



RESEARCH ARTICLE - BEES

Different Physiognomies and the Structure of Euglossini Bee (Hymenoptera: Apidae) Communities

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Abstract

Our aim was to evaluate the occurrence of orchid bees in remnants of the Atlantic Forest. We sampled specimens from five regions of Southeast Brazil, covering three different physiognomies of the Atlantic Forest (mixed Araucaria forests with high altitude fields, Atlantic Semi-deciduous Forest and Atlantic Rain Forest). The distances between the sampling sites ranged from 24 to 746 km. Male orchid bees attracted by fragrances were actively sampled monthly during one year using entomological nets and aromatic traps. A total of 1,482 bees were captured, including four genera and at least 31 species. We observed differences in the abundance and richness of species sampled among sites. Climatic variables, mostly relative humidity, explained twice more of the observed differences in the Euglossini communities than simple spatial variation. Our study found differences in the composition of euglossine bee communities as well as in their patterns of abundance and dominance among different vegetation formations. However, the level of pairwise similarity among the Euglossini communities sampled, although highly variable, was not related to climatic factors or geographical distances between the sampling sites. The greatest dissimilarities in the composition of the orchid bee communities were observed between sites around 400 km from each other rather than among sites that were further apart. A possible explanation is that the sampled areas that were 400 km from each other were also highly dissimilar regarding climate, especially altitude.

Introduction

Although the Atlantic Forest is one of the 25 hotspots of endemism and diversity of species in the world (Myers et al., 2000), it is one of the most devastated and threatened ecosystems on the planet (Ribeiro et al., 2009). The isolation of this area from the other two large blocks of South American wet forests, the Amazon and the Andean Forests, together with other factors, including its extensive latitudinal distribution (>27 degrees of latitude) and wide altitudinal variation (from 0 to 2,700 m above sea level), imbues considerable landscape diversity (Silva & Casteleti, 2005). As a result, this forest presents a high degree of biodiversity.

As part of this rich biodiversity, Euglossine bees (Hymenoptera: Apidae: Euglossini), commonly known as orchid bees, have been widely sampled in different Neotropical ecosystems in recent decades, mostly in fragments or remnants of the Atlantic Forest (e.g. Rebêlo & Garófalo, 1997; Tonhasca et al., 2002; Sofia et al., 2004; Aguiar et al., 2014; Rocha-Filho & Garófalo, 2013, 2014; Giangarelli et al., 2015; Costa & Francoy, 2017). Some these studies have shown structural differences in euglossine bee communities from distinct biogeographical regions, and differences have usually been attributed mainly to historical factors (Aguiar et al. 2014). However, comparative studies of orchid bee communities from different vegetation physiognomies have shown that regional



differences in community structure are also influenced by climatic, geomorphological, and/or vegetational parameters (Nemésio & Silveira, 2007; Sydney et al., 2010; Mattozo et al., 2011; Aguiar et al., 2014; Nemésio & Vasconcelos, 2013; Giangarelli et al., 2015; Costa & Francoy, 2017; Medeiros et al., 2017; Moreira et al., 2017).

Originally distributed throughout most of the Brazilian coast and parts of the interior in the southern region of the country, the Atlantic Forest is composed of a series of rather diverse vegetation physiognomies (Silva & Casteleti, 2005), which includes the Atlantic Rain Forest and the Atlantic Semi-deciduous Forest (Morellato & Haddad, 2000; Oliveira-Filho & Fontes, 2000). Although the Atlantic Forest is mostly composed of these two typical vegetation physiognomies, São Paulo State in southeast Brazil has varied biogeographic components, including the Atlantic component and elements of the biogeographic component of Central Brazil, the western component, constituting an unmatched mosaic of vegetation physiognomies. In this context, we examined the community structure of euglossine bees in three distinct vegetation types of the Atlantic Forest. We investigated the importance of the different vegetation types and different climatic conditions (temperature, humidity, precipitation) and geomorphological factors (altitude, latitude, longitude) on the species composition of those bee communities.

Materials and Methods

Study sites and field sampling – Sampling of male orchid bees was carried out in three different phytophysiognomies (Araucaria mixed forests with high altitude fields, Atlantic Semi-deciduous Forest and Atlantic Rain Forest) from five remnants of Atlantic Forest located in the state of São Paulo, in southeast Brazil (Appendix 1):

1- Campos do Jordão (22°44'19" S, 45°30'32" W), Araucaria mixed forests, is located in the Serra da Mantiqueira, at 1,628 meters of elevation. The study in this region was carried out in native forest Parque Estadual de Campos do Jordão (PECJ). According to Köoper's classification, the climate is Cwa, mesothermal with dry winter. It is characterized by steep slopes with scalloped cliffs covered by transition vegetation between high-altitude fields and moist Araucaria forests.

2- Pindamonhangaba (22°55'50" S; 45°27'22" W), Atlantic semi deciduous forests, is located at 567 meters of elevation. According to Köoper's classification, the climate is Cwa, humid subtropical, presenting average annual temperature of 22.4 °C, with warm temperatures in summer and mild winter. As a transition zone, it has a prevalence of vegetation characteristic of a seasonal forest, with environments that are less humid than those where dense rain forest develops.

3- Parque Estadual do Morro do Diabo (PEMD) (22°27'0" S, 52°10'0" W), Atlantic semi deciduous forests, is located in the Pontal do Paranapanema, municipality of Teodoro Sampaio city, west of São Paulo State, at 338 meters of elevation. According

to Köoper's classification, the climate is Cwa, dry weather with hot and humid summers. It presents average annual temperature of 21 °C, with warm temperatures in summer and mild winter. Mean annual precipitation ranges from 1,100 to 1,300 mm.

4- Ubatuba (23°26'13" S; 45°04'08" W), Atlantic rain forests, is located at sea level. According to Köoper's classification, the climate is Af, tropical rainforest climate, with warm temperatures in summer and mild winter. Mean annual precipitation is 2,650 mm, and even in the driest months, from June to August, the average monthly precipitation is never less than 80 mm. The vegetation has a high degree of plant species endemism, in the lower areas, trees tend to be robust and tall, whereas with increasing altitude, they tend to become thin and low; this occurs closer to the ocean. The trees of the slopes can grow to over 40 meters, due to the abundance of organic matter.

5- Parque Estadual Turístico do Alto Ribeira (PETAR) (24°27'36" S, 48°36'0" W), Atlantic rain forests, is located in the south of São Paulo State, in the Serra de Paranapiacaba, between the Baixada do Ribeira and the Planalto Atlântico. According to Köoper's classification, the climate is Cfb, humid subtropical without dry season and with cool summer. Mean annual precipitation ranges from 1,500 to 2,000 mm.

Once a month during one year, the bees were actively collected with entomological nets, from April 2014 to March 2015 in Campos do Jordão, Pindamonhangaba and Ubatuba, and from May 2014 to April 2015 in PEMD and PETAR, by two collectors. Specimens were collected on sunny days between 08:00 h and 15:00 h, in transects approximately 60 m in length. We chose chemicals traditionally used in similar studies, and that showed good attractiveness to euglossine males (e.g. Uehara-Prado & Garófalo, 2006; Rocha-Filho & Garófalo, 2013; 2014): benzyl acetate, eugenol, eucalyptol, methyl salicylate and vanillin. Sampling was conducted using methodology reported by Rebêlo and Garófalo (1991). We used baits with scents made from cotton wool wrapped in gauze and tied with a string; they were fixed in the branches of trees at the height of 1.5 m above the ground, at a distance of 5 m apart. The fragrance in each of the cotton wads was replaced every 60 min. All individuals were killed in 96% ethanol and preserved in this solution for subsequent molecular analysis (unpublished data). All specimens were stored in our laboratory, "Laboratório de Genética e Conservação de Abelhas" – Escola de Artes, Ciências e Humanidades – Universidade de São Paulo, at -20° C. The identification of specimens was based on the keys published by Kimsey (1979, 1982), Dressler (1982a), Rebêlo and Moure (1995), Oliveira (2006), Faria Jr and Melo (2007), Nemésio (2009), Nemésio and Engel (2012). We also followed the species distribution criteria presented in Moure's Bee Catalogue (Moure et al., 2008). Doubtful identifications were confirmed by a specialist.

Data analysis

Descriptive indices were estimated, including Shannon-Wiener diversity (H'), to quantify species diversity based on

the number of males collected, and the data were compared using Hutcheson's t-test (Hutcheson, 1970), as recommended by Magurran (2004) for comparing species assemblages. We also calculated Simpson's index (S') (Magurran, 2004) to estimate the probability of randomly collecting two individuals of the community that belong to different species. To determine uniformity, we calculated Pielou's measure of species evenness (J') (Pielou, 1969). The Berger-Parker dominance index (d) was calculated to species dominance (Magurran, 1988). For comparing the communities either qualitatively or quantitatively, we used β -diversity measures by similarity coefficients. The Sørensen (Sørensen, 1948) coefficient was used to compare community composition between the study areas. The quantitative similarity coefficient of Bray–Curtis was used to analyze the similarity in the fauna of the two sampled areas based on the relative abundance of the males.

The Mantel test statistic was calculated to analyze the variation of species composition among pairs of sampling sites about the geographic and the climatic distances between these sites. The Mantel test uses information about pairwise dissimilarities ($1 - \text{similarity}$) among sites; thus the male abundance dissimilarity matrices utilized in the Mantel tests were built using both the Bray–Curtis index (which takes species relative abundances into account) and the Sørensen index (which relies on presence–absence data). The geographic and climatic (based on precipitation, temperature and humidity) distances were calculated using the Euclidean distance between sites. We also ran partial Mantel tests to analyze the influence of the climatic variables independent of site location (geography) and vice versa.

Climatic data were obtained from the Centro Integrado de Informações Agrometeorológicas – CIIAGRO. To determine

if the climate or geographic variables of our study sites influenced the relative abundances of the different orchid-bee species, we performed a canonical correspondence analysis (CCA). Correlation tests were done to evaluate the associations among variables before performed CCA. The significance of each climatic and spatial variable in the CCA was evaluated using ANOVA. All of the tests of our study were performed using the statistical package R version 3.3.3 (R Development Core Team, 2017).

Results

We sampled 1,482 males, of four genera and at least 31 species. From this total, 1426 males, from 29 species were sampled using scent baits. It is important to note that 56 individuals were sampled on flowers and *Eufriesea surinamensis* and *Euglossa stellfeldti* were sampled only on flowers but not on the scent baits. The most attractive scent was eucalyptol, which attracted around 85% of the total visits and 28 species of bees. Vanillin was the second most attractive fragrance and eugenol was the third (Appendix 2). In PETAR, bees visited only eucalyptol. It is noteworthy that in one of our collection points, Campos do Jordão, no bees belonging to the tribe Euglossini were collected, despite monthly sampling efforts. Due to this fact, all the comparisons will be made using only the other localities, where it was possible to sample the Euglossini community. The abundance of individuals and the number of species were different among the areas, and they were also higher in the warmer months (November to March, Fig 1). Only two species were present in all four sites: *Euglossa fimbriata* Rebêlo & Moure and *Eulaema nigrita*

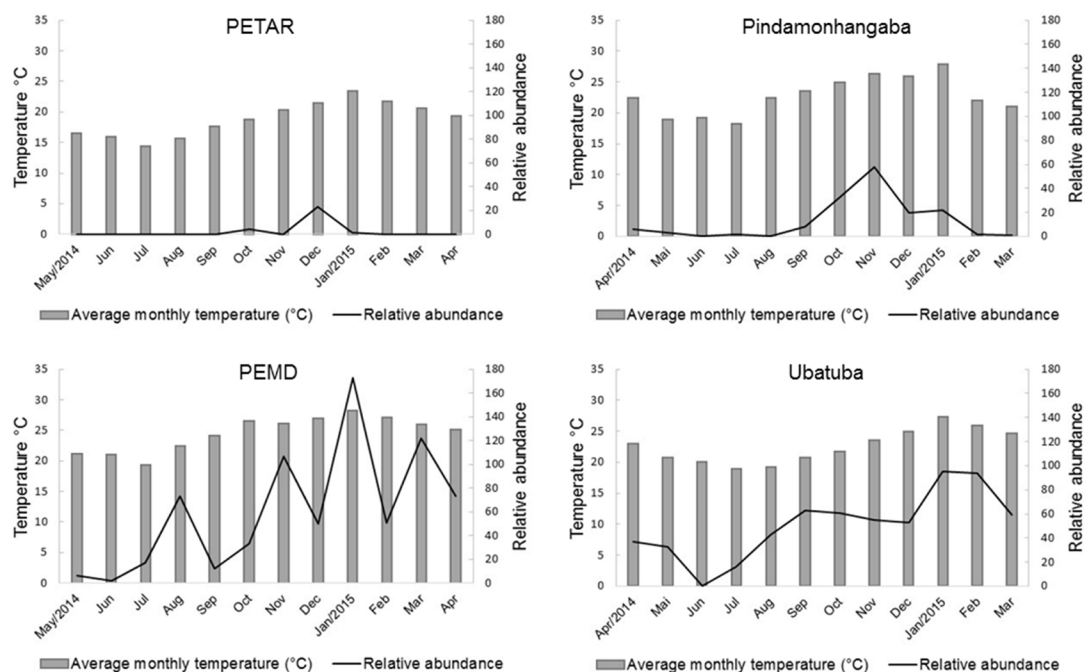


Fig 1. Monthly fluctuation of the abundance of bees and species richness of the Euglossini tribe as a function of temperature (in degrees Celsius) in areas with different forest vegetation types in São Paulo State, Brazil: (A) PETAR: Parque Estadual Turístico do Alto Ribeira; (B) Pindamonhangaba; (C) PEMD: Parque Estadual Morro do Diabo and (D) Ubatuba.

Lepelletier, and only seven other species were present in three sites: *Eufriesea violacea* (Blanchard), *Euglossa annectans* Dressler, *Euglossa cordata* (Linnaeus), *Euglossa leucotricha* Rebêlo & Moure, *Euglossa pleosticta* Dressler, *Euglossa securigera* Dressler and *Euglossa truncata* Rebêlo & Moure (Table 1).

When species diversity was quantified based on the number of collected individuals, the Shannon diversity index (H' index mean = 1.676, range = 0.881-2.523) was significantly different ($p < 0.01$) for the sampled communities when compared pair to pair, except between PEMD and PETAR. Likewise, the Simpson index (S') differed between

the sampling sites ($p < 0.01$), indicating a lower diversity in the PETAR community ($S' = 0.418$), while the Ubatuba area presented the highest diversity ($S' = 0.897$). The Pielou's evenness index (J') demonstrated a lower evenness in PEMD ($J' = 0.436$), while Pindamonhangaba was more uniform ($J' = 0.780$). Similarly, the dominant species representation, determined by the Berger-Parker dominance index, was high for the PEMD community ($d = 0.731$), dominated by *Eg. pleosticta*, accounting for 73.1% of all bees collected in this area. Dominance was lower in Ubatuba ($d = 0.151$), where the most abundant species, *Euglossa imperialis* Cockerell, represented 15% of all bees sampled at this location (Table 2).

Table 1. Euglossine bees collected in different sampling sites of the Atlantic Forest at São Paulo State, Brazil. PEMD: Parque Estadual Morro do Diabo; PETAR: Parque Estadual Turístico do Alto Ribeira.

Species	Pindamonhangaba		Ubatuba		PEMD		PETAR	
	N	%	N	%	N	%	N	%
<i>Eufriesea dentilabris</i> (Mocsáry, 1897)	-	-	-	-	-	-	1	3.57
<i>Eufriesea mussitans</i> (Fabricius, 1787)	-	-	-	-	-	-	1	3.57
<i>Eufriesea smaragdina</i> (Perty, 1833)	-	-	1	0.17	1	0.14	-	-
<i>Eufriesea surinamensis</i> (Linnaeus, 1758)	-	-	1	0.17	-	-	-	-
<i>Eufriesea violacea</i> (Blanchard, 1840)	-	-	2	0.33	50	7.09	3	10.71
<i>Euglossa analis</i> Westwood, 1840	-	-	2	0.33	-	-	-	-
<i>Euglossa annectans</i> Dressler, 1982	1	0.70	1	0.17	36	5.11	-	-
<i>Euglossa clausi</i> Nemésio & Engel, 2012	-	-	2	0.33	-	-	-	-
<i>Euglossa cordata</i> (Linnaeus, 1758)	38	26.57	75	12.38	17	2.41	-	-
<i>Euglossa crassipunctata</i> Moure, 1968	1	0.70	12	1.98	-	-	-	-
<i>Euglossa fimbriata</i> Rebêlo & Moure, 1996	5	3.50	10	1.65	18	2.55	2	7.14
<i>Euglossa ignita</i> Smith, 1874	0	0.00	2	0.33	-	-	-	-
<i>Euglossa imperialis</i> Cockerell, 1922	6	4.20	92	15.18	-	-	-	-
<i>Euglossa iopoecila</i> Dressler, 1982	4	2.80	81	13.37	-	-	-	-
<i>Euglossa ioprosopa</i> Dressler, 1982	1	0.70	6	0.99	-	-	-	-
<i>Euglossa iopyrrha</i> Dressler, 1982	-	-	1	0.17	-	-	-	-
<i>Euglossa leucotricha</i> Rebêlo & Moure, 1996	19	13.29	5	0.83	1	0.14	-	-
<i>Euglossa mandibularis</i> Friese, 1899	-	-	18	2.97	-	-	-	-
<i>Euglossa melanotricha</i> Moure, 1967	1	0.70	1	0.17	-	-	-	-
<i>Euglossa pleosticta</i> Dressler, 1982	14	9.79	70	11.55	516	73.19	-	-
<i>Euglossa roderici</i> Nemésio, 2009	1	0.70	44	7.26	-	-	-	-
<i>Euglossa sapphirina</i> Moure, 1968	0	0.00	56	9.24	-	-	-	-
<i>Euglossa securigera</i> Dressler, 1982	-	-	10	1.65	1	0.14	-	-
<i>Euglossa stellfeldi</i> Moure, 1947	2	1.40	-	-	-	-	-	-
<i>Euglossa townsendi</i> Cockerell, 1904	-	-	2	0.33	-	-	-	-
<i>Euglossa truncata</i> Rebêlo & Moure, 1996	4	2.80	7	1.16	2	0.28	-	-
<i>Euglossa viridis</i> (Perty, 1833)	13	9.09	77	12.38	-	-	-	-
<i>Eulaema cingulata</i> (Fabricius, 1804)	1	0.70	9	1.49	-	-	-	-
<i>Eulaema nigrata</i> Lepelletier, 1841	31	21.68	19	3.14	55	7.80	21	75.00
<i>Eulaema seabrai</i> Moure, 1960	1	0.70	1	0.17	-	-	-	-
<i>Exaerete smaragdina</i> (Guérin, 1844)	-	-	1	0.17	8	1.13	-	-
Total	143	100	606	100	705	100	28	100

Table 2. Shannon’s diversity (H’), Simpson’s diversity (S’), Pielou’s evenness (J’) and Berger-Parker dominance (d) for the four study areas.

Sampling Sites	Index Diversity			
	Shannon (H’)	Simpson (S’)	Evenness (J’)	Berger-Parker (d)
Pindamonhangaba	2.256	0.859	0.781	0.254
Ubatuba	2.523	0.897	0.757	0.151
PEMD	1.045	0.449	0.436	0.731
PETAR	0.881	0.418	0.547	0.750

The level of pairwise similarity among the sampled bee communities was low and showed considerable variation, ranging from 7.09 to 32.72 % (Bray–Curtis index mean = 17.96 %, Table3) when considering the relative abundances of all species. According to this index, Pindamonhangaba and Ubatuba were the most similar areas, with 17 species in common. When considering the presence or absence of species, the pairwise values of similarity among the areas were high (Sørensen index: mean = 42.24 %, range = 17.39-73.91%, Table 3). However, for the Sørensen index, Pindamonhangaba and PETAR were the least similar areas regarding species composition; while for the Bray–Curtis index, PETAR and

PEMD were the least similar areas. Further analyses were based solely on relative abundance data. Similarity in bee species composition among the different pairs of study sites was not significant both as function of the climatic (Mantel test: $r = -0.028$, $p = 0.625$) and geographic distances among these locations ($r = 0.485$, $p = 0.16667$). The greatest similarities in the composition of bee assemblages tended to be observed among pairs of sites located in similar physiognomies.

Our CCA analyses revealed that 75.5% of the total variation in the bee species composition could be explained by a combination of humidity and altitude; whereas an additional 24.5% remained unexplained or represented stochastic variation. The model with two climatic variables was significant (ANOVA: 1.546, $p = 0.041$) in explaining the observed variation based on the relative abundances of orchid bee species within our study region. It can be further seen in our CCA ordination graph that the species matrix and the climatic variables had a similar spatial structure. PEMD was relatively separated from the remaining sites regarding the composition of its fauna (Fig 2). Humidity tended to increase from interior to coastal regions; this may help explain the observed latitudinal differences in the community composition of the orchid bees, with several of these species occurring exclusively in some parts of the climatic gradients.

Table 3. Sørensen index (bottom of the table) and Bray–Curtis index (top of the table) for the four study areas. PEMD: Parque Estadual Morro do Diabo; PETAR: Parque Estadual Turístico do Alto Ribeira.

	Pindamonhangaba	Ubatuba	PEMD	PETAR
Pindamonhangaba		0.327	0.167	0.251
Ubatuba	0.739		0.189	0.072
PEMD	0.551	0.512		0.071
PETAR	0.173	0.181	0.375	

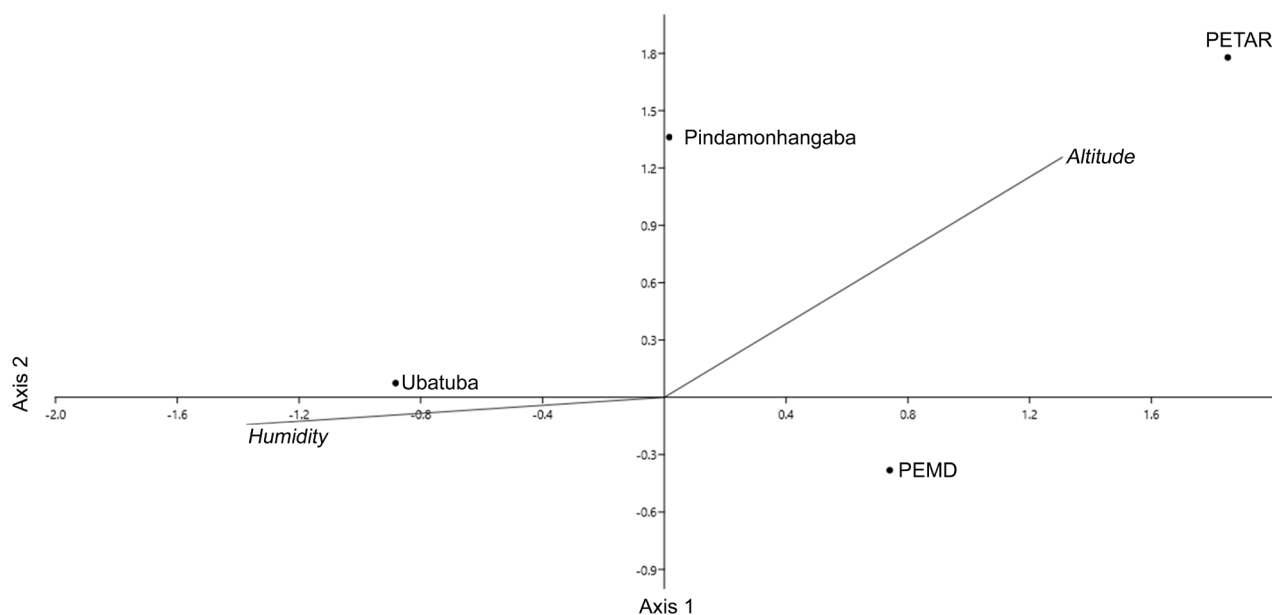


Fig 2. CCA ordination plot of the sampling sites in relation to the orchid bee and climatic and geographic variables. PEMD: Parque Estadual Morro do Diabo; PETAR: Parque Estadual Turístico do Alto Ribeira.

Discussion

Regarding Euglossini, Nemésio (2009) recognized around 54 species in the Atlantic forest; however, new species continue to be described (e.g. Nemésio, 2011; Hinojosa-Díaz et al., 2012; Faria Jr. & Melo, 2012; Nemésio & Engel, 2012). Assuming at least 62 orchid bee species inhabit this area, and 31 (approximately 50%) of these species were found in our study in a relatively small portion of the area, the sampled regions could be a refuge for a large number of Euglossini species. These data are similar to the richness pattern of this group reported for southeastern Brazil (Nemésio, 2009). In contrast, Campos do Jordão was characterized by a lack of Euglossini bees, probably as a consequence of the local geoclimatic characteristics since this region is characterized by Araucaria mixed forests with high altitude fields (for more details see Costa & Franco, 2017). Despite scarcity of information about orchid bee presence in Araucaria forests, Dias and Buschini (2013) indicated that these bees have a low diversity and abundance in Araucaria forest, being markedly smaller compared to other physiognomies. These authors (Dias & Buschini, 2013) sampled 35 male specimens belonging to two species, *El. nigrita* and *Eg. fimbriata*, in a similar area of Araucaria Forest in Paraná State. However, our area of Araucaria Forest in Campos do Jordão is located at an altitude of 1,628 m, what probably accounted to the absence of Euglossini bees, since altitudinal variation can drastically reduce abundance patterns and alter the species compositions of orchid bee communities (Abrahamczyk et al., 2011). Our data suggest that altitude is an important factor that induces variation in several other geomorphological and climatic features and therefore, helps to modify species composition and abundance of orchid bees, even at small scales of variation, however, this result has to be tested in future studies.

The efficiency of eucalyptol, or cineole, in attracting orchid bees is already well known (e.g. Dressler, 1982b; Rebêlo & Garófalo, 1991; Sofia et al., 2004; Rocha-Filho & Garófalo, 2014). However, eugenol, which was very attractive to male euglossine in other sites (e.g. Dressler, 1982b; Rocha-Filho & Garófalo, 2014), was poor attractant in our study. Geographical variation in fragrance preference of male orchid bees is common and was also reported by other authors (e.g. Pearson & Dressler, 1985; Sofia et al., 2004; Farias et al., 2007; Rocha-Filho & Garófalo, 2014). The distribution patterns of abundance in the sampled areas were similar to those of other studies made in other Atlantic Forest fragments; a few species had many individuals, and many species had few individuals (e.g., Rebêlo & Garófalo, 1997; Sofia & Suzuki, 2004; Sofia et al., 2004; Aguiar & Gaglianone, 2008; Ramalho et al., 2009; Giangarelli et al., 2015; Rocha-Filho & Garófalo, 2013). This tendency can be the result of the weak association of some species with the essences used (Viana et al., 2002) or can be the distribution pattern of these communities (Aguiar & Gaglianone, 2008).

This pattern was more evident in PEMD, where individuals of *Eg. pleosticta* represented 73.2% of the total, considered typical species of semi-deciduous areas. Also, species richness of orchid bees was characterized by a north-south gradient, with a gradual reduction from north to south direction, similar to other studies (Wittmann et al., 1988; Sofia & Suzuki, 2004; Mattozo et al., 2011; Cordeiro et al., 2013). Ubatuba was the area with the highest species richness of all areas sampled, even after the equalization efforts with rarefaction techniques; meanwhile, PETAR, the area furthest south, had the lowest species richness and abundance of orchid bees. Most of the sample areas included species with a wide distribution range along the north-south corridor of the Atlantic Forest, such as *Eg. cordata* and *El. nigrita*, which occurs along the entire coast of Brazil, as well as species that predominate in the southeastern region, such as *Eg. fimbriata* and *Eg. pleosticta* (Cordeiro et al., 2013). Several euglossine species found in the studied areas, such as *Eufriesea dentilabris* (Mocsáry), *Euglossa iopoecila* Dressler, *Euglossa stellfeldi* Moure and *Euglossa roderici* Nemésio, are endemic to the Atlantic Forest. *El. nigrita* and *Eg. fimbriata* were the only two species found in all sample areas. Also, the finding of *El. nigrita* in all the areas was also observed in other surveys made in the Atlantic Forest (e.g. Farias et al., 2008; Nemésio & Silveira, 2010; Aguiar et al., 2014). This species was abundant in areas in different conservation stages; it is tolerant to disturbances in the environment and vegetation (Peruquetti et al., 1999; Ramalho et al., 2009; Aguiar & Gaglianone, 2012). The great flight range could account for their prevalence in various areas (for more details see Dressler, 1982b; Roubik & Hanson, 2004). The relative abundance of *El. nigrita* varied between 3 and 75%; meanwhile for *Eg. pleosticta*, the predominant species in PEMD, abundance ranged from 9 and 73%. This variation in abundance affects the similarity between areas since we found values between 0.07 and 0.32 for Bray-Curtis index, which considers the relative abundances of all species. A similar result was found for the Sørensen index, which presented a high amplitude (0.17-0.74), due to the considerable variation in the species richness across the sampled areas.

The values of richness and/or abundance of euglossine bees are in disagreement with those of previous studies in similar areas of the Atlantic rain forests (Singer & Sazima, 2004; Rocha-Filho & Garófalo, 2013, 2014), including the low richness of the *Eufriesea* genus and the high abundance of two species, which frequently are recorded in semi deciduous forests (Rocha-Filho & Garófalo, 2013), *Eg. pleosticta* and *Eg. imperialis* in the coastal region. However, these comparisons should be viewed with wariness, since the sample design used in the studies is often different. According to Roubik (2001), reduced chances of resampling could reflect the dynamics of the bee communities on a short time scale. Additionally, our results revealed that the level of pairwise similarity among the Euglossini communities sampled, although highly variable, was not related to climatic or geographical distances

among the sampling sites. The greatest dissimilarities in the composition of the orchid bee communities were observed among areas distant around 400 km from each other rather than among the sites further apart. One reason for this fact could be that the sampled areas distant 400 km from each other were also highly dissimilar regarding climate-related variables, especially altitude. Besides, despite orchid bees show the large foraging range, becoming strong flyers (Janzen, 1971), several species of bees found in the Ubatuba were not collected in the Pindamonhangaba, although both areas are only 61 km apart and connected, largely, by areas of Eucalyptus and forest remnants.

In our study region, the Atlantic Forest is mostly characterized by three vegetation physiognomies, mixed Araucaria forests with high altitude fields, Atlantic Rain Forest and Atlantic Semi-deciduous Forest, which include several natural gradients within their latitudinal and longitudinal extensions, as well as an altitudinal variation from the coast to the interior. According to Lázaro and Totland (2010), vegetation types and differences in the availability of key resources can be one of the drivers of change population patterns of pollinators. Especially, in the Neotropical region, the floral landscape is spatially and temporally heterogeneous for foraging bees, promoting considerable change in the abundance pattern and amount of brood in the nests for bees (Smith et al., 2012). Climatic variables, mostly relative humidity, explained twice the observed differences in the Euglossini communities compared to spatial variation alone. Relative humidity seems to be the most important abiotic factor for our study, which was also found in another study that found the preference of orchid bees for humid forests (Roubik & Hanson, 2004). We found to a great richness of orchid bees in the Atlantic Rain Forest, even within a small spatial scale. This could be due to the high diversity of habitats, influenced by the wide geomorphological and climatic variation, besides the Atlantic and Occidental components, which extend throughout São Paulo State, from the coast to the interior, constituting a mosaic of landscapes that probably favors the occurrence of Euglossini in this region. Different physiognomies and, consequently, the variation in the availability of key resources can change population patterns of orchid bees (see Nemésio & Silveira, 2007); a thorough analysis of resource availability in the sampling areas would be important to clarify this issue. In addition to the abiotic factors that can affect orchid bee assemblages, other components, such as competition with similar species, historical occurrences, and habitat homogeneity (Roubik, 2001; Tonhasca et al., 2002; Roubik & Hanson, 2004) could also influence euglossine communities. The cleptoparasitic euglossine bees, such as genus *Exaerete*, involve additional biotic factors for their occurrence, such as the occurrence of host species in the genera *Eulaema* and *Eufriesea* (Aguiar et al., 2014); however, these factors have not been evaluated in this study, but should be considered in future studies.

Our data reinforces the general pattern that the euglossine fauna of the Atlantic forest changes according to the abiotic factors (Nemésio & Silveira, 2007; Abrahamczyk et al., 2011; Aguiar et al., 2014; Nemésio & Vasconcelos, 2013; Giangarelli et al., 2015, Medeiros et al., 2017). However, a lack of basic studies on Euglossini biology impedes an objective evaluation of the real influence of these factors on community composition (Nemésio & Vasconcelos, 2013). Nevertheless, our sampling area that can be considered floristically diverse, with drastic differences among physiognomies, suggests that variations in vegetation community composition can help to explain, at least in part, differences in the composition of euglossine communities.

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Appendix 1 - Information about their spatial location (latitude and longitude), altitude and climate (temperature, precipitation and humidity) of sampling sites at São Paulo state.

	Pindamonhangaba	Ubatuba	PEMD	PETAR	Campos do Jordão
Mean Temperature	22.75	22.60	24.52	18.82	15.34
Total Precipitation	1000.50	2023.80	1419.20	1262.30	1161.50
Mean Precipitation	83.38	168.65	118.27	105.19	96.79
Humidity	0.83	0.89	0.45	0.41	0.86
Altitude	567	31	338	915	1628
Latitude	-22.916	-23.376	-22.622	-24.383	-22.733
Longitude	-45.450	-45.873	-52.182	-48.616	-45.500

Appendix 2. Euglossine species sampled in areas of São Paulo State during one year, using the aromatic compounds benzyl acetate (BA), eucalyptol (Ep), eugenol (Eg), methyl salicylate (MS) and vanillin (Va). Pi: Pindamonhangaba; Ub: Ubatuba; PEMD: Parque Estadual do Morro do Diabo; PETAR: Parque Estadual Turístico do Alto Ribeira.

Species	BA			Ep			Eg			MS			Va			Total	
	Pi	Ub	PEMD	PETAR	Pi	Ub	PEMD	PETAR	Pi	Ub	PEMD	PETAR	Pi	Ub	PEMD		PETAR
<i>Eufriesea dentilabris</i>	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	1
<i>Eufriesea muscitans</i>	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	1
<i>Eufriesea smaragdina</i>	-	-	1	-	-	1	-	-	-	-	-	-	-	-	-	-	2
<i>Eufriesea surinamensis</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Eufriesea violacea</i>	-	-	-	-	2	37	1	3	-	-	1	-	-	-	12	-	55
<i>Euglossa analis</i>	-	-	-	-	-	-	-	-	2	-	-	-	-	-	-	-	2
<i>Euglossa annectans</i>	-	-	1	-	1	23	-	-	-	-	6	-	-	1	5	-	38
<i>Euglossa clausi</i>	-	-	-	-	2	-	-	-	-	-	-	-	-	-	-	-	2
<i>Euglossa cordata</i>	1	-	-	-	37	65	17	-	1	7	-	-	-	1	-	-	123
<i>Euglossa crassipunctata</i>	-	-	-	-	1	12	-	-	-	-	-	-	-	-	-	-	13
<i>Euglossa fimbriata</i>	-	-	-	-	5	10	18	2	-	-	-	-	-	-	-	-	35
<i>Euglossa ignita</i>	-	-	-	-	-	2	-	-	-	-	-	-	-	-	-	-	2
<i>Euglossa impertialis</i>	2	-	-	-	3	74	-	-	1	7	-	-	-	1	-	-	89
<i>Euglossa iopoeila</i>	-	-	-	-	4	77	-	-	-	-	-	-	-	1	-	-	82
<i>Euglossa ioprosopa</i>	-	-	-	-	1	6	-	-	-	-	-	-	-	-	-	-	7
<i>Euglossa iopyrrha</i>	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	1
<i>Euglossa leucotricha</i>	-	-	-	-	18	5	1	-	-	-	-	-	-	-	-	-	24
<i>Euglossa mandibularis</i>	1	-	-	-	-	5	-	-	-	10	-	-	-	-	-	-	16
<i>Euglossa melanoitricha</i>	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	1
<i>Euglossa pleosticta</i>	-	-	7	-	12	64	404	-	3	11	2	-	-	1	73	-	578
<i>Euglossa roderici</i>	5	-	-	-	1	29	-	-	1	-	-	-	-	6	-	-	42
<i>Euglossa sapphirina</i>	-	-	-	-	-	49	-	-	3	-	-	-	-	1	-	-	53
<i>Euglossa securigera</i>	-	-	-	-	12	9	1	-	-	-	-	-	-	1	-	-	23
<i>Euglossa stellfeldi</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Euglossa townsendi</i>	-	-	-	-	-	1	-	-	1	-	-	-	-	-	-	-	2
<i>Euglossa truncata</i>	-	-	-	-	3	5	2	-	1	-	-	-	-	-	-	-	11
<i>Euglossa viridis</i>	1	-	-	-	10	46	-	-	12	-	-	-	2	9	-	-	81
<i>Eulaema cingulata</i>	1	-	-	-	-	9	-	-	-	-	-	-	-	-	-	-	10
<i>Eulaema nigrita</i>	-	-	-	-	30	19	46	21	-	-	-	-	-	-	7	-	123
<i>Eulaema seabrai</i>	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	1
<i>Exaerete smaragdina</i>	-	-	-	-	-	1	5	-	-	-	-	-	-	-	2	-	8
Abundance	1	10	9	-	140	495	554	28	1	41	18	-	3	19	3	-	1426*
Richness	1	5	3	-	16	24	10	5	1	10	3	-	2	6	2	-	29**

*The total refers only to the individuals collected through the use of aromatic traps.

**The total refers only to the species collected through the use of aromatic traps. *Eufriesea surinamensis* and *Euglossa stellfeldi* were only collected in flowers of plants.