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Diversity and Abundance of Orchid Bees (Hymenoptera: Apidae, Euglossini) in a Tropical Rainforest Succession

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Composicion de Abejas Euglossinas (Hymenoptera: Apidae, Euglossini) en una Sucesión de Selva Tropical

RESUMEN - Las abejas euglossinas macho, son fácilmente atraídas por los cebos químicos que imitan las fragancias naturales recolectadas por las abejas, proporcionando así una medida de la diversidad y abundancia extensamente aplicada para estas abejas. En este estudio documento la composicion de las abejas euglossinas en tres hábitats de la selva baja del Perú (Loreto), tales como un bosque primario, un bosque reforestado y manejado, y un bosque muy deforestado. A partir de 2.072 abejas capturadas perteneciendo a 33 especies y cuatro géneros, encontré una diversidad comparable a otros estudios de la región Amazónica, pero no encontré ninguna diferencia significativa entre los hábitats muestreados. Quizás por que los muestreos de las abejas euglossinas de corta duración (< 3 meses), tal como este caso, no son buenos indicadores del estado del bosque sin datos adicionales. Comparado a otros estudios de la fauna de las abejas euglossinas, Loreto es el más similar en especies a las especies reportadas de Brasil (Manaus), de Perú central (Panguana) y luego de Perú meridional (Tambopata).

PALABRAS-CLAVE: *Euglossa, Eulaema, Eufriesea, Exaerete*, Jaccard indice, Sørensen indice

ABSTRACT - Euglossine bee males are easily lured to chemical baits imitating natural fragrances gathered by bees, providing a widely applied measure for estimating the diversity and abundance of euglossines. In here, I report the composition of euglossine bees in three lowland rainforest habitats of Peru, a primary old forest, a reforested and managed forest, and a very disturbed forest. A total of 2,072 males of euglossine were collected, belonging to 33 species and four genera. Although a comparable diversity relative to other studies from the Amazonian region was found, no significant differences among the sampled areas were detected. Perhaps, the short time and low intensity surveys here used (< 3 months) were not good enough indicators of forest disturbance without additional data. Compared to other major studies on the euglossine bee fauna, Loreto is most similar to the species assemblage reported from lowland rainforest in Brazil (Manaus), central Peru (Panguana) and southern Peru (Tambopata).

KEY WORDS: *Euglossa, Eulaema, Eufriesea, Exaerete*, Jaccard index, Sørensen index

The euglossine bees, or orchid bees, with their visually captivating metallic green and blue colors represent one of the better known groups of Neotropical bees (Cameron 2004, Roubik & Hanson 2004, Michener 2007). Male euglossine bees of most of the more than 200 species are easily lured to chemical baits imitating natural fragrances gathered from orchids and other plants, fungi, among others (Dressler 1968, 1982a, Roubik 1998, Cameron 2004). Ackerman (1983) showed that capture rates using artificial baits reflect actual bee abundance and baiting studies are therefore a widely applied measure of euglossine bee diversity and abundance. Studies in South and Central America have investigated the effect on euglossine communities from different habitats (Dressler 1985, Oliveira & Campos 1995), seasonality (Janzen *et al* 1982, Ackerman 1983, Oliveira 1999), fragmentation (Becker *et al* 1991, Tonhasca *et al* 2002), and agricultural effects (Otero & Sandino 2003, Hedström *et al* 2006a, b), providing information on the community structure and habitat changes. However, none of these studies addressed the community change between reforested and managed continuous forest patches. The euglossine bee fauna in Peru is one of the better known bee faunas of the country (Dodson 1965, Dressler 1985, Pearson & Dressler 1985, Bembé 2002), although new species are still regularly reported (Roubik

2004, Rasmussen & Skov 2006, Hinojosa-Díaz & Engel 2007). In this study, I report the diversity and abundance of euglossine bees in three lowland rainforest habitats of Peru, a primary old forest, a reforested and managed forest, and a disturbed forest. The overall diversity is also compared with other studies on euglossine bees, mainly from the western Amazon.

Material and Methods

Areas. This study was carried out at three continuous lowland (120 m) rainforest areas in different successional stages along the Iquitos-Nauta road, Loreto, Peru: 1) Allpahuayo-Mishana (AM), a primary forest with large trees, 2) Varillal (V), a disturbed habitat under reforestation, and 3) Peña Negra (PN), a very disturbed, shrubby habitat, with low canopy height (< 10 m). The AM area is located along the Instituto Nacional de Innovación Agraria trail in the Zona Reservada Allpahuayo-Mishana, 25 km S from Iquitos (3º57'S, 73º25'W). The second area is 15 km S from Iquitos, near Varillal village. This area had been used for timber and firewood extraction, as well as minor cultivation in transects through the forest. An area of 60 ha was reforested about 20 years ago and is managed for future logging. All samples were taken from the central part of the reforested area (3º54'S, 73º21'W). The PN site is 10 km S from Iquitos, near Peña Negra village. Exploitation of white sand for construction has led to the degradation of the entire area, and all samples were taken from a shrubby forest, near an approximately 20-year-old sand pit (3º51'S, 73º20'W). Rainfall variation in the Iquitos region is minor throughout the year, although January to May is the wettest season. The forest type was white sand, known as *varillal seco* in Peru (Encarnación 1993). In Loreto, *varillal seco* is characterized by white sand below a layer of humus, with good drainage. Most vegetation is dense, with low (3-18 m) and thin-stemmed plants (3-10 cm DBH) (Encarnación 1993, Kalliola *et al* 1993, Kalliola & Flores 1998). *Clarisia*, *Brosimum* (Moraceae), and *Virola* (Myristicaceae) are the dominant plant genera.

Sampling. The habitats sampled were heterogeneous with a mosaic of diverse microhabitats, created by the distribution and flowering patterns of orchids and other resources collected by euglossine bees (Armbruster 1993). The general hypothesis that there is variation in diversity among sites, despite heterogeneity within the areas, was tested by using a nested sampling design (several sampling units). Three sampling stations were established at least 300 m apart from each other in each area. Stations were sampled three times, yielding a total of nine samples per area during the study period.

According to Powel & Powel (1987) and Oliveira (1999) the optimal foraging conditions for collecting euglossines is 24.5-27ºC, with a peak activity between 09:00 and 12:00h. Baiting during this study was performed from approximately 08:45 until 12:45h. The temperature averaged 26.0ºC (±1.5ºC) at 09:30, and only during a cold period (June 18-23) no sampling were conducted. Sampling was never initiated during rain, but continued if light rain began during sampling. The five most efficient baits, according to Pearson & Dressler (1985), were prepared as follows: benzyl acetate, cineole (= eucalyptol), eugenol, methyl salicylate, and vanillin. Two ml of each bait were applied on a paper towel attached to a string, and baits were placed spread 1 m apart from each other at 2 m from the ground.

Male euglossine bees were sampled for a total of 108h with the above chemical baits during the end of the rainy season from May to June of 2001. An additional 2 ml of bait were supplied hourly, during the 4h of sampling, although eucalyptol evaporated faster and eugenol slower than any of the other baits. As suggested by Powell & Powell (1987), 2 g of vanillin were used in a perforated glassine envelope without refilling during sampling. It was later found (pers. obs.) that vanillin dissolved in ethanol was a more efficient attractant, but the method was not modified to improve attraction to vanillin. The specimens were preserved in ethanol 70% and later pinned for identification. Additionally, the Orchidaceae species were identified based on the attached pollinaria. The voucher specimens were deposited at the Museo de Historia Natural, Lima, Peru (MUSM) and in my personal synoptic collection.

Data analysis. In addition to the species abundance and non-parametric Kruskal-Wallis test statistics, α-diversity indices of Simpson (1/D, reciprocal value listed) and Shannon (H) were calculated (Magurran 2004). These indices were compared among sites with ANOVA, as recommended by Magurran (2004), for comparing species assemblages. To test how equally abundant species were in each of the three sites, an evenness measure ($E_{1/D}$) was calculated by dividing the Simpson index by the number of species in each sample (Magurran 2004). Lastly, I calculated the Jaccard and Sørensen indices to give a measure of the pairwise similarity between sites; a higher value indicates more similar sites. The β-diversity index is found by subtracting either of the two indices from 1 (Magurran 2004).

Results

A total of 2,072 male euglossine bees belonging to 33 species and four genera (Table 1) were collected. More specimens (abundance) were captured in the disturbed forest, but a similar number (diversity) of species was collected in each habitat. From the primary forest site (AM), 598 males (28.9%) belonging to 26 species were captured; at the reforested site (V), 635 males (30.6%) of 29 species were captured; and in the disturbed forest (PN), 839 males (40.5%) of 29 species were captured. The most abundant species, *Euglossa ignita* Smith, represented 41.8% of the total sample, while the second most abundant species, *Eufriesea pulchra* Smith and *Euglossa imperialis* Cockerell, each represented 6.1% of the total number of collected specimens. Four species were represented by a single specimen.

Species abundance among sites was compared using non-parametric tests, as there was no normal distribution of data when tested visually by histograms or by the Kolmogorov-Smirnov test (Sokal & Rohlf 1995). Resampling from each of the nine stations were treated as a single sample. There

Table 1 Number of male euglossine bees captured in three lowland tropical rainforest habitats in Peru. AM: Allpahuayo-Mishana (primary forest); VA: Varillal (reforested habitat); PN: Peña Negra (very disturbed habitat).

Species	Habitats			
	AM	V	PN	Total
Eufriesia ornata (Mocsáry)	5	12	2	19
Ef. pulchra (Smith)	29	52	47	128
Euglossa allosticta Moure	1	2	2	5
Eg. amazonica Dressler	5	23	19	47
Eg. analis Westwood	4	4	3	11
Eg. augaspis Dressler	6	12	31	49
Eg. aureiventris Friese	0	1	0	1
Eg. bidentata Dresssler	2	1	0	3
Eg. cognata Moure	0	2	1	3
Eg. crassipunctata Moure	10	2	13	25
Eg. gaianii Dressler	2	3	8	13
Eg. ignita Smith	299	224	344	867
Eg. imperialis Cockerell	50	38	39	127
Eg. intersecta Latreille	11	52	34	97
Eg. laevicincta Dressler	0	0	1	1
Eg. lugubris Roubik	6	2	11	19
Eg. mixta Friese	13	37	72	122
Eg. modestior Dressler	2	12	30	44
Eg. occidentalis Roubik	15	11	3	29
Eg. orellana Roubik	10	13	53	76
Eg. prasina Dressler	0	1	3	4
Eg. rugilabris Moure	6	10	0	16
Eg. singularis Mocsáry	0	4	1	5
Eg. sp.n. aff. *annectans* Dressler	0	0	3	3
Eg. sp.n. aff. *magnipes* Dressler	0	0	1	1
Eg. viridifrons Dressler	2	15	9	26
Eulaema bombiformis (Packard)	6	2	1	9
El. cingulata (Fabricius)	9	13	50	72
El. meriana (Olivier)	44	39	24	107
El. mocsaryi (Friese)	45	39	20	104
Exaerete frontalis (Guérin)	8	4	7	19
Ex. smaragdina (Guérin)	7	5	7	19
Ex. trochanterica (Friese)	1	0	0	1
Total				
Bee specimens	598	635	839	2072
Species	26	29	29	33
Simpson’s (1/D)	3.671	6.426	5.145	5.045
Shannon-Wiener (H)	2.042	2.463	2.314	2.360
Evenness ($E_{1/D}$)	0.127	0.177	0.222	0.002
Bees caught per hour sampling	16.6	17.6	23.3	19.2

was no significant difference among stations within each of the three sites (Kruskal-Wallis test: AM, F = 1.578, P = 0.454; PN, F = 3.992, P = 0.136; V, F = 0.048, P = 0.976), and all samples from each site were thus treated as a single sample. No significant differences (F = 0.233, P = 0.890) in the abundance of euglossine bees was found among sites. Pairwise comparison between each of the three sites using the Mann-Whitney U statistic revealed no significant differences: AM-PN (F = 346.500, P = 0.606); AM-V (F = 361.500, P = 0.793); PN-V (F = 430.000, P = 0.882). Also, no significant differences among sites were found for the Simpson (F = 2.446, *P* = 0.167) or Shannon indexes (F = 3.910, P = 0.082).

For each of the seven most abundant species (Table 1), comprising 74.9% of all specimens collected (1,552 specimens), the Kruskal-Wallis test revealed no significant difference in abundance across the three sites (*Ef. pulchra:* F = 3.339, P = 0.188; *Euglossa intersecta* Latreille: F = 5.067, P = 0.079; *Eg. imperialis:* F = 0.605, P = 0.739; *Eg. ignita:* F = 1.422, P = 0.491; *Eulaema meriana* (Olivier): F = 4.271, P = 0.118; *El. mocsaryi* (Friese): F = 5.445, P = 0.066), except for *Euglossa mixta* Friese (F = 6.056, P = 0.048).

As there was no significant difference among samples, species accumulation curve are presented based on pooled data (Fig 1). The Jaccard and Sørensen indices (Table 2) and a comparison of the results obtained here with similarity indices of other surveys (Table 3) are also available. As no standarized protocol has been proposed for euglossine surveys, these widely different surveys (duration and baits used) are the only presently available data for comparing the fauna. The euglossine bee fauna from Loreto is most similar to the species assemblage reported from lowland rainforest in Brazil (Manaus: Jaccard, 0.511; Sørensen, 0.676), central Peru (Panguana: Jaccard, 0.477; Sørensen, 0.646), and southern Peru (Tambopata: Jaccard, 0.423; Sørensen, 0.595); these are followed by Biodiversidad and Tingo Maria (640-950 m) on the transition between lowland rain forest and lower tropical montane rainforest in Peru.

Bait fragrance preferences from this study are included for comparative purposes for the most abundant species (*i.e.*, >10 specimens), with the most efficient being methyl salicylate (Table 4). The number of bees with pollinaria was higher (3.7%, PN) in the most disturbed area (Table 5).

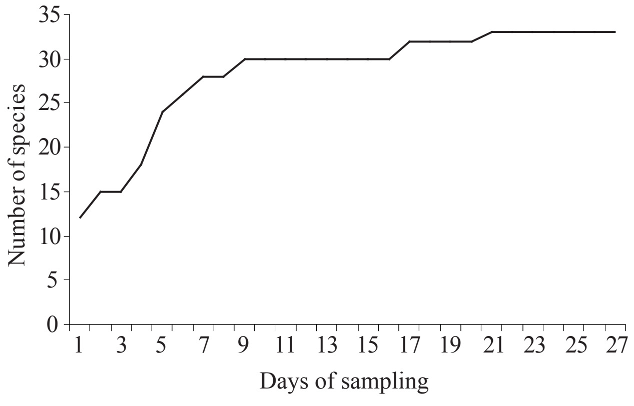

Fig 1 Species accumulation curve of 33 different species of euglossine bees based on 4h samplings for 27 d.

Table 2 Similarity coefficient of pairwise site comparisons at three lowland tropical rainforest habitats in Peru; AM: Allpahuayo-Mishana (primary forest); VA: Varillal (reforested habitat); PN: Peña Negra (very disturbed habitat).

Paired site comparisons	Coefficient of Jaccard (C_j)	Coefficient of Sørensen (C_s)
AM x V	0.833	0.909
V x PN	0.813	0.897
AM x PN	0.719	0.836

Discussion

Although the diversity in here reported is similar to that available in the literature, the actual species diversity of the Amazon region, however, must be higher around Iquitos as *Aglae caerulea* Lepeletier & Serville, *El. polyzona* (Mocsáry), *Ef. surinamensis* (L.), and *Ef. purpurata* (Mocsáry) were sampled from close areas without baits, and *Eg. bigibba* Dressler, *Ef. convexa* (Friese) and *Eg. magnipes* Dressler were reported from nearby (Dressler 1982b, Kimsey 1982). The richest known euglossine bee assemblage consists of approximately 50 species (Barro Colorado Island, Panama), although these may not all be present throughout the year. For example, *Eufriesea* bees are highly seasonal and may be missing as adults for most of the year (Roubik & Hanson 2004).

Table 3 Similarity coefficient of pairwise locality comparisons.

Paired site comparisons	Coefficient of Jaccard (C_j)	Coefficient of Sørensen (C_s)
IQ x MA	0.511	0.676
IQ x PA	0.477	0.646
IQ x TP	0.423	0.595
IQ x BI	0.400	0.571
IQ x TM	0.356	0.525
IQ x CH	0.164	0.281

IQ: Iquitos, Peru, in the present study (33 spp., 3º53'S, 73º22'W, 120 m, May to June 2001); BI: "Biodiversidad", Tarapoto-Yurimaguas, San Martín, Peru (29 spp., 6°34'S, 76°20'W, 950 m, April 2002 to April 2003) (Rasmussen, unpublished data); TM: Tingo María, Huánuco, Peru (28 spp., 9º18'S, 76º00'W, 670 m, April to September 1987) (Harold G. Hills and Carlos Atachahua, synoptic collection in MUSM); PA: Panguana and Llullapichis, Huánuco, Peru (32 spp., 9º37'S, 74º56'W, 260 m, September to October 2000) (Bembé 2002); TP: Tambopata Reserved Zone, Madre de Dios, Peru (41 spp., 12º50'S, 69º17'W, 300 m, September 1981 to August 1983) (Dressler 1985, Pearson & Dressler 1985); MA: Manaus, Brazil (35 spp., 2º30'S, 60ºW, 30-37 m, September 1989 to August 1990) (Oliveira & Campos 1995); CH: Chocó, Colombia (31 spp., 3º46'S, 76º57'W, 50-80m, June 1995 to July 1997) (Otero & Sandino 2003). Additional records for PA and TP were added from Roubik (2004).

Table 4 Bait preference for the most abundant species in all sites (> 10 specimens) at three lowland tropical rainforest habitats in Peru. Numbers indicate individuals collected in 108h of sampling. Total number of specimens is indicated in parenthesis after each species.

Species	Bait				
	BA	CI	EU	MS	VA
Eufriesia ornata (19)	7	1	11		
Ef. pulchra (128)		9	5	114	
Euglossa amazonica (47)	5	32	8	1	1
Eg. analis (11)	2		3	6	
Eg. augaspis (49)	10	4	15	13	7
Eg. crassipunctata (25)		19	2	2	2
Eg. gaianii (13)	3			10	
Eg. ignita (867)	155	175	27	510	
Eg. imperialis (127)		51	1	75	
Eg. intersecta (97)	88		6	1	2
Eg. lugubris (19)	11		3	5	
Eg. mixta (122)	3		3	116	
Eg. modestior (44)		43		1	
Eg. occidentalis (29)	20		1	7	1
Eg. orellana (76)	2	51	1	19	3
Eg. rugilabris (16)	2	10		4	
Eg. viridifrons (26)	6	10	7	3	
Eulaema cingulata (72)	11	3	53	2	3
El. meriana (107)	23	12	3	65	4
El. mocsaryi (104)	37	9	5	53	
Exaerete frontalis (19)	2	13		4	
Ex. smaragdina (19)	1	17		1	
Total for all species (2072)	267	587	159	1030	29

BA: benzyl acetate; CI: cineole (= eucalyptol); EU: eugenol; MS: methyl salicylate; VA: vanillin

The species accumulation curve quickly reached an asymptote (Fig 1), suggesting that most species occurring in the area were efficiently captured. The average capture rate of 19 bees/h is also comparable with the study of Pearson and Dressler (1985) from southern Peru, with 18 bees/h. These values are significantly less than that of Roubik and Ackerman (1987) in Panama, who recorded 104 bees/h during favorable periods, although specimens may have been counted multiple times during their catch and release survey (Roubik, pers. comm.). Previous reports show that a single species may comprise about 25% of the local species assemblage, and the three most abundant species from 54% to 61% of the total number of species captured per sample (Pearson & Dressler 1985, Otero & Sandino 2003, Roubik & Hanson 2004), as occurred with *Eg. ignita*, which was collected in 41.8% of the samples. Sampling throughout the year will be necessary to elucidate if abundance of this single species (or rareness of other species) relates to seasonal changes in the community composition. While *Eg. ignita* is known to chase other species away from baits (Roubik & Hanson 2004), this was not the case here, as all bees were captured as soon as they alighted on a bait.

Becker *et al* (1991) and Tonhasca *et al* (2002) found no significant differences in the euglossine communities among fragmented habitats, whereas Rincón *et al* (2000) and Otero & Sandino (2003) reported that bees were more abundant and diverse in secondary forest or farmland. Morato (1994) reported more bees in continuous forest and Hedström *et al* (2006a, 2006b) found that bees were more abundant in organic than in non-organic fields. Using abundance data (Kruskal-Wallis) and alpha-diversity indices (ANOVA) for all species, as well as individually for the seven most abundant species, I could not demonstrate that euglossine bees are susceptible to habitat disturbance like other tropical bees, such

Table 5 Fifty pollinariums recorded for 48 specimens (2.3% of all specimens caught) of twelve species of euglossine bees. Bees may carry several pollinariums of different or identical taxa.

Orchid genera (Orchidaeceae)	Bee species, number of specimens with pollinarium and location where deposited
Catasetum	1 *Euglossa ignita* (femur), 1 *Eg. gaianii* (paraocular area), 2 *Eg. lugubris* (dorsal thorax)
Catasetum (large)	1 *Eulaema cingulata* (dorsal thorax), 8 *El. cingulata* (2nd tergum), 1 *El. cingulata* (3rd tergum), 1 *El. mocsaryi* (dorsal thorax), 2 *El. mocsaryi* (2nd tergum), 1 *El. mocsaryi* (3rd tergum)
Catasetum (small, deposited dorsal)	5 *E. ignita*, 4 *Eg. mixta* (dorsal thorax on all specimens)
Catasetum (small, deposited ventral)	1 *Eg. ignita* (tibia), 2 *Eg. ignita* (ventral thorax), 5 *El. cingulata* (ventral thorax)
Catasetum aff. longifolium	1 *El. cingulata* (femur)
Chondrorhyncha complex	1 *Eg. orellana*, 1 *Eg. ignita*, 1 *Eg. imperialis* (legs on all specimens)
Coryanthes form 1	1 *Eg. ignita* (propodeum)
Coryanthes form 2	1 *El. cingulata* (1st tergum)
Galeandra or *Cyrtopodium*	2 *Eg. amazonica*, 2 *Eg. augaspis*, 1 *Eg. crassipunctata*, 2 *Eg. ignita*, 2 *Eg. modestior* (scutellum on all specimens)

as stingless bees of the genus *Melipona* (Brown & Albrecht 2001). Only *Eg. mixta* showed a preference for secondary forest, although this was not supported statistically. Perhaps, surveys of euglossine bees of short duration and sampling intensity, such as used here are not good enough indicators of forest disturbance without additional genetic data (diploidity, population genetic data) or seasonal survey data.

In addition to the limited sampling intensity, the finding that the local species assemblage of euglossine bees does not change across different adjacent habitats (*i.e.*, primary and secondary forest) may be related to their skills as fliers. Janzen (1971) demonstrated that female bees forage from 5 km to 23 km away from their nest, and thus, the spatial scale over which at least certain species are active may be larger than the small area studied here (the maximum distance between sites was less than 15 km). However, even if bees cover the whole area with primary forest as a source-area, as suggested by Roubik & Hanson (2004), other local factors may have promoted a patchy distribution pattern, e.g., foraging and nesting resources. Cane (2001) stressed the importance of available nesting sites, which may be equally or more abundantly available in secondary forest for stick or small-cavity nesting euglossine species like certain *Euglossa*. Resin sources used for constructing nest cells are abundantly available in secondary forest, where nests of many *Euglossa* and *Eufriesea* are frequent (Becker *et al* 1991). Nest factors should therefore not represent any limitation to the abundance of the bees across habitats. Long-term studies may provide insight into additional factors important for maintaining a diverse bee community, but so far habitat quality seem not to affect the diversity of euglossine bees if a continuous forest is available.

Seasonal differences could account for difference among habitats, although fragrance resources (Table 5) did not appear to be limited and the frequency of individuals with pollinaria attached were even slightly higher than reported elsewhere in South America (e.g., Pearson & Dressler 1985, Peruquetti *et al* 1999); the latter suggests a widespread flowering of orchids and availability of fragrance during the survey period. However, studies have shown the highest diversity of species is coincident with the rainy season and declines after this period (Pearson & Dressler 1985, Hedström *et al* 2006b, Roubik, pers. comm.), when the seasonally abundant species disappear. Seasonality may therefore be a factor as well in this study. The frequency of diploid males among samples was not tested, although Zayed *et al* (2003) reported such cases that could bias population estimates based on males alone, such as the present study.

Although not significant, the least similar habitat was the primary forest (AM) and the very disturbed forest (PN), with the reforested habitat (V) intermediate between the two (Table 2). When similarity indices were compared with other fragrance-based surveys of different duration (Table 3), the present study is most similar to the species assemblage reported from lowland rainforest in Manaus, Brazil, central Peru (Panguana), and southern Peru (Tambopata). These are followed by Biodiversidad and Tingo Maria (640-950 m) on the transition between lowland rain forest and lower montane rain forest in Peru. These Peruvian Andean foothills maintain a unique biological diversity, due to high precipitation, numerous disturbances, and great heterogeneity (Young & León 1999), and often represent a different assemblage of euglossine species than the lowland surveys (Rasmussen & Skov 2006). The only extra-Amazonian site in pacific Colombia (Chocó) was the least alike fauna.

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