

Stingless Bees (Meliponini) and Orchid Bees (Euglossini) in Terra Firme Tropical Forests and Forest Fragments

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Stingless Bees

Stingless bees are well known and familiar to many in the tropics because of their defensive habit of biting and entangling themselves in people's hair and beards. They are social bees living in organized hives that have a queen, males, and workers (females) that perform various functions inside and outside the nest. The sole function of males is to mate with the queen. After mating, which takes place in full nuptial flight, the queen lodges in the hive and dedicates herself to laying eggs that can generate new queens, males, or workers. The workers labor the most, cleaning the interior of the beehive, collecting resin, clay, or other materials used in nest construction, or even collecting water, nectar (source of sugars), or pollen (source of proteins) for themselves or to feed to other members of the hive. The nectar, through an enzymatic process that takes place in the worker's stomach, is transformed into honey. The ecological importance of these bees, however, is not the production of honey but rather their role in pollinating various natural or cultivated plant species.

Orchid Bees

Unlike stingless bees, orchid bees (Euglossini) are still poorly known because they do not live in hives; do not have a queen; do not produce honey; and fly at a very high speed, almost always near tree canopies, where they mostly visit orchids. In many species the body is metallic green or blue, and the tongue is longer than the body. The geographical distribution of these bees is restricted to the Neotropics, from northern Mexico to northern Argentina (Dressler 1982), and only Jamaica and Trinidad in the West Indies.

Euglossine males and females visit flowers to obtain nectar in at least twenty-three plant families, whereas the females visit flowers of nine families for pollen and three others for resin (Roubik 1989). All orchid species of the sub-tribes Stanhopeinae and Catasetinae, as well as members of the other sub-tribes, are pollinated exclusively by euglossine males that visit flowers to collect floral fragrances (Williams and Whitten 1983), which they probably convert biochemically into the pheromones that they in turn use to attract mates. Pollen is also collected from plant families besides the Orchidaceae, including Araceae, Euphorbiaceae, and Gesneriaceae (Williams and Whitten 1983).

According to Dressler (1982), at least 625 species of 55 genera of orchids exist in the Neotropical region that do not produce nectar and whose pollen is not consumed by bees. Floral fragrances, in these species, would be the principal resource offered for attracting their pollinators, the euglossine males (Roubik 1989). These bees also take part in the pollination of the Brazil-nut tree (*Bertholletia excelsa* H. B. K.), along with bees of the genera *Bombus*, *Centris*, *Xylocopa*, and *Epicharis*. Brazil-nut trees have shown reduced fruit production in areas where their pollinators are not present in sufficient numbers to promote cross-pollination (Nelson, Absy, et al. 1985; Mori and Prance 1987).

Methods

Collections of stingless bees were made in isolated forest fragments of 1, 10, and 100 ha, as well as in continuous forest sites and deforested areas as part of the BDFFP, north of Manaus. Samples taken in the deforested areas were in the vicinity of the Colosso isolates (1202 and 1104) and camp. The second-growth vegetation surveyed was dominated by *Vismia* spp. (plate 9). (A detailed description of the study area can be found in Lovejoy and Bierregaard [1990] and in Chapter 4; see fig. 4.1 and table 4.3.)

The bees were collected in six ways: (1) by using honey as bait; (2) by collecting clay; (3) by collecting sweat; (4) in flight; (5) in their nests; and (6) in flowers. A 100 ha continuous forest area, subdivided into 20 × 20 m squares (Reserve 1501, the Lecythidaceae subproject study area described by Mori, Becker, and Kincaid [Chapter 6]), was used to survey stingless bee nests.

The euglossine fauna of two terra firme forest areas were compared. The two study areas were outside the limits of reserves

1401 and 1501 to avoid interference with ongoing experiments within the reserves. Collections were made fortnightly between September 1989 and August 1990, using fruit-fly traps modified according to Campos et al. (1989), containing synthetic fragrances and placed at two heights: near the canopy (12–15m) and on the ground.

Results

RELATIVE ABUNDANCE, RICHNESS, AND DIVERSITY

Fifty-four stingless bee species were found in the BDFFP areas, two of which are new species, *Plebeia* sp.n. 1 and *Plebeia* sp.n. 2 (table 17.1). A few stingless bees that, surprisingly, entered the traps for the Euglossini, were included here.

Thirty-eight species of Euglossini were found, three of which appear to be new species (table 17.2). In addition to the thirty-eight species encountered, previous collections made in the same region have recorded an additional nine species: *Euglossa platymera* and *Eufriesea surinamensis* (Kimsey and Dressler 1986); *Eufriesea laniventris*, *E. xantha*, and *E. purpurata* (Powell and Powell 1987); *Euglossa* cf. *amazonica* (Becker, Moure, and Peralta 1991); *Euglossa* cf. *securigera* and *E. liopoda* (Morato, Campos, and Moure 1992); and *Eufriesea theresiae* (Morato 1993). About 68 percent of the species encountered were represented by fewer than 20 individuals and can be classified as uncommon to rare. Examples include *Euglossa laevicincta*, *Euglossa* sp. 3, and *Eufriesea vidua*, of which only one individual was collected during the entire year. Also, *Euglossa bidentata*, *E. piliventris*, *E. prasina*, and *Euglossa* sp.3 were found in only one of the areas studied.

TABLE 17.1. Stingless Bees in the BDFFP Areas by habitat Type

Species	Isolates			Continuous Forest	Deforested Area	Total
	1 ha	10 ha	100 ha			
<i>Aparatrigona impunctata</i> (Ducke 1916)				1		1
<i>Camargoia camargoi</i> Moure, 1989	4	1		1	1	7
<i>Celetrigona logicornis</i> (Friese 1903)	2				1	3
<i>Cephalotrigona capitata femorata</i> (Smith 1854)				2		2
<i>Duckeola ghiliani</i> (Spinola 1853)	? ¹	?	?	?	?	?
<i>D. pavani</i> Moure, 1963				1		1
<i>Frieseomelitta trichocerata</i> Moure, 1988	1			3	1	5
<i>Geotrigona subgrisea subnigra</i> (Schwarz 1940)	?	?	?	?	?	?
<i>Lestrimelitta limao</i> (Smith 1853)					1	1
<i>Leurotrigona pusilla</i> Moure & Camargo, 1988	?	?		?	?	?
<i>Melipona amazonica</i> Schulz, 1905	2					2
<i>M. captiosa</i> Moure, 1962	2	1			1	4
<i>M. fuliginosa</i> Lepeletier, 1836				1		1
<i>M. fulva</i> Lepeletier, 1836	1	3		4	1	9
<i>M. illustris</i> Schwarz, 1932				1		1
<i>M. lateralis</i> Erichson, 1848		1	2	7	1	11
<i>M. puncticollis puncticollis</i> Friese, 1902		1		1		2
<i>Nogueirapis minor</i> Moure & Camargo, 1982			1	2		3
<i>Oxytrigona obscura</i> (Friese 1900)		1	1	3		5
<i>Partamona</i> sp.	?	?	?	?	?	?
<i>P. mourei</i> Camargo, 1980		1	4	1		6
<i>P. cf. nigrilor</i> (Cockerell 1925)				1	1	2
<i>P. cf. pearsoni</i> (Schwarz 1938)	1	1			1	3
<i>P. pseudomusarum</i> Camargo, 1980	3	2	1	4		10
<i>P. testacea</i> (Klug 1807)	1			2	1	4
<i>Plebeia</i> sp. n. 1				1		1
<i>Plebeia</i> sp. n. 2				1		1
<i>P. minima</i> (Gribodo 1893)	1					1
<i>P. margaritae</i> Moure, 1962				1		1
<i>Plebeia</i> sp.				1		1
<i>Ptilotrigona lurida mocsaryi</i> (Friese 1900)	1	2		3	2	8
<i>Scaptotrigona bipunctata</i> (Lepeletier 1836)				2		2
<i>S. fulvicutis</i> Moure, 1964				2		2
<i>S. aff. Polysticta</i> (Moure 1950)				2	1	3
<i>Scaura tenuis</i> (Ducke 1916)					1	1
<i>S. latitarsis</i> (Friese 1900)	?	?	1	?	?	?
<i>Tetragona clavipes</i> (Fabricius 1804)					1	1
<i>T. dorsalis</i> (Smith 1854)	1			1	1	3
<i>T. essequiboensis</i> (Schwarz 1940)	3	1		1	1	6
<i>T. goettei</i> (Friese 1900)	2	2	1	2	1	8
<i>T. handlirschii</i> (Friese 1900)	4	1			1	6
<i>T. kaieteurensis</i> (Schwarz 1938)	1	2		1		4
<i>Tetragonisca angustula</i> (Latreille 1811)					1	1
<i>Trigona branneri</i> Cockerell, 1912		4		1	1	6
<i>T. cilipes</i> ² Fabricius, 1804				1	2	3
<i>T. crassipes</i> (Fabricius 1793)	4	4	1	5	1	15
<i>T. dallatorreana</i> Friese, 1900	1			1		2
<i>T. fulviventris</i> Guérin, 1835	4	3	1	6		14
<i>T. fuscipennis</i> Friese, 1900	1	3		1	1	6
<i>T. hypogea</i> Silvestri, 1902		1	2	4	1	8
<i>T. recursa</i> Smith, 1863		3		3		6
<i>T. williana</i> Friese, 1900	1	2		5	1	9
<i>Trigonisca dobzhanskyi</i> (Moure 1950)	?	?	1	?	?	?
<i>Trigonisca</i> sp.	1					1
TOTAL	41	41	14	80	17	203

Notes: ¹? = Unknown collection site. ²Dark wing tips, see Camargo 1988.

TABLE 17.2. Euglossine Bees Collected in Two Primary Terra Firme Forest Areas in the Central Amazon

Species	Reserve 1401	Reserve 1501	Percentage	Total
<i>Euglossa analis</i> Westwood, 1840	3	2	0.21	5
<i>E. augaspis</i> (Dressler 1982)	153	143	12.22	296
<i>E. avicula</i> (Dressler 1982)	136	143	11.52	279
<i>E. bidentata</i> (Dressler 1982)	—	3	0.12	3
<i>E. chalybeata</i> (Friese 1925)	121	231	14.53	352
<i>E. cognata</i> (Moure 1968)	2	14	0.66	16
<i>E. crassipunctata</i> (Moure 1970)	64	87	6.23	151
<i>E. decorata</i> (Smith 1874)	14	4	0.74	18
<i>E. gainii</i> (Dressler 1982)	8	8	0.66	16
<i>E. ignita</i> (Smith 1874)	14	10	0.99	24
<i>E. imperialis</i> (Cockerell 1922)	2	10	0.49	12
<i>E. intersecta</i> (Latreille 1938)	2	8	0.41	10
<i>E. ioprosopa</i> (Dressler 1982)	4	5	0.37	9
<i>E. iopyrrha</i> (Dressler 1982)	3	9	0.49	12
<i>E. laevectincta</i> (Dressler 1982)	—	1	0.04	1
<i>E. mixta</i> (Friese 1899)	27	40	2.77	67
<i>E. modestior</i> (Dressler 1982)	7	2	0.37	9
<i>E. mourei</i> (Dressler 1982)	23	19	1.73	42
<i>E. parvula</i> (Dressler 1982)	12	20	1.32	32
<i>E. piliventris</i> (Guérin 1845)	—	2	0.08	2
<i>E. prasina</i> (Dressler 1982)	—	2	0.88	2
<i>E. retroviridis</i> (Dressler 1982)	9	10	0.78	19
<i>E. stilbonota</i> (Dressler 1982)	311	474	32.41	785
<i>E. viridifrons</i> (Dressler 1982)	8	8	0.66	16
<i>E. viridis</i> (Perty 1833)	2	3	0.215	
<i>E. sp. 1</i>	—	3	0.12	3
<i>E. sp. 2</i>	2	—	0.08	2
<i>E. sp. 3</i>	—	1	0.04	1
<i>Eulaema bombiformis</i> (Packard 1869)	6	7	0.54	13
<i>E. meriana</i> (Olivier 1789)	42	38	3.30	80
<i>E. cingulata</i> (Fabricius 1804)	5	1	0.25	6
<i>E. mocsaryi</i> (Friese 1899)	17	11	1.16	28
<i>Eufriesea pulchra</i> (Smith 1854)	2	1	0.12	3
<i>E. ornata</i> (Mocsary 1896)	5	4	0.37	9
<i>E. vidua</i> (Moure 1976)	1	—	0.04	1
<i>Exaerete frontalis</i> (Guérin 1845)	50	30	3.30	80
<i>E. smaragdina</i> (Guérin 1845)	5	5	0.41	10
<i>E. trochantherica</i> (Friese 1900)	1	2	0.12	3
Total number of individuals	1,061	1,361		2,422
Total number of species	32	36		38

BEE FAUNA DISSIMILARITY

Comparing the Euglossini bee faunas of the two continuous forest areas, Reserve 1501 had more individuals, as well as more species; nevertheless, Shannon diversity index values (H') were significantly greater in Reserve 1401 (1401, $H' = 2.389$, and 1501, $H' = 2.257$; $t = 2.556$, $P = 0.005$, d.f. = 1). Eq-

uitability values J' (Ludwig and Reynolds 1988) were not different between the two areas (1401, $J' = 0.689$; 1501, $J' = 0.630$).

The two areas shared only thirty species (79 percent of the total species in the area) of euglossine bees (table 17.2), resulting in a dissimilarity coefficient of 0.22 between the two areas. This coefficient measures the dis-

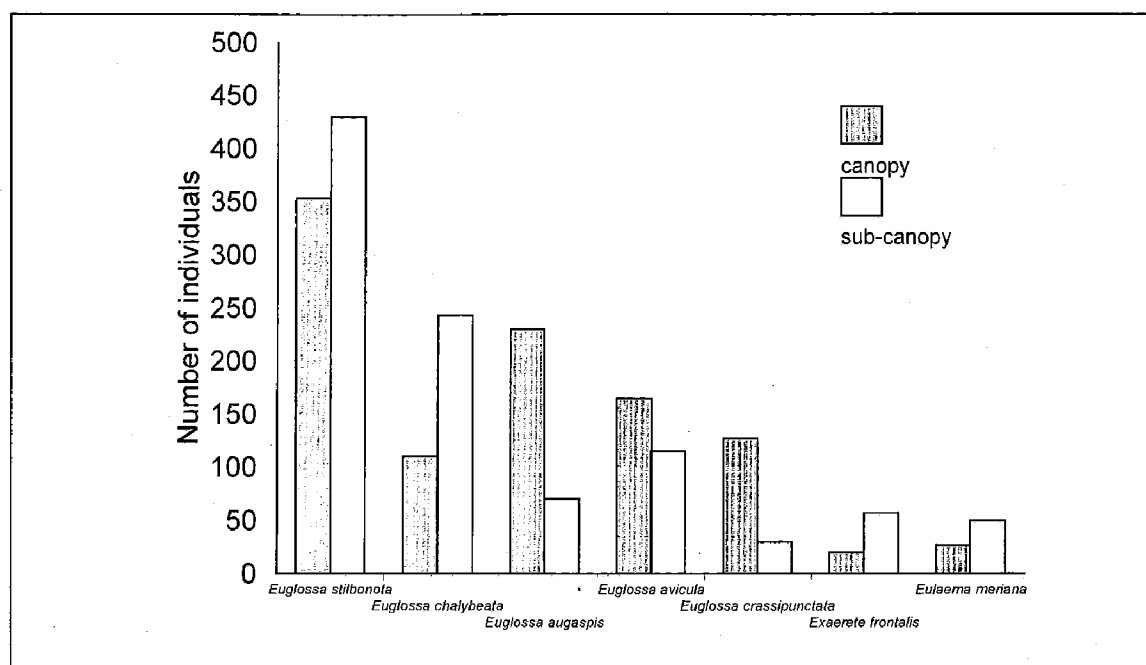


Fig. 17.1. Abundance of the most common Euglossini bee species in canopy and understory of terra firme continuous forest in central Amazon.

similarity between two samples and is based on the "chord distance" (Pielou 1984; Ludwig and Reynolds 1988). The maximum and minimum values for this distance are 1.41 and 0.0, respectively, in such a way that the greater the value obtained, the less similar the areas are. The value here obtained is relatively high, which is somewhat surprising, considering that the two areas are separated by a maximum of 10 km and are quite similar in their floristic composition; the value also shows considerable heterogeneity in the bee faunas over a fairly fine geographic scale (kilometers).

VERTICAL STRATIFICATION

In general, most of the euglossine species encountered in this study occurred in the forest canopy as well as in the understory. Species that were relatively uncommon or rare, such as *Euglossa laevecineta*, *E. prasina*, *E. viridis*, and *Euglossa* sp. 2, were captured exclusively in the canopy, whereas

E. piliventris, *Euglossa* sp.3, *Eufriesea vidua*, and *Exaerete smaragdina* were captured exclusively in the understory. Among the most abundant species, *Euglossa chalybeata*, *Exaerete frontalis*, and *Eulaema meriana* were much more common in the understory, whereas *E. augaspis* and *E. crassipunctata* were much more common in the canopy (fig. 17.1).

The number of individuals collected in the canopy was greater than in the understory, but the number of species was similar in the two strata. The diversity index value, however, was significantly greater in the canopy ($H' = 2.346$ and $J' = 0.660$) than in the understory ($H' = 2.123$ and $J' = 0.607$) ($t = 4.419$; d.f. 1; P less than 0.05).

EFFECTS OF FOREST FRAGMENTATION

Thirty-seven stingless bee species were found in continuous forest, 11 in 100 ha fragments ($n = 1$), 22 in 10 ha fragments ($n = 4$), 21 in 1 ha fragment ($n = 5$), and 25 in

the deforested areas (table 17.1). Interestingly, total species richness in the four 10 ha fragments, or in the five of 1 ha, surpass the number of species found in the 100 ha fragment. Even more surprising is the higher species richness in the deforested areas than in any one fragment, surpassed only by the sum total of all the fragments (31 species).

NEST DENSITY

Only 15 nests of nine stingless bee species were found in a 100 ha continuous forest area (table 17.3) at an average of about 0.15 nests/ha. This density is well below that encountered in other sites in the Neotropical region (table 17.4).

SEED DISPERSAL

In the terra firme forest near Manaus, at least five stingless bee species were observed visiting the ripe fruits of *Coussapoa asperifolia magnifolia* (Cecropiaceae) (Garcia, Oliveira, and Campos 1992). The workers of *Melipona seminigra merrillae*, *M. compressipes man-aosensis*, and *Trigona williana* removed the mucilaginous epicarp of ripe fruits, along with the minuscule seeds, while *Aparatrigona impunctata* and *Trigona fuscipennis* removed only the epicarp of ripe fruits. Moreover, nests of four stingless bee species, *M. lateralis*, *M. fulva*, *M. seminigra semini-gra*, and *M. rufiventris*, were constructed with a mixture of clay and mucilaginous epicarp containing seeds. On close analysis, these seeds were identified as those of *C. a. magnifolia*, although bees of these four species were never observed visiting fruits of *C. a. magnifolia*. Germination tests on these seeds were positive, suggesting that bees actually play a role in seed dispersal of these plant species.

Table 17.3. Stingless Bee Nest Density in a 100 ha Continuous Terra Firme Forest Area in the Central Amazon

Species	Nests/ha
<i>Melipona captiosa</i>	0.01
<i>Partamona pseudomusarum</i>	0.01
<i>Ptilotrogona lurida mocsaryi</i>	0.03
<i>Scaptotrigona</i> aff. <i>polysticta</i>	0.01
<i>Tetragona dorsalis</i>	0.01
<i>T. goettei</i>	0.01
<i>T. kaieteurensis</i>	0.02
<i>Trigona crassipes</i>	0.04
<i>T. fulviventris</i>	0.01

Discussion

RELATIVE ABUNDANCE, RICHNESS, AND DIVERSITY

The large number of stingless bee species found in the BDFFP areas (about 36,000 ha) is larger than the entire bee fauna of other areas, such as Madagascar, which has only four species; New Guinea with five; Australia with eight to ten; central Sumatra with 24; and Africa with 50 (Salmah, Inoue, and Sakagami 1990; Camargo and Pedro 1992). Only French Guiana has more known species, with 69 (Roubik 1989). It is also worth noting that the number of species found corresponds to about 21 percent of those previously registered for the Neotropical region as a whole (Camargo 1990).

Further, this abundance and richness of euglossine bee species is greater than anywhere else in Brazil (table 17.5). The 47 euglossine species known from the Manaus area is the highest total for the Neotropics, with the exception of Barro Colorado Island and Cerro Campana on Panama, where 53 species were recorded (table 17.6). It is likely that even richer faunas might be found in Amazonia as more and larger areas are surveyed. Recently, J. C. Brown (unpublished data) found 53 euglossine species in the state of Rondônia, but in a significantly larger area than that reported on in this chapter.

TABLE 17.4. Stingless Bee Nest Densities in Neotropical Forests

Area (ha)	Nest density (per ha)	Species density (per ha)	Locality	Author
5.0	5.88	2.78	Panama	Roubik 1983
36.7	1.82	0.25	Costa Rica	Hubbell and Johnson 1977
1.0	1.00	1.00	Amazonas	M. V. B. Garcia (pers. comm.)
64.7	2.17	0.14	Panama	Michener 1946
100.0	0.15	0.09	Amazonas	M. Oliveira, Morato, and Garcia 1995

TABLE 17.5. Published Studies Using Synthetic Fragrance Baits in Brazil on Euglossine Bees

State	Number of			Studies
	baits	specimens	species	
Amazonas ¹	4	76	10	Braga 1976
Amazonas ²	3	992	15	Powell and Powell 1987
Amazonas ²	3	290	16	Becker, Moure, and Peralta 1991
Amazonas ²	4	1,242	27	Morato, Campos, and Moure 1992
Amazonas ²	8	2,422	38	M. Oliveira and Campos 1995
Maranhão ²	4	1,728	13	Gomes 1991
Paraíba	7	1,082	10	Bezerra 1995
Bahia	5	1,285	5	Raw 1989
Bahia	5	280	9	Aguilar 1990
Bahia	5	1,144	12	Neves and Viana 1997
Minas Gerais	4	896	11	Abrantes 1990
São Paulo	3	892	8	Rebello and Garófalo 1991
Rio Grande do Sul	3	639	5	Wittmann, Hoffmann, and Scholz 1988

Notes: ¹Campina, campinarana, and forest area. ²BDFFP areas.

BEE FAUNA DISSIMILARITY

The results highlight the spatial heterogeneity in bee species composition and the need to include different sites to estimate species diversity in a given area (see also Chapter 16). This spatial heterogeneity is surprising given that Euglossine bees are robust and capable of flying long distances (Janzen 1971; Raw 1989; Williams and Dodson 1972). However, Armbruster (1993) argued that although the tropical forest seems homogeneous to the human eye, from a bee's point of view the forest is a mosaic of diverse microhabitats characterized by the distribution and phenology of diverse plant species and by the sources of floral fragrances. Becker, Moure, and Peralta (1991) also emphasize that it is difficult to charac-

terize the euglossine bee fauna of a forest by taking samples from only one location. It is possible that some euglossine species do not move between two proximate areas even though these bees possess great flying capacity and are able to cover large distances. Research in the Manaus region has shown that four euglossine species did not cross the 100 m of pasture that separated continuous forest from some forest fragments (Powell and Powell 1987). Moreover, Becker, Moure, and Peralta (1991) suggested that, on a small scale, the abundance of bees can vary completely in response to unknown factors, since they encountered substantial differences between sites separated by only 300 to 700 m sampled during the same day. Morato (1994) showed a reduction in the abundance

TABLE 17.6. Published Studies on Euglossini Bees in the Neotropics That Used Synthetic Fragrance Baits

Country	Number of			Studies
	baits	specimens	species	
Colombia (East Region)	3	160	42	Dodson et al. 1969
Costa Rica	5	961	27	Janzen et al. 1982
El Salvador	4	31	6	Dodson et al. 1969
Equador (East Region)	5	427	18	"
Guatemala	5	68	6	"
Guiana	23	713	45 ¹	Williams and Dodson 1972
Honduras	14	147	13	E Bennett 1972
Mexico (East Region)	5	203	9	Dodson et al. 1969
Nicaragua	4	73	4	"
Panama	16	27,874	53	Ackerman 1989
Peru	20	2,917	38	Pearson and Dressler 1985
Trinidad	5	244	13	Dodson et al. 1969
Venezuela (East Region)	4	89	18	"

Note: ¹Collections in flowers were included.

of euglossine males that were attracted by floral fragrances from the interior of the forest to the edge and to an adjacent deforested area. Morato (1994) concluded that, although the Euglossini are considered long-distance pollinators, open and deforested areas could constitute barriers to their dispersal, limiting pollination by bees in these areas. Lower gene flow in plant populations that require Euglossini as their principal or exclusive pollinator (e.g., orchids) could thus result.

The significant difference between the diversity of the euglossine fauna in the two areas is probably related to differences in floristic composition. However, microclimatic factors or the presence of parasites in nests might also play important roles (Folsom 1985). Finally, it should be mentioned that the dispersion of the synthetic fragrances used as bait is more effective in ventilated, well-lit, open vegetation areas (Folsom 1985). Thus, a greater number of sites should be sampled to correct for or to minimize these effects.

VERTICAL STRATIFICATION

Although the height difference between the understory and the canopy traps was only 12 to 15 m, it was sufficient to observe the preference of some species for one of these strata. It is possible that the use of traps at heights greater than 30 m, which is the average canopy height of these forests (Bierregaard and Lovejoy 1988) would show a more distinct stratification.

Various studies on tropical forests have found that the number of bee species in the forest canopy is much greater than in the understory. Erwin (1982) estimated that in tropical forests, the arthropod fauna (which includes bees) in the canopy should be two times greater than in the understory. In the tropical forests of Panama, Papua New Guinea, and Brunei, Sutton, Ash, and Grundy (1983) found a clear stratification and a marked preference of some insect groups, including Hymenoptera (which includes bees), for the canopy. In most cases, the insects were found between 20 and 30 m in the trees. Wolda and Roubik (1986) found that bee species of the genus *Rhinetula* and *Ptiloglossa*, which build nests in the ground,

were mainly captured by 3 m high traps, whereas *Megalopta*, which build nests in wood, was more abundant at 27 m. These authors postulated that such factors as food and nest sites could influence the stratification of bees in a forest. Frankie, Vinson, and Barthell (1988) placed nest-traps for bees of the genus *Centris* at 0.5 and 2.5 m heights and found that a large percentage of these bees built nests at the latter height. Morato (1993) placed nest-traps for bees and solitary wasps at 1.5, 8, and 15 m, in the same forests as the present study, and found that most species built nests at heights of 8 and 15 m.

Bees and wasps seem to prefer the forest canopy, but the reasons for such a preference are unclear. Salmah, Inoue, and Sakagami (1990) have shown that the microclimatic conditions in primary forest vary between the interior of the understory and the edges of the canopy. The understory is characterized by cooler, darker, and more humid conditions, with very little fluctuation in these conditions. Forest canopy conditions show opposite trends and vary much more. These microclimatic gradients may produce a series of microhabitats in which various animals, including bees, have adapted themselves in different ways.

Of course, because orchids, from which Euglossini males remove floral fragrances, also show vertical distribution gradients (Braga 1987), it is possible that the Euglossini fauna simply respond to the distribution of orchids.

The understory faunas of the two forest areas showed a greater similarity to each other than did the canopy faunas. This similarity was greater than that between the understory and canopy of the same area (table 17.7), suggesting that most species show a clear preference for one stratum or the other.

TABLE 17.7. Values of a Dissimilarity Index of Euglossini Bee Faunas Between the Forest Canopy and Understory in the Two Study Areas

	Canopy 1401	Understory 1501	Canopy 1501
Understory 1401	0.51	0.21	0.37
Canopy 1401		0.65	0.23
Understory 1501			0.48

Notes: Large values indicate less similar species composition. The index used varies between 0.0 and 1.41.

EFFECTS OF FOREST FRAGMENTATION

At first glance it would seem that the continued deforestation of terra firme forest area in the central Amazon would not cause any major impact on the stingless bee populations. This is misleading because 11 species were found exclusively in the continuous forest (*Aparatrigona impunctata*, *Cephalotrigona capitata femorata*, *Duckeola pavani*, *Melipona fuliginosa*, *M. illustris*, *Plebeia margaritae*, *Plebeia* sp., *Plebeia* sp. n. 1, *Plebeia* sp. n. 2, *Scaptotrigona bipunctata*, and *S. fulvicutis*). These species would be very sensitive to any deforestation or fragmentation of their habitats. Although *Melipona amazonica*, *Plebeia minima*, and *Trigonisca* sp. were found in the 1 ha fragments, which suggests some tolerance to fragmentation, we know nothing about the persistence of these species in such small areas through time. Long-term monitoring of these bee populations would be important.

Lestrimellita limao, *Scaura tenuis*, *Tetragona clavipes*, and *Tetragonisca angustula* were captured exclusively in deforested areas. These species probably represent recent invasions to the modified BDFFP landscape due to the appearance of farmland and pasture, and of young second growth (see also Brown and Hutchings 1997; Chapter 19). *Tetragonisca angustula*, for example, is a well-known species, perfectly adapted to

large urban centers where it builds its nests in cavities of walls, posts, and the like.

The low species richness in the 100 ha fragment is more difficult to explain. Probably the niches occupied by some *Meliponini* species are somewhat discontinuous in forests (J. M. F. Camargo, pers. comm.), perhaps by chance alone being underrepresented in isolated forest patches.

NEST DENSITY

The nest density encountered is well below that reported for other regions (see table 17.4). Again this may reflect very patchy distribution of resources needed by bees in primary forests and is intriguing, given the high number of species in the area.

RISK OF EXTINCTION

The process of deforestation and the expansion of agricultural frontiers have the potential to reduce populations of *Meliponini* bee species, which may lead to extinction (Roubik 1983). In areas of natural low population density this risk is even greater. Kerr and Vencowsky (1982) estimated that a minimum of forty colonies are necessary in an area to maintain a stable population and decrease the risk of inbreeding. In areas of lower abundance, inbreeding favors the emergence of male diploids. In this case, workers kill the queen when the first diploid males emerge and kill other diploid males later (Carvalho et al. 1995). This behavior, of course, may mean the end of the colony.

SEED DISPERSAL

Vertebrate seed dispersal is a well-known phenomenon, and recently observations of seed dispersal by invertebrates has increased. LaSalle and Gauld (1993) showed that seed dispersal by ants occurs in at least eighty-seven genera of twenty-three plant

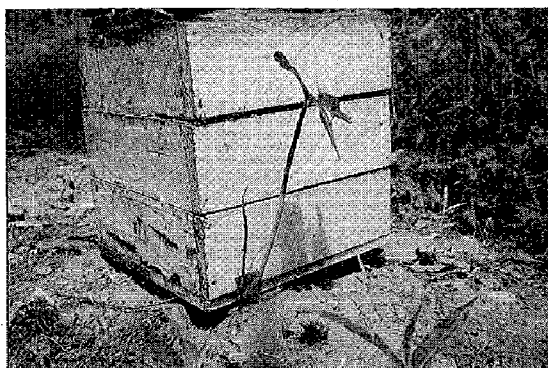


Fig. 17.2. *Melipona eburnea fuscopilosa* hive with seedlings of *Coussapoa* sp. growing out of a lateral wall.

families in Australia and that seeds of about 35 percent of all the herbaceous plant species and many tree species are dispersed by ants. A few years ago, Wallace and Trueman (1995) reported that workers of *Trigona carbonaria*, a stingless bee, are the effective agents of seed dispersal in the eucalypt tree, *Eucalyptus torelliana*, in the rainforests on the east coast of Australia.

Although not observed in the BDFFP area, it is common to find *Coussapoa* sp. seedlings sprouting in wooden boxes with *Melipona eburnea fuscopilosa* nests (fig. 17.2) or in natural *Partamona* sp. nests around Rio Branco, Acre, also in Amazonia. These findings confirm the role of stingless bees in dispersing seeds of *Coussapoa*. As this plant has epiphytic habits and strangling roots, it is probable that their seeds can germinate inside nests located in tree cavities and that *Coussapoa* seedlings subsequently spread out onto these trees, strangling them, as has been observed in nature.

Conservation Lessons

1. Euglossine bees have been recognized as keystone species, or, rather, species that play major roles in ecosystem structure and functioning. The removal or extinction of such species would lead to a

domino effect in nature (LaSalle and Gauld 1993). Gilbert (1980, cited by LaSalle and Gauld 1993) suggested that euglossine bees are among the most important "linking organisms" known in the Neotropical forests, because of their association with plants of all stages and strata in a forest.

2. The role of native bees in maintaining the tropical forest by means of pollination must be fully acknowledged. Tropical forests, unlike temperate forests, are characterized by a prevalence of dioecious plants (male and female in separate individuals) (Opler and Bawa 1978), and pollination tends to be performed by animals (Lovejoy and Rankin 1981). Bees as a group clearly play a major role in maintaining the forest, and the Euglossini represent 15–20 percent of these bee species (Ackerman 1985).
3. As deforestation in the Amazon continues at alarming rates (INPE 1998), the demarcation of forest reserves and parks becomes all the more necessary to protect natural resources. Because the euglossine bee fauna appears heterogeneous within a tropical forest, and the Meliponini bee fauna shows very low densities in many sites, the survival of many bee species, as well as the plants that they pollinate (or disperse), can be threatened without adequate protection, which includes large forest reserves that contain much of the spatial heterogeneity in natural resources needed by bees.
4. When planning and designing conservation areas, large forest areas are necessary to offer adequate conditions for the survival of those Meliponini species that have low nest densities. For example, *T. fulviventris*, which had only 0.01 nests/ha (see table 17.3), would require an estimated 4,400 ha as a minimum area capable of maintaining at least forty-four colonies to avoid the undesirable effects of inbreeding (Kerr and Vencowsky 1982; Carvalho et al. 1995).