly symmetrical interaction strength, while values close to 1 or -1 indicate high asymmetry.

The richness estimators (Chao 1, Chao 2, Jack, and Bootstrap) and the Mao Tau rarefaction curve were calculated using the EstimateS program version 9 (Colwell, 2013), with 1000 randomizations.

Results

A total of 72 hours of sampling effort were conducted, during which 444 bees were collected, representing 18 species from five subfamilies (Table 1). Throughout the study, the temperature ranged from 32.2 to 15.1 °C, relative air humidity ranged from 99 to 61%, and wind speed varied between 37.5 and 0 m/s.

Table 1. List of collected bee species, abundance of sampled individuals, and sampling method at Praia do Cardoso, Laguna, Santa Catarina State, Brazil. Legend: E: entomological net; T: trap dishes; A: aromatic bait; S: sighting.

Subfamily	Tribe	Species	E	T	A	S	Total
Andreninae	Panurgini	*Callonychium (Callonychium) luteimaculatum* (Strand, 1910)	15	152			167
Apinae	Apini	*Apis mellifera* Linnaeus, 1758		3		166	169
	Xylocopini	*Ceratina (Neoclavicera) asunciana* cf	2				2
		Xylocopa (Neoxylocopa) brasilianorum (Linnaeus, 1767)	1				1
		Xylocopa (Megaxylocopa) frontalis (Olivier, 1789)				2	2
	Euglossini	*Eufriesea auriceps* (Friese, 1899)			1		1
Colletinae	Neopasiphaeini	*Hexantheda enneomera* Urban & Graf, 2000		1			1
Halictinae	Augochlorini	*Augochloropsis (Paraugochloropsis)* sp. 1	2				2
		Augochloropsis (P.) sp. 2	1				1
		Augochloropsis (P.) sp. 3	5	1		2	8
		Augochloropsis (P.) sp. 4	8	1	1		10
		Augochloropsis (P.) sp. 5	1				1
		Pseudaugochlora graminea (Fabricius, 1804)	1				1
		Thectochlora hamata Gonçalves & Melo, 2006	5	1			6
	Halictini	*Dialictus* sp. Robertson, 1902	7	21			28
		Pseudagapostemon (Pseudagapostemon) pampeanus (Holmberg, 1886)	34	6			40
Megachilinae	Megachilini	*Coelioxys (Glyptocoelioxys)* sp. Mitchell, 1973	1				1
		Megachile (Grafella) crotalariae (Schwimmer, 1980)	3				3
Total	8	18	86	186	2	170	444

It should be noted that although the majority of bees are associated with plants, only three individuals of the following species have been sampled without showing any interaction with flora: *Hexantheda enneomera* Urban & Graf, 2000, collected only in a trap dish; *Eufriesea auriceps* (Friese, 1899), only with aromatic bait; and *Coelioxys (Glyptocoelioxys)* sp. Mitchell, 1973, in flight. Concerning plants, 16 species belonging to nine families were sampled (Table 2).

Diversity

Eighteen bee taxa were collected and distributed across five subfamilies, and their abundance, along with the collection method employed, is presented in Table 1. Among the collected species, one is considered exotic (*Apis mellifera* L.), one is parasitic (*Coelioxys* (*Glyptocoelioxys*) sp.), two were highly abundant (*Ap. mellifera* and *Callonychium (Callonychium) luteimaculatum* (Strand, 1910)), and none are considered threatened. The species *Ca. luteimaculatum* and *Megachile (Grafella) crotalariae* (Schwimmer, 1980) are not listed for the state of Santa Catarina (Moure et al., 2024).

The species accumulation curve is shown in Fig 1A, and in Fig 1B, it is possible to observe bees' abundance and species richness concerning the seasons. The months with the highest abundances were March and December (with 115 and 114 individuals, respectively). February and March had the highest recorded species (12 and 8, respectively). The absence of bees in the field marked the months of July, August, and October.

Table 2. Botanical species sampled than interacted with the bees.

Family	Specie
Anacardiaceae	*Schinus terebinthifolia* Raddi
Asparagaceae	*Yucca filamentosa* L.
Asteraceae	*Baccharis dracunculifolia* DC.
	Baccharis trimera (Less.) DC
	Mikania involucrata Hook. & Arn.
	Noticastrum hatschbachii Zardini
	Porophyllum ruderale (Jacq.) Cass.
	Senecio platensis Arechav.
	Symphyopappus casarettoi B. L. Rob.
Boraginaceae	*Varronia curassavica* (Jacq.) Roem. & Schult.
Commelinaceae	*Commelina erecta* L.
Fabaceae	*Desmodium incanum* (Sw.) DC.
	Lupinus albescens Hook. & Arn.
Melastomataceae	*Pleroma urvilleanum* (DC.) P.J.F. Guim. & Michelang.
Onagraceae	*Oenothera mollissima* L.
Solanaceae	*Petunia integrifolia* (Hook.) Schinz & Thell.
Total	16

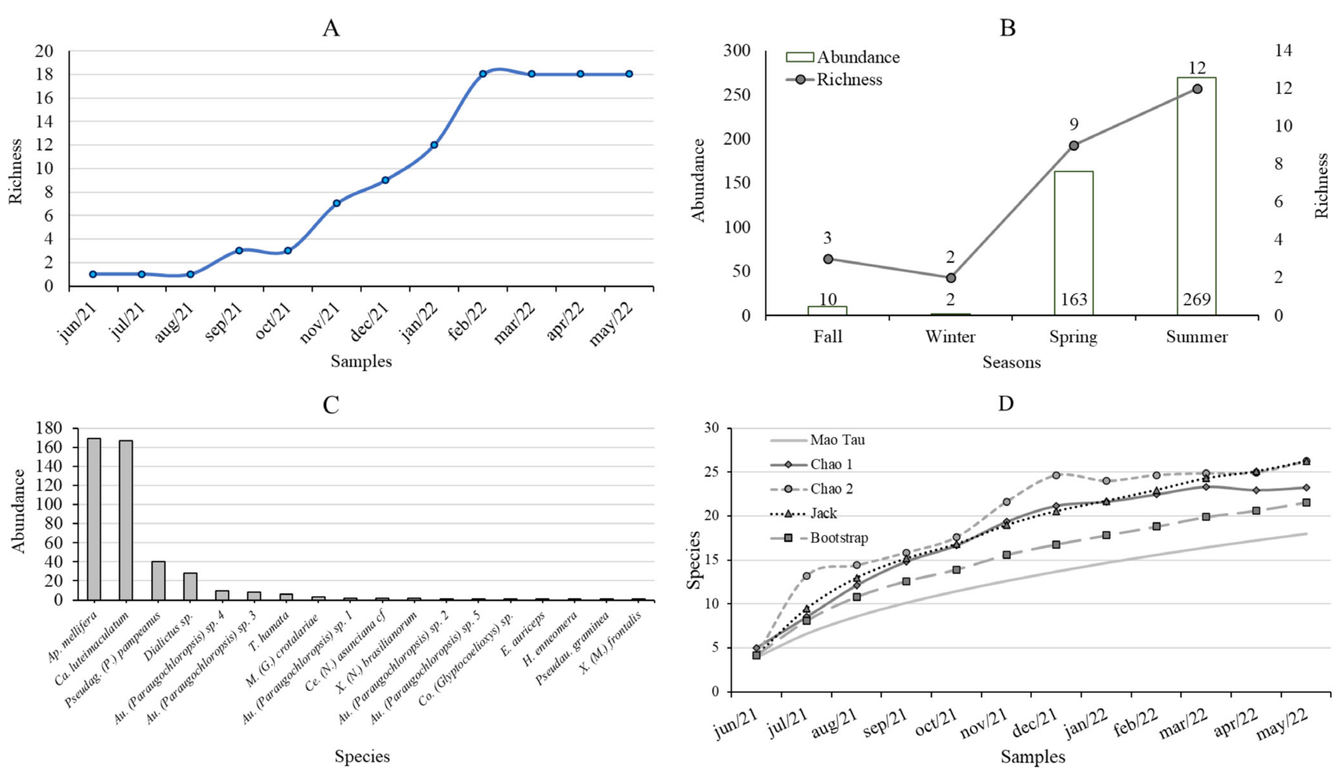

Fig 1. A: collector's curve graph; B: abundance and richness of bees graph in the seasons; C: graph with the total abundance of bees per species; and D: graph related to richness estimators.

The most abundant species was *Ap. mellifera*, followed by *Ca. luteimaculatum* and *Pseudagapostemon (Pseudagapostemon) pampeanus* (Holmberg, 1886) (169, 167, and 40 individuals, respectively) (Fig 1C).

In Fig 1D, richness estimators are grouped. In the final sample of estimators, Chao 1 indicated a richness of 23.24 species, Chao 2 and Jack indicated the same value of 26.25 species, and Bootstrap indicated 21.57 species. Regarding collection efficiency, Chao 1 and Bootstrap showed values above 70% (77.45% and 83.45%, respectively), and Chao 2 and Jack showed a collection efficiency of 68.57%.

Regarding the trap dishes, only the red plate did not attract bees. Except for the red plate, the species *Ca. luteimaculatum* was collected on all other colored plates, *Dialictus* sp. Robertson, 1902 appeared in four colored plates (blue, white, yellow, and purple), *Pseudag. pampeanum* was collected in only two plate colors (blue and white). Three bee species were collected only on the blue plate (*H. enneomera*, *Augochloropsis (Paraugochloropsis)* sp. 3, and *Thectochlora hamata* Gonçalves & Melo, 2006), *Augochloropsis (P.)* sp. 4 was collected only on the white plate, and *Ap. mellifera* only on the yellow plate (Figure 2A). The abundance of bees concerning trap dishes is shown in Figure 2B.

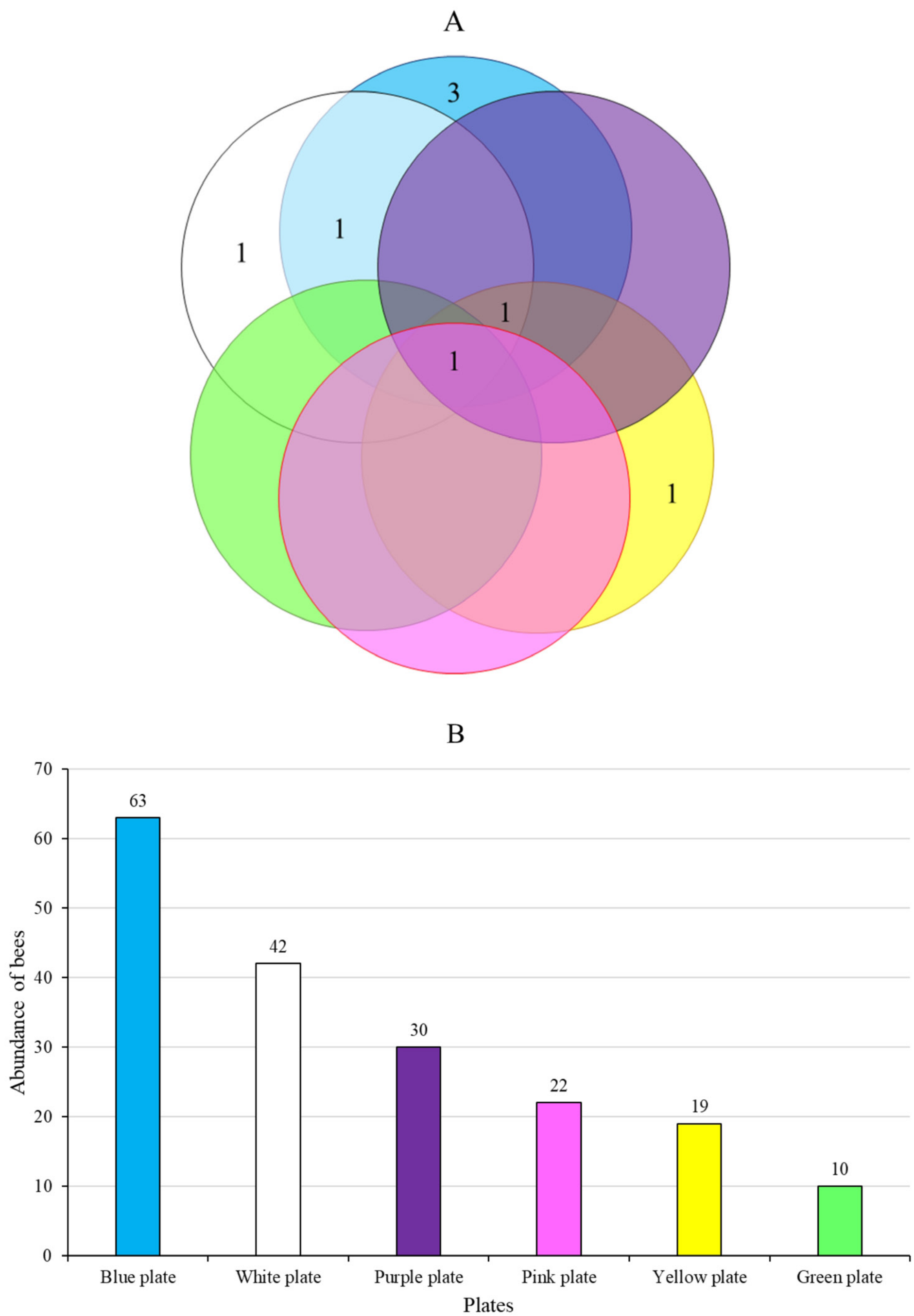

Fig 2. A: Venn diagram with different plate colors; and B: graph showing the abundance of bees in different plate colors. In both (A and B), each color is represented as the color of respective plate used in the methodology.

Abiotic factors, abundance, and richness

Pearson tests revealed that temperature influences bee richness over the months ($r < 0.05$). This abiotic factor, which varies significantly throughout the year, conditions the appearance of species, emphasizing the influence of the advent of plant species. Furthermore, considering only the averages of each season, a positive correlation was observed between the richness of plants and the richness and abundance of bees; bee richness showed a positive correlation with bee abundance, and the abundance of bees showed a positive correlation with temperature ($r < 0.05$).

The Spearman test showed a very high correlation between plants' richness and bees' abundance over the months ($r > 0.9$).

Ecological indices

Considering the presence of *Ap. mellifera*, the diversity index (H') was 1.56, and the equitability index (J) was 0.54. If the presence of *Ap. mellifera* is disregarded, the H' index was 1.45, and the J index was 0.51.

Similarity

The Soerensen index (similarity) applied to the data from this study concerning studies conducted in similar environments is presented in Table 3. The site with the highest bee fauna similarity (38%) in this study is the closest to Laguna (Lima, 2016) at 13.8 km. The least similar is that of Alves-dos-Santos (1999) (9%), which is located 117 km away from the current study, although it is not the most distant environment.

Table 3. Sorensen similarity index, comparing the current study with those from other coastal regions (*restinga*s) in Santa Catarina.

Author	Altitude (m)	Taxa	Distance (km)	Municipalities	Sorensen
Alves-dos-Santos, 1999	3	199*	117	Torres (and others)	0,09
Kamke et al., 2011	4	64	86,7	Palhoça	0,23
Patricio et al., 2014	5	39	67,7	Araranguá	0,35
Mouga & Nogueira-Neto, 2015	5	86/74	257	São Francisco do Sul	0,19/0,22**
Lima, 2016	17	24	13,8	Jaguaruna	0,38
Mouga et al., 2018	0	60/48	261	São Francisco do Sul	0,10/0,12**
Silva et al., 2022	13	50	259	São Francisco do Sul	0,29
Praia do Cardoso (present)	9	18	-	Laguna	-

*Only species collected in lowlands are considered here.
**The first value corresponds to the total number of species described in the article, and the second, after identification adjustments.

Associations between bees and plants

Nine botanical families with 16 species were sampled: Asteraceae was represented by seven species (*Baccharis dracunculifolia* DC., *Baccharis trimera* (Less.) DC, *Mikania involucrata* Hook. & Arn., *Noticastrum hatschbachii* Zardini, *Porophyllum ruderale* (Jacq.) Cass., *Senecio platensis* Arechav. and *Symphyopappus casarettoi* B. L. Rob.), Fabaceae by two species (*Desmodium incanum* (Sw.) DC. and *Lupinus albescens* Hook. & Arn.), and the remaining families by only one species, with Anacardiaceae (*Schinus terebinthifolia* Raddi), Asparagaceae (*Yucca filamentosa* L.), Boraginaceae (*Varronia curassavica* (Jacq.) Roem. & Schult.), Commelinaceae (*Commelina erecta* L.), Melastomataceae (*Pleroma urvilleanum* (DC.) P.J.F.Guim. & Michelang.), Onagraceae (*Oenothera mollissima* L.) and Solanaceae (*Petunia integrifolia* (Hook.) Schinz & Thell.).

The plants associated with the bees observed in this study are listed in Table 4. The botanical family most visited by bees was Asteraceae (which included seven botanical species), followed by Fabaceae (two), and the remaining botanical species associated with bees (seven in total) belonged to various families. The botanical species *Mikania involucrata* Hook. & Arn. (Asteraceae) was visited only by *Ap. mellifera*.

The number of botanical species visited by bee species is shown in Fig 3A. The number of bee species that visited botanical species is depicted in Fig 3B. *Pleroma urvilleanum*, *Baccharis trimera*, and *Schinus terebenthifolius* Raddi received more bee species than the other plant species. These three botanical species received eleven bee species, while the others totaled nine. The species *Pleroma urvilleanum*, *Baccharis trimera,* and *Schinus terebenthifolius* received 1.22-fold more species than the other plants.

The bee species with the highest number of plant species it interacted with was *Pseudag. pampeanus* (with ten species), followed by *Ap. mellifera* (nine), *Augochloropsis (P.)* sp.4 (four), and the remaining species were sampled in three or fewer plant species (Figure 4C).

Table 4. Bees and associated plants, verified through visits to flowers by bees.

Bee subfamily	**Bee species**	Botanical family	Botanical species	Abundance of bee species
ANDRENINAE	***Callonychium luteimaculatum***			
		Asteraceae	*Noticastrum hatschbachii* Zardini	3
		Solanaceae	*Petunia integrifolia* (Hook.) Schinz & Thell.	10
		Asteraceae	*Senecio platensis* Arechav.	1
APINAE	***Apis mellifera***			
		Asteraceae	*Baccharis dracunculifolia* DC.	30
		Asteraceae	*Baccharis trimera* (Less.) DC	94
		Commelinaceae	*Commelina erecta* L.	1
		Fabaceae	*Lupinus albescens* Hook. & Arn.	1
		Asteraceae	*Mikania involucrata* Hook. & Arn.	1
		Asteraceae	*Noticastrum hatschbachii* Zardini	1
		Anacardiaceae	*Schinus terebinthifolia* Raddi	16
		Asteraceae	*Senecio platensis* Arechav.	1
		Asteraceae	*Symphyopappus casarettoi* B. L. Rob.	21
	***Ceratina (Neoclavicera) asunciana* cf**			
		Asteraceae	*Baccharis trimera* (Less.) DC	1
		Fabaceae	*Desmodium incanum* (Sw.) DC.	1
	Xylocopa (Megaxylocopa) frontalis			
		Boraginaceae	*Varronia curassavica* (Jacq.) Roem. & Schult.	1
	Xylocopa (Neoxylocopa) brasilianorum			
		Melastomataceae	*Pleroma urvilleanum* (DC.) P.J.F. Guim. & Michelang.	2
HALICTINAE	***Augochloropsis (Paraugochloropsis)* sp. 1**			
		Melastomataceae	*Pleroma urvilleanum* (DC.) P.J.F. Guim. & Michelang.	2
	***Augochloropsis (Paraugochloropsis)* sp. 2**			
		Onagraceae	*Oenothera mollissima* L.	1
	***Augochloropsis (Paraugochloropsis)* sp. 3**			
		Melastomataceae	*Pleroma urvilleanum* (DC.) P.J.F. Guim. & Michelang.	6
		Anacardiaceae	*Schinus terebinthifolia* Raddi	1
	***Augochloropsis (Paraugochloropsis)* sp. 4**			
		Asteraceae	*Baccharis dracunculifolia* DC.	1
		Asteraceae	*Baccharis trimera* (Less.) DC	2
		Melastomataceae	*Pleroma urvilleanum* (DC.) P.J.F. Guim. & Michelang.	1
		Anacardiaceae	*Schinus terebinthifolia* Raddi	4
	***Augochloropsis (Paraugochloropsis)* sp. 5**			
		Melastomataceae	*Pleroma urvilleanum* (DC.) P.J.F. Guim. & Michelang.	1
	***Dialictus* sp.**			
		Asteraceae	*Baccharis trimera* (Less.) DC	4
		Anacardiaceae	*Schinus terebinthifolia* Raddi	3
	Pseudagapostemon (Pseudagapostemon) pampeanus			
		Asteraceae	*Baccharis dracunculifolia* DC.	1
		Asteraceae	*Baccharis trimera* (Less.) DC	11
		Fabaceae	*Lupinus albescens* Hook. & Arn.	1
		Asteraceae	*Noticastrum hatschbachii* Zardini	1
		Solanaceae	*Petunia integrifolia* (Hook.) Schinz & Thell.	6
		Melastomataceae	*Pleroma urvilleanum* (DC.) P.J.F. Guim. & Michelang.	1
		Asteraceae	*Porophyllum ruderale* (Jacq.) Cass.	1
		Anacardiaceae	*Schinus terebinthifolia* Raddi	4
		Asteraceae	*Symphyopappus casarettoi* B. L. Rob.	5
		Asparagaceae	*Yucca filamentosa* L.	2
	Pseudaugochlora graminea			
		Melastomataceae	*Pleroma urvilleanum* (DC.) P.J.F. Guim. & Michelang.	1
	Thectochlora hamata			
		Asteraceae	*Baccharis trimera* (Less.) DC	3
		Commelinaceae	*Commelina erecta* L.	1
		Solanaceae	*Petunia integrifolia* (Hook.) Schinz & Thell.	1
MEGACHILINAE	***Megachile (Grafella) crotalariae***			
		Asteraceae	*Senecio platensis* Arechav.	1

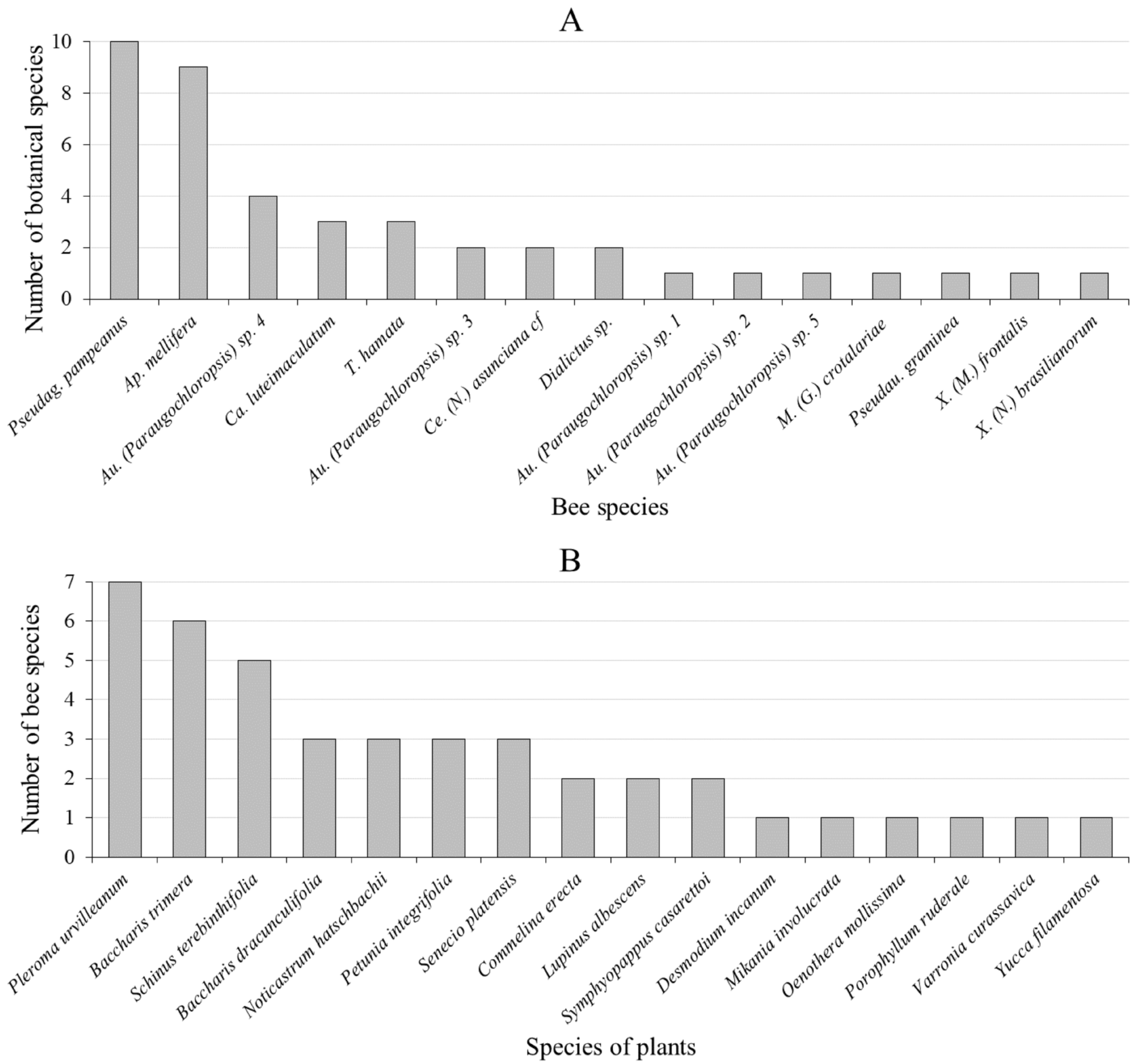

Fig 3. A: Number of plant species that interacted with bee species; B: Number of bee species that interacted with plant species.

Interaction network

The interaction network between bees and plants and the total number of interactions is shown in Figure 4. The species *Ap. mellifera* and *Ca. luteimaculatum* can be considered keystones in terms of abundance and *Pseudag. pampeanus* and *Ap. mellifera* also, but in terms of the number of interactions with plants.

The total number of possible interactions in the studied community would be 288, but only 18% were observed. If the presence of *Ap. mellifera* is disregarded, the total becomes 272, with only 16% confirmed. Thus, the connectance values are 0.18 and 0.16 (with and without *Ap. mellifera*, respectively).

The specialization index was 0.44 with *Ap. mellifera*, and without this bee, the value becomes 0.46. The NODF (nestedness) obtained was 33.33, but without *Ap. mellifera*, the value drops to 29.80. Considering the presence of *Ap. mellifera*, the robustness of the bee community was 0.59, and that of the botanical community was 0.58. If the presence of *Ap. mellifera* is disregarded, the robustness value of the apicultural community is 0.58, and that of the botanical community is 0.55.

Regarding the push-pull interaction in bees, four species were considered "*pusher*" (> 0) (*Ap. mellifera*, *Pseudag. pampeanus*, *Ca. luteimaculatum*, *Ceratina asunciana* cf), and nine were considered "*puller*" (< 0) (*Augochloropsis* sp.1,

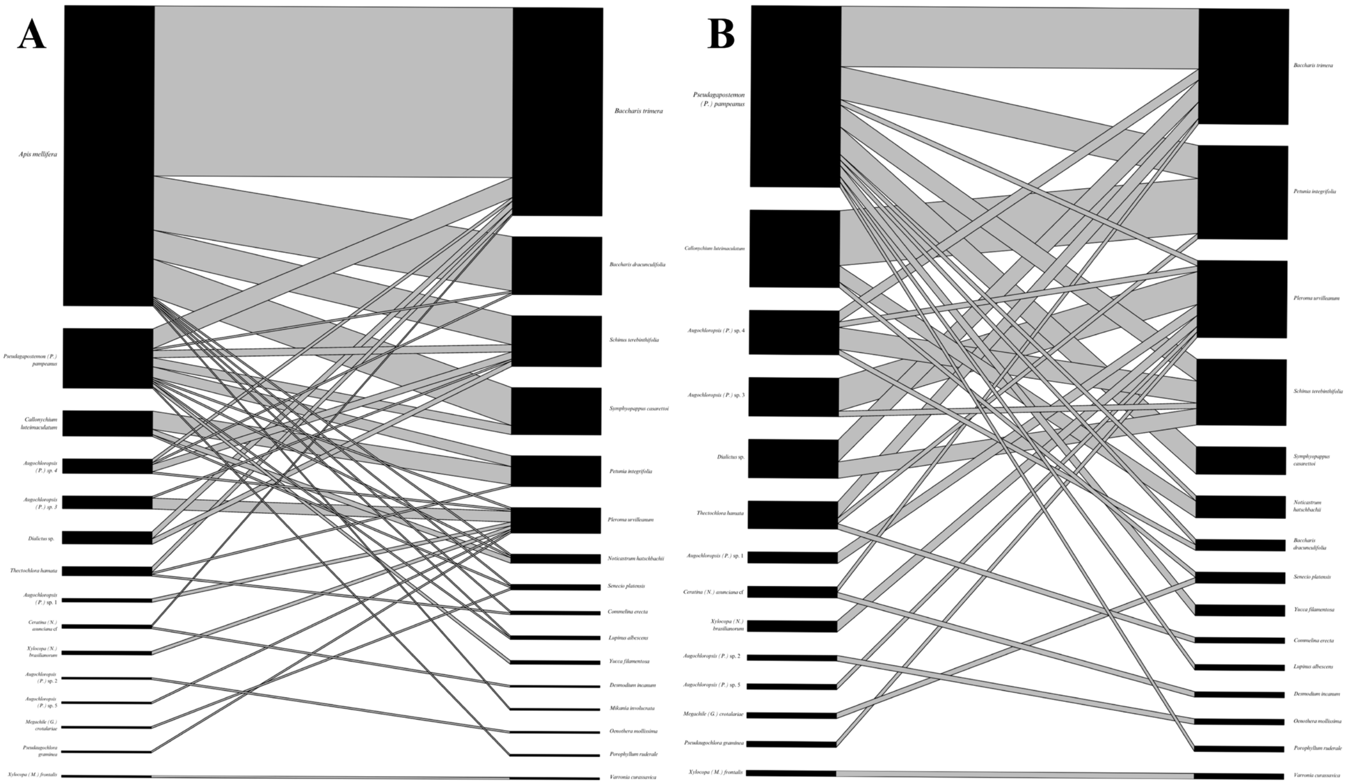

Fig 4. A: Graph of interactions between bee species and plants, including the honeybee species *Apis mellifera*; B: Graph of interactions between bee species and plants, without the honeybee species *Apis mellifera*.

Augochloropsis sp.3, *Augochloropsis* sp.4, *Augochloropsis* sp.5, *Dialictus* sp., *M. crotalariae*, *Pseudau. graminea*, *T. hamata*, *X. brasilianorum*). Additionally, two species maintained a value of 0 (*Augochlora (P.)* sp. 2 and *Xylocopa (Megaxylocopa) frontalis* (Olivier, 1789) as they showed interaction only with one botanical species each. In plants, five species were considered "*pusher*" (> 0) (*B. trimera*, *Sc. terebinthifolia*, *Pe. integrifolia*, *Pl. urvilleanum*, and *Senecio platensis*), and nine were considered "*puller*" (< 0). Also, two species maintained a value of 0 (*O. mollissima* and *Varronia curassavica*), maintaining interaction with only one bee species each. The ISA (Interaction Strength Asymmetry) values were -0.02 and -0.04 (in the presence and absence of *Ap. mellifera*, respectively).

Discussion

Diversity

Halictinae and Apinae were the most represented subfamilies of bees, with nine and five species, respectively, and 97 and 175 individuals, respectively. However, in terms of abundance, a species of Andreninae (*Ca. luteimaculatum*) was extensively collected, surpassing Halictinae. It is possible that the intense collection of this species in the present study did not occur in other works, as they may not have used trap dishes.

The pattern of prevalent subfamilies observed here was quite similar to that of other studies, where Apinae and Halictinae remained at the top in terms of the number of species and abundance (Alves-dos-Santos, 1999; Kamke et al., 2011; Patricio et al., 2014; Lima, 2016; Mouga et al., 2018; Silva et al., 2022). In this sense, it is understood that these groups are common in the southern region of Brazil, showing greater morphological variety, different social organizations (ranging from solitary to highly social), and generalist foraging habits (Roubik, 1989; Michener, 2007). Additionally, Steiner et al. (2006) mentioned that, concerning the richness of bee subfamilies in the Southern Region of Brazil, two groups can be distinguished: inventories where Apinae prevails (coastal regions) and inventories where Halictinae prevails (inland regions of Santa Catarina State). It is observed that, in the current study, the pattern expected in coastal regions was not found, as the highest number of species is attributed to Halictinae, as well as Mouga and Nogueira-Neto (2015) have also found in their study. However, in terms of abundance, Apinae prevails over Halictinae.

Only one genus of cleptoparasite was sampled in this study, namely, *Coelioxys*, which was also reported by Alves-dos-Santos (1999), Kamke et al. (2011), Patricio et al. (2014), Lima (2016), and Mouga et al. (2018). According to Silveira et al. (2022), this genus can parasitize nests of *Megachile* (present in the studied environment).

Among the most collected species are *Ap. mellifera* and *Ca. luteimaculatum*; however, in other studies, the species *T. hamata* was frequently sampled in dune areas of Santa Catarina State (Kamke et al., 2011; Patricio et al., 2014; Lima, 2016). In the present study, *T. hamata* was collected infrequently, as it was sampled only during summer. Gonçalves & Melo (2006) cited this species in continental Rio Grande do Sul State and Uruguay continental areas. Alvarez et al. (2024), on the other hand, found *T. hamata* in Argentina (Missiones and Entre Ríos). This fact reinforces the importance of surveys of species that allow verifying and confirming the extent of geographic distributions.

The high number of collected individuals of *Ap. mellifera* corresponds to findings in similar regional studies (Kamke et al., 2011; Patricio et al., 2014; Lima, 2016; Mouga et al., 2018; Silva et al., 2022). However, in the mentioned studies, other species had high abundance alongside *Ap. mellifera*. Near the studied environment (i.e., inland), there is greater vegetation coverage (observed visually and on maps), and the location may be characterized as shrubby coastal vegetation (*restinga arbustiva*). Thus, there is the possibility of sufficient resources for *Ap. mellifera* to establish itself near the sampling area (or even to be kept in apiaries), explaining its strong presence there.

In the present study, bees from the tribe Meliponini (stingless bees) were not sampled. This was also observed by Silva et al. (2022) in a study conducted on an island in Santa Catarina State. In the case of the current study, the absence of sampling Meliponini bees may be related to the lack of nesting sites in the dunes. These bees primarily nest in tree hollows (which are absent in dunes) but also in termite nests, rock crevices, and soil cavities (scarce in the environment) (Roubik, 1989; Kleinert-Giovannini, 1989; Nogueira-Neto, 1997).

Samplings conducted using trap dishes allowed the collection of a species-specific to this method, namely *H. enneomera*, which was not collected using other methods. However, trap dishes also facilitated a high sampling for another species (*Ca. luteimaculatum*), with the majority of the individuals being collected by the blue plate, followed by the white and then the purple ones (although it was present in all other colors). The latter species heavily visited the botanical species *Pe. integrifolia,* which has lilac-colored petals, explains the significant interaction with these colors. Additionally, it is essential to highlight the interaction of this bee species with *Noticastrum hatschbachii*, a threatened botanical species visited only by *Ca. luteimaculatum* and two other bee species (*Ap. mellifera* and *Pseudag. pampeanus*), emphasizing the importance of these bee species for the conservation of this plant.

According to Kamke et al. (2011), bees from the Euglossini group have populations considered low in restinga areas. In the present study, only one individual (male) from this group (species *E. auriceps*) was collected using scent baits with methyl cinnamate. Another study also used compounds to attract this type of bee (Silva et al., 2022). The explanation for the presence of this taxon in the dune area could be attributed to the ability of many species in this group to fly long distances, moving through different habitats (Añino et al., 2019).

The species accumulation curve (collector's curve, Fig 1) showed stability only in the last samplings (specifically in the last months: March, April, and May). Similar observations were made by Mouga et al. (2018), where the last samplings also did not record new species. However, it is essential to note that the last two samplings in the current study had few collections (April with six individuals and May with only one, corresponding to the beginning of autumn).

The low number of bee species observed (18) is likely due to the inhospitable nature of the environment. When referring to richness estimators, it is noted that two of them showed equal values in terms of collection efficiency (Chao 2 and Jack, both at 68.57%). Still, the others showed distinct values, with values exceeding 70% in terms of collection efficiency. Among the richness estimators, Chao 2 and Jackknife showed the highest values, both at 26.25 species (equal for both), which is considerably lower than what many similar studies have calculated (values above 40 species) (Kamke et al., 2011; Patricio et al., 2014; Silva et al., 2022). Lima's study (2016) showed a similar value (26.55 for Bootstrap).

The Sorensen similarity index calculated for studies conducted in similar environments highlights that the distance between locations alters the resident bee community, as environments tend to differ with distance. It was observed that the closest location to the studied environment, 13.8 km away (Jaguaruna), had the highest similarity (38%). Despite this, even those more distant environments are not necessarily the most different, as Moldenke (1975) states that contiguous habitats that are more physiognomically distinct exhibit lower structural similarities than distant analogous habitats, thus demonstrating the possibility that, under similar physical conditions in geographically distant environments, communities may similarly organize themselves, as climate controls the phenology of floral resource availability, which in turn largely determines the abundance and diversity of flower-herbivores (*sic*), as explicitly mentioned by the afore author.

Seasonality and abiotic factors

The highest number of species and individuals were collected in December and March, but January and February also showed high abundance. Thus, spring and summer were the seasons that provided more intense results. Other studies have shown similar patterns, consistently reporting higher abundance between November and February (Alves-dos-Santos, 1999; Kamke et al., 2011; Patricio et al., 2014; Lima, 2016; Mouga et al., 2018; Silva et al., 2022). According to Nimer (1989) and Monteiro (2001), the State of Santa Catarina exhibits significant variations in its climate, clearly showing the four seasons, and thus, the climate is considered characteristically temperate.

Over the months, plant richness positively correlated with bee abundance. Additionally, over the months, temperature showed a positive correlation with bee richness, similar to the observation made by Patricio et al. (2014). Among the seasonal averages, three positive correlations were observed: one between temperature and bee abundance, another between plant richness and bee abundance, and finally, between bee richness and bee abundance. Considering that the correlations are positive, the increase in temperature and richness of both plants and bees increased bee abundance, making these seasons more distinctly marked.

Ecological indices

In this study, the diversity indexes (H') were 1.56 and 1.45 (with and without *Ap. mellifera*). Other studies produced H' values higher than ours, and despite that, H' values without *Ap. mellifera* in other studies was always higher than with its presence, which differs from the current study. This difference may have occurred because of the high abundance of *Ca. luteimaculatum* that was observed in the sampling. In other studies, *Ap. mellifera* typically has a high abundance, and removing it from the calculation eliminates its dominance. However, in this study, *Ca. luteimaculatum* has an abundance as high as *Ap. mellifera* and, consequently, even if *Ap. mellifera* is removed, the high abundance of *Ca. luteimaculatum* still influences the results. When the calculation is performed without both species, the H' value increases to 1.99. Among different studies, Kamke et al. (2011) obtained the highest H' values, which were 3.41 and 3.43 (with and without *Ap. mellifera*, respectively). Others presented values lower than three (Patricio et al., 2014; Mouga et al., 2018; Silva et al., 2022). However, Lima (2016) showed values that were closest to ours. It is important to remember that this diversity calculation is influenced by community species richness and the relative abundance of each species, which can affect the diversity index result for the site (Magurran, 2004).

This study's J index (evenness) was 0.54 and 0.51 (with and without *Ap. mellifera*). Similar to H', the J values also decreased with the removal of the bee *Ap. mellifera*. In other studies in similar environments, the opposite pattern was observed. Mouga et al. (2018) reported the highest value, 0.88, among the studies compared. Other studies with values close to those of Mouga et al. (2018) include Kamke et al. (2011), with 0.821 and 0.828, respectively (with and without *Ap. mellifera*), and Patricio et al. (2014), with 0.628 and 0.756 (with and without *Ap. mellifera*). The values closest to the present study (considering the presence of *Ap. mellifera*) were found in Lima (2016) and Silva et al. (2022), but without this bee species, both studies produced results higher than the current study. The decrease in evenness with the removal of *Ap. mellifera* indicates that this species, in terms of dominance (along with *Ca. luteimaculatum*), is a significant component in the community. The obtained value suggests that the community appears moderately even in dominance.

The values obtained for both indices in this study are lower than those in similar environments. This difference could be attributed to the low species richness sampled, as the studied environment appears less favorable for the survival of several species, whether bees or plants (the latter reason possibly being the main factor).

Associations of bees and plants

Regarding the flora, the Asteraceae family was the most prevalent, as observed in other studies in similar environments and using similar methods (Alves-dos-Santos, 1999; Kamke et al., 2011; Lima, 2016; Mouga et al., 2018; Silva et al., 2022). Two sampled botanical species are non-native (*Yucca filamentosa* and *Desmodium incanum*), four are endemic (*Noticastrum hatschbachii*, *Symphyopappus casarettoi*, *Pl. urvilleanum*, and *Solanum reineckii* Briq.), and one is endangered (*N. hatschbachii*) (Tietz et al., 2023).

Despite its high abundance, *Ap. mellifera* was not the species that interacted with the greatest number of botanical species. Instead, *Pseudag. pampeanus* took the lead, interacting with ten species, while *Ap. mellifera* showed nine interactions, followed by *Augochloropsis (P.)* sp. 4, with four interactions. An adaptive advantage for interacting with more species may arise from the ability to perform *buzz pollination*, a behavior *Ap. mellifera* does not exhibit (Vinícius-Silva et al., 2017). On the other hand, species of the genus *Pseudagapostemon* have been observed performing this behavior (Hoffmann, 1990; Netto-Silva, 2015). The bee *Ca. luteimaculatum* interacted with three botanical species, two of them from the Asteraceae family (*Noticastrum hatschbachii* and *Senecio platensis*) and another from the Solanaceae family (*Pe. integrifolia*), with the latter having the highest number of visits (ten), demonstrating a great interest in this plant. It has been observed that species of this bee genus show a strong interest in plants of the *Petunia* genus, exhibiting oligolectic behavior towards these plants (Wittmann et al., 1990). Another bee that visited three botanical species was *T. hamata*, all from different plant families but with more visits to *Baccharis trimera*. Lima (2016) reported that this bee species visited a botanical species belonging to the Rubiaceae family (*Borreria palustris* (Cham. & Schltdl.) Bacigalupo & E.L.Cabra). Still, this family was not sampled in the current study.

The botanical species *Pl. urvilleanum* (Melastomataceae) did not receive a high abundance of visits. Still, it was the one that attracted the highest number of bee species (seven), followed by an Asteraceae species interacting with six bee species and an Anacardiaceae species with five (*Baccharis trimera* and *Schinus terebinthifolia*, respectively). *Pl. urvilleanum* is a species with poricidal anthers, meaning it needs to be pollinated through *buzzing*, and the bee genus *Augochloropsis* was quite present, with four species visiting this plant. The ability of this genus to perform this behavior has been reported in the literature (Portman et al., 2019). Another bee species that visited this plant was *Pseudag. pampeanus*, *Xylocopa (Neoxylocopa) brasilianorum* (Linnaeus, 1767), and *Pseudaugochlora graminea* (Fabricius, 1804).

Throughout the summer, the plant *Baccharis trimera* was in bloom (Tietz et al., 2023) in many individuals (visual observation). This likely promoted the high number of visits received, both in abundance and in bee species richness. The botanical species *Schinus terebinthifolia* has been the subject of studies by Lenzi et al. (2003) regarding bee species that visit it on the Island of Santa Catarina State; in the cited study, 20 bee species were recorded, with Halictinae being the most abundant and diverse, but Apinae, Colletinae, and Megachilinae were also present. In the current study, only Apinae and Halictinae made visits to *Schinus terebinthifolia*, with Apinae being the most abundant (only *Ap. mellifera* visited) and Halictinae being the most diverse, with four species (*Augochloropsis (P.)* sp. 3, *Augochloropsis (P.)* sp. 4, *Dialictus* sp., and *Pseudag. pampeanus*).

In a study carried out in the zone of this studied environment, Oliveira et al. (2017) verified that there has been an increase in vegetation along the dunes from 1938 to the present, occurring concurrently with an expansion of urbanized areas, and variations in the coastline have been observed, with a retreat of approximately 0.5 m per year that, cumulatively, ranged between 10 and 50 m in the mentioned period. In the long term, the bee and plant communities may not be excessively affected by the coastline retreat, although the vegetation expansion is positive for the bees. However, the expansion of urbanized surfaces could pose a greater threat, as land use affects areas where plants can develop and stabilize the dunes. On the other hand, it is crucial to consider that the sandy soil in the region, combined with the dunes, may negatively impact the urban area, preventing or diminishing it.

Interaction network

In the present study, connectivity can be considered low, both in the presence and absence of *Ap. mellifera* (0.18 and 0.16, respectively). In other studies, connectivity showed values much higher than those obtained here (Mouga et al., 2018) and others considerably lower (Silva et al., 2022). Nevertheless, not very high values have been reported in network analyses, which are considered a standard in interactive communities, suggesting low connectivity in interaction networks (Donatti, 2011).

The specialization index (H_2') showed a slight variation when *Ap. mellifera* was excluded from the analyses, being 0.44 with and 0.46 without this bee species. These values are higher than those obtained by Mouga et al. (2018) and Silva et al. (2022). Thus, the studied community cannot be considered highly generalist or highly specialist.

The NODF (nestedness of the interaction network) value also showed variation with the absence of the species *Ap. mellifera* indicates a slight decrease, as Silva et al. (2022) observed. Even though they sampled a greater number of species (both for bees and plants), the NODF values obtained in the cited study and by Mouga et al. (2018) were lower than those in the current study, suggesting a higher nestedness in the herein studied community. However, these values cannot be considered high, as the maximum NODF value is 100 (Morrison, 2013). Since this index did not show significant changes in nestedness when *Ap. mellifera* was excluded from the analyses. It can be stated that this bee species does not cause (or did not cause) significant changes in the community. However, due to the lack of records before the appearance of this exotic species in the area, it is impossible to measure how much this species interferes with the native bee fauna.

The robustness values, like NODF, varied slightly with the absence of *Ap. mellifera*. Silva et al. (2022) described only one value regarding robustness for the community they studied, which was higher than that in the current study. The values obtained here are relatively closer to 1, indicating less susceptibility to extinction, or, in other words, more resistant than prone to extinction, as a value of 0 implies a higher susceptibility to extinction. Thus, the communities of bees and plants studied here are moderately robust (Burgos et al., 2007).

These values are unusual, likely due to the limited number of sampled species. This can be explained by the fact that the bee species are generalists and likely originate from nearby, more vegetated areas, like the case reported by Faria-Mucci et al. (2003).

The push-pull index (Vázquez et al., 2007) ranges from -1 to 1, where positive values indicate that a species affects its interaction partners more strongly than it is affected by them (it is a "*pusher*" species), negative values indicate that a species experiences strong effects from its interaction partners but does not exert a strong reciprocal effect on them (it is a "*puller*" species), and 0 indicates symmetry of total dependence.

Many plants considered "*pusher*" here received numerous visits due to the abundance of visiting individuals or the number of visiting species. These plants are *Baccharis trimera*, *Sc. terebinthifolia*, *Pe. integrifolia*, *Pl. urvilleanum*, and *Se. platensis*. Ten were considered "*puller*" (<0), and two species maintained a value of 0 (*O. mollissima* and *V. curassavica*), interacting with only one bee species each. Regarding push-pull interaction in bees, four species were considered "*pusher*" (>0) (*Ap. mellifera*, *Pseudag. pampeanus*, *Ca. luteimaculatum*, and *Ce. Asunciana* cf), and nine were considered "*puller*" (<0); in addition, two species maintained a value of 0 (*Augochlora (P.)* sp. 2 and *X. frontalis*) as they showed interaction only with one plant species each. Thus, several species were considered "*pusher*" due to the high number of visits they performed and the number of plant species they visited. It is essential to note that most species considered "*pusher*" are, in some way, generalists, but there are also specialist "*pusher*" species, indicating their importance to the community.

Conclusion

The apifauna and the associated plant community are small (with less than 20 species each). The greatest richness of the bee community is concentrated in Halictinae and non-corbiculate Apinae (prevalent in southern Brazil). Two species of bees were very abundant: *Ca. luteimaculatum* (Andreninae) and *Ap. mellifera* (Apinae), with many plant species associated with and constituting keystones. The collector curve reached stability, demonstrating that there were not many more bee species (collection efficiency of around 70%), and the estimators suggested having between 21 and 26 species. The absence of Meliponini must be attributed to the lack of nesting sites. The bee fauna studied was more similar to the nearest site, 13.8 km away. There was only greater bee activity and flower visualization during spring and summer, demonstrating strong seasonality. Sampling using trap dishes showed bee preferences. The most visited botanical family was Asteraceae, a recurring result. A few bee species visited many plant species, but, for the most part, bee species were sampled from only one to two botanical species. Plants showed the same pattern, with some botanical species receiving many bee species and most with few bee species, a pattern in pollinator communities. The bee fauna showed average uniformity in terms of dominance. Regarding interactions, the network showed low connectivity (common in interactive communities), moderate network specialization, and, although little nested, shows relatively high robustness. As for the "pusher-puller" species of bees, there are twice as many "*puller*" species as there are "*pusher*" species and the same can be said for plants, showing that the most influential species in both communities are a minority. The values presented in ISA (interaction strength asymmetry) are negative, implying little dependence and/or specialization. The bee community studied has species in common with nearby vegetated areas of the region, which are found further into the continent, in a situation similar to that found in isolated places; that is, these bee species very possibly come from nearby (or adjacent areas), visiting the environment under study at appropriate times. These data suggest a bee community that, as it is established in an area not very favorable regarding environmental conditions and food resources, is organized in moderately generalist terms, without particular specializations, which allows a range of interactions to be developed without restrictive commitments. Having a small number of specialist species suggests greater resilience of the community. However, this occurrence should not mask the fact that the studied site constitutes an inhospitable environment and that low diversity possibly implies little functional redundancy, causing vulnerability of the ecological functioning of the environment and its continuity in the case of absence/decrease of taxa. The area where the studied environment is located must be considered for protection and conservation, as bee species not yet designated for the State were found, and a botanical species at risk of extinction is also present.

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Authors' Contribution

ALT: Conceptualization, methodology, formal analysis, investigation, data curation, writing-original draft, writing-review and editing, design of the figures.

DMDSM: Conceptualization, formal analysis, resources, data curation, writing-original draft, writing-review and editing, supervision.

Declaration of Conflict of Interest:

The authors declare no competing interests.

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