

ECOLOGY, BEHAVIOR AND BIONOMICS

Edge Effects on the Orchid-Bee Fauna (Hymenoptera: Apidae) at a Large Remnant of Atlantic Rain Forest in Southeastern Brazil

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*Neotropical Entomology 35(3):313-323 (2006)*

Efeitos de Borda sobre a Fauna de Abelhas Euglossinas (Hymenoptera: Apidae) em um Grande Remanescente Florestal de Mata Atlântica no Sudeste do Brasil

RESUMO - Machos de abelhas euglossinas foram atraídos mensalmente com o auxílio de iscas aromáticas e coletados no período de julho de 1999 a abril de 2000 em seis pontos amostrais situados a diferentes distâncias da borda da mata (0 a 4.000 m) no Parque Estadual do Rio Doce, o maior remanescente florestal de Mata Atlântica de Minas Gerais, sudeste do Brasil. O objetivo deste estudo foi avaliar possíveis diferenças na abundância, riqueza e estrutura das comunidades de euglossinas a diferentes distâncias da borda. No total, foram coletados 1.183 machos de 20 espécies. Apenas variações pequenas e insignificantes na riqueza e abundância foram observadas entre os pontos amostrais. Duas espécies dominantes, *Euglossa analis* Westwood e *Eulaema cingulata* (Fabricius), apresentaram distribuições contrastantes com relação ao hábitat: enquanto os machos da primeira espécie foram coletados em maior número no interior da mata, machos de *E. cingulata* foram mais comuns na borda ou próximo a esta. As respostas de espécies como essas, e não índices de riqueza e abundância, são mais informativas com relação à integridade da floresta e efeitos de borda.

PALAVRAS-CHAVE: Insecta, bioindicador, conservação

ABSTRACT - Male orchid bees were sampled with chemical baits monthly from July 1999 to April 2000 at six sites situated at different distances from the forest edge (0 to 4,000 m) at Parque Estadual do Rio Doce, the largest remnant of Atlantic Forest in the state of Minas Gerais, southeastern Brazil. The main goal of this study was to assess the abundance, richness, and the community structure of the orchid-bee fauna at different distances from the edge. In all, 1,183 males from 20 species were collected. Only minor and insignificant variation in richness and abundance were observed among the sites. Two dominant species, *Euglossa analis* Westwood (Hymenoptera: Apidae) and *Eulaema cingulata* (Fabricius) (Hymenoptera: Apidae), showed strongly opposing habitat associations: while males of the former were most collected in the interior of the forest, the latter was most found at or close to the edge. The responses of individual species, such as these, and not composite measures of richness and abundance, are more informative regarding forest integrity and edge effects.

KEY WORDS: Insecta, Euglossina, bioindicator, conservation

Orchid-bee sampling has changed spectacularly since the late 1960's, when male-attracting aromatic compounds were discovered, artificially synthesized and employed as lures in the field (e.g. Dodson *et al.* 1969). It was soon realized that this methodology could be a powerful tool for testing theoretical ecological hypotheses. Powell & Powell (1987), Becker *et al.* (1991), and Morato (1994), for instance, tested effects of fragmentation in the Amazonian Forest using orchid bees. The use of chemical baits to attract male orchid bees also contributed to increase our taxonomic

knowledge of these bees, with several new species being described since then (e. g. Dressler 1978, 1982 a,b,c; Moure 1989, 1995, 1999; Rebêlo & Moure 1995; Dressler & Ospina-Torres 1997; Ospina-Torres & Sandino-Franco 1997; Moure *et al.* 2001; Moure & Schlindwein 2002; Oliveira & Nemésio 2003; Roubik 2004). Systematic sampling started in Central America in the late 1960's and early 1970's, focused on Amazonia in the 1980's and early 1990's, and are more recently being carried out especially in the Atlantic Rain Forest (e. g. Rebêlo & Garófalo 1991, 1997; Peruquetti *et*

*al.* 1999; Bezerra & Martins 2001; Tonhasca Jr. *et al.* 2002; Nemésio 2003, 2004) and adjacent domains (Neves & Viana 1997, 1999; Nemésio & Faria Jr. 2004).

However, most of those surveys were carried out at a single site within each studied area, and it has been hypothesized that a single site might not represent accordingly the community structure of a given area (Armbruster 1993). Besides, due to logistic conditions, samplings are generally done quite close to the forest edge. Morato (1994), for example, sampled three sites at an area in the Amazonian Forest: one outside the forest, the second one at the forest edge, and the third one 50 m inside the forest, which he considered “the interior of the forest”. But is 50 m enough to avoid edge effects? If any orchid bee species exhibit any association to habitats in the interior of the forests, forest patches large enough to avoid the edge effects should be chosen and sites deep in the forest, as well as at the edge, should be sampled for comparison.

Our goal was to compare the male orchid bee fauna at several sampling sites at different distances from the edge of a large forest fragment in order to establish (i) if the orchid-bee community structure varies according to the distance to the edge, (ii) if the orchid-bee abundance varies at different distances to the edge, and (iii) if other biotic and abiotic factors may explain the observed effects on richness and/or abundance of orchid bees.

## Material and Methods

**Study sites.** This study was conducted at the Parque Estadual do Rio Doce (PERD), the largest Atlantic Forest reserve in the state of Minas Gerais, southeastern Brazil. This park, situated in the municipalities of Dionísio, Marliéria, and Timóteo (19°30' - 19°48'S, 42°30' - 42°36'W), covers 35,973 ha, between elevations of 236 m and 515 m (Freitas 2000). Most of the vegetation at PERD consists of tropical semideciduous forest, including 3,000 ha of pristine forest (Andrade *et al.* 1997). Regional climate is warm and humid, with temperatures oscillating between 28°C and 39°C in the warm rainy season and between 7°C and 20°C in the cool dry season. Annual precipitation varies between 1,350 mm and 1,900 mm (Godinho 1996).

Six sampling sites were located in the park (Fig. 1). They were situated: *site-1*, exactly at the west edge of the forest (19°39'04"S - 42°35'05"W); *site-2*, 50 m inside the forest measured from the west edge (19°39'04"S - 42°35'04"W); *site-3*, 400 m inside the forest from the west border (19°39'16"S - 42°34'59"W); *site-4*, at 4,000 m from both the west and east borders of the forest (19°42'31"S - 42°33'50"W); *site-5*, at 2,000 m from the east border (19°41'02"S - 42°31'23"W); and *site-6*, at about 500 m measured from the east border of the park (19°41'54"S - 42°30'17"W).

**Sampling.** At each sampling site, 13 scent baits 2-m apart from each other were exposed to the bees at about 1.5 m above the soil. These baits were made of cotton waddings soaked with one of the following substances, known or believed to be attractive to orchid bees: benzyl acetate, 1,8-cineole, *p*-cresol acetate, dimethoxybenzene, eugenol,

$\beta$ -ionone, methyl benzoate, methyl *trans*-cinnamate, methyl salicylate,  $\beta$ -myrcene, skatole, *p*-tolyl acetate and vanillin. Both  $\beta$ -ionone and  $\beta$ -myrcene were kept below 8°C in a refrigerator until they were taken to the field. Baits with cineole and  $\beta$ -myrcene, the most volatile compounds, were recharged every hour.

Sampling was carried out between July 1999 and April 2000 at sites 1, 2, 3, and 5. Sampling was missed in July and September 1999 at site 4 and in July, September, and December 1999 at site 6. When sampling was carried out by two people, sites 1 and 3 were sampled in the same day, sites 2 and 5 in the following day and sites 4 and 6 in the third consecutive day; when carried out by three individuals, sites 1, 3, and 4 were sampled in one day and sites 2, 5, and 6 in the day after or before. Sampling the closest sites (1 and 2 or 2 and 3) in the same day was thus avoided.

Bees arriving at the baits between 6:00h and 18:00h were collected with insect nets, killed with ethyl acetate and deposited at the Taxonomic Collections of the Universidade Federal de Minas Gerais (UFMG).

Air temperature and relative humidity were measured every 30 min, with a digital thermo-hygrometer. The leaf area index (LAI) and visible sky fraction (VSF) were measured at each sampling site with the aid of a LAI-2000 Plant Canopy Analyzer (LiCor, USA). Those measurements were taken on May 2002 (beginning of the dry season), so that the correlation between an estimate of canopy cover and bee abundance and diversity could be evaluated.

**Data analysis.** The effect of the distance to the forest edge on bee abundance and species richness was estimated through the rank correlation (Spearman coefficient) between the distance to the border and total number of bees and species captured at each site. Since the sampling effort differed among sites, two data sets were analyzed separately: Set-1 – the 10-consecutive-month data set obtained in sites 1, 2, 3, and 5, and Set-2 – a seven-month data set obtained in all sites.

To measure the effect of the distance to the border on the composition of the fauna, the similarity between the fauna of each pair of sampling sites was estimated by means of the Renkonen percent similarity index, which was recommended by Wolda (1981) to be applied to small samples. Sites were clustered using the “unweight pair-group method using arithmetic averages” (UPGMA - Sneath & Sokal 1973) using the similarities calculated above.

The similarity matrices (of each dataset) were correlated to a matrix of geographic distance (in meters) among the sites (a matrix with the four sites of Set-1 and another one with the six sites of Set-2). However, since the elements are not independent (Fortin & Gurevitch 1993), the Mantel permutation test was used for these correlations (Manly 1994, Sokal & Rohlf 1995). For calculating statistic *Z*, 1,000 permutations were used, as recommended by Fortin & Gurevitch (1993).

The frequencies of each one of the most common species (those with more than one per cent of all euglossine individuals) were analyzed under two perspectives: 1) – by calculating the relative abundance of a given species at each site relative to the orchid bee community of that

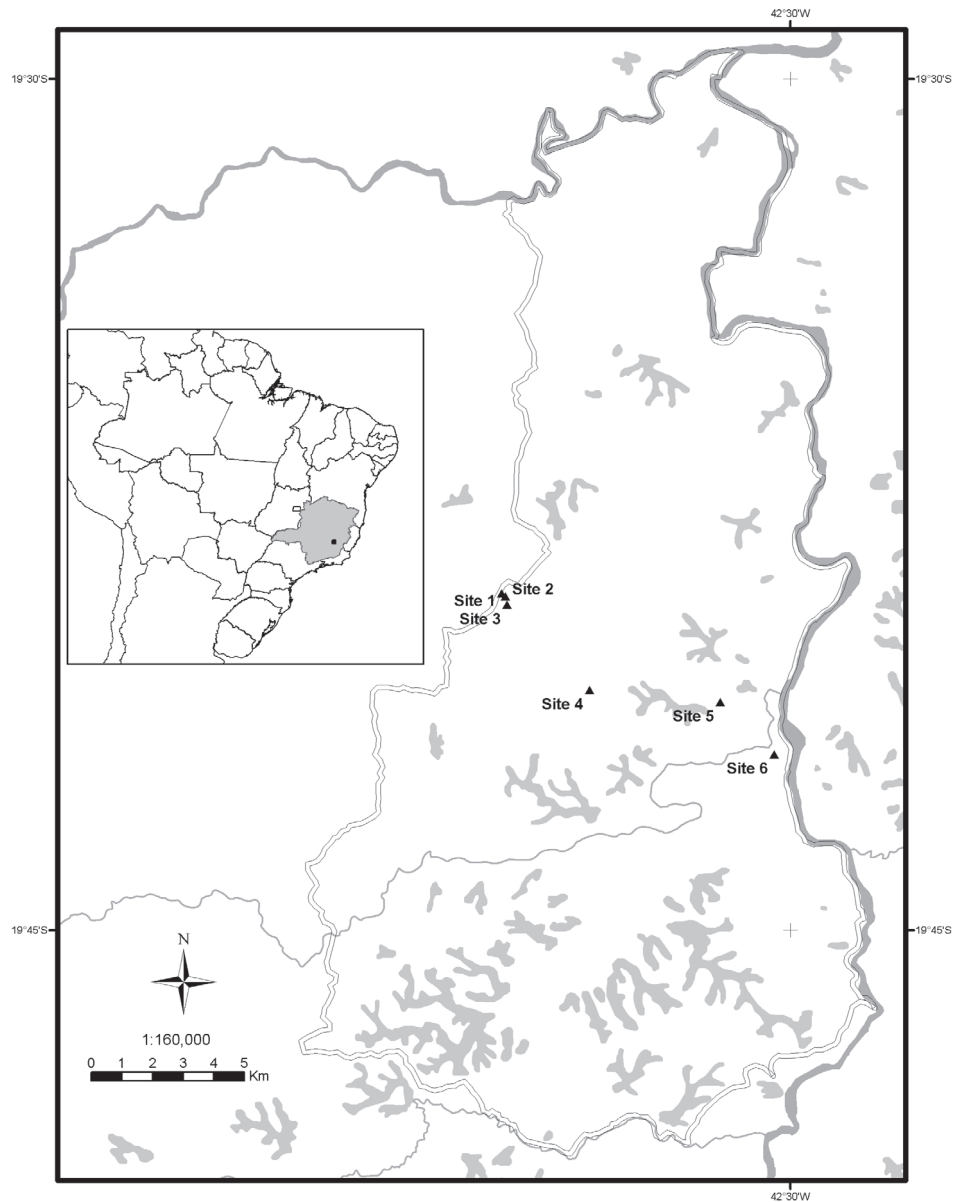


Fig. 1. Map showing the exact location of Parque Estadual do Rio Doce and the six sampling sites. Site 1 = edge; site 2 = 50 m from the edge; site 3 = 400 m from the edge; site 4 = 4,000 m from the edge; site 5 = 2,000 m from the edge; site 6 = 500 m from the edge.

particular site, and 2) – by calculating the relative abundance of a given species at each site in relation to the total number of individuals of that particular species in all sites. To avoid bias due to potentially seasonal species, and since in sites 4 and 6 some months were not sampled, only Set-1 (four sites sampled for 10 consecutive months) was employed in this specific analysis. This had the advantage of using larger samples of each species at each site.

The association between the leaf area index and fraction of visible sky and the abundance and species richness of bees was also evaluated through the Spearman rank correlation.

## Results

A total of 1,183 bees of 20 species of Euglossina were collected at the six sampling sites during the 10 months. Results obtained for the two sets of sampling sites were similar. The most common species was *Euglossa analis* Westwood (45% of all specimens collected for Set-1, and 51% for Set-2), followed by *Eulaema cingulata* (Fabricius) (23% and 19%, respectively) and *Eulaema nigrita* Lepelletier (10% and 9%, respectively). In all sites, the community was characterized by the dominance of two or three species (relative abundances > 10% of all bees caught – Tables 1 and 2). At the edge of the forest, *El. cingulata* was the most

Table 1. Relative abundance of each orchid bee species at each sampling site at different distances to the forest edge at the Parque Estadual do Rio Doce during 10 consecutive months (July 1999 – April 2000).

Species	Distance from the forest edge (m)								Total	
	0		50		400		2000			
	N	%	N	%	N	%	N	%	N	%
<i>Eufriesea aeneiventris</i> (Mocsáry)	1	0.4	0	0	0	0	0	0	1	0.1
<i>Ef. dentilabris</i> (Mocsáry)	1	0.4	0	0	0	0	0	0	1	0.1
<i>Ef. surinamensis</i> (L.)	1	0.4	0	0	0	0	0	0	1	0.1
<i>Ef. ornata</i> (Mocsáry)	1	0.4	0	0	0	0	0	0	1	0.1
<i>Euglossa analis</i> Westwood	36	16	33	26	55	43	291	67	415	45
<i>Eg. cognata</i> Moure	2	1	0	0	0	0	4	1	6	0.7
<i>Eg. cordata</i> (L.)	0	0	1	1	1	1	0	0	2	0.2
<i>Eg. despecta</i> Moure	15	7	10	8	6	5	29	7	60	7
<i>Eg. fimbriata</i> Rebêlo & Moure	2	1	1	1	1	1	0	0	4	0.4
<i>Eg. hemichlora</i> Cockerell	0	0	0	0	0	0	1	0.2	1	0.1
<i>Eg. pleosticta</i> Dressler	17	7	11	9	3	2	13	3	44	5
<i>Eg. sapphirina</i> Moure	2	1	3	2	5	4	31	7	41	4
<i>Eg. securigera</i> Dressler	13	6	2	2	1	1	2	0.5	18	2
<i>Eg. truncata</i> Rebêlo & Garófalo	5	2	3	2	4	3	6	1	18	2
<i>Euglossa</i> sp.	0	0	0	0	0	0	1	0.2	1	0.1
<i>Eulaema cingulata</i> (Fabricius)	87	38	39	31	32	25	52	12	210	23
<i>El. nigrita</i> Lepageletier	43	19	25	20	19	15	5	1	92	10
<i>Exaerete smaragdina</i> (Guérin-Méneville)	1	0.4	0	0	1	1	0	0	2	0.2
Total (N)	227		128		128		435		918	
Abundance (specimens/h)	1.9		1.1		1.1		3.6		1.9	
Mean temperature (°C)	26.9		24.6		24.2		24.0		–	
Mean humidity (%)	65		73		78		78		–	
Leaf area index	0		2.80		3.41		2.27		–	
Visible sky fraction (%)	100.0		9.5		5.6		15.3		–	
Frequency of dominant species (n)	73(3)		77(3)		83(2)		79(2)		78(3)	
Frequency of <i>Eulaema</i> (%)	57		51		40		13		33	

common species (38% and 40% for Set-1 and Set-2, respectively) and the two species of *Eulaema*, together, represented 57% and 53% of all individuals collected, respectively, for Set-1 and Set-2. At this site, *Eg. analis* contributed with 16% and 19% of the individuals, respectively. However, at site-5, the relative abundance of *Eulaema* dropped to 13% and 10%, while that of *Eg. analis* rose to 67% and 69% (Table 1). At site-4 (included only in Set-2), the relative abundance of *Eulaema* was 20%, whereas that of *Eg. analis* was 59%.

Only eight species contributed with one per cent or more individuals (Table 1) to the sample, totaling 898 bees, when Set-1 is analyzed. Table 3 shows the relative abundances of each one of the eight most common species based only on

the total number of individuals of each particular species in Set-1. Based on Tables 1 and 3, seven of the eight most common orchid-bee species at PERD may be divided in three broad groups: (i) those with no clear association to any specific environment (*Euglossa pleosticta* Dressler and *Euglossa truncata* Rebêlo & Moure), (ii) those common at the edge (*Euglossa securigera* Dressler, *El. cingulata* and *El. nigrita*), and those most common in the interior forest (*Eg. analis* and *Euglossa sapphirina* Moure). *Euglossa despecta* Moure was slightly more common in the interior forest. No species was most abundant at the intermediate (50 m and 400 m) sites.

In general, temperatures were highest close to the edge and lowest inside the forest. This trend holds when averages

Table 2. Frequencies of each euglossine species at each sampling site at different distances of the forest edge at the Parque Estadual do Rio Doce for seven months (August, October, November, 1999; January, February, March, and April, 2000).

Species	Distance from the forest edge (m)										Totals				
	0		50		400		500		2000				4000		
	N	%	N	%	N	%	N	%	N	%	N	%	N	%	
<i>Eufriesea aeneiventris</i>	1	0.7	0	0	0	0	0	0	0	0	0	0	1	0.1	
<i>Ef. dentilabris</i>	1	0	0	0	0	0	0	0	0	0	0	2	2	2	0.3
<i>Ef. surinamensis</i>	1	0.7	0	0	0	0	0	0	0	0	0	0	2	0.3	
<i>Ef. violacea</i> (Blanchard)	0	0	0	0	0	0	0	0	0	0	0	2	2	2	0.3
<i>Euglossa analis</i>	27	19	18	38	29	50	58	50	174	69	74	59	380	51	
<i>Eg. cognata</i>	2	1	0	0	0	0	2	2	1	0.4	0	0	5	0.7	
<i>Eg. cordata</i>	0	0	1	2	0	0	0	0	0	0	0	0	1	0.1	
<i>Eg. despecta</i>	7	5	4	8	0	0	5	4	14	6	8	6	38	5	
<i>Eg. fimbriata</i>	2	1	0	0	1	2	1	1	0	0	0	0	4	0.5	
<i>Eg. hemichlora</i>	0	0	0	0	0	0	0	0	1	0.4	1	1	2	0.3	
<i>Eg. pleosticta</i>	8	6	4	8	2	3	4	3	12	5	7	6	37	5	
<i>Eg. sapphirina</i>	0	0	1	2	3	5	10	9	17	7	2	2	33	4	
<i>Eg. securigera</i>	1	1	1	2	0	0	3	3	2	1	0	0	7	1	
<i>Eg. cf. townsendi</i>	0	0	0	0	0	0	0	0	0	0	1	1	1	0.1	
<i>Eg. truncata</i>	2	1	2	4	3	5	1	1	6	2	6	5	20	3	
<i>Eulaema cingulata</i>	57	40	13	27	13	22	16	14	25	10	15	12	139	19	
<i>El. nigrita</i>	32	23	4	8	6	10	16	14	1	0.4	10	8	69	9	
<i>Exaerete smaragdina</i>	0	0	0	0	1	2	0	0	0	0	0	0	1	0.1	
Total (N)	141		48		58		116		253		126		742		
Abundance (specimens/h)	1.7		0.6		0.7		1.4		3		1.5		1.5		
Mean temperature (°C)	27.3		25.0		24.6		24.6		24.2		24.2		–		
Mean humidity (%)	65		73		78		81		78		79		–		
Leaf area index	0		2.80		3.41		2.61		2.27		2.86		–		
Visible sky fraction (100%)	100.0		9.5		5.6		12.7		15.3		8.6		–		
Freq. of spp. >10% (n)	82(3)		65(2)		82(3)		78(3)		79(2)		71(2)		70(2)		
Freq. of <i>Eulaema</i> (%)	63		35		32		28		10		20		28		

are calculated considering all ten months or only the months in which all six areas were sampled (Table 4). Furthermore, the amplitude of temperature variation along the day was by far greater at the edge. At sites 4 and 6 temperatures were not measured in July, one of the coldest months, and this probably accounts for their comparatively high average temperatures. On the other hand, relative humidity was lowest the closer to the edge (Table 5).

There was no correlation between distance to the edge and bee abundance, richness, temperature, humidity (correlation was only estimated for this variable for Set-1 since many data were lacking for sites 4 and 6, see Table 5), leaf area index, and visible sky fraction. There was a significant correlation, however, between temperature and

abundance of *El. cingulata* ( $r_s = 1.00$  for Set-1, and  $r_s = 0.97$  for Set-2;  $P < 0.05$ ) and *Eg. analis* ( $r_s = -1.00$ ,  $P < 0.05$ , for Set-1; but no correlation for Set-2,  $r_s = -0.50$ ,  $P > 0.05$ ), and between humidity and abundance of *Eg. analis* ( $r_s = 0.95$  for Set-1,  $P < 0.05$ ). Correlation between humidity and abundance of *El. cingulata* was high but not significant ( $r_s = -0.85$ ,  $P > 0.05$ , for Set-1).

Abundance of all orchid-bee species taken together changed erratically among sites, while the number of species tended to remain constant. However, the composition of the fauna (regarding both presence and abundance of species) progressively changed from the edge to the interior of the forest. Thus, the similarity between the edge fauna and those at the other sites tended to decrease



Table 3. Distribution of the eight most abundant euglossine species (in %) at PERD, according to different distances from the forest edge.

Species	Distance from the forest edge (m)				Totals N
	0	50	400	2000	
	%	%	%	%	
<i>Euglossa analis</i>	9	8	13	70	415
<i>Eg. despecta</i>	25	17	10	48	60
<i>Eg. pleosticta</i>	39	25	7	30	44
<i>Eg. sapphirina</i>	5	7	12	76	41
<i>Eg. securigera</i>	72	11	6	11	18
<i>Eg. truncata</i>	28	17	22	33	18
<i>Eulaema cingulata</i>	41	19	15	25	210
<i>El. nigrita</i>	47	27	21	5	92

inward the forest. When similarity was correlated to geographic distance through the Mantel test, the results obtained for Set-1 showed a marginally significant correlation ( $r = -0.81$ ;  $n = 4$ ;  $P = 0.04$ ), but those obtained for Set-2 ( $r = -0.13$ ;  $n = 6$ ;  $P = 0.30$ ) were not correlated, i.e., the groupings observed in Fig. 2 seems to be more related to distance from the edge than to distance among sites.

The site cluster (Figs. 2 and 3) shows a great overall similarity among sites, with the most distinctive of them (the edge) still sharing more than 50% similarity with the others. This is due to the fact that the two most common species were the same at all sites and that the same three species were the most common ones in all but one site. In spite of this, the clustering clearly reflects the tendency of progressive change in the fauna composition, calling attention to the fact that the edge fauna is the most distinct of all site faunas.

### Discussion

**Species richness.** Twenty species were recorded in this study. Bonilla-Gomez (1999) recorded 31 species for the Reserva Florestal de Linhares, state of Espírito Santo, and Tonhasca Jr. *et al.* (2002) recorded 21 species for the Desengano region, state of Rio de Janeiro, both 22,000 ha-remnants of Atlantic Forest on the Brazilian coast, differently of PERD, which is situated in the interior.

Peruquetti *et al.* (1999) recorded four *Euglossa* species in PERD which are not present in our study. However, one of us (AN) has checked the bees collected by Peruquetti and colleagues and concluded that the difference in both lists is due to misidentification of some species in Peruquetti and colleagues' list. Thus, what they called *Euglossa avicula* Dressler, in fact is *Euglossa townsendi* Cockerell (moreover, presently, *Eg. avicula* is considered a junior synonym of *Eg. heterosticta* Moure – see Bembé 2004); *Eg. amazonica* Dressler specimens are, in fact, *Eg. pleosticta*; *Eg. modestior* Dressler is *Eg. securigera*, and the single *Eg. liopoda* Dressler specimen was not found for examination and remains as a doubtful record. Moreover, the specimen assigned by Peruquetti and colleagues as *Eufriesea* sp. 1 is currently deposited at the entomological collection of the Universidade Federal do Paraná. One of us (AN) had the opportunity of studying this specimen and concluded it is *Eufriesea dentilabris* (Mocsáry), also collected in the present study. Kimsey & Dressler (1986) considered *Ef. dentilabris* a junior synonym of *Eufriesea distinguenda* (Gribodo) but, after examining specimens of both species, one of us (AN) concluded that they are separate species. However, *Eufriesea violascens* (Mocsáry) and *Eufriesea smaragdina* (Perty) were collected by them and not by us, and a specimen of *Exaerete dentata* (Linnaeus) was collected at PERD in 1990 and is currently deposited at UFMG, raising the richness of PERD to, at least, 23 species.

The most striking difference between our sample and that obtained by Peruquetti *et al.* (1999) lays on the community structure. In their study, *Eg. analis* represented only 2% of the total orchid bee fauna and *El. cingulata*

Table 4. Minimum (-), maximum (+) and mean (M) temperatures at each sampling site between July 1999 and March 2000.

	Edge			50 m			400 m			500 m			2000 m			4000 m		
	-	+	M	-	+	M	-	+	M	-	+	M	-	+	M	-	+	M
Jul	19.0	24.2	21.6	17.8	26.1	22.0	18.0	21.9	20.0	-	-	-	16.5	24.3	20.4	-	-	-
Aug	15.7	26.0	20.9	12.1	24.8	18.5	17.0	22.8	19.9	14.0	23.0	18.5	12.4	23.3	17.9	12.0	24.0	18.0
Sep	24.5	31.4	28.0	21.2	28.0	24.6	23.2	25.4	24.3	-	-	-	21.7	27.1	24.4	-	-	-
Oct	23.8	31.9	27.9	21.6	32.4	27.0	21.1	27.5	24.3	21.5	31.3	26.4	20.6	29.9	25.3	18.2	30.2	24.2
Nov	19.3	35.9	27.6	21.4	25.7	23.6	21.0	25.3	23.2	21.6	26.1	23.9	22.5	24.2	23.4	20.0	25.0	22.5
Dec	23.1	34.1	28.6	23.1	26.2	24.7	23.9	28.3	26.1	-	-	-	25.6	27.5	26.6	24.4	27.2	25.8
Jan	27.9	33.7	30.8	22.6	32.4	27.5	26.0	29.2	27.6	23.5	31.5	27.5	21.4	31.4	26.4	24.5	29.7	27.1
Febr	24.5	29.9	27.2	24.1	30.7	27.4	24.0	28.0	26.0	24.3	27.9	26.1	24.4	28.7	26.6	24.6	29.0	26.8
Mar	27.1	32.1	29.6	23.6	28.9	26.3	26.1	27.1	26.6	24.0	27.0	25.5	24.0	27.2	25.6	24.2	28.5	26.4
M	22.8	31.0	<b>26.9</b>	20.8	28.4	<b>24.6</b>	22.3	26.2	<b>24.2</b>	21.5	27.8	<b>24.6</b>	21.0	27.1	<b>24.0</b>	21.1	27.7	<b>24.4</b>

Table 5. Minimum (-), maximum (+) and mean (M ) relative humidity at each sampling site between July 1999 and March 2000.

	Edge			50 m			400 m			500 m			2000 m			4000 m		
	-	+	M	-	+	M	-	+	M	-	+	M	-	+	M	-	+	M
Jul	66	82	74	76	95	86	76	91	84	-	-	-	84	93	89	-	-	-
Aug	47	87	67	59	90	75	68	86	77	-	-	-	69	90	80	-	-	-
Sep	44	63	54	53	78	66	73	80	77	-	-	-	59	76	68	-	-	-
Oct	50	80	65	51	79	65	75	87	81	39	67	53	60	80	70	45	80	63
Nov	33	87	60	60	77	69	64	85	75	-	-	-	57	78	68	-	-	-
Dec	52	91	72	74	80	77	65	86	76	-	-	-	85	93	89	75	89	82
Jan	44	55	50	46	80	63	68	71	70	79	98	89	58	90	74	-	-	-
Febr	69	90	79	72	87	80	79	92	86	86	96	91	82	89	86	83	92	88
Mar	61	77	69	68	86	77	-	-	-	83	97	90	-	-	-	75	92	84
M	52	79	<b>65</b>	62	84	<b>73</b>	71	85	<b>78</b>	72	90	<b>81</b>	69	86	<b>78</b>	70	88	<b>79</b>

accounted for 53% (n = 308). This outstanding difference is probably related to the differences between both studies. In the present study, bees were collected with insect nets, while in Peruquetti and colleagues' study baited traps were used. Nemésio & Morato (2004) have quantitatively shown that insect nets are almost five times more efficient than bait traps and that these latter present a drastic bias, increasing by a factor of two the frequency of individuals of the genus *Eulaema*. In some instances, species of *Euglossa* which were common and even dominant species at a site when sampling is performed with insect nets were rarely caught in bait traps (Nemésio & Morato 2004).

It is remarkable that none of the large *Euglossa* belonging to the subgenus *Glossura* was ever collected at PERD. *Eg. imperialis* Cockerell occurs in the Belo Horizonte region (Nemésio 2004) and Parque Estadual do Rio Preto (northeast

of PERD) (Nemésio & Faria Jr. 2004) and northeastern state of São Paulo (south of PERD). *Euglossa imperialis*, *Euglossa chalybeata* Friese and *Eg. ignita* Smith are abundant at the Reserva Florestal de Linhares (state of Espírito Santo), the latter two also occur at the Desengano region (state of Rio de Janeiro, both west of PERD), and the former two are also present in southern state of Bahia (north of PERD – unpublished data, specimens deposited at UFMG).

Rebêlo & Moure (1995) also considered *Euglossa annectans* Dressler as a member of the subgenus *Glossura*. This species is common in Minas Gerais (see Nemésio 2004) and northeastern São Paulo (see Rebêlo & Garófalo 1991, 1997), but it was not collected at PERD. One of us (AN) has recently treated *E. annectans* as a junior synonym of *Euglossa stellfeldi* Moure (Nemésio & Faria Jr. 2004). However, males recently collected by Dr. S. C. Augusto in

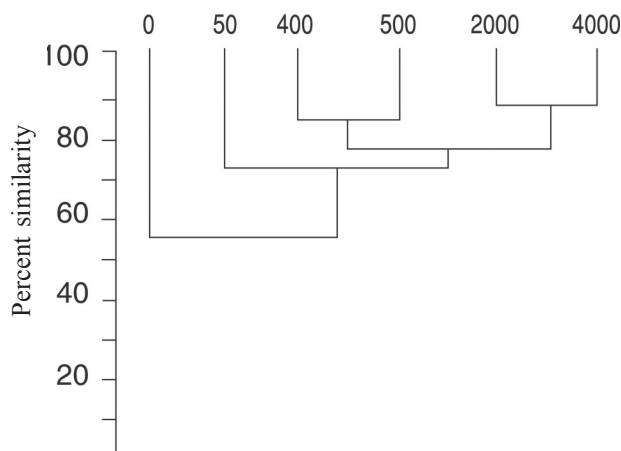


Fig. 2. Clustering of six sites at Parque Estadual do Rio Doce, southeastern Brazil, according to the similarity of their fauna of male orchid bees. Numbers in site acronyms refer to the distance, in meters, from the nearest edge.

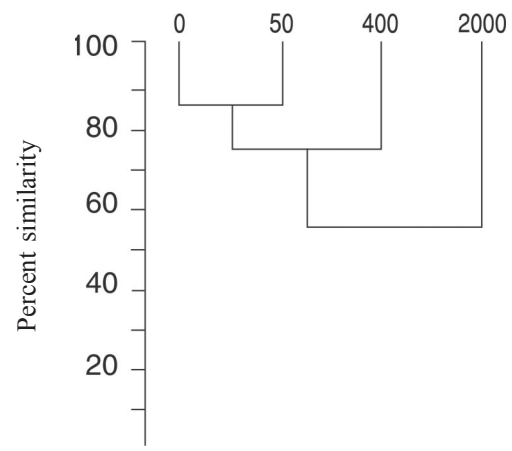


Fig. 3. Clustering of four sites at Parque Estadual do Rio Doce, southeastern Brazil, according to the similarity of their fauna of male orchid bees. Numbers in site acronyms refer to the distance, in meters, from the nearest edge.

Ilha do Cardoso, southern state of São Paulo, southeastern Brazil, some 50 km far from the type locality of *E. stellfeldi*, have shown that both species are really distinct, as Dressler (1982) and Rebêlo & Moure (1995) maintained. Thus, in this paper, *E. annectans* is reinstated as a valid species by the first author and the individuals treated as *Eg. stellfeldi* in Nemésio & Faria Jr. (2004) work are now understood as *Eg. annectans* individuals.

In spite of having the most extreme climatic conditions and the largest daily amplitudes of both temperature and relative humidity, the edge yielded the most species (15). This may be an ecotone effect, with males of species both typical of the interior of the forest and those which prefer open areas both being attracted by the baits at the forest edge. This is further supported by the fact that many of the most common species at the forest edge were the same found at small, narrow, riparian forest fragments composed of shorter trees and with canopy more open than those at PERD. These fragments, sampled at the Belo Horizonte Metropolitan area (Nemésio 2004), are immersed in a matrix of savannas and fields and, in recent times, urban areas. Another example of such ecotone effect, in the Belo Horizonte region, is *Eufriesea nigrohirta* (Friese), normally occurring in the “campo rupestre” (rocky montane field) formations, which was attracted once inside a small forest fragment surrounded by “cerrado” and “campo rupestre” areas, to a cineole bait. This also suggests that orchid bees may try incursions in different areas seeking for the aromatic compounds. However, it is not known whether those species would naturally occur at the edge (or at any other site), attracted by their usual aromatic sources, since in the baits these substances are in their pure forms. Consequently, these conclusions should be treated with care, at least until the attractive power of these baits is fully understood.

The results obtained at PERD show that species richness is a poor indicator of edge effects. This conclusion is the same reached by Morato (1994), who also found similar species richness of orchid bees in open areas and at the edge and in the interior of the Amazon forest. However, faunistic composition, considering presence and relative abundance of the various species, may be indicative of environmental condition inside forest fragments, provided that composition of regional faunas at relatively undisturbed habitats is known.

**Abundance.** Contrary to Morato’s (1994) findings, our data suggest that the distance to the forest border does not directly affect orchid bee abundance. It should be emphasized that the “interior” sample of Morato’s study (where he recorded the largest bee abundance) was taken at only 50 m inside the forest (Morato 1994). Our data suggest, however, that at this point the orchid bee fauna might still be heavily affected by edge effects. The erratic changes observed at PERD suggest that orchid bee abundance may be responding to subtle variations in light incidence, temperature, humidity and/or other unmeasured variables, including those influencing odor dispersion inside the forest. The fact that no correlation between abundance and/or richness and any of these variables was found is probably due to the differential behavior of different species, as shown by the eight most

common species. It also could be a consequence of the fact that measurements taken at the sampling sites may not represent the average condition to which the bees are exposed in their whole (probably large) habitats. The significant correlations between temperature and humidity with abundance of *Eg. analis* and temperature with abundance of *El. cingulata* are obvious, since these species presented strong associations to the inner and the outer sites (respectively), regarding forest edge, and temperature and humidity are correlated with distance to the edge (see Tables 1 and 2) – which is in agreement with other studies (Lovejoy et al. 1986, Kapos 1989). Whether or not temperature and/or humidity are the factors that determine environment associations by those bees is a subject for further study.

Armbruster (1993) suggested that a sample obtained by baiting a single spot may not be a good representative sample of the structure of the orchid bees of an area. Our data, however, suggest the opposite. At PERD, although abundance varied greatly from site to site, if one excludes the edge, the community composition of the sites was extremely similar, as shown in Tables 1 and 2 and Figs. 1 and 2. Thus, apparently, sampling one site at the edge and one site in the interior of the forest (as deep as possible) would give us a good idea of the general pattern of the orchid bee community of a given area.

Other authors (Powell & Powell 1987, Morato 1994) have shown that different orchid bee species prefer environments at different distances in and out the forest edge. Thus, Morato (1994) classified orchid bee species as a) intolerant to the forest edge; b) tolerant to the forest edge but intolerant to open spaces; c) indifferent (tolerant to forest edge and to open spaces) and d) intolerant to the forest interior. At PERD, where more points at different distances to the forest border were sampled, as compared to Morato’s (1994) work, the differences were not as straightforward. *Euglossa analis* and *Eg. sapphirina* did show a strong association to the farthest environments into the forest, but the former was still at the edge relatively abundant. On the other hand, *El. cingulata* and *El. nigrita* (the former rare and the latter absent in Morato’s sample) seem to prefer the environments close to the border than those in the interior of the forest. *El. nigrita* may be what Morato (1994) defined as tolerant to the forest edge and to open spaces; however, considering all that is written about it (Morato 1994, Tonhasca Jr. et al. 2002), the species may actually prefer open spaces (not sampled in this study). *Euglossa pleosticta*, *Eg. truncata* and, apparently, *Eg. despecta* are clearly tolerant to the forest edges. However, since we did not sample the open areas out of the forest at PERD, they may either be intolerant to open spaces or indifferent to them.

As observed in the Amazonian Forest by Morato (1994), and despite the fact that the same three species were dominant at almost all sites, this variable tolerance of varying habitat conditions, and the consequent changes in the relative frequencies of the species lead to a progressive change in the composition of the fauna along the gradient edge-interior of the forest. This is seen in Fig. 3, when sites 3 and 6 (400 and 500 m from the forest edge, but in opposite sides of the park – see Fig. 1) appears as the most similar to each other. Both these areas presented different visible sky fractions



and leaf area indexes, but very similar mean temperature and humidity (Table 2), suggesting these two latter factors might have a stronger influence on these bees.

**Overall similarity.** In general, similarity among sites was quite high, with the most distinct site, the edge, still sharing more than 50% of similarity with the other sites (when six sites are considered). However, in this situation, Mantel test has revealed that the similarity among sites seems to be more associated to the distance from the edge than to the distance among them. It is outstanding that site-3 (400 m from the edge) was highly similar (84%) to site-6 (500 m from the edge) which is situated more than 9,000 meters far away (Fig. 1), but both are approximately the same distance from an edge. The marginally significant result in the opposite direction found when Set-1 was tested could be an effect of the small number of sites and, more important, because they present very different distances from the edge. On the other hand, it reinforces the ambiguous position of site-2 (50 m from the edge), that tends to associate to the edge when Set-1 is analyzed but also tends to associate to the other sites when Set-2 is considered. It shows that, at 50 m from the edge, the orchid bee fauna may still be under strong effect from the edge.

**Individual species.** In conservation terms, a better understanding of the ecology of *El. nigrata* is particularly important. If it really is a species which prefers disturbed and/or open environments, it could be an excellent bioindicator for several reasons: (i) its wide geographic distribution in the Neotropics, from Central America (Oliveira 2000) to the state of Rio Grande do Sul, southern Brazil (Wittmann *et al.* 1988), and from sea level (Bezerra & Martins 2001) to high altitudes (Silveira & Cure 1993) – which means a tool of broad geographic utilization; (ii) its easy identification in the field, and (iii) the easy use of chemical baits to attract male orchid bees, which makes field studies easy. Finding a few reliable bioindicators may be an important tool for conservation efforts. Other organisms in other taxa have also been suggested as bioindicators, but few are as widespread as *El. nigrata* [e. g. *Atta cephalotes* (L.) (Hymenoptera: Formicidae), for well preserved Atlantic Forest environments, and *Atta sexdens* (L.) (Hymenoptera: Formicidae), for disturbed areas – see Corrêa *et al.* 2005].

Concerning *El. cingulata*, also a widespread species – from Central America to the state of Paraná, southern Brazil (Oliveira 2000), overlapping with the distribution of *El. nigrata* – there is some controversy regarding its habitat. Oliveira (2000) states that this species is typical of dense and undisturbed environments, which suggests an example of ecological exclusion (with *El. nigrata*). Contrarily to Oliveira's ideas, however, our data, as well as those obtained by other authors (Tonhasca Jr. *et al.* 2002), suggest that this species may be dependent on some sort of forest environment but is perfectly tolerant to ill developed forests and open environments. On the other hand, we have noticed that this species is more abundant in lower elevations, becoming rarer above 800 m elevation (unpublished data). If any kind of

ecological exclusion occurs between these two species, it may involve altitude and, perhaps, the kind of floral resources used by them. Thus, the presence of *El. cingulata* in the interior of fragments might also indicate some degree of disturbance.

If *El. nigrata* and *El. cingulata* may constitute bioindicators of disturbed environments on one hand, finding one or more species which play the reverse role is not as simple. Species with wide distributions have quite different frequencies over their distribution and it is not a simple matter to establish why. *Eg. pleosticta*, for example, is the dominant species in a fragment in northeastern state of São Paulo (Rebêlo & Garófalo 1991) and in a well preserved area of the state of Maranhão, northeastern Brazil (Silva & Rebêlo 1999), but it is absent or occurs in very low frequencies in the rest of the Atlantic Forest (e. g. PERD, this study, Bonilla-Gomez 1999, Bezerra & Martins 2001, Tonhasca Jr. *et al.* 2002), regardless of the size of the fragment. In Belo Horizonte metropolitan region, where several fragments were sampled (Nemésio 2004), the dominant *Euglossa* species varies largely from place to place and the reasons for this are unknown.

Tonhasca Jr. *et al.* (2002) suggested *Eg. analis* to play the role of a bioindicator of healthy environments, since it occurs in good numbers in the large and relatively well preserved, 22,000 ha forest remnant of Desengano region, state of Rio de Janeiro but is absent from or occurs only in low frequencies in the disturbed fragments sampled in the same region. This species is also abundant at the Reserva Florestal de Linhares, state of Espírito Santo, southeastern Brazil (22,000 ha, Bonilla-Gomez 1999, 17% of the orchid bee fauna), a well preserved Atlantic Forest remnant. Based on our own data, it is tempting to agree with Tonhasca Jr. *et al.* (2002). PERD is, perhaps, the largest and best preserved Atlantic Forest fragment ever sampled for orchid bees. *Eg. analis* is the dominant species there. However, its absence from other areas in the Atlantic Forest domain leaves the following question: is it absent because the environment quality is too poor to sustain viable populations of *Eg. analis* (in this case it would really be an excellent example of a bioindicator of healthy environments) or is it absent because it never occurred at those areas? Given the available data, this species seems to occur only in well preserved, large fragments of the typical coastal Atlantic Forest or in fragments in the interior at low elevations (specimens of this species from well preserved fragments in southern state of Bahia, northeastern Brazil, are also deposited at UFMG, and reinforce this hypothesis).

On the other hand, our data suggest that *Eg. sapphirina* could also play the same role as a bioindicator of healthy environments, but the results obtained by Tonhasca *et al.* (2002) go on the opposite direction. It means that further investigation on this topic is needed, especially in areas not yet sampled, such as the non-studied region of northeastern state of Minas Gerais, where some relatively well preserved fragments of Atlantic Forest still exist but are virtually unprotected.

### Acknowledgments

Instituto Estadual de Florestas de Minas Gerais and

PERD administration allowed us to sample the area (through license IEF-MG #018/1999). Companhia Agrícola Florestal (CAF) permitted us to use their installations and gave us support at the region of the PERD. Alexandre G. Damasceno, Bruno Q. Sander, and Júnio Damasceno helped with field work. Dr. Elder F. Morato, two referees of Neotropical Entomology, and two referees from another journal to which a first version of this manuscript had been submitted made important comments and suggestions which greatly improved this final version. Dr. Gabriel A. R. Melo helped with the identification of some specimens and examined the *Eufriesea dentilabris* and *Ef. distinguenda* synonymy. Dr. Solange C. Augusto kindly sent the individuals from Ilha do Cardoso which helped to re-evaluate the status of both *Euglossa annectans* and *Euglossa stellfeldi*. Dr. André Hirsch provided the map appearing as Figure 1. Field studies were supported by a grant from PROBIO (a program financed by the World Bank and the Brazilian Ministry for the Environment), which also provided the first author with a fellowship (CNPq process #380678/1999-3).

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Received 19/VIII/05. Accepted 25/X/05.