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Does Forest Phisiognomy affect the Structure of Orchid Bee (Hymenoptera, Apidae, Euglossini) Communities? A Study in the Atlantic Forest of Rio de Janeiro state, Brazil

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Abstract

We describe and discuss the composition, abundance and diversity of euglossine in three vegetation types of the Atlantic Forest (Lowland Seasonal Semideciduous, Submontane Seasonal and Dense Montane Ombrophilous Forest) in Rio de Janeiro state, Brazil, compare them to previous studies in the region and investigate the importance of the vegetation types, climatic and geomorphological factors on the species composition. Male euglossine bees attracted by fragrances were sampled monthly from August/2008 to July/2009 using entomological nets and traps. Euglossine bee communities exhibited differences in their species composition and abundance along the year and in the vegetation types. The precipitation, altitude and vegetation types demonstrated a significant influence on the ordination of the euglossine communities. 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, stressing the importance of the conservation of landscape mosaics in the region.

Introduction

Orchid bee communities have been widely sampled in different neotropical ecosystems in recent decades, including the Atlantic Forest (Tonhasca et al., 2002a; Sofia & Suzuki, 2004; Nemésio & Silveira, 2006a; Ramalho et al., 2009; Mattozo et al., 2011; Silveira et al., 2011; Aguiar & Gaglianone, 2012; Ramalho et al., 2013), the Amazonian Forest (e.g., 1985; Powell & Powell, 1987; Storck-Tonon et al., 2009; Abrahamczyk et al., 2011), Central American forests (e.g., Ackerman, 1983; Brosi 2009), the savannas of central Brazil (Cerrado) (Souza et al., 2005; Alvarenga et al., 2007; Faria & Silveira, 2011), and the dry forest of northeastern Brazil (Caatinga) (Souza et al., 2005; Alvarenga et al., 2007; Andrade-Silva et al., 2012). These studies have shown structural differences in bee communities from distinct biogeographical regions, particularly in relation to composition, richness, patterns of dominant species and numbers of endemic species. The differences have usually been attributed mainly to historical factors, although regional differences in community structure at less encompassing spatial scales can be analyzed based on current ecological characteristics related to climatic, geomorphological, and/or vegetational parameters (Silveira et al., 2002; Sydney et al., 2010). Recently, Nemésio and Vasconcelos (2013) evaluated the beta diversity of Euglossina in the Atlantic Forest and noted that climate variations explain twice as much variation in the species data than the spatial variation in species distribution. Nevertheless, part of the observed latitudinal changes in community composition appears to be explained by a concomitant seasonal gradient of precipitation. Similarly, low temperatures and a seasonal rainfall may help explain the relative specificity of the fauna of some of the most western Atlantic Forest. This Tropical Forest extends along almost the entire eastern coast of Brazil and it is composed of a mosaic of rainforest, “restinga” (coastal vegetation on Quaternary sandy soils) and mangrove swamp ecosystems (Galindo-Leal & Câmara, 2003).

The wide latitudinal extension and significant longitudinal width of this biome, associated with altitudinal variations throughout the region, constitute important factors that define different vegetation types (Galindo-Leal & Câmara,

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2003; Ribeiro et al., 2009) and likewise favor the high diversity and endemism of animals found there (Myers et al., 2000).

Comparative studies of orchid-bee communities between different vegetational formations have been carried out, and, in the Atlantic Forest, include those by Nemésio and Silveira (2007), Sydney et al. (2010), Mattozo et al. (2011) and Nemésio and Vasconcelos (2013). These authors reported differences between euglossine bee species composition in Dense Ombrophilous and Semideciduous forests, along the northern and the southern coast of Brazil. Additionally, Nemésio (2008) demonstrated the strong influence of altitude on spatial distributions and species composition of communities living in the same geographical region.

Dense ombrophilous forest areas within the Atlantic Forest biome generally occur from the scarps of the coastal mountains, which are directly influenced by masses of humid air moving in from the sea, to the coastline inland. Forested regions in the northern part of Rio de Janeiro State, however, exhibit somewhat unusual features due to the occurrence of the "Campos dos Goytacazes Gap", which designates a geographic transition between the Serra do Mar forest domain (which extends from north of Paraná to Rio de Janeiro) and the Central Atlantic forest domain (which covers the state of Espírito Santo, small areas of eastern Minas Gerais and southern Bahia).

The low humidity associated with this geographical transition (gap) between the two Atlantic forest domains favors the appearance of seasonal forests that extend to the coast (Oliveira-Filho & Fontes, 2000; Oliveira-Filho et al., 2005). This incursion of semideciduous forest to the coast in the northern region of the state of Rio de Janeiro makes the vegetation show limited number of species common to both areas of dense Ombrophilous forest in the state of Rio de Janeiro (Silva & Nascimento 2001).

Oliveira-Filho and Fontes (2000) consider the weather and especially the temperature as the factor most strongly related to the floristic variation observed. This interposition of a seasonal forest between two large belts of ombrophilous forests might be expected to result in differences in the composition, richness and abundance of the orchid bee communities, as these bees are highly dependent on local floral resources for food, nesting, and reproductive resources (see Roubik & Hanson, 2004).

The present study was therefore designed to: (1) Describe and discuss the community structure of euglossine bees in three distinct vegetation types of the Atlantic Forest in the northern portion of Rio de Janeiro State; (2) Comparatively analyze the structure of those bee communities with other communities previously studied in the same region (Tonhasca et al., 2002a; Aguiar & Gaglianone, 2008, 2011, 2012; Ramalho et al., 2009;); (3) Investigate the importance of the different vegetation types and different climatic conditions (temperature, humidity, precipitation) and geomorphological factors (altitude) on the species composition of those bee communities.

Materials and Methods

Study Sites

We selected three forest fragments, from the three different Atlantic Forest vegetation types that originally covered the northern portion of the Rio de Janeiro state (Veloso et al., 1991), based on their large area, the advanced stage of regeneration, and their degree of conservation, considering that they have not been completely devastated in the past.

1- "Mata do Carvão" (21º24'S - 41º04'W), located in the conservation unity "Estação Ecológica Estadual Guaxindiba", in the municipality of São Francisco de Itabapoana, is a fragment of Lowland Seasonal Semideciduous Forest (LSSF) covering approximately 1,200ha, and situated at 40 m.a.s.l. (Silva & Nascimento, 2001).

2- "Mata da Prosperidade" (21º24'S - 42º02'W), located within a private farm in the municipality of São José de Ubá, is a fragment of Semideciduous Submontane Seasonal Forest (SSSF) covering approximately 900 ha, and situated between 350 and 500 m.a.s.l. (Dan et al., 2010).

3- "Mata da Cabecinha" (22°05'S - 42º05'W), located in the municipality of Trajano de Moraes, is a fragment of Dense Montane Ombrophilous Forest (DMOF) covering approximately 900ha, at 750 to 1,000 m.a.s.l. (RioRural/GEF, 2007).

The climate in the first two areas (LSSF and SSSF) is classified as Aw (Köppen & Geiger, 1928), with an average total annual rainfall of approximately 1,100 mm (RadamBrasil, 1983) and a well-defined dry season from May to September (Radam Brasil, 1983). During the study year, the total precipitation was 1,600mm, with average temperatures of 25.3ºC and 24.8ºC in the two areas respectively (Data: Instituto Nacional de Meteorologia).

In the DMOF area, the climate is classified as Cwa (Köppen & Geiger, 1928), with an average total annual rainfall of approximately 1,300 mm and a predominantly humid climate with no (or only small) water deficits during the year. During the study year, the precipitation was 1,600mm, with an average temperature of 21.4°C (Data: Instituto Nacional de Meteorologia).

Data Collection

Male euglossine bees were sampled once a month from August, 2008 to July, 2009. At each collecting day, fragrance baits (methyl cinnamate, vanilla, eucalyptol, benzyl acetate, and methyl salicylate) were exposed from 09:00 to 15:00h, using two quantitative sampling methods: insect nets and traps, totaling 144 sampling hours (72 hours with an insect net and 72 with traps). The traps and sampling methodologies were the same described in Aguiar and Gaglianone (2011); baits were applied to cotton balls and inserted in the traps or hung on bushes for direct capture using the net. In the capture using an insect net, a single collector inspected the cotton balls throughout the sampling period and all bees that landed on cotton were collected. The attractors were placed 1.5m from the ground and 2m apart from each other. The minimum distance between collection stations was approximately 500m. Two different capture methods were used to maximize the number of captured species. The data were used together to characterize the euglossine bee community. Previous studies in the region (Aguiar & Gaglianone, 2011, 2012) suggested that the methodologies can be complementary, as traps collect more individuals of *Eulaema* while more *Euglossa* are captured with nets.

Sampling was consistently undertaken on sunny days, and never during periods of atypical low temperatures. All voucher specimens are deposited in the Zoological Collection of the Laboratory of Environmental Sciences at the Universidade Estadual do Norte Fluminense.

Data analysis

Community descriptions

Three descriptive indices were estimated, Shannon-Wiener diversity (H´), Berger-Parker dominance (d), and Pielou's evenness (J) (Magurran, 2003), using the software Past version 1.91 (Hammer et al., 2001).

In order to compare the diversity among the three euglossine communities in the study area, we generated a 95% confidence interval for the Shannon-Wiener diversity index using the Jackknife method (Zahl, 1977) and sites with non-overlapping confidence intervals were considered significantly different. Diversity estimates were generated using the software Spade (Chao & Shen, 2005).

Species abundance distribution patterns were determined using the Rank-Abundance Plot, with their relative abundance plotted in descending order (Whittaker, 1965). All species whose relative abundance was larger than 10% were considered dominant for that area.

Rarefaction curves for species richness of each study area were obtained using 999 randomizations, following Magurran (2003). This procedure was undertaken to evaluate the sampling effort based on the species richness in the study areas. The analyses were carried out with the software EcoSim 7 (Gotelli & Entsminger, 2001) and the results plotted using Statistica 8.0 (StatSoft, 2007). The nonparametric richness estimators (Chao1, Jack1 and Bootstrap) were also calculated using EstimateS 8.0 (Colwell, 2006).

Comparative analyses with other Atlantic Forest communities

The structure of the euglossine communities sampled were compared with those reported in studies previously undertaken in Rio de Janeiro State, based on the following criteria: (1) We considered surveys that used baited traps or direct capture with entomological net in baits, that undertook sampling at least on a monthly basis for at least one year, and used at least five fragrance baits (and at least one of which was cineol or eucalyptol); (2) In the case of surveys on a quarterly basis, we considered only those that lasted for at least two years. The study areas examined in the present work, as well as those selected for comparisons (according to the criteria delimited above), are presented in Table S1 (available online as supplemenatry material).

Detrended Correspondence Analysis (DCA) was used to evaluate the ordination of the communities being compared and a data matrix was built to that end containing abundance data for the individuals in each area (considering the methodological criteria described above for comparisons between areas).

The first two axes of the DCA were correlated with climatic (temperature, humidity, precipitation) and geomorphological (altitude) parameters using Pearson's linear correlations. The same axes were utilized to evaluate the influence of the forest vegetation types on the ordination of the euglossine bee communities using nonparametric variance analysis (Kruskal-Wallis); the vegetation types were categorized according to Table S1. These analyses provided representations of the patterns of gradual species substitutions along environmental gradients, as suggested by Ter Braak (1995), and were carried out in Statistica 8 (StatSoft, 2007). Some of the species names used in the original publications were updated to correct identification, or in response to taxonomic changes.

Results

Description of the studied communities

A total of 1,710 male euglossine bees were collected, belonging to four genera and 15 species. *Euglossa cordata* (Linnaeus), *Eulaema nigrita* Lepeletier and *Eulaema cingulata* (Fabricius) were the dominant species, representing more than 80% of the individuals collected (Table 1).

In the SSSF fragment 978 individuals belonging to four genera and 11 species were collected; 444 individuals belonging to four genera and 10 species were collected in the LSSF fragment and 288 individuals belonging to three genera and 12 species were collected in the DMOF forest fragment (Table 1).

The estimated Shannon diversity in SSSF (H' = 1.52, d.f = 0.024) significantly differed from the LSSF and DMOF sites (H' = 1.23, d.f = 0.05 and H' = 1.36, d.f = 0.08, respectively). Similarly, the evenness in the SSSF area showed a higher value than those in LSSF or DMOF (Table 1).

Species composition differed in the three forest fragments: *Eulaema atleticana* Nemésio was sampled only in the LSSF site, *Eufriesea violacea* (Blanchard) only in SSSF, and *Euglossa annectans* Dressler, *E. bembei* Nemésio, and *E. truncata* Rebêlo & Moure were restricted to the DMOF site; *Euglossa clausi* Nemésio & Engel was found only in SSSF and DMOF (Table 1).

Euglossa cordata was dominant in LSSF (52% of the total), while *Eulaema cingulata* was dominant in both SSSF and DMOF (31% and 59%, respectively) (Table 1). Four species were dominant in SSSF, three species in LSSF, and two species in DMOF (Fig 1). In spite of the differences in species dominance, the curves obtained for species importance did not demonstrate significant differences among the different vegetation types (Kolmogorov-Smirnov test, $P > 0.05$), suggesting essentially the same distribution patterns in all three studied sites (Fig 1).

The rarefaction curves based on species richness as a function of abundance revealed that the DMOF site requires a higher sampling effort (Fig 2). This result was also corroborated by the richness estimators (Table 2). The rarefaction curves in the other two areas demonstrated a tendency toward stabilization beyond the abundance of 400 individuals, confirming the results of the richness estimators, which likewise indicated values very close to those actually observed (Table 2). Comparisons of the richness curves calculated for the study areas indicated that species richness was significantly greater in DMOF than in the other two areas (Fig 2).

The studied euglossine communities exhibited differences in their species composition and abundance along the year and among the different vegetation types (Fig 3). In LSSF and SSSF, the communities showed a peak of abundance during the dry season, as well as another smaller peak during the rainy season (although less prolonged in SSSF). The highest abundance in the DMOF area was observed between December and February, during the rainy season (Fig 3B).

Temporal variation in abundance was largely determined by the dominant species. *Eulaema cingulata* was more abundant during the dry season in SSSF and LSSF, but did not demonstrate a noticeable temporal pattern in the DMOF site (Fig 3D). The abundance peak of *Eulaema nigrita* occurred during the rainy season (January to April) in LSSF and DMOF, while its abundance in SSSF varied very little along the year (Fig 3E).

Euglossa cordata showed a peak of abundance in the LSSF site only during the dry period; this species showed two similar abundance peaks in the SSSF site, one during the dry season and one in the rainy season, while a single peak was observed in DMOF during the rainy season (Fig 3F). *Euglossa securigera* Dressler demonstrated two peaks of abundance in SSSF (Fig 3C) that were similar to those of *Euglossa cordata*; a few individuals were collected in the other two areas, making interpretations of its abundance more difficult. *Eufriesea violacea* and *E. surinamensis* (Linnaeus) were sampled only during the rainy period (between November and January).

Comparative analyses with other Atlantic Forest communities and correlation with abiotic factors

The correspondence analysis (DCA) of euglossine communities resulted in four major groupings (Fig 4): (1) one group clustered all of the Lowland Seasonal Semideciduous Forest areas (LSSF), between 0.0 and 0.4 on axis 1 and between -0.2 and -0.4 on axis 2, plus one of the Seasonal Semideciduous Submontane Forest sites (SSSF-5); (2) the second group encompassed the areas of Dense Lowland Ombrophilous Forests (DLOF) between -0.3 and -0.6 on axis 1 and between 0.0 and -0.4 on axis 2; (3) the third group, represented by the ar-

Table 1: Composition, abundance (Ab.), relative frequency (fr), richness, diversity, dominance, and evenness of the bee communities of the subtribe Euglossina in different vegetation types of the Atlantic Forest in Rio de Janeiro State, Brazil. LSSF: Lowland Seasonal Semideciduous Forests; SSSF: Submontane Seasonal Semideciduous Forest; DLOF: Dense Lowland Ombrophilous Forest; DSOF: Dense Submontane Ombrophilous Forest; and DMOF: Dense Montane Ombrophilous Forest.

Species	LSSF		SSSF		DMOF		TOTAL	
	Ab.	fr	Ab.	fr	Ab.	fr	Ab.	fr
***Eufriesea surinamensis* (Linnaeus)**	1	0.2	1	0.1	4	1.4	6	0.4
***E. violacea* (Blanchard)**	0	0	3	0.3	0	0	3	0.2
***Euglossa annectans* Dressler**	0	0	0	0	9	3.2	9	0.5
***E. bembei* Nemésio**	0	0	0	0	1	0.3	1	0.1
***E. cordata* (Linnaeus)**	230	51.8	171	17.5	20	7	421	24.6
***E. clausi* Nemésio & Engel**	0	0	6	0.6	1	0.3	7	0.4
***E. despecta* Moure**	5	1.1	2	0.2	1	0.3	8	0.5
***E. fimbriata* Moure**	2	0.5	22	2.3	4	1.4	28	1.6
***E. pleosticta* Dressler**	23	5.2	10	1.0	5	1.7	38	2.2
***E. securigera* Dressler**	12	2.7	213	21.8	9	3.1	234	13.7
***E. truncata* Rebêlo & Moure**	0	0	0	0	1	0.3	1	0.1
***Eulaema atleticana* Nemésio**	1	0.2	0	0	0	0	1	0.1
***E. cingulata* (Fabricius)**	48	10.8	306	31.3	170	59	524	30.5
***E. nigrita* Lepeletier**	120	27.0	242	24.7	63	22	425	24.9
***Exaerete smaragdina* (Guérin-Méneville)**	2	0.5	2	0.2	0	0	4	0.2
TOTAL	444	100	978	100	288	100	1710	100
Richness	10		11		12		15	
Diversity (H')	1.26		1.52		1.32		1.61	
Dominance (D)	0.518		0.313		0.590		0.306	
Evenness (J)	0.570		0.650		0.528		0.595	

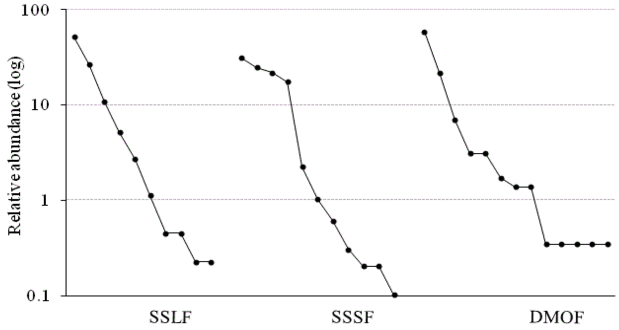

Fig 1. Abundance of orchid bee species in three forest communities in Rio de Janeiro State. LSSF: Lowland Seasonal Semideciduous Forests; SSSF: Submontane Seasonal Semideciduous Forest; and DMOF: Dense Montane Ombrophilous Forest. For descriptions of the areas, refer to Table S1.

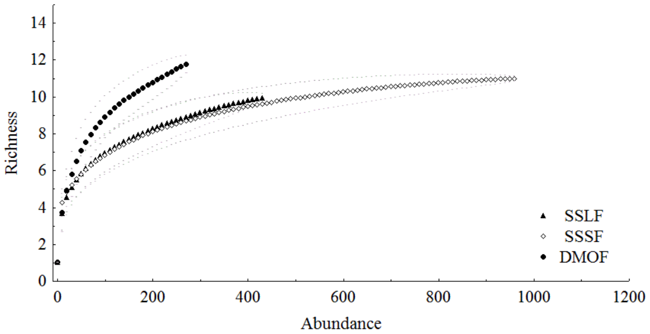

Fig 2. Rarefaction curves (1,000 simulations) for the species richness of orchid bees as a function of their abundance in areas with different vegetation types of forest in Rio de Janeiro State. Dotted lines indicate the upper and lower limits (95%) of each curve. The abbreviations follow those of Table S1.

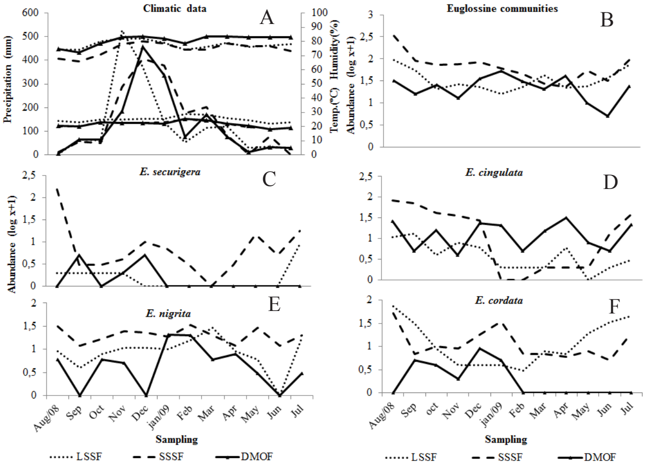

Fig 3. Climatic data (A) and temporal variations of Euglossine communities (B) in three vegetation types of forest in northern and northwestern Rio de Janeiro State, between August/2008 and July/2009. 3C to 3F represent the temporal variations of the most abundant species.

eas of SSSF and DMOF, was situated between 0.6 and 1.3 on axis 1 and between 0.0 and 0.4 on axis 2; (4) the fourth group, which encompassed the areas of DSOF, was more scattered in the diagram, with clear indication of subgroups within it. The eigenvalues of axis 1 and axis 2 were 0.20 and 0.19, respectively, while the percentage of variance explained by axis 1 was 24.9%, and 23.7% by axis 2.

The correlation between axis 1 of the DCA with the abiotic variables demonstrated a significant negative influence of precipitation (Person's r = - 0.56, N = 21, p = 0.001) and a positive influence of altitude (Pearson's r = 0.523, N = 21, *P* = 0.003) on the ordination of the euglossine communities. Only altitude had a significant positive influence on the second axis of the DCA (Pearson's r = 0.61, N = 21, *P* = 0.0004) (Table 3). The vegetation type likewise demonstrated an influence on the ordination of the euglossine communities on both axes 1 and 2 (Kruskal-Wallis test: H= 7.85, *P* = 0.049 and H= 15.39, *P*= 0.0015 respectively).

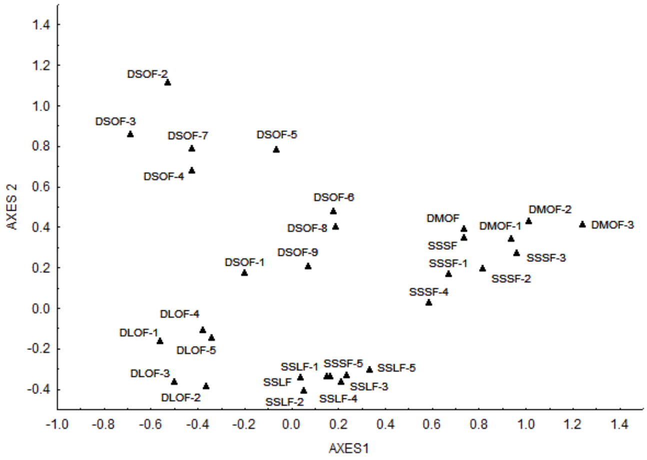

Fig 4: Diagram of the Detrended Correspondence Analyses (DCA) based on the composition of the orchid bee fauna found in areas in northern and northwestern Rio de Janeiro State. LSSF: Lowland Seasonal Semideciduous Forests; SSSF: Submontane Seasonal Semideciduous Forest; DLOF: Dense Lowland Ombrophilous Forest; DSOF: Dense Submontane Ombrophilous Forest; and DMOF: Dense Montane Ombrophilous Forest. The abbreviations follow those of Table S1.

Table 2 - Richness estimators for euglossine bee communities sampled between August/2008 and July/2009 in three different vegetation types of forest in Rio de Janeiro State, Brazil. The abbreviations follow those of Table S1.

Richness Estimator	LSSF	SSSF	DMOF
Jack1	12.75 ± 1.43	13.75 ± 1.97	17.6 ± 2.85
Chao1	10.33 ± 0.92	11 ± 0.16	23 ± 10.2
Bootstrap	11.17 ± 0	12.2 ± 0	14.93 ± 0

Table 3 - Pearson correlations between axes 1 and 2 of the Detrended Correspondence Analysis (DCA) and the variables of precipitation, temperature, humidity, and altitude in study areas in the northern and northwestern regions of Rio de Janeiro State, Brazil, relative to the compositions of their orchid bee fauna.

	Precipitation	Temperature	Humidity	Altitude
Axis 1	r = -0.56; *P* = 0.001	r = 0.014; *P* = 0.94	r = 0.24; *P* = 0.20	r = 0.52; *P* = 0.003
Axis 2	r =- 0.009; *P* = 0.96	r = -0.20; *P* = 0.291	r = 0.08; *P* = 0.632	r = 0.61; *P* = 0.0004

Discussion

The results of the present study, plus those obtained by Tonhasca et al. (2002a), Aguiar and Gaglianone (2008, 2011, 2012), and Ramalho et al. (2009) in other areas in the northern portion of the Rio de Janeiro State, revealed a total of 32 euglossine bee species for this region. This number corresponds to about 60% of the total orchid-bee fauna reported by Nemésio (2009) for the Atlantic Forest biome. Considering the result of the rarefaction curves and richness estimators, the orchid bee fauna in Dense Montane Ombrophilous Forest was underestimated and the real number of species is probably higher in the region.

Studies in other ombrophilous forests in Rio de Janeiro State (Tonhasca et al., 2002a; Ramalho et al., 2009) indicated higher number of species. In addition to insufficient sampling in the studied area, its regeneration time (approximately 60 years, according to local inhabitants), may not have been sufficient for more restrictive species to recolonize it. Species such as *Euglossa marianae* Nemésio and *Euglossa iopoecila* Dressler are known from areas of well-preserved Ombrophilous Forest (Tonhasca et al., 2002a; Ramalho et al., 2009).

These results point out to a great richness of orchid bee species in Dense Montane Ombrophilous Forest of the Atlantic Forest biome, even at the small spatial scales examined. This is possibly due to the great diversity of habitats, influenced by the wide geomorphological and climatic variation, besides the "Campos dos Goytacazes Gap", extending the Lowland Seasonal Semideciduous Forest to the coastline. This configuration forms a mosaic of landscapes probably favoring the occurrence of orchid bees in the region. The euglossine bee communities sampled in Dense Montane Ombrophilous Forest demonstrated the highest species richness among the studied physiognomies. The greatest average relative humidity values (up to 80%) seem to be the most important abiotic factor for this result. It was expected given the fact that other studies have indicated preference for humid forests by orchid bees (see Roubik & Hanson, 2004).

Eufriesea surinamensis and *Eulaema atleticana* were not found in Lowland Seasonal Semideciduous Forest in a previous study (Aguiar & Gaglianone, 2008) using the same methodology. Also four other species previously found there (*Eulaema niveofasciata* (Friese), *Euglossa gaianii* Dressler, *Euglossa leucotricha* Rebêlo & Moure, and *Euglossa truncata*) were not present in the current study. This reflects the dynamics of the bee communities in a short time scale, which might result in smaller chances of resampling rare species (Roubik, 2001).

Euglossa annectans (treated as a junior synonym of *Euglossa stellfeldi* Moure in Nemésio, 2009) had not been cited in previous surveys undertaken in Rio de Janeiro State although the species has been originally described from specimens collected at the Tijuca Forest, RJ (Dressler, 1982b). This species is endemic to the Atlantic forest domain, being distributed from the states of Bahia to Santa Catarina, and then into Argentina (Faria & Melo, 2007; Andrade-Silva et al., 2012). In this study *E. annectans* along with *E. bembei* were found only in Dense Montane Ombrophilous Forest, which, together with data from other studies (Tonhasca et al., 2002a; Darrault et al., 2006; Moure et al., 2007; Ramalho et al., 2009; Cortopassi-Laurino et al., 2009), indicates their close association with dense ombrophilous forests in Brazil. *Eulaema atleticana,* also endemic to the Atlantic Forest, has been considered restricted to coastal areas in northeastern and southeastern Brazil (Nemésio, 2009). However, more recent surveys have indicated that this species is common at altitudes above 700m (A. Nemesio, personal communication). The occurrence of *Eulaema atleticana* in the Lowland Seasonal Semideciduous Forests in Campos dos Goytacazes Gap may represent the southern limit of its distribution.

Eufriesea violacea was collected only in Submontane Seasonal Semideciduous Forest. This species has been previously found in other vegetation type of the Atlantic Forest domain (Tonhasca et al., 2002a; Nemésio & Silveira, 2006a; Giangarelli et al., 2009), but always in well-preserved areas. Giangarelli et al. (2009) reported that it was sensitive to habitat fragmentation and that its abundance becomes significantly reduced in small forest fragments. This can explain its reduced abundance in the present study.

Effects of fragmentation in the orchid bee communities were detected by Aguiar and Gaglianone (2012), who found changes in the pattern of species dominance in small fragments of Atlantic Forest. Originally the Lowland Seasonal Semideciduous Forests extended from southern Rio Grande do Norte to northern of Rio de Janeiro state. This forest was severely fragmented and the studied fragment represents only a very small portion of its original cover in the region (Silva & Nascimento, 2001). The number of species recorded by Bonilla-Gómez (1999) for this vegetation type was much higher and some relatively common species in this physiognomy have become rare in small forest fragments.

The dominance of *Euglossa cordata*, *Eulaema nigrita* and *Eulaema cingulata* in the present study was likewise observed in other surveys in the Atlantic Forest (Peruquetti et al.,1999; Aguiar & Gaglianone, 2008; Farias et al., 2008; Ramalho et al., 2009; Nemésio & Silveira, 2010). Ramalho et al. (2009) and Aguiar and Gaglianone (2012) demonstrated that these species were abundant in areas at different stages of conservation and do not confirm that they are indicators of disturbed areas, as suggested previously (e.g. Morato et al., 1992; Peruquetti et al., 1999). However, their tolerance to disturbance areas is unquestionable. Furthermore, the communal nesting or social behavior could favor their dominance in many of the communities studied (Zucchi et al., 1969; Garófalo, 1992; 1994; Augusto & Garófalo, 2004; Roubik & Hanson, 2004), as well as the great flight distance of Eulaema nigrita and E. cingulata (Dressler, 1982).

Despite exhibiting high relative abundances in all of the vegetation types studied, *Euglossa cordat*a and *Eulaema cingulata* showed variations in their dominance patterns. *Euglossa cordata*, for example, was not dominant in Dense Montane Ombrophilous Forest, although its abundance was greater than 50% in Lowland Seasonal Semideciduous Forest. *Eulaema cingulata* was the most abundant species in Dense Montane Ombrophilous Forest but the third one in Lowland Seasonal Semideciduous Forests. *Euglossa securigera* also showed great variation in their dominance patterns, represented 23% of the individuals collected in Submontane Seasonal Semideciduous Forest but only about 3% of the individuals sampled in Lowland Seasonal Semideciduous Forests and

Dense Montane Ombrophilous Forest. Vegetation types and differences in the availability of key resources can change population patterns of pollinators (Lázaro & Totland, 2010), including euglossine communities (Ramirez et al., 2002; Souza et al., 2005; Nemésio & Silveira, 2007); detailed analyses of resource availability in the forests would be important to clarify this issue. According to Smith et al. (2012) the floral landscape in the neotropical forest is spatially and temporally heterogeneous for foraging bees, promoting considerable change in the abundance pattern and amount of brood in the nests for bees.

The abundance distribution patterns observed in the present study were similar to those described by other authors in different Atlantic Forest areas: few dominant species; usually two to four species, each one with more than 10% of abundance and many rare species (Rebêlo & Garófalo, 1997; Sofia et al., 2004; Aguiar & Gaglianone, 2008; Nemésio, 2007; Ramalho et al., 2009). However, this pattern differs from that found by Aguiar and Gaglianone (2012) for small fragments of Atlantic Forest, where most species had each more than 10% of abundance, suggesting the loss of rare species in small forest fragments.

The euglossine communities in Lowland Seasonal Semideciduous Forests and Submontane Seasonal Semideciduous Forest demonstrated seasonal peaks of abundance, with one conspicuous peak during the dry period that was influenced by the abundances of *Euglossa cordata*, *E. securigera* and *Eulaema cingulata*, as well as another peak in the rainy season with a predominance of *Eulaema nigrita* (thus similar to data presented by Aguiar and Gaglianone [2008, 2011]). The peak of abundance in Dense Montane Ombrophilous Forest occurred during the rainy season but the same was not demonstrated for the studied semideciduous forests. Long-term studies are necessary to confirm the different seasonal pattern observed in these areas.

Short periods of adult activity were observed for *Eufriesea violacea* and *E. surinamensis*. Seasonality of *Eufriesea* species was observed in different regions in Brazil, for example, semideciduous forest in Paraná (Giangarelli et al., 2009), ombrophilous forest in the Rio de Janeiro (Tonhasca et al., 2002a; Ramalho et al., 2009) and sandbanks in Maranhão state (Silva et al. 2009). Our data corroborate the seasonality of these bees in different physiognomies of Atlantic Forest.

Three of the four main groups detected in the Detrended Correspondence Analysis (DCA) (groups 1, 2 and 4 in the Results) showed a close correspondence of the euglossine communities with the predominant vegetation types. A single group combined fragments from distinct vegetation types, Seasonal Semideciduous Submontane Forest and Dense Montane Ombrophilous Forest. This grouping may be partly explained by their uniquely sharing of *Euglossa clausi*, as well as a higher relative abundance of *Eulaema cingulata*.

As stressed by Linsley (1958) and Abrahamczyk et al. (2011), different distribution patterns along natural gradients reflect different responses to changes in the biotic and abiotic factors acting along those gradients. In the case of the present study, the original Atlantic Forest was a continuum of forest, "restinga", and mangrove swamp ecosystems stretching along the entire eastern coast of Brazil (Galindo-Leal & Câmara, 2003) and included diverse natural gradients within its latitudinal and longitudinal extensions, as well as altitudinal variation going from the coast to inland (Galindo-Leal & Câmara, 2003).

Rainfall and altitude, and also vegetation types, were the main factors influencing the ordination of the euglossine communities in the study areas. According to Abrahamczyk et al. (2011), these factors were found to have a significant effect on the ordination of euglossine communities in the western Amazon region. Altitudinal variation, can drastically reduce abundance patterns and alter the species compositions of euglossine communities. Our data suggest that altitude is important and can modify species composition and abundance of euglossine bees, even at small scales of variation. This result has to be tested in future studies. Temperature is influenced by altitudinal variations, and it is an important factor in the regulation of flowering time in the Atlantic Forest (Talora & Morellato, 2000; Pereira et al., 2008), altering plant resource availability for bees. According to Hegland and Boeke (2006) and Lázaro and Totland (2010) the diversity and density of plants affect the foraging behavior and community of pollinators. Indeed, the incursion of the Lowland Seasonal Semideciduous Forests, due to the Campos of Goytacazes Gap, significantly modified the structure of vegetation in the region and can represent a great influence on the community structure of euglossine bees.

Precipitation has been found to be significantly related to the abundance and species richness of euglossine bees in the western Amazon region (Abrahamczyk et al., 2011). The Lowland Seasonal Semideciduous Forests area has relatively high average temperatures (25.3ºC) associated with lower relative humidity levels (70%), which influenced the ordination of euglossine communities.

In addition to the climate and type of vegetation identified as strong influences on euglossine bee communities, other components, such as competition with similar species, historical occurrences, and habitat homogeneity (see Armbruster, 1993; Rosenzweig, 1995; Roubik, 2001; Tonhasca et al., 2002b; Roubik & Hanson, 2004) are also determinant for these bees. Also cleptoparasitic euglossine bees, such as those of the genus *Exaerete*, require additional biotic factors for their occurrence (such as the occurrence of host species in the genera *Eulaema* and *Eufriesea*) (Wcislo & Cane, 1996; Nemésio & Silveira, 2006b); however these factors have not been evaluated in this study, but should be considered in future studies.

Our data confirmed that a set of climatic, geomorphological and vegetational factors act to strongly influence euglossine species richness and composition (Ramirez et al., 2002; Souza et al., 2005; Nemésio & Silveira, 2007). *Euglossa annectans* and *E. bembei*, for example, were found only in Dense Montane Ombrophilous Forest, the survey region with the highest altitude (850 m) and humidity and the lowest average temperature (21 ºC). Altitude, however, does not appear to be a determinant factor in the geographical distribution of these species, as they have been also found in areas of dense ombrophilous forest at lower altitudes in southern Brazil (with warmer temperatures) (Cortopassi-Laurino et al., 2009).

Our study reinforces the importance of the conservation of landscape mosaics that include various vegetation types, as the composition of euglossine bee communities as well as their patterns of abundance and species dominance have been found to differ among these distinct sites. Furthermore, the occurrence of rare species, such as *Eulaema atleticana* in the Lowland Seasonal Semideciduous Forest, demonstrates the need to preserve these areas, as was similarly observed for *Euglossa annectans* and *E. bembei* in Dense Montane Ombrophilous Forest and for *Eufriesea violacea* in Seasonal Semideciduous Submontane Forest. The conservation of this important group of neotropical pollinators is essential for the maintenance of ecological services and the genetic diversity of their host plant populations, and attention should be given to studies focusing on these points.

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Supplementary Material

Table S1 available at: http://periodicos.uefs.br/ojs/index.php/sociobiology/rt/suppFileMetadata/231/0/418

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