



## RESEARCH ARTICLE - BEES

## The bee community (Hymenoptera, Apidae) of Ilha Grande, Babitonga bay, Santa Catarina State, Brazil: structure, insularity and interaction network

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### Abstract

Island biotic communities tend to be less diverse than mainland communities. This work aimed to describe the bee community of Ilha Grande, Babitonga Bay, Santa Catarina, Brazil, and its interactions with floral resources. Entomological net-sweeps were used to collect bees in flight or on flowering plants for 7 hours a day, monthly, for two years. A total of 785 specimens were sampled in the field, belonging to 50 species or morphotypes with four indeterminate individuals. The most representative subfamilies were Apinae (58.59%), Halictinae (40.43%), Colletinae (0.8%) and Megachilinae (0.1%), while the most abundant species were *Apis mellifera* (305 individuals), *Dialictus* sp. 1 (182) and *Dialictus* sp. 2 (32). The presence of *Apis mellifera* decreased diversity throughout the year. Relative abundance and richness of Halictinae were greater on the island on mainland. Richness of Apinae was lower on the island than that on the mainland due to the absence of Meliponina. A total of 55 botanical species were identified in association with bees, with *Schinus terebinthifolius* (105 visits) being the most visited. Interaction network metrics indicate an asymmetric, nested, and poorly specialized network. The results corroborate the Theory of Island Biogeography and demonstrate little interference/favoring of some taxa as well as the absence of others.

### Introduction

There are about 20,000 species of bees in the world (Michener, 2007; Imperatriz-Fonseca & Nunes-Silva, 2010) with about 1,500 being recorded in Brazil (Silveira et al., 2002). There is concern about the reported global decline in bee populations, since at least 75% of important crops for human consumption depend on their services (McCravy & Ruhoff, 2017; Geldmann & González-Varo, 2018). In addition, bees are important for the maintenance of biodiversity and are culturally valued by indigenous peoples (Quezada-Euán et al., 2018).

Among insects, bees stand out with regard to pollination as they provide an essential service to angiosperms while

depending on the resources of these plants for food, generating a fundamental interaction among plant, pollinator and ecosystem functioning (Dalsgaard, 2020). Many flowering plants do not reproduce or do not produce seeds if there is no exchange of pollen, thus bees act at the base of ecosystem food chains (Imperatriz-Fonseca et al., 2012).

The availability of food and nesting resources is a determining factor for the survival and establishment of bees (Oertli et al., 2005). In addition, a greater diversity of food resources and habitats favors a greater richness of these insects, and a positive correlation has been documented between food abundance and apifauna abundance (Spengler et al., 2011). Thus, one way to analyze interactions between plants and pollinators is through a mutualistic interaction



network. For Bascompte et al. (2003), nesting generates an asymmetric and cohesive structure of interactions around a generalist core of species. Furthermore, network metrics make it possible to understand robustness against extinctions in both guilds (Almeida-Neto et al., 2008).

In the period from 2017 to 2018, 11,399 hectares of Atlantic Forest were deforested throughout Brazil. Nonetheless, the state of Santa Catarina, inserted entirely within the Atlantic Forest biome, still retains 28.8% of its natural area (Fosma, 2019). The Atlantic Forest is one of 36 global biodiversity hotspots for conservation, and is under constant threat from habitat fragmentation and loss (Esser et al., 2019). Bees can be affected by fragmentation, as they need good landscape structure for locomotion (Ferreira et al., 2015).

The Theory of Island Biogeography (McArthur & Wilson, 1963), by which colonization and extinction rates are related to island size and degree of isolation, made it possible to generate predictions about species richness in these environments, which have already been corroborated by several authors. Serafini et al. (2010) point out that, in the case of oceanic islands, endemism is greater and genetic variability and the number of populations are smaller than in continental places, so the introduction of exotic species and the loss of habitats are among the factors that most cause a decrease in diversity.

Few studies have been carried out on bee communities on islands in South and Southeast Brazil: Zannella et al. (1998) as well as Schwartz and Laroca (1999) in the state of Paraná; Lorenzon et al. (2006) in the state of Rio de Janeiro; and Mouga et al. (2018a) in the state of Santa Catarina (SC), plus two on genetic diversity (Francisco, 2012; Boff et al., 2014). Works related to apifauna in the focal region of the present work, Ilha Grande, encompass Mouga et al. (2018a) and Dec and Vivallo (2019) on the island Ilha das Flores (2.43 km away from Ilha Grande; the latter being a bionomy study) and on the mainland, Mouga et al. (2015) at the locality of Vila da Glória (5.37 km away), Mouga and Warkentin (2016) in Caieira Municipal Natural Park (9.54 km away) and Possamai et al. (2017) at the University of the Region of Joinville/ Univille (14.9 km away).

Thus, the objective of this work was to understand and compare insular apifauna by describing the diversity of bees and their foraging resources, and to assess community structure and plant-pollinator relationships, in hourly and seasonal terms, on Ilha Grande, a continental island in Babitonga Bay, state of Santa Catarina, Brazil.

## Material and Methods

### Study area

Babitonga Bay (26° 15' 25.63" S, 48° 41' 17.91" W) is the second largest estuarine formation in the state of Santa Catarina (160 km<sup>2</sup> of water surface) and the last large mangrove formation in the Southern Hemisphere (62 km<sup>2</sup>)

(Grose et al., 2014). The climate in the region is of the Cfa type, according to Köppen, with hot summers and no defined dry season (Alvares et al., 2013). The annual average temperature is 20.3°C, with July being considered the coldest month with an average temperature of 16.5°C (Feldhaus JR. et al., 2020). Rainfall is high, with about 1,800 mm per year corresponding to 180 days of rain, being favored by proximity to the Serra do Mar mountain range and the ocean (Knie, 2002).

The bay includes 206 islands (Fava, 2016), one of which is Ilha Grande (IG) (Figure 1). Ilha Grande is located in the central portion of the bay (26°16'11.09"S, 48°42'30.94"W), 1.6 km from Vila da Glória on the coast and 2.5 km from the island of São Francisco do Sul. It has an area of 329,506 m<sup>2</sup>, a variable width ranging from 233 to 447 m and is about 1,300 m long (Silva & Mouga, 2020). The vegetation is Atlantic Forest in transition with arboreal *restinga* (dune formation) (Melo Jr. et al., 2018) and mangrove (Silva & Mouga, 2020).

Ilha Grande houses several summer residences and some fixed dwellings, with gardens of ornamental and fruit plants (Silva & Mouga, 2020).

### Field sampling

Collections were carried out monthly, on days with favorable weather conditions, between July 2018 and May 2020, for seven hours a day, totaling two samplings *per* month of the year, except for October, January, April and June, which had only one sampling due to logistical difficulties and rainy periods. Sampling employed an entomological net and followed the method of Sakagami et al. (1967), with adaptations. The method consists of active scanning for bees on flowering plants or in flight along a predefined 2.5-km path. Individuals of *Apis mellifera* Linnaeus, 1758, were not collected, although those observed on plants were recorded. The sampled bees were placed in flasks with ethyl acetate and received an identification label containing the date, place, time and plant number. Temperature and humidity were recorded every hour in the field with a Simpla TH01 thermo-hygrometer.

Trap dishes (Moerick, 1955), in the colors white, yellow, blue and orange and with water and detergent, were also used for sampling open areas in accessible places. The dishes were placed in a group of different colors from 9 am to 4 pm on each sampling day.

Odoriferous baits (embedded cotton tufts placed in a pet bottle) were installed at 1.5 meters above the ground and used during samplings in summer and spring. Aromatic compounds (methyl salicylate, cineol, vanillin, eugenol and methyl cinnamate) were alternated at random on every day of sampling (adapted from Dec & Mouga, 2014).

The sampled bees were prepared and identified according to Michener et al. (1994) and Silveira et al. (2002), using the classification of Melo and Gonçalves (2005). The material was listed and stored in the Bee Laboratory Collection



**Fig 1.** Map of the location of Ilha Grande, Babitonga Bay, Santa Catarina State. Source: Primary (2021).

at Univille (Joinville, SC). The plants were photographed, collected, herborized, listed and stored at the Herbarium Joinvillea of Univille (Joinville, SC). Specialized literature was used to identify plants, such as Lorenzi and Souza (2001), Lorenzi (2006), Lorenzi and Matos (2008), Moreira and Bragança (2011) and Binfaré (2016), among other more specific works. The samples were compared at the Herbarium Joinvillea of Univille (Joinville, SC).

#### Data analysis

A Mao Tau species accumulation curve was constructed, with standard deviation and 95% confidence interval, to identify sampling sufficiency (Colwell, 2004). Total species richness was estimated using Chao 1 and Jackknife 1 richness estimators (Gotelli & Cowell, 2011), which were also calculated for the seasons. The accumulation curve and the richness estimators were generated using the EstimateS 9.1.0 program (Cowell, 2013).

Diversity was measured using the Shannon-Wiener index ( $H'$ ), dominance using the Simpson index ( $1-D$ ) and evenness using the Pielou index ( $J$ ) (Magurran, 2004); the first two both with and without *A. mellifera*. For each sampling date, the corresponding season was assigned, data were grouped and indices were calculated. Diversity, dominance

and evenness indices were calculated using PAST software version 2.17 (Hammer et al., 2001).

Similarity with other studies was determined using the coefficients of Dice (1945) and Sorensen (1948), calculated using PAST software version 2.17. Only data obtained by the same sampling methodology (entomological net) were considered for similarity and relative abundance analyses. Only *taxa* identified to the level of species, morphotype or subspecies were considered. Comparisons were made among the localities Vila da Glória (Mouga et al., 2015), Ilha das Flores (Mouga et al., 2018) and Ilha Grande.

Community structure was analyzed by relative abundance, which shows the most representative group within a sample, using the equation  $(n/N) \cdot 100$  (Zanella et al., 1998; Mouga et al., 2018a).

To analyze the structure of interactions, an interaction network was built and its metrics calculated using the Bipartite package of R software (Dormán et al., 2008; Dormán et al., 2009). Nestedness was calculated as the NODF index (Nestedness Metric Based on Overlap and Decreasing Fill) (Almeida et al., 2008), using ANINHADO software version 3.0.3 (Guimarães & Guimarães, 2006). NODF and degree of specialization ( $H'^2$ ) were calculated both with and without including the exotic species *Apis mellifera*.

## Results

A total of 20 days of collection and 140 hours of sampling effort acquired a total of 785 individual bees, with 603 collected on flowers, seven sighted/collected in flight or attracted with the help of aromatic essences and 175 collected in trap dishes.

A total of 50 species of bees could be identified (Table 1). Three individuals of *Dialictus* that could not be differentiated into morphotype/species and one individual bee that could not be identified (NI = not identified) were included in Table 1 but not considered as identified species. The species are distributed among four apid subfamilies: Apinae, Halictinae, Colletinae and Megachilinae. Halictinae and Apinae were the most representative subfamilies for richness and abundance, with 31 species (not considering the NI Individual) and 421 individuals for the former and 16 species and 359 individuals for the latter. Colletinae was represented by three species and Megachilinae by only *Dicranthidium seabrai* Urban, 2002. The total of species represents ten tribes, with Apini (324 individuals), Halictini (239) and Augochlorini (182) having the greatest representation. From the 485 specimens sampled (excluding *A. mellifera* identified in the field), 378 were female and 107 were male.

The most abundant species was *Apis mellifera* with 305 individuals/observations, followed by *Dialictus* sp. 1 (182) and *Dialictus* sp. 2 (32). The genera with the greatest number of species/morphotyps were *Augochlora* (8 morphotypes), *Augochloropsis* (7) and *Dialictus* (7). Stingless bees (subtribe Meliponina) and bees of the subfamily Andreninae were not sampled sighted during the study.

Subfamilies in decreasing order of abundance, with Apinae separated into corbiculated and non-corbiculated and Halictinae into Augochlorini and Halictini, is as follows: corbiculated Apinae (324) > Halictini (239) > Augochlorini (182) > non-corbiculated Apinae (35) > Colletinae (4) > Megachilinae (1) ajshd.

Subfamilies in decreasing order of species richness is as follows: Augochlorini (21) > non-corbiculated Apinae (12) > Halictini (9) > corbiculated Apinae (4) > Colletinae (3) > Megachilinae (1). It should be noted that these numbers do not include the NI individual of Augochlorini nor the three individuals of *Dialictus* that could not be differentiated.

The species accumulation curve (Figure 2) indicates a possible stabilization between collections 12 and 16, however, 13 new species were added from collection 17 onward, thus increasing the curve and not indicating stabilization. Thus, the accumulation curve (Mao Tau) does not indicate stabilization. The estimated richness values were 63.84 species by Chao 1 and 67.1 by Jackknife 1, such that the sampling performed here (50 species) was equivalent to 78% and 75% of the estimated richness, respectively.

Diversity ( $H'$ ) was 2.30 ( $J = 0.58$ ) with *A. mellifera* and 2.68 ( $J = 0.68$ ) without. Differences were also noted for dominance (Simpson index 1-D), with 0.78 with *A. mellifera* and 0.83 without. According to season, the greatest diversity (Shannon-Wiener index), considering *A. mellifera*, was during summer ( $H' = 2.48$ ) and lowest during spring ( $H' = 1.58$ ) (Figure 3). According to month, the greatest diversity was for February ( $H' = 2.14$ ) and the lowest for November ( $H' = 1.46$ ). The highest dominance (lowest Simpson value 1-D) was for November, when the abundance of *A. mellifera* reached its highest.

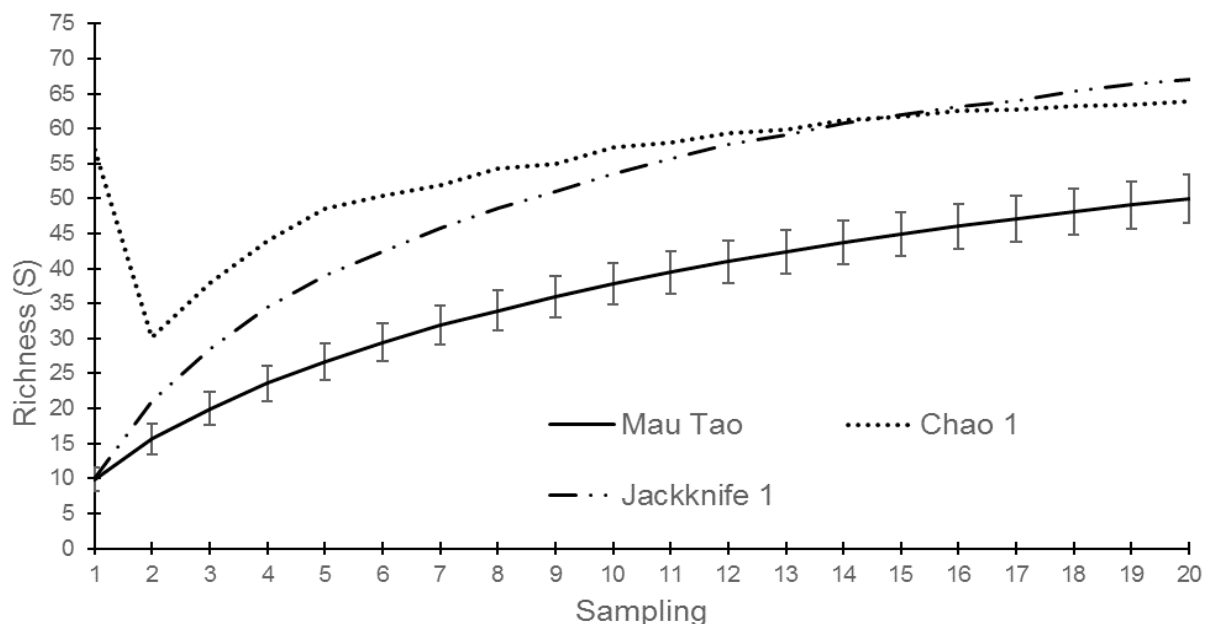


Fig 2. Mao Tau, Chao 1 and Jackknife 1 species accumulation curve, with respective standard deviations.

**Table 1.** List of bee species from Ilha Grande, São Francisco do Sul, SC, following the classification by Melo & Gonçalves (2005). Caption: n = number of individuals.

Subfamily	Tribe	Specie	n	Subfamily	Tribe	Specie	n	
<b>Apinae</b>	Apini	<i>Apis mellifera</i> Linnaeus, 1758	305	<b>Halictinae</b>	Augochlorini	<i>Augochlora</i> (A.) sp.24	3	
		<i>Bombus (Fervidobombus)</i> <i>morio</i> Swederus, 1787	12			<i>Augochlora</i> ( <i>Oxystoglossella</i> ) sp.1	26	
		<i>Euglossa (Glossura)</i> <i>annectans</i> Dressler	6			<i>Augochlora</i> (O.) sp.12	5	
		<i>Euglossa (Glossurella)</i> <i>stellfeldi</i> Moure, 1947	1			<i>Augochlorella ephyra</i> Schrottky, 1910	20	
	Centridini	<i>Centris (Centris) flavifrons</i> Fabricius, 1775	2			<i>Augochloropsis sparcilis</i> Vachal, 1903	3	
		<i>Centris</i> sp.1	1			<i>Augochloropsis</i> sp.1	17	
		<i>Epicharis (Anepicharis)</i> <i>dejeanii</i> Lepageletier, 1841	4			<i>Augochloropsis</i> sp.3	21	
	Emphorini	<i>Melitoma segmentaria</i> Fabricius, 1804	3			<i>Augochloropsis</i> sp.14	29	
		Exomalopsini	<i>Exomalopsis</i> ( <i>Exomalopsis</i> ) sp.1			3	<i>Augochloropsis</i> sp.27	1
	<i>Exomalopsis</i> ( <i>Exomalopsis</i> ) sp.2		2			<i>Augochloropsis</i> sp.33	1	
	<i>Exomalopsis</i> ( <i>Phanomalopsis</i> ) sp.		1		<i>Augochloropsis</i> sp.34	1		
	Tapinotaspidini	<i>Lophopedia nigrispinis</i> Vachal, 1909	4		<i>Ceratalictus camargoi</i> Coelho & Gonçalves, 2010	1		
		Xylocopini	<i>Ceratina (Crewella)</i> <i>maculifrons</i> Smith, 1854		2	<i>Neocorynura</i> sp.1	3	
	<i>Ceratina (Crewella)</i> sp.16		1		<i>Pereirapsis</i> sp.1	2		
	<i>Xylocopa (Neoxylocopa)</i> <i>brasilianorum</i> Linnaeus, 1767		11		<i>Pseudaugochlora</i> <i>graminea</i> Fabricius, 1804	18		
	<i>Xylocopa (Neoxylocopa)</i> <i>frontalis</i> Olivier, 1789		1		<i>Temnosoma</i> sp.1	2		
					N.I.	1		
	<b>Colletinae</b>	Hylaeini	<i>Hylaeus</i> sp.1		2	Halictini	<i>Agapostemon</i> sp.1	1
			<i>Hylaeus</i> sp.2		1		<i>Caenohalictus</i> sp.1	6
			Morfotipo sp.1		1		<i>Dialictus</i> sp.1	182
<b>Halictinae</b>	Augochlorini	<i>Augochlora</i> ( <i>Augochlora</i> ) sp.1	4	<i>Dialictus</i> sp.2	32			
		<i>Augochlora</i> (A.) sp.3	3	<i>Dialictus</i> sp.3	3			
		<i>Augochlora</i> (A.) sp.4	11	<i>Dialictus</i> sp.4	3			
		<i>Augochlora</i> (A.) sp.7	7	<i>Dialictus</i> sp.5	7			
		<i>Augochlora</i> (A.) sp.12	3	<i>Dialictus</i> sp.6	1			
				<i>Dialictus</i> sp.	3			
				<i>Pseudagapostemon</i> ( <i>Pseudagapostemon</i> ) <i>arenarius</i> Schrottky, 1902	1			
				<i>Dicranthidium</i> cf. <i>seabrai</i> Urban, 2002	1			
				<b>Total</b>	785			

With regard to time and season, the average temperature for all samplings together was 26.25 °C (Figure 4), while the highest average temperature was in January 2019 (31.15 °C) and the lowest in August 2018 (21.65 °C). The period between 2 pm and 3 pm was the hottest (27.55 °C). The greatest abundance of bees (without *A. mellifera*) was for February and March, while February also had the greatest species

richness (Figure 4). The greatest abundance was sampled between 09:00 and 11:00 hours (Table 2), when a total of 135 individuals were sampled between 10:00 and 10:59 h (of the total of 608 specimens whose sampling allowed time determination because it was not possible to do so for those collected by dish trap or bottle trap) (Table 2). Summer had the greatest abundance and richness.

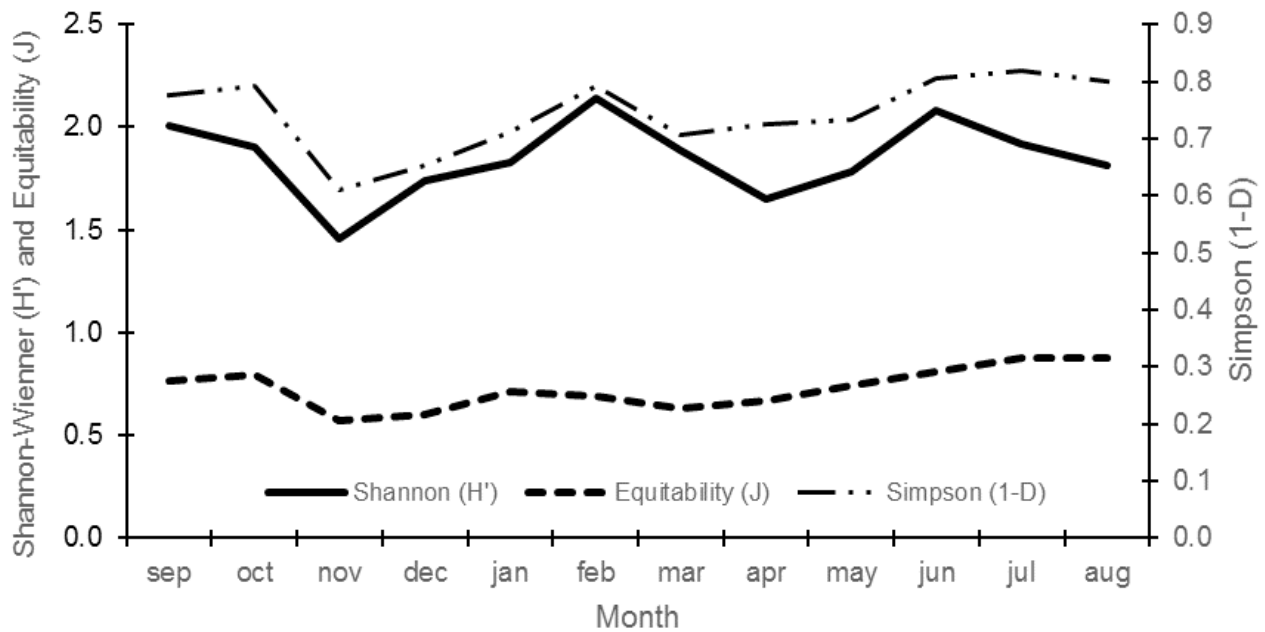


Fig 3. Shannon-Wiener ( $H'$ ), Simpson (1-D) and evenness (J) diversity over the months.

Table 2. Number of sampled individuals (grouped data from samplings, without trap plates), average temperature and humidity per time of day, in Ilha Grande, São Francisco do Sul, SC.

Hour	8h	9h	10h	11h	12h	13h	14h	15h
Number of individuals	3	112	135	111	77	88	56	27
Temperature (°C)	23.52	25.30	26.57	27.17	26.81	27.55	26.96	25.76
Relative humidity (%)	74.70	68.75	65.10	64.65	66.85	62.55	63.79	69.53

The communities of Ilha das Flores and Ilha Grande were the most similar (Sorensen similarity index 0.45), while Ilha Grande and Vila da Glória were the least (0.24), thus Ilha das Flores was more similar to Vila da Glória than was Ilha Grande.

The relative richness and abundance of subfamilies observed in the present work differs from that of nearby communities (Figure 5). For example, the subfamily Andreninae only occurred in the mainland community (Vila da Glória)

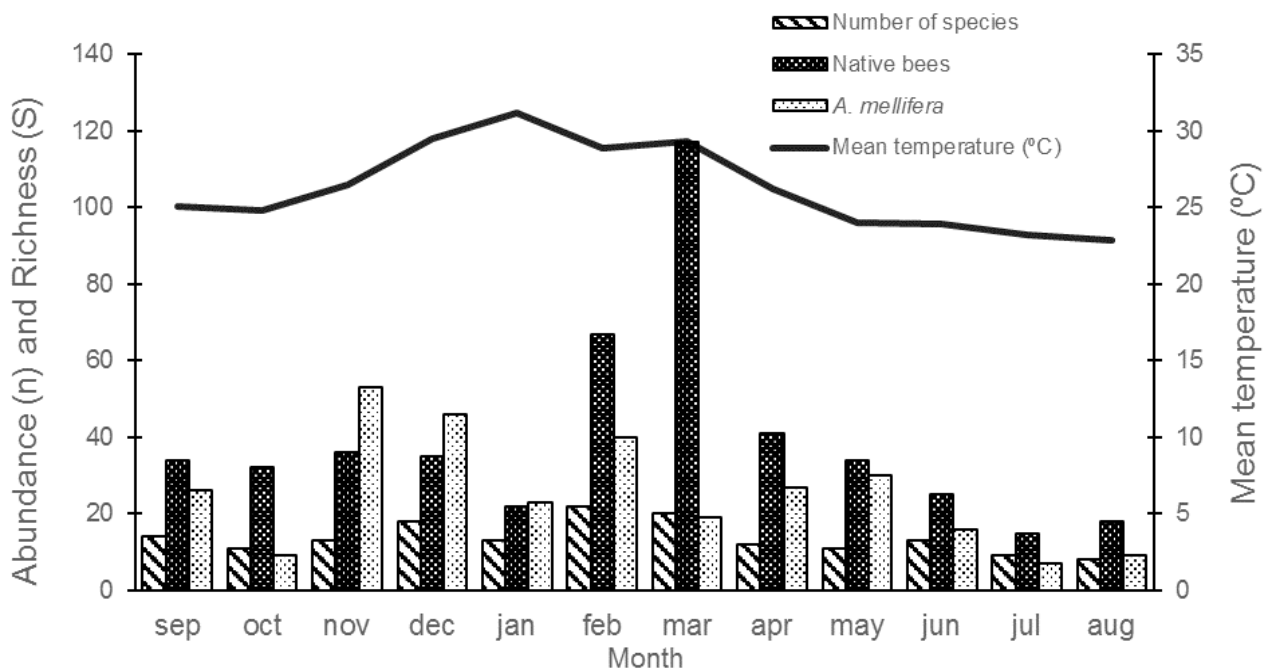


Fig 4. Richness, abundance and average temperature over the months, from Ilha Grande, São Francisco do Sul, SC.

and with a low relative abundance (0.06%), hardly appears in Figure 5.

Plant richness totaled 55 species distributed among 34 botanical families (Table 3). Among these, the most visited were of Asteraceae and Anacardiaceae, with 161 and 105 visits, respectively, with Asteraceae represented by seven species and Anacardiaceae by only *Schinus terebenthifolia* Raddi. The most visited plant species were *S. terebenthifolia* (n = 105

visits), *Sphagneticola trilobata* (L) Pruski (n = 75), *Cyrtocymura scorpioides* (Lam.) H. Rob. (n = 43), *Euphorbia milii* des Moul. (n = 41) and *Psidium cattleianum* Sabine (31). The greatest number of visits took place during summer and autumn.

Bee species with the highest number of interactions were *A. mellifera*, *Augochloropsis* sp.14, *Augochlora* (*O.*) sp.1, *Dialictus* sp.1, *Augochlorella ephyra* and *Augochloropsis* sp.3.

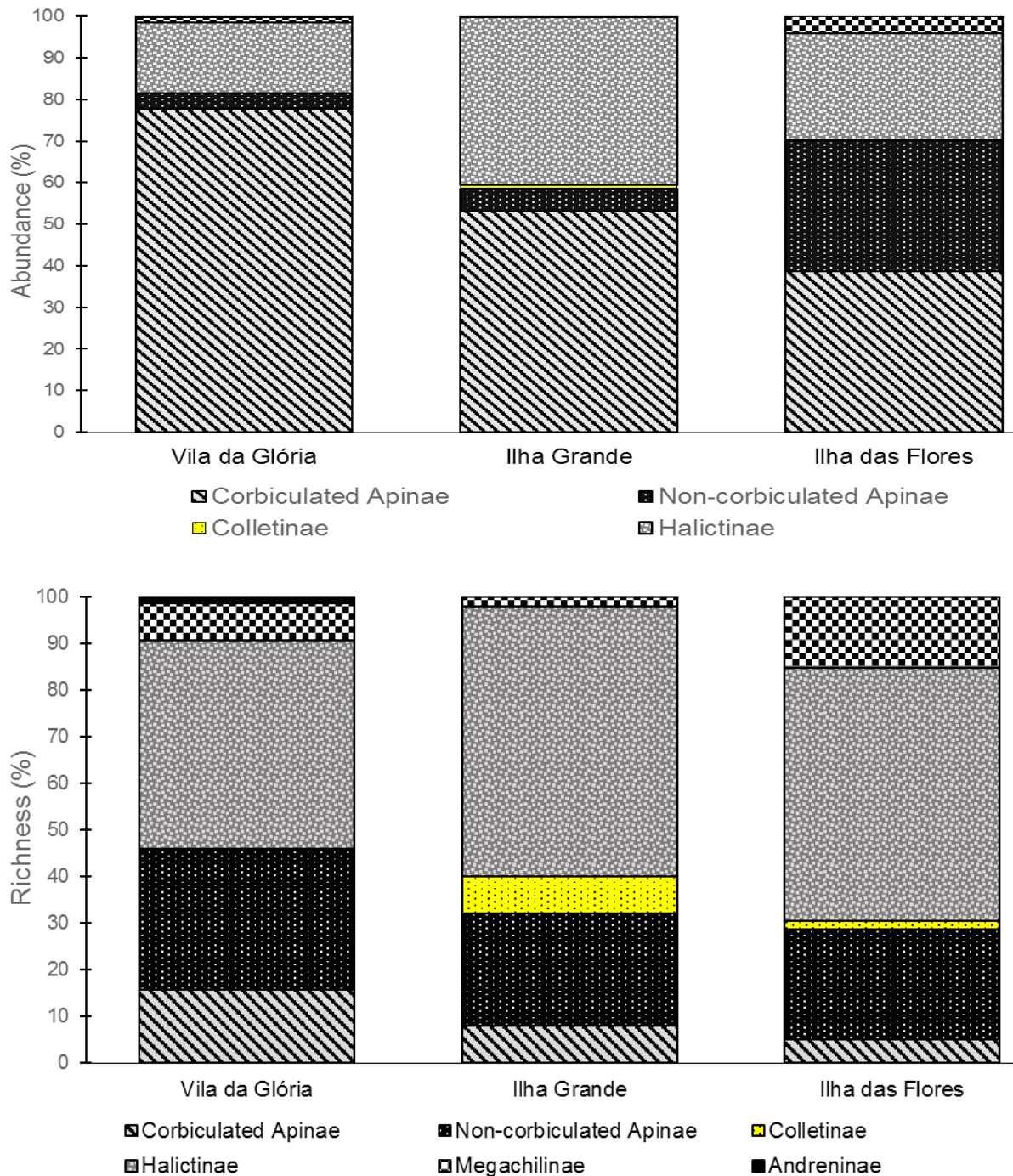


Fig 5. Abundance and relative richness of subfamilies in the communities Vila da Glória (Mouga et al. 2015), Ilha Grande and Ilha das Flores (Mouga et al., 2018a).

**Table 3.** List of plant species visited by bees in Ilha Grande, São Francisco do Sul, SC.

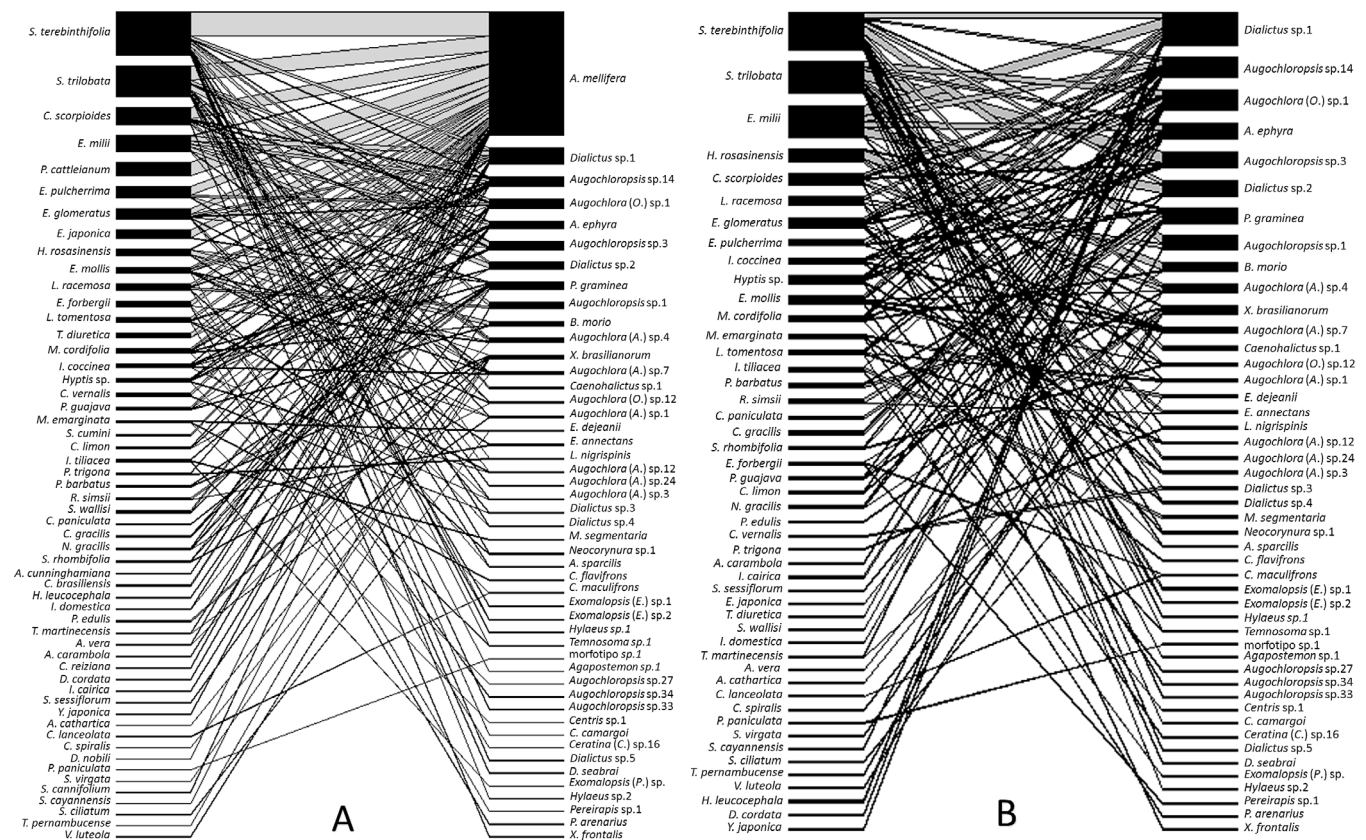
Family	Plant specie	Number of visits	Family	Plant specie	Number of visits
Anacardiaceae	<i>Schinus terebinthifolia</i> Raddi	105	Iridaceae	<i>Iris domestica</i> (L.) Goldblatt & Mabb.	3
Apocynaceae	<i>Allamanda cathartica</i> L.	1		<i>Neomarica gracilis</i> Sprague	4
Araceae	<i>Spathiphyllum cannifolium</i> (Dryand.) Scott	1		<i>Trimezia martinecensis</i> (Jacq.) Herb.	3
	<i>Spathiphyllum wallisi</i> Regel	5	Lamiaceae	<i>Hyptis</i> sp.	9
Araliaceae	<i>Hydrocotyle leucocephala</i> Cham. & Schltldl.	3		<i>Plectranthus barbatus</i> Andr.	5
			Lythraceae	<i>Cuphea gracilis</i> Kunth	4
Arecaceae	<i>Archontophoenix cunninghamiana</i> (H. Wendl.) H. Wendl. & Drude	3	Malpighiaceae	<i>Malpighia emarginata</i> DC	6
Asphodelaceae	<i>Aloe vera</i> (C.) Burm. F.	2		<i>Stigmaphyllon ciliatum</i> (Lam.) A. Juss.	1
Asteraceae	<i>Coreopsis lanceolata</i> L.	1	Malvaceae	<i>Hibiscus rosa-sinensis</i> L.	18
	<i>Cyrtocymura scorpioides</i> (Lam.) H. Rob.	43		<i>Sida rhombifolia</i> L.	4
	<i>Elephantopus mollis</i> Kunth	16		<i>Talipariti pernambucense</i> (Arruda) Bovini	1
	<i>Emilia forbergii</i> Nicolson	13	Myrtaceae	<i>Campomanesia reitziana</i> D. Legrand	2
	<i>Mikania cordifolia</i> (L. F.) Willd.	11		<i>Psidium cattleianum</i> Sabine	31
	<i>Sphagneticola trilobata</i> (L) Pruski	75		<i>Psidium guajava</i> L.	7
	<i>Youngia japonica</i> (L.) DC.	2		<i>Syzygium cumini</i> (L.) Skeels	6
Calophyllaceae	<i>Calophyllum brasiliense</i> Cambess.	3	Orchidaceae	<i>Dendrobium nobile</i> Lindl.	1
Cannaceae	<i>Canna paniculata</i> Ruiz & Pav.	4	Onagraceae	<i>Ludwigia tomentosa</i> (Cambess.) H.Hara	12
Caryophyllaceae	<i>Drymaria cordata</i> (L.) Willd. ex Roem. & Schult	2	Oxalidaceae	<i>Averrhoa carambola</i> L.	2
Combretaceae	<i>Laguncularia racemosa</i> (L.) C. F. Gaertn.	16	Passifloraceae	<i>Passiflora edulis</i> Sims	3
Commelinaceae	<i>Tripogandra diuretica</i> (Mart.) Handlos	12	Polygalaceae	<i>Polygala paniculata</i> L.	1
Convolvulaceae	<i>Evolvulus glomeratus</i> Nees & Mart.	27	Rosaceae	<i>Eriobotrya japonica</i> (Thumb.) Lindl.	20
	<i>Ipomoea cairica</i> (L.) Sweet	2	Rubiaceae	<i>Ixora coccinea</i> L.	10
	<i>Ipomoea tiliacea</i> Willd. Choisy	5	Rutaceae	<i>Citrus limon</i> (L.) Osbeck	5
Costaceae	<i>Costus spiralis</i> (Jacq.) Roscoe	1	Sapindaceae	<i>Cupania vernalis</i> Cambess	8
Ericaceae	<i>Rhododendron simsii</i> Planch	5		<i>Paullinia trigonia</i> Vell.	5
Euphorbiaceae	<i>Euphorbia milii</i> des Moul.	42	Solanaceae	<i>Solanum sessiflorum</i> Dunal	2
	<i>Euphorbia pulcherrima</i> Willd.ex Klot.	28	Verbenaceae	<i>Stachytarpheta cayannensis</i> (Rich.) Vahl	1
Fabaceae	<i>Sesbania virgata</i> (Cav.) Pers.	1		<b>Total</b>	<b>604</b>
	<i>Vigna luteola</i> (Jacq.) Benth.	1			

Note: The number of visits is less than the total number of bees due to non-exclusive bee sampling in flowers.

The network was not highly nested (NODF = 24.01 with *A. oeficie* and 16.90 without) nor highly specialized ( $H2' = 0.37$  with *A. oeficie* and 0.43, without). The average number of links *per* species was 1.66 (Figure 6). There was an average of 10.59 plant species *per* bee species and 3.84 bee species *per* plant species. Network connectivity was 0.064 and the robustness for both bees and plants was 0.67. The

clustering oeficiente (0.036) and the number of compartments (3) indicated few subsets disconnected from the network. Only the bee species *Melitoma segmentaria* shows exclusive visitation on *Ipomoea tilleacea* (Convolvulaceae), however, a species from the tribe Hylaeini (morphotype 1) has a specific reciprocal relationship with *Polygala paniculata* (Polygalaceae).





**Fig 6.** Network of interactions between bees and plants from Ilha Grande, São Francisco do Sul, SC. Caption: A = with *A. mellifera*; B = without *A. mellifera*.

## Discussion

Some of the bee species found on Ilha Grande have no previous record of occurrence in the state Santa Catarina (Moure et al., 2012), namely *Centris flavifrons*, *Ceratalictus camargoi*, *Ceratina maculifrons*, *Xylocopa frontalis*, *Dicranthidium seabrai* and *Augochloropsis sparcilis*. It is noteworthy that some of these species have already been reported in other studies carried out in the region of this study (Mouga et al., 2015; Mouga et al., 2016; Mouga et al., 2018a; Dec & Vivallo, 2019).

The rarefaction curve does not show a tendency towards stabilization, which is supported by the richness estimators, although the Chao 1 estimator shows a greater tendency towards stabilization. The rarefaction curve shows an increase over the last samplings, which occurred in the summer when greater bee activity is expected in South Brazil (Krug & Santos, 2008; Dec & Mouga, 2014; Mouga et al., 2015; Mouga et al., 2018a). According to the richness estimators, at least 76% of the species richness was sampled. This result is consistent with that found by Krug and Santos (2008), who sampled between 64 and 83% of the estimated richness, for samples with more than one capture technique. The first seven samplings of the present study were responsible for works more than 50% of the species.

The Shannon-Wiener index ( $H'$ ) (diversity) was similar to that obtained by Mouga et al. (2015) and below other works carried out in the region in rain forest (Mouga & Warkentin, 2016; Possamai et al., 2017; Mouga et al., 2018a) and araucaria forest (Mouga et al., 2016; Liebl et al., 2019).

Diversity decreased in the months of November and April of the present study, as was also observed by Mouga and Krug (2010) in montane rain forest. The mainland (Vila da Glória) and Ilha das Flores experienced decreased diversity between May and November, with the mainland having its lowest diversity in July, August and September and Ilha das Flores having its lowest diversity in May, June and July (Mouga et al., 2015; Mouga et al., 2018a).

Analysis of the results of the present study using the Simpson index (1-D) of dominance, which is more sensitive to variation in abundance than species richness (Magurran, 2004), demonstrates an antagonistic relationship between diversity and *A. mellifera* abundance (Figure 7), with lower diversity with a greater abundance of *A. mellifera*. This high abundance of *A. mellifera* decreases evenness (J) in abundance among taxa (Magurran, 2004). This was confirmed by calculating the same index with the exclusion of *A. mellifera*. Patricio et al. (2014) and Somavilla et al. (2018) attributed the low diversity of samples to the great abundance of a few taxa, such as the exotic *Apis mellifera*. It should be noted that this

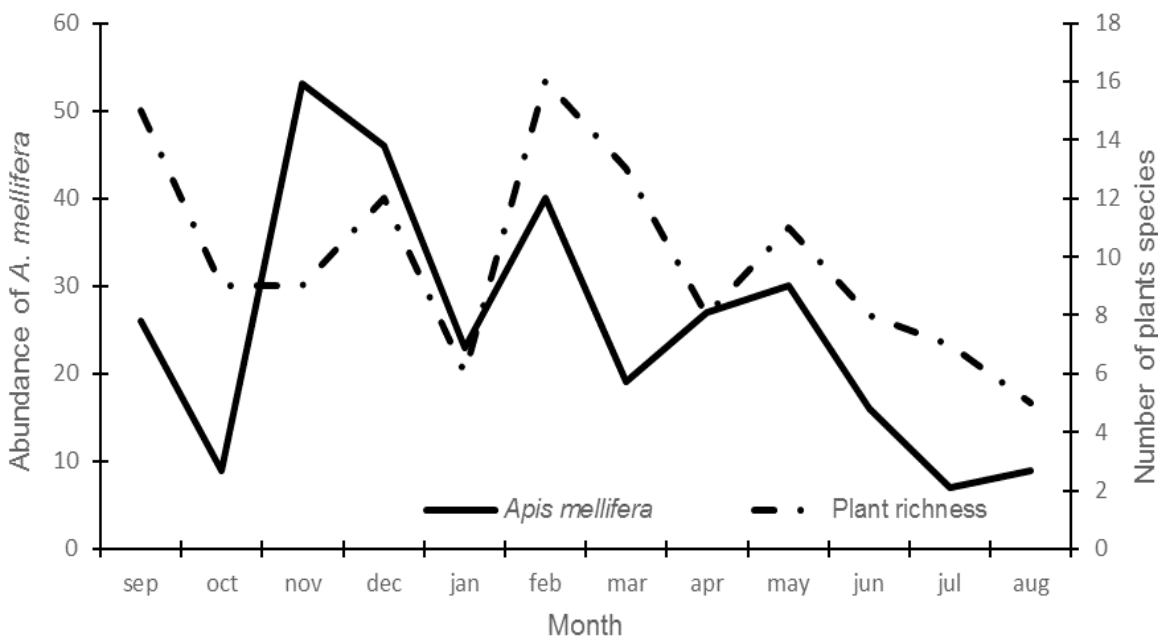


Fig 7. Floral richness and abundance of *Apis mellifera* over the months.

drop in diversity occurred during the two transition seasons (autumn and spring), when there is a change in temperatures, which is more unfavorable for certain *taxa* and, thus, favors the abundance of others.

Richness and abundance were found to be associated with temperature, especially in the warmer months, as observed in other studies carried out in the region (Kamke et al., 2011; Mouga et al., 2011; Dec & Mouga, 2014; Mouga et al., 2015; 2018a). This correlation is expected for inventories in South Brazil, as there is inactivity of some *taxa* in the cold months and greater availability of flowers in the warm months, usually starting in spring (Krug & Santos, 2008; Patricio et al., 2014). Unlike the bivoltine pattern found for Vila da Glória (Mouga et al., 2015), the results of the present work show only a single peak of abundance and richness, which could signal seasonality possibly related to plant richness, following the trend already reported in the literature (Silveira et al., 2002).

Some species showed seasonal patterns, appearing in only one or two seasons of the year, such as *E. dejeanii* and *Exomalopsis (E.)* sp.2, which occurred only in spring and summer. *Epicharis dejeanii* is indicated as being univoltine (Kamke et al., 2011), appearing only in summer months. It should be noted that, in the present work, *E. dejeanii* was collected in late spring, when the mean temperature is higher. Taxa of Halictinae, for the most part, were found to occur throughout the year, mainly *Augochlora* spp., *Augochlarella ephyra*, *Augochloropsis* spp. And *Dialictus* spp., which appeared in all or almost all seasons, corroborating the literature (Kamke et al., 2011; Patricio et al., 2014).

In hourly terms, foraging activity tends to decrease in hours of higher temperatures (Silveira et al., 2002), that is, with high insolation, which was observed in the present work.

Ilha Grande and Ilha das Flores had the greatest similarity, in the comparisons of richness. The same result was found by Zanella et al. (1998) when comparing Ilha do Mel and Ilha das Cobras, which suggests selectivity of similar species between nearby islands. Besides, the results of the present work demonstrate less similarity between the more distant Ilha Grande and Vila da Glória.

The Theory of Island Biogeography (MacArthur & Wilson, 1963) predicts a higher rate of immigration for larger islands and islands closer to the source of species (mainland). From a geographical point of view, Ilha Grande is more isolated, both from the source of species and from other islands, in relation to Ilha das Flores, which is located close to a subset of islands with larger areas.

The community structure found on Ilha Grande demonstrates patterns similar to those found in studies carried out on other continental islands (Zanella et al., 1998; Schwartz & Laroca, 1999; Mouga et al., 2018a). Specifically, the species richness of Ilha Grande is lower than that of the nearby continental area, and the total richness of Apinae and Halictinae is lower, although the difference in abundance of Halictinae between Ilha Grande and the mainland is small. The sequence of richness obtained in this study differs from that obtained by other studies carried out in the region (Mouga et al., 2015; Mouga et al., 2018a) (Table 4), due to the superposition of Colletinae in relation to Megachilinae and, consequently, the same can be observed for abundance.

The lower richness of Apinae on Ilha Grande is due to the absence of the subtribe Meliponina. In contrast, Vila da Glória (Mouga et al., 2015) had eight species (66.66% of the Apinae) belonging to Meliponina, while Ilha das Flores had only *Trigona spinipes*, which was the fourth most abundant bee species on the island. (Mouga et al., 2018a).

Bee species of Meliponina are considered eusocial and nest in preexisting cavities (Silveira et al., 2002), which depends on the availability and distribution of substrates, ecological aspects and swarming occurring close to the mother colony (Serra et al., 2009). Correia et al. (2016) found a low density of nests in an area of 132 hectares (Rio Branco, state of Acre) and suggested it may be related to the low availability of suitable substrates, even with the supply of floral resources. In addition, stingless bees may be unable to overcome small geographic barriers and to maintain genetically stable populations in small and isolated areas (Zanella et al., 1998; Schwartz & Laroca, 1999), which would make the permanence of these species on islands unlikely due to the increased probability of extinction. Mouga et al. (2018a) found only one species of Meliponina (*Trigona spinipes*) on Ilha das Flores and suggested that its great abundance was related to its eusocial habit and the large number of individuals *per* nest.

*Apis mellifera* accounted for 49.92% of the abundance of bees (sampled from flowers) and, consequently, is the species with the greatest interaction with plants. Kato (1999) and Abe et al. (2010) showed that the presence of *A. mellifera* and the lizard *Anolis carolinensis* (predator of native bees) has negative impacts on the native apifauna of in oceanic islands (Bonin or Ogasawara Islands, Japan). Native bees were predominant on islands where *A. mellifera* and the lizard were scarce or absent, thus demonstrating changes in mutualistic dynamics due to biological invaders.

In contrast to the studies just mentioned, Lorenzon et al. (2006) found a different community structure for eusocial Apinae on Ilha Grande of the state of Rio de Janeiro, due to the predominance of Meliponina in relation to *A. mellifera*. These authors did not mention the presence of any meliponiculture activity taking place on the island and suggest that the occurrence of Meliponina there is as old as the formation of the island itself. In addition, the *A. mellifera* found on that island were found to be more associated with areas of human residence and not so common in forests. The studied island has an area of 5,594 hectares (Lorenzon et al., 2006), and so is much larger than the Ilha Grande of the present study, and the fact observed by the mentioned authors may be related to the species-area effect demonstrated by MacArthur and Wilson (1963).

The relative richness of non-corbiculate Apinae of Ilha Grande differed little from that of Vila da Glória. Due to its great diversity of social and resource-gathering behavior, this group can explore a wider range of niches, thus reducing the chance of extinction (Schwartz & Laroca, 1999). There is a notable difference in abundance of this group among islands, with it being 3.85% on Vila da Glória, 5.56% on Ilha Grande and 31.53% on Ilha das Flores. However, aggregations of nests of *Epicharis dejeanii* were reported on Ilha das Flores during reproductive periods, thus overestimating the population (Mouga et al., 2018a; Dec & Vivallo, 2019).

Individuals of *E. dejeanii* were sampled in flowers between December 2018 and January 2020 on Ilha Grande,

with no records of nests or aggregations as described by Dec and Vivallo (2019) for Ilha das Flores with nest aggregations reaching 8 nests/m<sup>2</sup>.

The relationship between richness and abundance found by the present work shows greater relative representation of Halictinae compared to the continent. Zanella et al. (1998) as well as Schwartz and Laroca (1999) witnessed significant greater absolute abundance and density of this group on the islands they studied, corroborating the hypothesis of density compensation. Density compensation (MacArthur et al., 1972) implies in an increase in the density of a given species on species-poor islands compared to the mainland. The mean density of Halictinae varied little between Ilha Grande and Vila da Glória (mainland) with 25.8 and individuals/km<sup>2</sup>, respectively, but was much greater on Ilha das Flores with 87.15 individuals/km<sup>2</sup>. Thus, the results of the present study suggest that the isolation and area of Ilha Grande have little influence on the existence of the taxon Halictinae, with the insular environment having a community similar to that on the mainland.

Mouga and Warkentin (2016) inferred that the presence of kleptoparasitic species may indicate a favorable environment with available resources. Species of the genus *Temnosoma* (Augochlorini) parasitize other species of Augochlorini (Silveira et al., 2002). Thus, the presence of this genus may be related to the found diversity of Augochlorini, since species of this tribe accounted for 28.47% of total bee abundance. The tribe Augochlorini is more diverse in the Southeast Region of Brazil (Michener, 2007) and has high richness in the *restinga* formations there (Kamke et al., 2011). The results of the present work corroborate Zanella et al. (1998), who state that the presence of kleptoparasites probably does not interfere with the abundance of other species.

Apifauna data from Ilha das Flores (Mouga et al., 2018a) show a relative richness of Megachilinae and that this island shares some species of this group with Vila da Glória (mainland). This result differs from that obtained in the present work for Ilha Grande, which has only one species of Megachilinae, of the genus *Dicranthidium*, not shared with the aforementioned locations, while 83.33% and 77.77% of the species of Megachilinae on Vila da Glória and Ilha das Flores, respectively, belong to *Megachile*. For Schwartz and Laroca (1999), the decrease in relative richness observed on islands is related to the rapid disappearance of this taxonomic group (Megachilinae) in altered environments (anthropized, see below), which could be the case for Ilha Grande.

Patricio et al. (2014), Mouga et al. (2015) and Mouga et al. (2018a) associate the low richness of Colletinae and Andreninae that they sampled with the biogeography and the latitude of the places they studied, where a hot and humid climate predominated, which is the opposite of the environment preferred by the two subfamilies (Silveira et al., 2002). The results obtained in the present work corroborate those reported above for Andreninae as none were found. The richness and abundance of Colletinae, however, was greater

on the studied islands, which could be related to vegetation (Zanella et al., 1998) or to sandy environments (Mouga et al., 2015; Mouga et al., 2018a).

The diversity of native plants tends to be low due to changes in the environment and to the introduction of species, as state Possamai et al. (2017), in respect to the anthropization of natural environments and, in this case, of the island. Of the 55 botanical species sampled, 38.18% (21) are considered exotic, being mostly used as ornamentals in the study area. Although the highest frequency of flower visits occurred during summer, some botanical species, such as *Euphorbia millii*, *Euphorbia pulcherrima* and *Evolvulus glomeratus*, had higher frequencies of bee visits in autumn and winter, especially *E. millii*, which was the most visited species during the cold seasons. Thus, exotic plants can offer resources during periods when native species are not flowering (Mouga et al., 2015).

The botanical family Asteraceae is highly attractive to the apifauna of Ilha de Santa Catarina (Steiner et al., 2010) and Brazil (Mouga et al., 2012) – a relationship that was observed in the present study since it was the most visited family. The species *Schinus terebinthifolius* (Anacardiaceae) was reported by Steiner et al. (2010) to be highly interactive with bees on Ilha de Santa Catarina. Which was also observed for the coast of the state of Paraná, especially on Ilha das Cobras and Ilha do Mel, where this plant species proved to be one of the main floristic resources for bees (Zanella et al., 1998; Schwartz & Laroca, 1999).

The bee species with the highest number of floral visits, other than *A. mellifera*, have solitary, communal or primitive eusocial habits (Silveira et al., 2002).

Nestedness occurs when a certain specialist species interacts with a subset of species that interact with generalists (Bascompte et al., 2003). Although the results for Ilha Grande

do not indicate a high degree of nestedness, it is greater than that obtained for Ilha das Flores (NODF = 11.88). Nested networks are cohesive and comprise groups of interactions between generalists to which specialists are linked, with the asymmetric pattern (specialists interacting with generalists) favoring the survival of rare species (Bascompte et al., 2003), in addition to increasing robustness against the random loss of species (Almeida-Neto et al., 2008). The present results indicate a 29.61% loss of NODF when *A. Mellifera* is not considered, which is similar to the results of Santos et al. (2012), who claim that their calculated values attest to the significant impacts of the presence of *Apis mellifera* in *caatinga* vegetation.

The exclusion of *A. Mellifera* from calculations in the present work implied the removal of seven plant species, of which *Archontophoenix cunninghamiana* and *Dendrobium nobile* are exotics introduced for ornamental purposes and the others are of the native flora. Therefore, *A. Mellifera* certainly has significant impacts on network structure, apparently making it more stabilized, especially in the case of fragmented areas (Santos et al., 2012), such as Ilha Grande. On the other hand, since nestedness can be a result of the abundance of individuals, and the co-elimination of plants with the removal of *A. Mellifera* can be due to a small amount of links with generalist bees (Lewinsohn et al., 2006; Almeida-Neto et al., 2008), further studies are needed to better understand the network of interactions on the island.

Robustness values were close to 1, which means a slow decrease in the plant extinction curve if all pollinators are eliminated, reflecting a characteristic resistance of the studied network (Burgos et al., 2007).

The degree of specialization ( $H'2 = 0.37$ ) for Ilha Grande was higher than that obtained for Ilha das Flores ( $H'2 = 0.0$ ) (Mouga et al., 2018a) and lower than that obtained

**Table 4.** Classification of richness and abundance, obtained in several studies carried out.

Authors	S	N	H'	City	Veg.	Dist. (Km)	Richness ranking	Abundance ranking
Mouga et al. (2018a)	60	1.120	2.77	SFS (SC)/Ilha das Flores	FOD	2.43	Hal>Api>Meg>Col	Api>Hal>Meg>Col
Mouga et al. (2015)	80	1.519	2.3	SFS (SC)/Vila da Glória	FOD	5.37	Hal>Api>Meg>And	Api>Hal>Meg>And
Mouga & Warkentin (2016)	60	1.503	2.63	Joinville (SC)	FOD	9.52	Api>Hal>Meg	Api>Hal>Meg
Possamai et al. (2017)	78	3.073	3	Joinville (SC)	FOD	14.9	Hal>Meg>Api>And	Api>Hal>Meg>And
Mouga et al. (2016)	93	2.749	2.65	Mafra (SC)	FOM	111.97	Api>Hal>And>Meg>Col	Api>Hal>And>Col>Meg
Liebl et al. (2019)	56	1.304	2.18/2.56	Mafra (SC)	FOM	111.97	Api>Hal>Meg>And>Col	Api>Hal>Meg>And>Col
Somavilla et al. (2018)	88	2.772	2.6	Santa Cruz do Sul (RS)	FED	529.76	Api>Hal>Meg>And>Col	Api>Hal>Meg>And>Col

Caption: S = richness; N = total number of individuals; H' = Shannon-Wiener; SFS = São Francisco do Sul; SC = Santa Catarina; Veg. = vegetation; Dist. = distance; FOD = Rain Forest; FOM = Araucaria Forest; FED = Deciduous Season Forest. Api = Apinae; Hal = Halictinae; Meg = Megachilinae; Col = Colletinae; And = Andreninae.

in a transitional forest ( $H^2 = 0.51$ ) by Mouga et al. (2012). The latter authors considered their value to represent high specialization in the network, when compared to the  $H^2 = 0.24$  and  $0.63$  obtained by Blütghen et al. (2006, for networks) in England and Argentina, respectively.

The presence of bees with a high number of interactions can reduce specificity since rare interactions may not appear (Valido et al., 2019). Thus, *Apis mellifera* reduced the degree of specialization on Ilha Grande by 14%, if we compare to the situation without this species.

## Final Considerations

Our results raise questions, such as: How insular are the islands of Babitonga Bay for certain bee species and how does this interfere with community structure?

The simple crossing of a water barrier can be a limiting factor for some *taxa*, especially for those with tiny individuals, such as *Dialictus*, as well as those with eusocial reproductive individuals, such as species of Meliponina (Zanella et al., 1998). In addition, bees of Meliponina need a relatively large space to support a genetically sufficient number of colonies (Schwartz & Laroca, 1999).

For other species, such as *Bombus morio*, body size and flight capacity favor worker foraging between islands and the mainland (Francisco, 2012). The same can be considered for *Centris*, *Epicharis* and *Xylocopa*, which may have the capacity to carry out daily flights between islands (Schwartz & Laroca, 1999). Francisco (2012) found no negative correlations between geographic distance and genetic diversity for most of the bee populations he studied. On the other hand, Boff et al. (2014) found reduced genetic variability for *Euglossa cordata*, but there is an indication that the species maintains sex locus variation. In other words, populations can maintain genetic variability, and flee the vortex of extinction, by inbreeding through gene flow, for which males play an important role (Kraus et al., 2009).

Considering community structure, the hypothesis raised by Spengler et al. (2011) for Indonesian islands – where species with good dispersal capacity, but which are not good competitors, could become well established on more isolated islands due to the absence of competitors – can be thought of as a modeling factor for the community. Furthermore, the same authors report that habitat diversity may be more correlated with the richness of the biota than with the MacArthur and Wilson's (1963) species area-relationship. We remarked, in the present study, on the oligolectic relationship between the genus *Hylaeus* (Colletinae) and the species *Schinus terebinthifolius*, a plant already reported by Zanella et al. (1998) as a favoring this group of bees.

Considering landscape evolution, the verified variation of species composition among islands may be related to the paleoenvironmental processes of the bay that formed the islands (Souza et al., 2001). Mazzer and Gonçalves (2011)

describe Babitonga Bay as an estuary with a valley profile, drowned by the relative rise of sea level during the Holocene marine transgression about 5,100 years ago (Oliveira & Horn-Filho, 2001). These fluctuations of sea level may have had negative impacts on taxonomic groups, such as the destruction of nests and reproductive individuals (Mouga et al., 2018a). Thus, the fauna of Ilha Grande may be relictual, in part, with, on the other hand, some species that can migrate or disperse, frequently or rarely, according to their bionomic characteristics.

It is worth emphasizing the limiting factors of the sampling methodology of Sakagami et al. (1967), which considers only the lowest vegetation substrate, and not the forest canopy, could explain the absence of some *taxa* or the non-stabilization of the accumulation curve.

This study helps to understand the apid communities of isolated areas and can be used to better comprehend changes in fragmented areas of the Atlantic Forest. More in-depth research is needed to further increase knowledge on the topic in the interest of conservation.

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