

# Diversity of Euglossini (Hymenoptera, Apidae) in primary and secondary lowland rainforests in south-western Costa Rica

## Diversidad de Euglossini (Hymenoptera, Apidae) en bosques lluviosos de tierras bajas primarios y secundarios en el sudoeste de Costa Rica

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**Abstract:** Orchid bees are a small group of Hymenoptera which occurs only in South and Central America. They play a very important role in the long-distance pollination of orchids from which they collect aromatic fragrances thought to play a role in territorial display and courtship. We present initial data of a collection of euglossine bees in the Piedras Blancas National Park in the south-west of Costa Rica during the dry season, in January 2007. The species diversity and abundance of two primary forest sites and one secondary forest habitat are compared. Male orchid bees were attracted with four different fragrances and collected for one hour at each site. A total of 23 species of the genera *Euglossa*, *Eulaema* and *Exaerete* were recorded, representing a third of all species known from Costa Rica, and all but one genus, *Eufriesea*. This genus is known to be strongly seasonal, flying only in the wet season. Species diversity and abundance were significantly higher in primary forest than in secondary forest, and all species found in the secondary forest were also recorded in the primary forest. These results suggest that secondary forests are only colonised by a subset of the orchid bee assemblage from primary forests, probably due to fewer resources in secondary forest and the inability of many euglossine bees to cross open grassland.

**Key words:** Apidae, Euglossini, orchid bees, biodiversity, chemical baits, mobility.

**Resumen:** Las abejas de las orquídeas son un pequeño grupo de Hymenoptera, que se encuentra sólo en centro y sudamérica. Ellos tienen un importante rol en la polinización de larga distancia de las orquídeas, desde las cuales colectan fragancias aromáticas que tendrían un rol en el despliegue territorial y el cortejo. Presentamos el primer dato de colecta de abejas euglossine en el Parque Nacional Piedras Blancas, en el sudoeste de Costa Rica durante la estación seca, en enero de 2007. Se compara la diversidad específica y abundancia en dos sitios de un bosque primario y en un hábitat de un bosque secundario. Los machos de las abejas de las orquídeas fueron atraídos con cuatro diferentes fragancias y colectados durante una hora en cada sitio. Se colectaron 23 especies de los géneros *Euglossa*, *Eulaema* y *Exaerete*, que representan un tercio de todas las especies conocidas en Costa Rica, excepto el género *Eufriesea*. Este género es conocido por ser muy estacional, volando solo durante la estación seca. La diversidad de especies y la abundancia fue significativamente mayor en los bosques primarios que en los secundarios, y todas las especies encontradas en el bosque secundario también se hallaban en el bosque primario. Estos resultados sugieren que los bosques secundarios son sólo colonizados por un subgrupo de las abejas de orquídeas desde un bosque primario, probablemente debido a los pocos recursos en el bosque secundario y la incapacidad de muchas abejas euglossine para cruzar pastizales abiertos.

**Palabras clave:** Apidae, Euglossini, abejas de orquídeas, biodiversidad, cebos químicos, movilidad.

### Introduction

Orchid bees (apid tribe Euglossini) are brightly-coloured, long-tongued bees inhabiting the Neotropics, which constitute a relatively well studied group of tropical insects. The common name of these bees derives from the fact that males are the exclusive pollinators of

nearly 700 orchid species (DRESSLER 1982a, ROUBIK & HANSON 2004). The pollen of most orchids is compacted into more or less solid pollinia that cannot be eaten by bees. Nectar is the reward offered by most orchids, but a surprising array of other rewards is offered, e.g. oil, pseudopollen and perfume. Perfume is usually used as an advertisement rather than a reward, but male euglossine bees gather floral perfumes and store them

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in special organs on their hind legs. A number of orchids offer perfume as a reward and are normally pollinated only by male euglossine bees (DRESSLER 1993). The orchids, from which the males collect their fragrances, may even lack nectaries; they usually allure the bees only with fragrance (VOGEL 1963, ROUBIK & HANSON 2004). The bees collect these fragrances with their front tarsi and store them in their hind tibiae (DODSON et al. 1969, EVOY & JONES 1971). For foraging fragrances, male bees have specialised foraging structures that are absent in the females (DRESSLER 1982a, ROUBIK & HANSON 2004, BEMBÉ 2007). Some of these foraging structures are very important characters for identifying genera and species of euglossine bees. The reason for collecting fragrance, which is limited to the males, is not totally clear, but it is suggested that the fragrances are important in the mating behaviour of the bees (DODSON et al. 1969). Female euglossines are not attracted to the aromatic compounds that attract males (DODSON et al. 1969, DRESSLER 1982a), and therefore it seems unlikely that these are used as volatile lures, like pheromones. However, it has been suggested that they are modified in the body of the male bee to produce a female-attractive pheromone (DRESSLER 1982a). It is also possible that the collected scents are used to attract other males to form leks – groups of males performing courtship displays (DODSON et al. 1969, ROUBIK & HANSON 2004). BEMBÉ (2007) postulated that fragrances are sprayed during the so-called “ventilating” behaviour at the bee courtship sites, but the real function and biological importance of the fragrances remains unclear.

The close relationship between certain orchids and male Euglossini is very important for both partners suggesting a co-evolution between the two (ROUBIK & HANSON 2004). DRESSLER (1982b) pointed out that euglossine males are well adapted to gathering perfume from the surfaces of flowers, but none of them is adapted to a particular type of flower. The knowledge of the fragrance-dependence of the bees makes it possible to attract the male bees for ecological and biogeographical studies (WILLIAMS & DODSON 1971, DRESSLER 1982a, JANZEN et al. 1982).

### Foraging and pollination

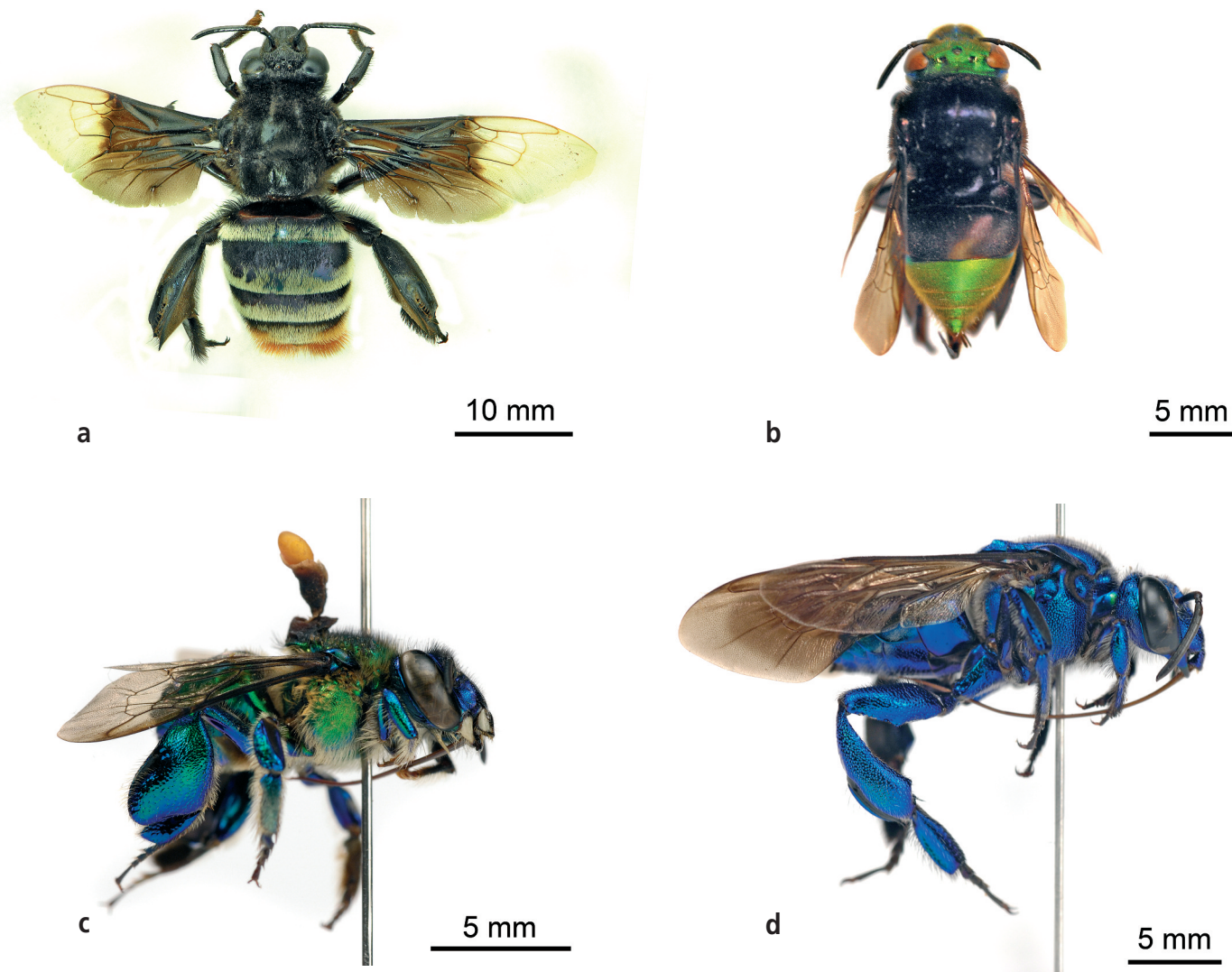
In spite of the long proboscis characteristic of the tribe, female euglossines visit various flowers for pollen and nectar, including some that contain nectar in a short corolla where the long proboscis would appear to be a hindrance. The females also pollinate some nectar-producing orchids, but they are far less important in orchid pollination than the males (DRESSLER 1982b). The males visit the same flowers for nectar but are strongly attracted to certain perfumes as well (DRESSLER 1993). The precise positioning of orchid pollen on the fragran-

ce-collecting bee is made possible by complex mechanisms which direct the bee into the proper place. DRESSLER (1993) exemplifies in his book ‘The Orchids’ some pollination scenes, e.g. in *Catasetum*, an orchid genus, the stipe that connects the pollinia to the sticky viscidium is elastic and is stretched over a knob. When a bee touches the trigger the viscidium is released and is thrown from the column with considerable force. The pollinia hit the pollinator with such force that the bee may be reluctant to approach another male flower. The female flowers, however, are quite different in appearance. Small bees of the genus *Euglossa* pollinate some *Catasetum*, and they may not be able to fly away until the anther cap falls off the pollinia and the pollinia have dried a bit.

Male euglossine bees use a wide variety of chemical sources, including many that are not from orchids. ROUBIK & HANSON (2004) mention four families of monocotyledons and six families of dicotyledons (e.g. Euphorbiaceae, Araceae, Gesneriaceae, Solanaceae) as chemical sources. In most cases the floral fragrance components are commonly-occurring plant products, either terpenoids or aromatic compounds (WILLIAMS & DODSON 1971). But also non-floral sources provide the bees with scents: rotting logs, certain fungi, sap from plant wounds or fruit (DRESSLER 1982a, CAMERON 2004). Cadavers of conspecific males are another source of chemicals, offered from the hind tibia of the dead bee (ROUBIK & HANSON 2004).

### Mobility of orchid bees

According to ROUBIK & HANSON (2004) orchid bees are most abundant in the lowlands up to about 1000 m above sea level. They are well known for flying long distances and for being very strong fliers. Details on observed flight ranges of male and female orchid bees are given in several publications. Orchid bees have been observed to fly up to 5 km over water (DRESSLER 1968, DODSON in DRESSLER 1968, JANZEN 1971, ACKERMAN 1981 in DRESSLER 1982a) and to come from habitats 50 km away (ACKERMAN 1981 in DRESSLER 1982a). Other studies show that the home range of male bees is confined to a small area, at least for certain periods of time (KROODSMA 1975), and the bees return daily to rewarded fragrance and food sources (JANZEN 1971, ACKERMAN 1982). This behaviour appears reasonable, because suitable orchids are often very widely scattered (BEMBÉ 2007) and have several long-living flowers (JANZEN 1981). In many euglossine-pollinated orchids, the flowering season is not sharply defined at all and the inflorescences are usually quite short-lived, but they are highly attractive to pollinators. Such a system seems especially well suited to promote cross-pollination over considerable distances (DRESSLER 1968, WILLIAMS &



**Fig. 1:** Photos of typical specimens of the four Euglossini genera occurring in Costa Rica. All specimens except for the *Eufriesea* are males. (a) *Eulaema meriana*, a large hairy bee, which has similarities with bumblebees at first glance; (b) *Eufriesea* sp., the head and the metasoma are brilliantly metallic; (c) *Euglossa championi* (with orchid pollinarium on the thorax) belongs to the most glittery genus of the Euglossini including the smallest orchid bees; (d) *Exaerete smaragdina* is a cleptoparasite, which has a clearly less swollen hind tibia than the non-parasitic genera.

DODSON 1972). Several orchids show synchronous flowering. They have short-lived flowers but coordinate their flowering time to the same days in the population. The synchronously flowering orchids are probably a much more effective stimulus for the pollinators (DRESSLER 1993). Orchid bees exhibit a spectrum of behaviour from transient to resident depending on the abundance and dispersal of resources (ACKERMAN 1982). Thus, bees can be attracted from the nearer surroundings as well as from habitats at great distances, which needs to be taken into account in fragrance baiting experiments.

### The 5 Euglossini genera

Euglossine bees occur only in the Neotropics, where there are currently 180 to 200 described species

(ROUBIK & HANSON 2004, CAMERON 2004, BEMBÉ 2007). Of these, 76 species occur in Central America (ROUBIK & HANSON 2004) (Table 1). They belong to the five genera *Euglossa*, *Eulaema*, *Exaerete*, *Eufriesea* and *Aglae* (Fig. 1).

*Euglossa* is the largest genus of orchid bees with over 100 described species, 43 of which occur in Central America and Mexico.

The second largest genus of Euglossini with over 60 species in the Neotropics, over 20 of which occur in Central America and Mexico, is *Eufriesea* (ROUBIK & HANSON 2004). Due to the pronounced seasonality of adults (ROUBIK 1989), they are poorly represented in collections. Previously, most species of *Eufriesea* were included in *Euplusia*, which was synonymised with the

older name *Eufriesea* by KIMSEY 1979 (in ROUBIK & HANSON 2004). Most *Eufriesea* are about 15-20 mm long, roughly intermediate between *Euglossa* and *Eulaema* in size. *Eufriesea* are darker and have more hair than *Euglossa* but are more metallic than *Eulaema* (ROUBIK & HANSON 2004).

*Eulaema* comprises at least 16 species, eight of which occur in Central America and Mexico. They include the largest euglossines and those with the least metallic coloration. Most *Eulaema* are superficially similar to bumblebees (CAMERON 2004): they are large bees – mostly greater than 20 mm in length – with predominantly black face and mesosoma, and mostly only slight metallic coloration on the metasoma.

Five of the six described species of *Exaerete* occur in Central America and Mexico. All of them are cleptoparasites in the nests of *Eufriesea* and *Eulaema*. Bees of the genus *Exaerete* are large (20-25 mm in length) green or blue bees with uniformly blackened wings, whereas smaller (15 mm or less in length) metallic bees with clear wings are usually *Euglossa*.

The fifth genus, *Aglae*, which consists of just one species, is restricted to the Amazon region. One eastern Panama report of *Aglae* is doubtful but the genus certainly occurs in Colombia. *Aglae*, like *Exaerete*, is a cleptoparasitic species with *Eulaema* as host (MICHENER 2000). It is coloured metallic blue-grey and has a long (25 mm) and slender body (CAMERON 2004).

In this study, one main intention was to carry out an initial assessment of species diversity in the Piedras Blancas National Park. At the same time, we tried to investigate differences in species composition and abundance between primary and secondary forest and within the former between the two habitat types riverine and ridge forest.

## Material and Methods

### Study area and Climate

The study was conducted in the southwestern part of Costa Rica in the Piedras Blancas National Park near the village of La Gamba which is at an altitude of about 70 m, characterised by tropical lowland rainforest. The Golfo Dulce region where the study area is situated is one of the most humid areas in Costa Rica. The average number of rainy days is 286.5 per year and the average annual rainfall is about 6000 mm. The months December to March are the driest months with an average rainfall of about 300 mm. During the months with the highest precipitation (August-November) it rains nearly every day. The mean monthly temperature averages 26.7°C in January and 27.3°C in February (WEIS-

SENHOFER & HUBER 2001). The relative humidity is constantly high, averaging 88.3% at the station and 97.7% inside the forest. Mist forms daily at dawn, sometimes at dusk and after heavier rainfalls. Under these conditions, air temperature is lower.

### Sampling sites

We conducted the sampling at three different locations, two of them in the middle of two types of primary forest (riverine and ridge forest), the third in secondary forest (gallery woodland) as defined in WEISSENHOFER et al. (2001) and WEISSENHOFER (2005). The two locations in primary forest are at a distance of 1 to 2 km to each other; the first place is located on the waterfall trail next to the 1<sup>st</sup> waterfall from the Esquinas lodge and the other on the crossing of 'fila trail' and 'ocelot trail'. The secondary forest is located next to the road connecting the research station and the village La Gamba and is situated at a distance of about 3 km from the riverine forest site surrounded by grassland and agricultural area.

### Sampling design

We used four different aromas which are present in orchid flower fragrances (WILLIAMS & DODSON 1971) to attract male bees. Based on ROUBIK & HANSON (2004), these aromas were chosen such that almost every orchid bee known from Central America was attracted by at least one of them. Only two orchid bees occurring in this region – *Euglossa variabilis* and *Eulaema seabrai* are not known to be attracted by our chosen combination. All four were bought at an Austrian pharmacy; therefore they had usual commercial quality. Three of them, methylsalicyl acid, cineole and eugenol, were dissolved, vanillin was bought as a powder and dissolved in alcohol until the solution was saturated.

The survey was carried out on sunny days from 27 to 31 January 2007, in times of cloudless sky, because under these conditions the flight activity is highest (JANZEN et al. 1982, GRUBER & MORAWETZ personal observation). The sampling activities were performed between 9:00 and 12:00 in the morning, at peak bee activity (ACKERMAN 1983, POWELL & POWELL 1987, MILET-PINHEIRO & SCHINDWEIN 2005). At each sampling site, all four chemical baits were put at an average height of 2 m (scented napkins attached to branches with twine), at an average distance of about 4-5 m. The baits were monitored simultaneously and constantly, the sampling lasted one hour per sampling site. The sampling time was subdivided in time units of 10 minutes to obtain the time pattern of bee arrival. Not all bees were captured immediately, but within the time unit in which they arrived. The attracted bees were captured with an insect net after visiting the baits and killed in a jar with ethyl

acetate (C<sub>4</sub>H<sub>8</sub>O<sub>2</sub>). They were kept in labelled glasses (tagged with capture time and sampling site).

## Data analysis

EstimateS (COLWELL 2006) was used to generate the estimators for true species richness. True species richness for each site was estimated using the incidence-based coverage estimator (ICE), Chao 2 and second order jack-knife, three common nonparametric richness estimators that use species-by-sample data. For identification, we used the key of ROUBIK & HANSON (2004) and for species of the *Euglossa cordata* group, the key of BEMBÉ (2007), which provides a totally revised key of this group.

## Results

### Species richness

From Costa Rica, 66 species of Euglossini are known (Table 1), but little research has been done on Euglossini in the south-west of Costa Rica, where our experiments were conducted. There, we found half of the *Euglossa* (= *Eg.*) species occurring in Costa Rica, two *Eulaema* (= *Eu.*) and two *Exaerete* (= *Ex.*), but no species of *Eufriesea*. In total, we collected 23 species (Table 3). One of them was found outside the sample periods and therefore it does not appear in the statistical tests (*Eg. despecta*). In the two primary forest habitats, we caught noticeably more species and individuals than in the secondary forest: 112 individuals from 20 species were collected in riverine forest, 166 individuals from 19 species in ridge forest. On the other hand we collected only 19 individuals from 9 species in the secondary forest during the same amount of time.

*Eulaema* and *Exaerete* were only caught in primary forest, but we saw one individual of *Eulaema* in secondary forest, which we were unable to catch. *Euglossa* was found at all three locations, with eight species in all three habitats, nine species in both primary forests and

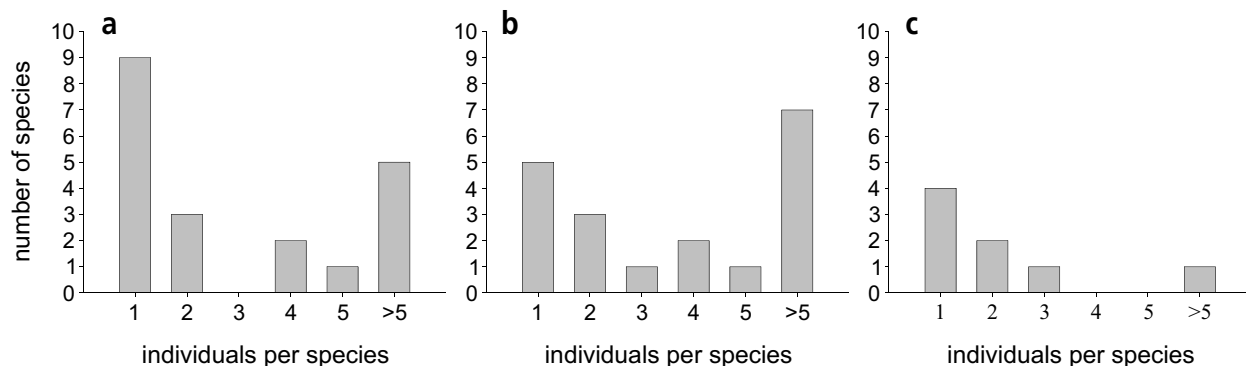
**Table 1:** Comparison of Euglossini species richness. The data about the Neotropics and Costa Rica are taken from ROUBIK & HANSON (2004), the data "La Gamba" are own data from a collection in January 2007 in primary and secondary forests around the village La Gamba in the southwest of Costa Rica.

Genus	Neotropis	Costa Rica	La Gamba
<i>Aglae</i>	1	0	0
<i>Eufriesea</i>	58	15	0
<i>Euglossa</i>	103	40	19
<i>Eulaema</i>	16	8	2
<i>Exaerete</i>	6	3	2

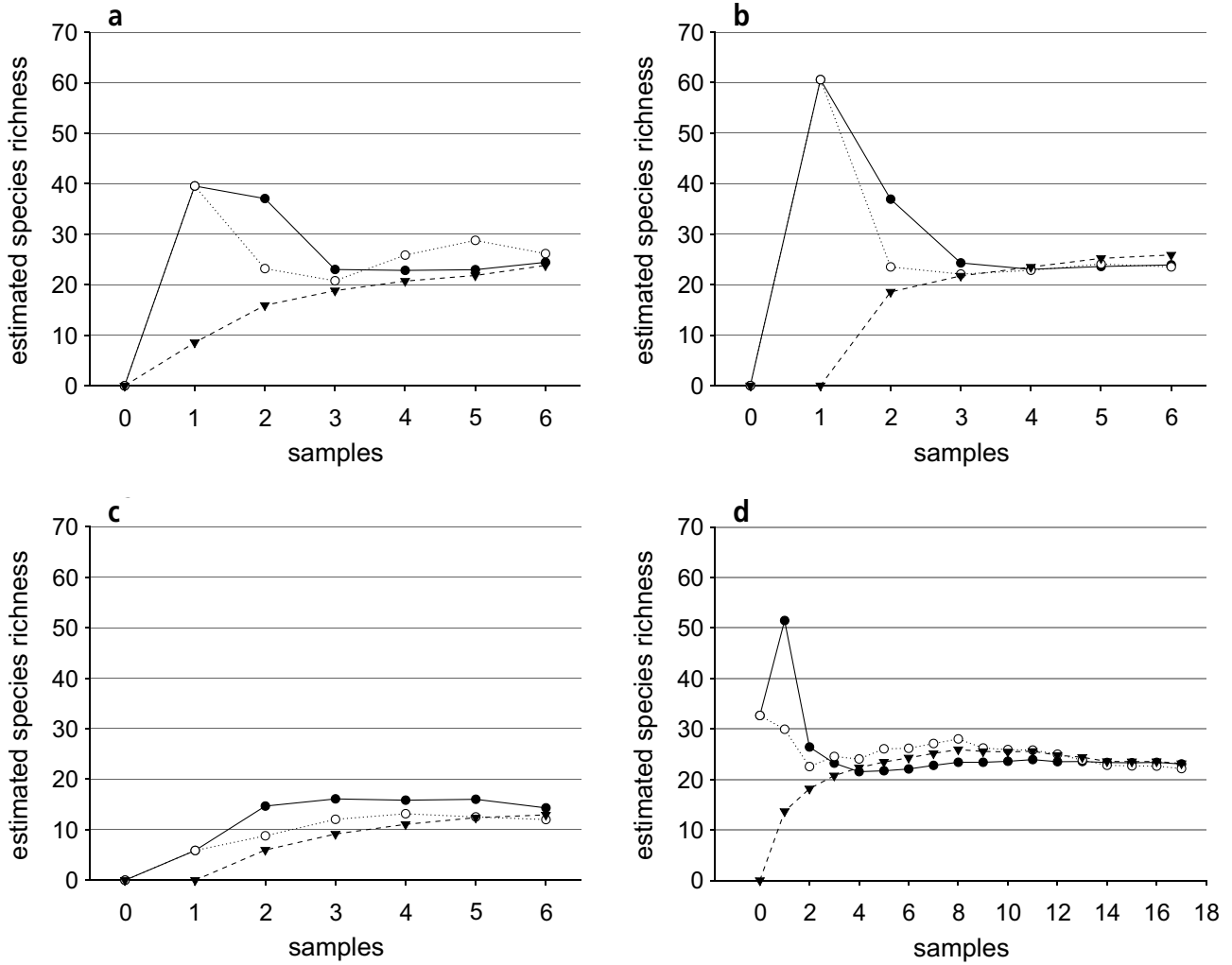
five species at only one location (Table 3). No species was limited to the secondary forest.

The most common bee in the primary forest was *Eg. dodsoni*. This species made up about a third of the collected individuals in both locations. It was rare in secondary forest, where only one individual was collected. Another very abundant bee was *Eg. sapphirina*. This species was most common in the secondary forest and constituted nearly half of the collected individuals there, but was also found in primary forest in large numbers. With about half of all collected individuals, *Eg. dodsoni* and *Eg. sapphirina* were the dominant species in the primary forest. Most of the other frequent species recorded in the primary forest were also found in the gallery woodland. Only *Eg. gorgonensis*, which is the third most common species in primary forest and made up nearly 10% of the collection in both primary forest habitats, was not sampled in the secondary forest at all.

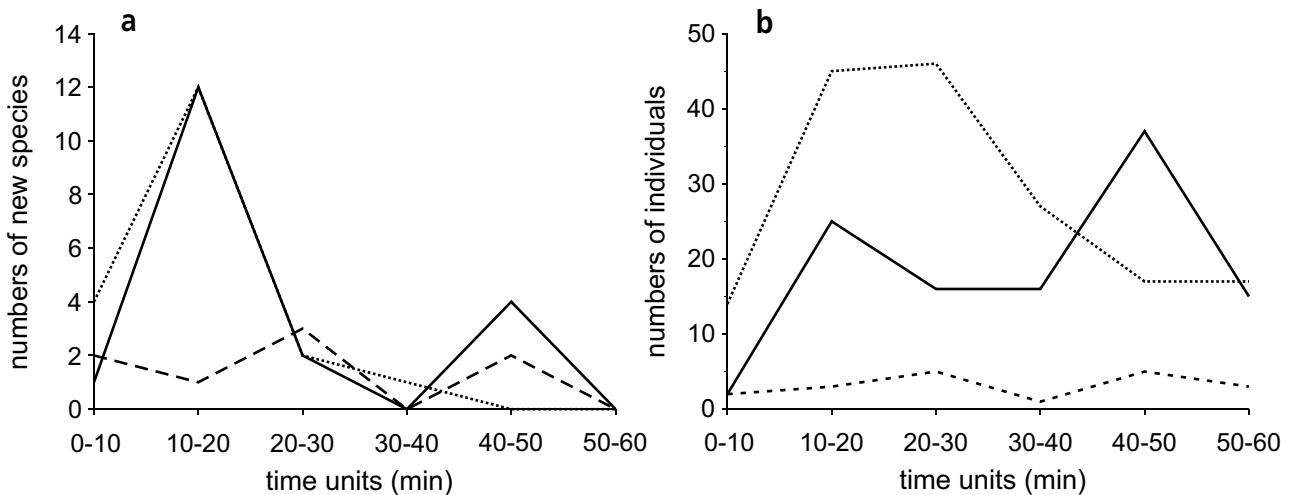
In the gallery woodland, very few individuals were collected, such that two thirds of all collected species were represented by a single individual (singletons, Fig. 2). In the ridge forest, there were approximately the same numbers of singletons, but the total number of species was higher in this habitat including many frequent species. In the riverine forest, we found twice as many singletons as in the other two habitats, although the number of collected species was the same as in the rid-



**Fig. 2:** Occurrence of Euglossini species in the Southwest of Costa Rica. The collection took place both in primary forest (a, b) and secondary forest (c). (a) riverine forest: 20 species, 112 individuals; (b) ridge forest: 19 species, 166 individuals; (c) gallery woodland: 9 species, 19 individuals.



**Fig. 3:** Estimated richness of the Euglossini genera *Euglossa*, *Eulaema* and *Exaerete* in three habitats of the Piedras Blancas NP. ICE: solid line, closed circles; Jackknife 2: dashed line, triangles; Chao 2: dotted line, open circles. (a) riverine forest; (b) ridge forest; (c) gallery woodland; (d) all habitats together.



**Fig. 4:** Time structure of the arriving male orchid bees during a collection with fragrant baits in the woods of southwestern Costa Rica. The collections took place twice in primary forest (solid line: riverine forest; dotted line: ridge forest) and once in secondary forest (dashed line: gallery woodland). (a) newly arrived species per time unit; (b) individuals caught per time unit.

**Table 2:** Collected and estimated number of species of Euglossini in the southeast of Costa Rica. The collections were conducted two times in primary forest (riverine forest, ridge forest) and one time in a secondary forest (gallery woodland), each collection was separated into 6 periods of 10 minutes.  $N_s$ : the number of recorded species,  $N_i$ : the number of caught individuals. The mean number of individuals was calculated using the three given estimators. The percentage shows how many species were found in comparison with the mean estimated number of species

Habitat	$N_s$	$N_i$	ICE	Chao 2	Jack 2	Mean $\pm$ SD	%
Riverine forest	19	111	27.4	27.0	28.9	27.8 $\pm$ 1.0	68.3
Ridge forest	19	166	23.9	23.5	25.9	24.4 $\pm$ 1.2	77.9
Gallery woodland	8	19	14.3	12.0	12.9	13.1 $\pm$ 1.2	61.1
<b>Total</b>	<b>22</b>	<b>296</b>	<b>25.2</b>	<b>24.0</b>	<b>26.0</b>	<b>25.1 <math>\pm</math> 1.0</b>	<b>87.6</b>

ge forest. Comparing singletons between primary and secondary forest (Table 3) shows that most of the species of the secondary forest are more abundant in primary forest, e.g. *Eg. imperialis* was collected only once in gallery woodland, but 11 times in ridge forest. Furthermore, species which were rare in primary forest did not occur in the secondary forest at all.

### Estimation of species number

At the two locations in the primary forest, we attracted five and respectively eight times more individuals than in the secondary forest during the same length of time (Table 2) but we only collected twice as many species than in the secondary forest. The results of the species richness estimations show little differences between the two habitats in the primary forest, but the riverine forest habitat seems to contain slightly more species than the ridge forest. They indicate that in secondary forest the number of species present is clearly lower than in primary forest, but in all three cases, the curves of Chao 2 and second order jack-knife are still relatively unstable (Fig. 3). Furthermore, it must be remembered that the data do not include the genus *Eufriesea* which is therefore not included in the estimates. The estimates of the total data, which show stable curves, suggest that the figures for the riverine forest might be slightly overestimated, because they exceed those estimated from the total data.

### Arrival time and distance estimation

The time it takes the bees to arrive at the bait can be used as an indication of their flight distance to the bait. It is known that the orchid bee *Eufriesea surinamensis* (formerly known as *Euplusia surinamensis*) can reach a speed of 5 m/sec (JANZEN 1971), and thus orchid bees could fly a distance of 3 kilometres within 10 minutes. But these velocity calculations are from measurements of one moderate sized *Eufriesea* species and might differ for species of a different size or of a different genus.

In the ridge forest, many bees appeared within a short time from the beginning, most of them 10 to 30 minutes after placing the baits (Fig. 4). After this the

**Table 3:** Euglossini collected in the forests near La Gamba, Costa Rica. The numbers of collected individuals are indicated, the percentage of the total number of species per location is given in brackets. Species in bold letters were found in all three locations, the species marked grey was found at the riverine forest, but not during the sampling periods.

Species	Riverine forest	Gallery woodland	Ridge forest
<i>Eulaema meriana</i> (OLIVIER, 1789)	4 (3.6)		2 (1.2)
<i>Eulaema polychroma</i> (MOCSÁRY, 1899)			1 (0.6)
<i>Euglossa alleni</i> MOURE, 1968/ <i>Euglossa hansonii</i> MOURE, 1965	1 (0.9)		3 (1.8)
<b><i>Euglossa allosticta</i> MOURE, 1969</b>	2 (1.8)	1 (5.6)	1 (0.6)
<i>Euglossa bursigera</i> MOURE, 1970	4 (3.6)		7 (4.2)
<b><i>Euglossa championi</i> CHEESMAN, 1929</b>	7 (6.3)	2 (10.5)	15 (9.0)
<i>Euglossa cordata</i> (LINNAEUS, 1758)	1 (0.9)		
<b><i>Euglossa cybelia</i> MOURE, 1968</b>	2 (1.8)	1 (5.3)	4 (2.4)
<b><i>Euglossa dodsoni</i> MOURE, 1965</b>	31 (27.9)	1 (5.3)	53 (31.9)
<i>Euglossa despecta</i> MOURE, 1968	1		
<i>Euglossa flammea</i> MOURE, 1969			2 (1.2)
<i>Euglossa gorgonensis</i> CHEESMAN, 1929	10 (9.0)		16 (9.6)
<b><i>Euglossa hemichlora</i> COCKERELL, 1917</b>	1 (0.9)	2 (11.1)	4 (2.4)
<i>Euglossa heterosticta</i> MOURE, 1968	1 (0.9)		2 (1.2)
<b><i>Euglossa imperialis</i> COCKERELL, 1922</b>	5 (4.5)	1 (5.3)	11 (6.6)
<i>Euglossa milenae</i> BEMBÉ, 2007	1 (0.9)		1 (0.6)
<i>Euglossa mixta</i> FRIESE, 1899	1 (0.9)		1 (0.6)
<b><i>Euglossa sapphirina</i> MOURE, 1968</b>	28 (25.2)	8 (42.1)	30 (18.0)
<i>Euglossa townsendi</i> COCKERELL, 1904			5 (3.0)
<b><i>Euglossa tridentata</i> MOURE, 1970</b>	8 (7.2)	3 (15.8)	8 (4.8)
<i>Euglossa villosiventris</i> MOURE, 1968	1 (0.9)		
<i>Exaerete frontalis</i> (GUÉRIN-MÉNEVILLE, 1845)	1 (0.9)		
<i>Exaerete smaragdina</i> (GUÉRIN-MÉNEVILLE, 1845)	2 (1.8)		1 (0.6)

number of arriving bees slowed down, but we always collected more than 15 bees per time unit. In the first 10 minutes, four species arrived: *Eg. dodsoni*, *Eg. gorgonensis*, *Eg. heterosticta* and *Eg. imperialis*. In the riverine forest, the number of individuals was lower than in the ridge forest and it took more time before most of them arrived; most individuals were collected in the fifth time unit. Most species were first collected 10-20 minutes after the beginning. The species collected first after more than 40 minutes were represented by only one or two individuals. In the riverine forest, only one species, *Eg. gorgonensis*, arrived in the first time unit. In gallery woodland, where very few orchid bees were collected,

only one to three new species were recorded per time unit. There is no meaningful difference between the time units in the number of approaching species and individuals. The species which approached in the first ten minutes were *Eg. sapphirina* and *Eg. allosticta*.

## Discussion

### Species Abundance

In general, this study shows that orchid bees have impressive species diversity in the Piedras Blancas National Park. We found more than a third of all species known from Costa Rica, although we collected only for 3 hours in the dry season. Some of the Euglossini show a seasonal behaviour: they are less active in the wet and late wet season, but from the middle of the dry season to the early wet season the bee abundance peaks (DRESSLER 1982a, ACKERMAN 1983). Although we collected in the best season of the year, we have to be careful with assumptions about abundance because of this short observation period. Some species have a stable abundance during the year, while others do not (DRESSLER 1982a, JANZEN et al. 1982, ACKERMAN 1983, SOFIA et al. 2004). *Eg. dodsoni*, which was the most common bee in our collection, was found to have very unstable populations in Panama during the year, whereas *Eg. sapphirina* and *Eg. imperialis* had very stable populations (ROUBIK & ACKERMAN 1987). Therefore, it is not clear whether *Eg. dodsoni* is the dominant species throughout the year, because species dominance might vary with the season.

We found no individuals of the genus *Eufriesea*, although this is the second largest genus in Euglossini. This is attributed to the strong seasonality of most of its species. JANZEN et al. (1982) found them only in two months of the year and in Central Panama they occur mainly in the wet season (ACKERMAN 1983). According to WEISSENHOFER & HUBER (2001), August to November are the months with the highest precipitation. Our sampling was conducted in January, one of the driest months. For more significant results concerning species diversity and abundance, additional sampling in the rainy season would be important.

In all three habitats, we found a high dominance of a few species. This is a typical pattern for Euglossini communities. Certain species, such as *Eg. imperialis*, can constitute 25% of the local Euglossini community (ROUBIK & HANSON 2004) and in Central Panama the two most abundant species accounted for 45-50% of the individuals observed (ACKERMAN 1983). Our results also confirm this pattern. In the ridge forest and the riverine forest *Eg. dodsoni* and *Eg. sapphirina* account for ca. 50% of all collected individuals, in gallery woodland only *Eg. sapphirina* is dominant (43% of all individuals).

### Differences between the habitats

Species diversity and abundance was found to be much lower in secondary forest than in primary forest. The reason for this might be the higher plant diversity in the primary forests, especially for epiphytes (WEISSENHOFER et al. 2001) which is probably correlated with a higher resource availability for orchid bees. It has been shown in several studies (JANZEN 1971, ACKERMAN 1982, ARMBRUSTER 1993) that orchid bees remember locations of successful collection and exhibit temporary site constancy for these places. Therefore, we suggest that high resource availability is the reason for the higher number of individuals and species in primary rainforest. It would be interesting to compare the availability of potential perfume flowers, which are strictly dependent on euglossine pollination, in the different habitats.

Another difference between the primary forests and the gallery woodland is seen in the species assemblage. Interestingly, all species which were found in secondary forest also occur in primary forest. This suggests that the secondary forest has been colonised by a subset of the species diversity found in primary forest, possibly only on a temporary basis by regular migrations. We do not know what distances orchid bees cross over open pasture. Some of the larger bees were observed to cross open water (DRESSLER 1968, DODSON in DRESSLER 1968, JANZEN 1971, ACKERMAN 1981 in DRESSLER 1982a), and these bees should be able to use both primary and secondary forest as resources as suggested by JANZEN (1981). This may be especially the case with *Eulaema*, which is frequently found outside the forest (POWELL & POWELL 1987, MILET -PINHEIRO & SCHINDWEIN 2005, NEMÉSIO & SILVERA 2006) and in very fragmented areas (TONHASCA et al. 2002b), but there are species of *Euglossa* which are unable to cross cleared areas of 100 m (POWELL & POWELL 1987) and in the study of MILET-PINHEIRO & SCHINDWEIN (2005) only the most abundant *Euglossa* out of fourteen *Euglossa* species could be lured into a sugar cane plantation next to the closed forest. Our data confirm these observations, because we mostly found those *Eulaema* and *Euglossa* species in secondary forest which were also frequent in primary forest. We therefore assume that few species are able to cross the pasture between the two forests which could explain the low species diversity and abundance in the gallery forest.

The main difference between the two primary forest habitats is the different number of collected individuals. The reason for this is unclear, because the distance between the two collection sites was only two kilometres, a distance regularly covered by collecting orchid bees (DRESSLER 1968, JANZEN 1971), but it is obvious that the individuals arrived more quickly and in greater



numbers in the ridge forest than in the riverine forest, although almost the same number of species were sampled. TONHASCA et al. (2002a) explained sample differences of two nearby sites through sampling variability caused by changes in wind speed and direction, temperature and cloud cover. Therefore, the exposure may be an important factor. The site in the riverine forest was below a small waterfall and therefore more protected against wind. This was not the case in the ridge forest; due to the exposed position, wind plays an important role in this type of forest (WEISSENHOFER et al. 2001). It can be assumed that the fragrances were distributed better in the ridge forest and could attract more bees. Unfortunately we did not measure the wind speed and direction, factors which could have had a strong influence on our results.

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