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RESOURCE PARTITIONING BETWEEN HIGHLY EUSOCIAL BEES AND POSSIBLE IMPACT OF THE INTRODUCED AFRICANIZED HONEY BEE ON NATIVE STINGLESS BEES IN THE BRAZILIAN ATLANTIC RAINFOREST

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ABSTRACT

The highly eusocial bee community of the neotropical Atlantic Rainforest was studied at Boracéia Biological Station in the state of São Paulo, Brazil. In this reserve, 17 species of stingless bees and the introduced Africanized honey bee were found, the latter being the most abundant flower visitor. Of all flowering plants, Asteraceae and Myrtaceae were particularly important as resources for bees. Trophic niche overlap between the various species of stingless bees is evident, and it was generally larger within the tribes Meliponini and Trigonini than between members of different tribes. Nevertheless, in the stingless bee community the competitive pressure is rather uniformly spread. The trophic niche of the Africanized honey bee can be positioned between those of Meliponini and Trigonini. Today this introduced species represents the main competitor in this bee community. However, its impact on native stingless bee populations is apparently buffered by mass-flowering trees which are the most important food plants of the indigenous highly eusocial bees.

KEYWORDS: Atlantic Rainforest of Brazil, bee community, stingless bees, Africanized honey bee, nutritional resource partitioning, mass-flowering.

INTRODUCTION

Highly eusocial bees have permanent colonies often comprising large numbers of individuals which represent the main flower visitors and pollinators in tropical ecosystems (Roubik 1989; Pedro & Camargo 1991; Wilms 1996). Stingless bees (Meliponinae) are highly eusocial bees of pantropical distribution, though they are most species-rich in the Neotropics (Roubik 1989). Honey bees (*Apis mellifera* L.) were introduced to the Americas in historical times (Crane 1990). The accidental release of the African honey bee subspecies *A. m. scutellata* in Brazil 40 years ago gave rise to the Africanized honey bee. Possible impacts of this introduced eusocial species on the native bee community were not investigated during its initial spread. In the context of ecosystem functioning, competition with the similarly highly eusocial stingless bees is particularly important but still poorly understood. Only after the arrival of the Africanized honey bee in the northern parts of South

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and Central America was competition between it and native bees studied and claimed to exist (Roubik 1978, 1980, 1983), and a decline of stingless bee colonies was predicted (Roubik *et al* 1986). However, Roubik (1988) concluded that the real long-term effect of the Africanized honey bee, especially in wild habitats, had yet to be documented. Since all eusocial bees have evolved generalized patterns of foraging but also exhibit some flower preferences (Ramalho *et al* 1990), Africanized honey bees potentially compete for nutritional resources with either all, many, or only a few of the indigenous social bees and, consequently, they will affect the abundance of sympatric species in quite different ways. These alternative hypotheses could hopefully be evaluated by trophic niche overlap calculations.

The aim of this study was to analyse such trophic relationships in the highly eusocial bee community of an undisturbed area in the Brazilian Atlantic Rainforest. In this unique neotropical ecosystem, the apifauna and the exploitation of floral resources have never been investigated. The data were also used to estimate the possible impact of the Africanized honey bee on populations of native stingless bees.

MATERIAL AND METHODS

Study site

The study was conducted at Boracéia Biological Station which is located between 800 and 900 m NN in the Serra do Mar of São Paulo State (23°38' S, 45°52' W), circa 90 km east of the city of São Paulo and 10 km from the Atlantic Ocean coast. Boracéia lies in the Atlantic Forest Morphoclimatic Domain (Ab'Sáber 1977), in the middle of a forest-covered water reserve of over 16,000 ha. Sampling of bees was carried out mostly in an area of approximately 5 km in diameter around the station. The vegetation consists mainly of primary Atlantic Rainforest with some patches of secondary growth. The upper canopy is approximately 15 m high with few emergents. A total of over 650 plant species was recorded, including the survey of Custodio-Filho (1989). Of these, 240 are trees, mainly of the families Myrtaceae, Melastomataceae and Lauraceae. The similarly species-rich Asteraceae include many climbers. The overall picture of the plant distribution is that of a mosaic structure without dominance by a single species. Only the palm *Euterpe edulis* is exceptionally abundant.

Bee sampling

From September 1991 through March 1994, over 7,000 bees were collected when visiting flowers. Nets attached to long poles were used to reach the upper canopy. In our random sampling approach, bees were captured wherever plants were encountered in bloom, taking in mind, as far as possible, the overall abundance and flowering periods of plant species in the study area. In a sampling effort, all bees visiting flowers were collected. However, for standardization, not more than 50 bee individuals were taken on a single plant specimen. Of the total sample, 4,465 bees were of highly eusocial species. For identification of bee species the collections of the Zoological Museum of the University of São Paulo, the Camargo collection at the University of São Paulo at Ribeirão Preto and the Moure collection at the Federal University at Curitiba were used. Voucher specimens of our survey will be deposited in the Zoological Museum of the University of São Paulo. Branches of the flowering plants visited by bees were sampled and dried. Identification was carried out in the Botanical Institute of the State of São Paulo and samples will be deposited there.

Ecological indices

For calculation of the trophic niche breadth of a bee species, the number of different resources used as well as their frequency of use were considered. This is because analysis of purely the number of used plant species is only of limited value. In fact, use by a bee species of many resources of low importance can suggest a broad trophic niche when, in reality, most food is supplied by only one resource.

Trophic niche breadth (NB) was calculated as the *Shannon index* (Pielou 1969):

$$NB_i = -\sum_k p_{ik} \times \mathrm{eln}p_{ik}$$

where i = a particular bee species, $p_{ik} = N_{ik}/Y_i$, N_{ik} = number of individuals of bee species i collected on flowers of species k, and Y_i = total of all individual bees of species i that were collected on flowers.

Trophic niche overlap (NO) was calculated from the formula of Colwell and Futuyama (1971) as:

$$NO_{ih} = 1 - \tfrac{1}{2} \sum_k \left| p_{ik} - p_{hk} \right|$$

where i and h represent the two species under comparison.

The values for the relative use of a particular flower, p_{ik} and p_{hk}, may be somewhat dependent on the absolute number of foragers collected. Transformation to equal sample size, i.e. to the smaller number of collected bees of the two species, that is $\min(Y_i, Y_h)$, and recalculating the NO index revealed a deviation of less than 1% from the uncorrected NO values. Differences in sample size are therefore negligible.

The trophic niche overlap indices were used to create a matrix of dissimilarities or "niche distances" calculated as 1 – NO. This distance matrix was used to visually represent the trophic niche relationships between the species by ordination (Orloci 1973) using the multidimensional scaling procedure (Kruskal 1964) in the SPSS statistics program (SPSS for Windows, release 6.0, SPSS Inc. Chicago).

Niche overlap alone does not indicate the extent of interspecific competition very well because abundance and body size are also important factors in modulating competition. Considering these factors, we calculated the competitive load (CL) imposed by one species (i) upon another (h) as:

$$CL_{ih} = NO_{ih} \times \text{relative abundance}_i \times \text{body weight}_i \text{ [g]}$$

Notice that, in contrast to niche overlap, the competitive load is uni-directional. The corollarly of the competitive load (CL) of species i on species h is the competitive pressure (CP) that species h suffers from species i.

Within the bee community, if one species would, in part or even completely, replace another by occupying a trophic niche common to both, then interspecific competition can be expressed simply in terms of biomass: species x would become rare, and instead species y more abundant. Accordingly, the present population of the Africanized honey bee can be transformed into a biomass of hypothetically replaced native stingless bees in relation to particular plant resources. If, for example, 1g of Africanized honey bees was reared on a certain amount of collected pollen, this biomass may be regarded as equivalent to 1g of stingless bees. The hypothetical relative population decline (PD) of a bee species can then be calculated as:

$$PD_i = 1 - \frac{B_i}{EB_i}$$

where B_i = the actual biomass of bees of species i, given as: number of bees captured × body weight, and EB_i = the potentially expected biomass of species i before the arrival of the Africanized honey bee, where:

$$EB_i = \sum_k \frac{B_{ik} \times TB_k}{(TB_k - B_{ak})}$$

where B_{ik} = the actual biomass of stingless bee species i on flowers of plant species k, TB_k = total biomass of highly eusocial bees (stingless bees and Africanized honey bees) foraging on flowers of plant species k, and B_{Ak} = biomass of Africanized honey bees foraging on flowers of plant species k.

All calculations were carried out only for the 11 most abundant stingless bee species and the Africanized honey bee. Data of flower visitations for the remaining highly eusocial species were not sufficient to warrant inclusion in the analyses.

RESULTS

The highly eusocial bee community as part of the apifauna at Boracéia

Altogether 255 bee species (Apoidea) were recorded at Boracéia. Of these, 18 belong to the highly eusocial group (Fig. 1), 17 species of native stingless bees and the introduced Africanized honey bee. Despite the relatively small species number, highly eusocial bees make up approximately 2/3 of all flower visiting bees. The Africanized honey bee turned out to be the most abundant species, representing about 20% of all individuals, or 30% of all highly eusocial bees (Fig. 2). Thus, today, the Africanized honey

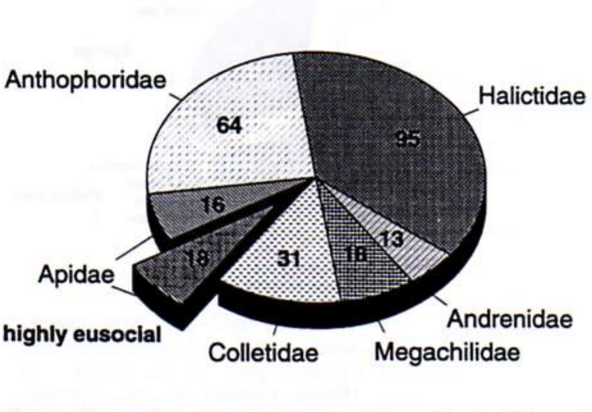

Fig. 1. Composition of the apifauna of Boracéia: families and number of species per family.

bee is predominant in this tropical rainforest ecosystem.

Of the indigenous stingless bees, 11 species can be ranked as abundant flower visitors representing 1% or more of the sample, and 5 species are rare (Fig. 2). The workers of an additional stingless bee species present at Boracéia, the kleptoparasitic *Lestrimelitta limao*, do not visit flowers but instead rob pollen and honey stores from the nests of other eusocial bees.

Resource exploitation by the highly eusocial bees
In order to elucidate the nutritional basis of this highly eusocial bee community, resource use was monitored for the 16 species of flower-visiting meliponines and the Africanized honey bee. Pollen or nectar foraging bees were observed on the flowers of 207 species of angiosperm plants belonging to 56 plant families (Table 1). According to forager abundance, Asteraceae and Myrtaceae contributed most to the nutritional input of highly eusocial bee colonies (Fig. 3). Plant genera that can be considered as important food resources are: *Mikania* and *Vernonia* (Asteraceae), *Myrcia* and *Eugenia* (Myrtaceae), *Bathysa* and *Psychotria* (Rubiaceae) and several others such as *Ocotea*, *Euterpe*, *Solanum*, *Didymopanax* and *Guapira* belonging to different plant families (Table 1).

Solitary bees visited more flowering herbs and climbers in comparison to workers of the highly eusocial species that collected resources more on flowering trees (Fig. 4). These trees usually exhibit a mass-flowering syndrome, in which a burst of numerous blossoms lasting for rather a short period was observed in the majority of trees of a particular species. For instance almost all the flowers of a *Myrcia tomentosa* tree opened on the same day and, for some hours, were heavily frequented by foraging bees. For the rest of the year, hardly any flowers could be observed on that tree. In other mass-flowering trees, flowering lasted up to a few weeks, but the peak of abundant flowering was always rather restricted. Of all the melittophilous tree species which were visited by stingless bee foragers when in blossom, over 30% exhibited a pronounced, and more than 50% a moderate mass-flowering syndrome (Table 1). However, quantifying the degree of mass-flowering was subjective and was carried out more in a comparative manner.

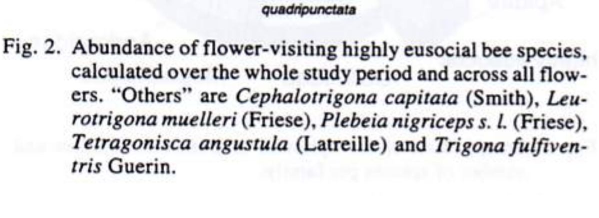

Fig. 2. Abundance of flower-visiting highly eusocial bee species, calculated over the whole study period and across all flowers. "Others" are *Cephalotrigona capitata* (Smith), *Leurotrigona muelleri* (Friese), *Plebeia nigriceps s. l.* (Friese), *Tetragonisca angustula* (Latreille) and *Trigona fulfiventris* Guerin.

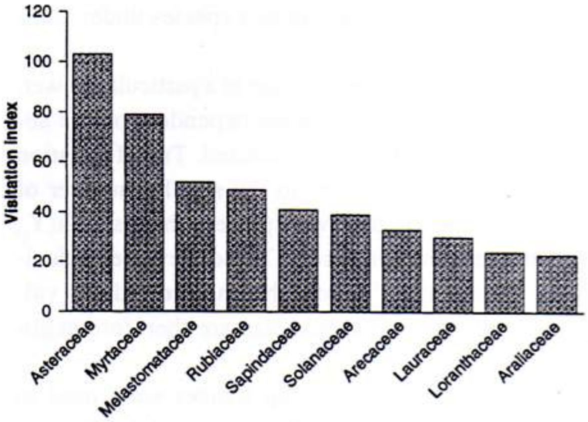

Fig. 3. Ranking of food plant families according to their importance for highly eusocial bees. The ten most-visited plant families for each bee species, indicated by the number of captured individuals, were given rank points, i. e. 10 points for the most important family, 9 points for the second most important, and so on. Addition of rank points gives the visitation index.

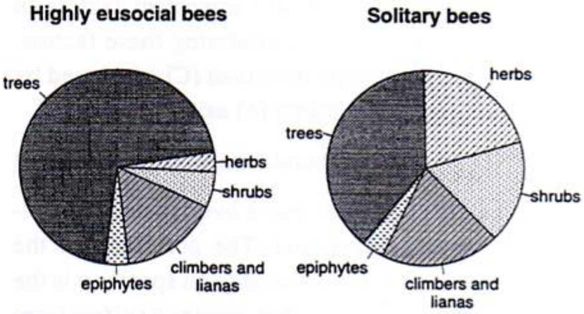

Fig. 4: Distribution of bee captures per life-form of food plants. "Solitary bees" include all non-highly eusocial bees, regardless of their different levels of social organization. Grouping of plant life-forms as described in the legend of Table 1.

Table 1. Food plant spectra of highly eusocial bee species at Boracéia. Data given are frequency classes of relative flower use: + = < 1%, • = 1 – <2%, •• = 2 – <5%, ••• = ≥5%. Plant species with non-bee flowers are marked with an asterix (*). Plant life-forms are: t = trees, c = climbers, climbing shrubs, and lianas, s = shrubs (more than 1m in high), e = epiphytes (including parasitic and hemi-parasitic life-forms), h = herbs, semi-shrubs and shrubs less than 1m in height. Observed degree of mass-flowering (subjective classification): ◇ = moderate mass flowering, ◇◇ = pronounced mass-flowering. Abbreviations for bee species' names: Am = Africanized *Apis mellifera* L., Mb = *Melipona bicolor* Lepeletier, Mm = *Melipona marginata* Lepeletier, Mq = *Melipona quadrifasciata anthidioides* Lepeletier, Mr = *Melipona rufiventris* Lepeletier, Pd = *Plebeia droryana* (Friese), Ph = *Partamona helleri* (Friese), Pr = *Plebeia remota* (Holmberg), Ps = *Paratrigona subnuda* Moure, Sb = *Scaptotrigona bipunctata* (Lepeletier), Sq = *Schwarziana quadripunctata* (Lepeletier), Ts = *Trigona spinipes* (Fabricius).

Plant families and species	Life-form	Mass-flowering	Highly eusocial bee species											
			Am	Mb	Mm	Mq	Mr	Ps	Ph	Pd	Pr	Sb	Sq	Ts
Amaranthaceae														
Pfaffia pulverulenta	c	◇	+								••	•	•	+
Apocynaceae														
Mandevilla funiformis *	c													+
Aquifoliaceae														
Ilex paraguariensis	t	◇	+	+					•					+
Ilex theezans	t	◇◇	+		••									+
Araliaceae														
Didymopanax angustissimus	t	◇	••					•	•••	••		••		••
Oreopanax capitatum	t	◇	+		•			+		•	••	••		•
Arecaceae														
Acrocomia spec.	t													
Arecastrum romanzoffianum	t	◇	+					••		•	•			•
Euterpe edulis	t	◇	••						•••	•••	••			•••
Geonoma gamiova	t								+	+	•			
Asclepiadaceae														
Asclepias curassavica *	h													+
Orthosia urceolata	c			••	+	•			•				+	+
Asteraceae														
Baccharis anomala	s	◇	+					••		••		+	+	+
Baccharis grandimucronata	s	◇	+		•			+	+	•		•		
Baccharis cf. microdonta	s	◇						•		+				
Baccharis spec.	t	◇	+		•			•	+	+		+	+	•
Bidens segetum	h, (c)		+			•		+						
Erigeron bonariensis	h				+					•				
Erigeron maximus	h									+			+	
Erigeron spec.	h		+											
Eupatorium itatiayense	h, s		+					+					•	
Eupatorium vauthierianum	h, s		+							+				+
Jaegeria hirta	h									+				
Mikania biformis	c	◇◇	+							+		•	+	•
Mikania catharinensis	c	◇	+		•			••	+	•		•	••	
Mikania conferta	c	◇◇	+	•				+	••	•	•			+
Mikania cynanchifolia	c	◇	+					•				••		
Mikania eriostrepta	c	◇◇	••		••		••	••	••	•		••	••	+
Mikania cf. hoffmanniana	c	◇	+						+	+		+	•	+
Mikania laevigata	c	◇	+			•			+					
Mikania lanuginosa	c	◇◇	+						+					
Mikania lindbergii	c	◇◇			•									
Mikania pachylepsis	c	◇	+					+						
Mikania cf. smaragdina	c	◇◇	•		+			•		+	•		•	+
Mikania trinervis	c	◇◇	+		+				+	+	•	+	+	
Mikania aff. trinervis	c	◇◇	+						+		+			
Mikania ulei	c	◇			•			+	+	•	•	••	+	+
Piptocarpha axillaris	t	◇	+		••				•					
Piptocarpha macropoda	t	◇◇								+				+
Piptocarpha oblonga	c	◇◇	+	•				•	•	•	+		••	••
Piptocarpha obovata	t	◇	+											
Senecio brasiliensis	h		•						+				••	+
Senecio desiderabilis	c	◇◇						+		••	••	•	•	•

Table continues

Table 1. (continued)

Plant families and species	Life-form	Mass-flowering	Highly eusocial bee species											
			Am	Mb	Mm	Mq	Mr	Ps	Ph	Pd	Pr	Sb	Sq	Ts
Trixis pinnatifida	h		+											
Vernonia diffusa	t	◇◇	●●	●	●●	●●	●●●	●●	●	+				
Vernonia discolor	t	◇◇	+					+		+			+	
Vernonia petiolaris	s	◇	+			●●●	●●	+	●					+
Vernonia puberula	t	◇	●			●		●	●	+				
Vernonia aff. puberula	t	◇◇	●●	●●			●●●	●	+	+				+
Vernonia quinqueflora	t	◇	●						●					
Vernonia westiniana	s	◇	+			●●●			+					
not identified	h		+					+					+	
Balsaminaceae														
not identified *	h		+							+				+
Begoniaceae														
Begonia boraceiensis	h		+	●										
Begonia fruticosa	c			+	+		●						●	
Begonia integerrima	e, c						●							
Begonia luxurians	h			+							●			●
Begonia solananthera	e						●							
Begonia spec.	h													+
Bignoniaceae														
Arrabidaea rego	c							+						
Clytostoma cf. callistegioides	c									+				
Jacaranda puberula	t	◇						●●		+				+
Lundia nitidula	c													+
Boraginaceae														
Cordia sellowiana	t	◇◇				●		●●	+	●			●	
Cordia trichoclada	t	◇	●	+			●●		●	●			●●	
Bromeliaceae														
Vriesea friburgensis *	e								+					+
Vriesea cf. platynema *	e													+
Caesalpiniaceae														
Bauhinia microstachya	c		+									+		
Sclerolobium denudatum	t	◇◇	+	●●	●●	●●	●●●			●●	●	●●		●
Celastraceae														
Maytenus cf. subalata	t	◇								+				
Chloranthaceae														
Hedyosmum brasiliense *	s, t	◇	●							●●	●●		+	●●
Clethraceae														
Clethra scabra	t	◇	●●	+	●●			●●	●	●	●	●●●	+	
Commelinaceae														
Dichorisandra thyrsiflora	h									+				+
Tripogandra diuretica	h									+				
Concolvulaceae														
Ipomoea spec.	c													+
Cucurbitacae														
Cayaponia spec.	c		+	●		●●			+					+
Cunoniaceae														
Lammanonia ternata	t	◇	+					+	+					
Weinmannia discolor	t	◇◇						+		+		●	+	+
Weinmannia pauliniifolia	t	◇◇	+							+	+			+
Weinmannia pinnata	t	◇◇	●		●●			●	+	+	●●●	+	●●	

Table continues

Table 1. (continued)

Plant families and species	Life-form	Mass-flowering	Highly eusocial bee species											
			Am	Mb	Mm	Mq	Mr	Ps	Ph	Pd	Pr	Sb	Sq	Ts
Ericaceae														
Gaylussacia spec.	s													+
Euphorbiaceae														
Actinostemon spec.	t	◇	+					+		+			●	
Alchornea triplinervia	t	◇	+					+						+
Croton floribundus	t	◇	●	+			●		●			●	●	+
Croton macrobothrys	t	◇	+								●			
Croton cf. paulinianus	t	◇	●	●	+			+				●		
Croton priscus	t	◇	+	+				+	+	●				●
Sapium glandulatum	t	◇	+							+			+	
Fabaceae														
Andira anthelmia	t	◇						+		+				
Dahlstedtia pinnata *	t							+						+
Dalbergia frutescens	c	◇	●	●	●	●								
Dioclea rufescens	c								+					
Erythrina speciosa *	s									+				+
Machaerium oblongifolium	c	◇	●●	●●		●								
Flacourticaceae														
Casearia decandra	t	◇◇						+			●	●●		
Casearia sylvestris	t	◇◇	●●	+	●●		●	●●	●●	+		●●●	●●●	+
Lauraceae														
Aiouea cf. trinervis	t	◇	+					+			●	+		+
Ocotea dispersa	t	◇	+	+	●			●●	●●	●			●	●●
Ocotea glaziovii	t	◇	●	●				●●	+	+	●●	+	●●	●●
Ocotea cf. paranapiacabensis	t	◇	+					●	+		●		+	
Persea alba	t	◇									●●			
Liliaceae														
not identified *	h									+				+
Loranthaceae														
Struthanthus concinnus	e	◇	●●	●●	●●●		●	●	+			●	●●	
Struthanthus confertus	e	◇	+	+										
Struthanthus salicifolius	e							+		+			+	
Struthanthus staphylinus	e				+			●●		●●	+		+	●●
Struthanthus uraguensis	e	◇	●					●		+			+	+
Malpigihiaceae														
Byrsonima ligustrifolia	t													●
Malvaceae														
Sida rhombifolia	h		+							+				+
Marcgraviaceae														
Marcgravia polyantha *	c								+					+
Norantea brasiliensis *	c									+				●
Melastomataceae														
Miconia cabucu	t	◇		●●	●●	●	●●	●	+				●●	
Miconia fasciculata	t	◇◇		●	●	●●							+	
Miconia inaegidans	t	◇◇		●●	●	●●●	●	+	+				+	
Miconia rigiduscula	t	◇◇							●●			●		
Miconia theaezans	s, t	◇◇	●	●	●●		●●		+	●●	+	●●		●●
Tibouchina cerastifolia	h							●●						
Tibouchina kuhlmannii	s, t	◇						+						
Tibouchina pulchra	t	◇						+						●●
Tibouchina scaberrima	t	◇						●●						+
not identified	s			+				●						●●

Table continues

Table 1. (continued)

Plant families and species	Life-form	Mass-flowering	Highly eusocial bee species											
			Am	Mb	Mm	Mq	Mr	Ps	Ph	Pd	Pr	Sb	Sq	Ts
Meliaceae														
Cabralea canjerana	t	◇	+						+	+	●			●
Guarea macrophylla	t	◇								+				
Trichilia silvatica	t	◇						+	+					
Mimosaceae														
Inga capitata *	t	◇						+	+					
Inga lenticellata *	t	◇	+											
Inga marginata	t	◇◇	●	+			●●		●			●		
Inga sessilis *	t							+		●				+
Inga vulpina *	s, t	◇	+					+	+	+	●		+	
Pithecellobium langsdorffii *	t		+							+				
Monimiaceae														
Mollinedia triflora	t							+						
Mollinedia spec.	t		+					+		+	+		●	
Myrsinaceae														
Rapanea gardneriana	t	◇								●				●●
Rapanea umbellata	t	◇		+						+	+			●●
Myrtaceae														
Calyptranthes lucida	t	◇◇	+						●	●	●	●●		
Campomanesia phaea	t	◇	+	●●	+				+					
Campomanesia xanthocarpa	t	◇◇	●		+		●●●		●					●●
Eugenia brasiliensis	t	◇	+											
Eugenia oblongata	t	◇◇	+				●	+	●		●		+	+
Eugenia reitziana	s			●		●●					+			
Eugenia riedeliana	s	◇	+											
Eugenia spec. a	t	◇◇	+	●		●●	●		●●	+	●	●●	●	
Eugenia spec. b	t	◇◇	+	●		●●			●	+		●●		
Gomidesia schaueriana	s, t	◇						+						
Marlierea spec.	t	◇	+	+			●			+	●		●	
Myrceugenia myrcioides	s, t	◇	+			●	●●	+				●		
Myrcia glabra	t	◇				●●		●		+	●●	+		
Myrcia pubipetala	t	◇◇	+	●●	+			+	●●	●	●●●	+	●	+
Myrcia rostrata	s, t	◇◇	+		●●		●●	+	●●	+	●●●	●	●●	+
Myrcia tomentosa	t	◇◇	●●	●●		●●●			●●	+	●		●●●	+
Psidium cattleyanum	s, t		+											
Nyctaginaceae														
Guapira opposita	t	◇	+					+	+	●●	●●		●	●
Guapira spec.	t		+						●	●	●●			
Olacaceae														
Heisteria silvianii	t		+		+			+		+				+
Onagraceae														
Fuchsia regia *	c		+						●	●				+
Passifloraceae														
Passiflora alata	c									+				
Piperaceae														
Piper spec. a	s		+							+				
Piper spec. b	s									+				
Piper spec. c	s		+						+					
Poaceae														
Chusquea spec. *	s									+				+
Setaria poiretiana *	h									+				
Polygalaceae														
Polygala paniculata	h							+						

Table continues

Table 1. (continued)

Plant families and species	Life-form	Mass-flowering	Highly eusocial bee species											
			Am	Mb	Mm	Mq	Mr	Ps	Ph	Pd	Pr	Sb	Sq	Ts
Polygonaceae														
Coccoloba martii	t	◇	●			●	●	+	●●	●●	●●	●●	●	+
Coccoloba aff. ovata	t	◇◇	●		●●	●	●●	+	●●	●	●	+	●	+
Proteaceae														
Euplassa hoehnei *	t	◇						●		●●	●●		●	
Ranunculaceae														
Clematis dioica	c												●	
Rhamnaceae														
Rhamnus sphaerosperma	t		+					+		+				●●
Rosaceae														
Prunus sellowii	t	◇	+					+	●	+	●	●●	+	●
Rubus rosaefolius	s			●										+
Rubiaceae														
Alseis floribunda	t	◇◇	+					●		+				
Bathysa australis	t	◇	+	●●●		●●●	●●●	+	+	+				
Bathysa meridionalis	t	◇	●	●●	●	●	●●●	●●	●●	●		+		
Borreria verticillata	h		+	+	+			●						●
Diodia schumannii	h		+		+									
Emmeorhiza umbellata	c		+					+		+		●●	●	●●
Psychotria suterella	s, t	◇	●	+		●	●●		+					
Psychotria cf. vellosiana	t	◇◇	●●	●●	+	●●●	●●●	+	●●		●			+
Rutaceae														
Zanthoxylum hiemalis	t	◇◇	+					+		+	●●	●	+	
Sapindaceae														
Allophylus petiolulatus	t	◇	+	+	●●●			●		+		●●	+	●
Cupania oblongifolia	t	◇	●	●●	●●●	●	●●	●				●●	●	
Cupania vernalis	t	◇	+	●		●						+	●	
Cupania zanthoxyloides	t	◇	+					●				+		
Matayba elaeagnoides	t	◇	+									●		+
Paullinia carpopodea	c	◇	+	●			●●	+		+				
Paullinia seminuda	c	◇						+				●		+
Paullinia trigonia	c	◇	+											
Serjania gracilis	c	◇		+					+					
Serjania multiflora	c	◇	+	+										
Solanaceae														
Capsicum spec. a	s, t							+		●				
Capsicum spec. b	s									●				
Capsicum spec. c	s, t		+						+					
Solanum americanum	s	◇			+			+						
Solanum concinnum	s	◇	+	●●		●●		+						
Solanum cf. falcatum	t	◇		+						+				
Solanum inaequale	t	◇		●●		●●●	●●							
Solanum martii	s							+						
Solanum megalochiton	s, c	◇		●●●	●●●	●●	●●●	+	+	+	+		+	
Solanum rufescens	t			●										
Solanum variabile	s						●	●●						
not identified	c									+				
Symplocaceae														
Symplocos spec.	t	◇	●	+			●●		●	+	+	●		+
Theaceae														
Laplacea semiserrata	t	◇	●	+	●				●	+				+
Thymelaeaceae														
Daphnopsis gemmiflora	t	◇◇	+					+	●	●●		+	●●	●
Daphnopsis spec.	s	◇												+
Verbenaceae														
Aegiphila sellowiana	t	◇	●	●				●	+	+			+	●
Verbena litoralis	h							●						

Trees with a mass-flowering syndrome provide extremely rich floral resources. In spite of the limited period of full blossom in a particular species, the numerous species of trees within the forest of Boracéia give rise to several consecutive flowering periods. Thus, over the year, these stochastic resources together constitute a rather constant nutritional resource supply with a peak of flower abundance during springtime, October through December.

Trophic niche overlap

Workers of the Africanized honey bee foraged upon a remarkably wide floral resource spectrum, visiting flowers of 122 plant species. This represents the largest niche breadth of all highly eusocial bees (Fig. 5). Trophic niches of similar width were recorded in the stingless bees *Plebeia droryana*, *Paratrigona subnuda* and *Trigona spinipes*. In comparison with these species, the somewhat smaller trophic niche breadth of *Partamona helleri* apparently does not depend upon its lower abundance, because the number of captured individuals per plant species visited is rather high. The same is true for *Scaptotrigona bipunctata*. This points to more restricted forage spectra for these two species. Concerning the remaining stingless bee species, their smaller calculated trophic niche breadthes may be related to their increased rareness.

The trophic niche overlap (NO) calculations are based on the congruence of floral resource use. For most of the highly eusocial bee species, the NO index ranges between 0.2 and 0.4 (Table 2). In any pairwise comparison of stingless bees, this value does not surpass 0.5. The relations in resource sharing among the highly eusocial bees become more evident by multidimensional scaling of the niche distances (Fig. 6). A 3-dimensional arrangement was choosen over a 2-dimensional one because of the better fit of the scaled distances. Pearsons' correlation coefficient between the values of the dissimilarity matrix and the scaled distances is 0.95 ($p < 0.001$). Also the stress value for the goodness of fit of 0.073 indicates that the 3-dimensional arrangement gives an accurate representation of species' relationships (Kruskal 1964). Two major groups can be recognized: the large *Melipona* bees (Mb, Mr, Mq) which form a homogenous cluster, and all the other highly eusocial species with more diffuse relations among them. However, noteable as a central group combining the floral preferences of Meliponini and Trigonini are *Partamona helleri* and the Africanized honey bee.

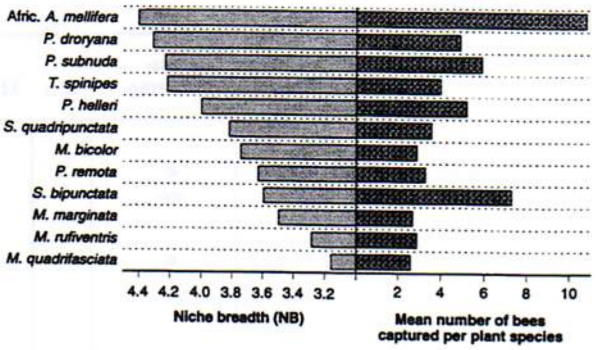

Fig. 5. Trophic niche breadth (NB) of highly eusocial bees in relation to the mean number of worker bees captured per plant species.

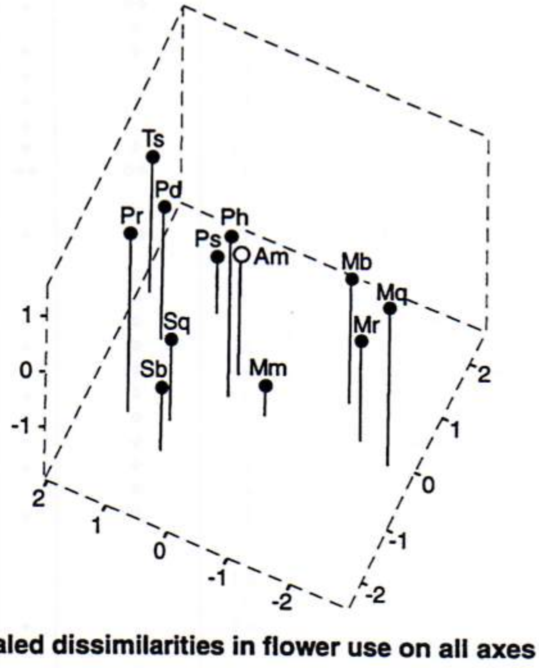

Fig. 6. Three-dimensional arrangement of the trophic niche relationships between highly eusocial bees at Boracéia. Axes are arbitrary and not directly related to particular variables. For abbreviations of species' names see Table 1.

It is of special interest that the introduced honey bee does not occupy a more dissimilar trophic niche to the native social bees. In contrast, its central position is due to it having the largest average trophic niche overlap to all other species. The niche overlap between the Africanized honey bee and *Partamona helleri* is particularly pronounced. The index exceeds 0.5 (Table 2), which represents the greatest similarity in flower visitation between highly eusocial bees

Table 2. Matrix of trophic niche overlap between highly eusocial bee species. Niche overlap (NO) is given in absolute values and, for better representation, in classes: + = <0.2, ○ = 0.2 – <0.3, • = 0.3 – <0.4, •• = 0.4 – <0.5, ••• = ≥0.5.

	Am	Mb	Mm	Mq	Mr	Pd	Ph	Pr	Ps	Sb	Sq	Ts
Africanized *Apis mellifera* (Am)	–	0.39	0.33	0.23	0.34	0.41	0.51	0.31	0.41	0.35	0.40	0.33
Melipona bicolor (Mb)	•	–	0.38	0.46	0.45	0.21	0.33	0.17	0.22	0.19	0.24	0.19
Melipona marginata (Mm)	•	•	–	0.20	0.34	0.25	0.27	0.21	0.33	0.34	0.34	0.19
Melipona quadrifasciata (Mq)	○	••	○	–	0.38	0.10	0.25	0.12	0.14	0.14	0.16	0.05
Melipona rufiventris (Mr)	•	••	•	•	–	0.17	0.31	0.13	0.20	0.23	0.21	0.11
Plebeia droryana (Pd)	••	○	○	+	+	–	0.40	0.42	0.36	0.31	0.34	0.49
Partamona helleri (Ph)	•••	•	○	○	•	••	–	0.32	0.29	0.33	0.38	0.31
Plebeia remota (Pr)	•	+	○	+	+	••	•	–	0.21	0.28	0.35	0.31
Paratrigona subnuda (Ps)	••	○	•	+	○	•	○	○	–	0.27	0.37	0.34
Scaptotrigona bipunctata (Sb)	•	+	•	+	○	•	•	○	○	–	0.34	0.27
Schwarziana quadripunctata (Sq)	••	○	•	+	○	•	•	•	•	•	–	0.26
Trigona spinipes (Ts)	•	+	+	+	+	••	•	•	•	○	○	–

in this ecosystem. It is also noteworthy that the very abundant *Trigona spinipes* is found in the periphery of the community. From our observations in Boracéia this is not mainly due to aggressive foraging behaviour and rejection of other bees from flowers visited by it, but instead more a result of its pronounced tendency to visit non-bee flowers, which it often did in an illegitimate manner.

DISCUSSION

The Boracéia bee community

The vegetation and the bee community of the Boracéia Atlantic Rainforest are characterized by a high biodiversity which is as yet little disturbed. Since no comparable data exist in the literature, our survey of this apifauna can be discussed only with respect to distinctly different tropical areas of Brazil, and also secondary forests, and parks, generally representing habitats with a reduced native flora and fauna (Pedro & Camargo 1991; Pedro 1996; Ramalho in prep). The species richness of Apoidea at Boracéia certainly exceeds the 255 species recorded, and species discovery curves (Wilms in prep.) suggest a total of over 300 sympatric bee species. This is regarded as a good example of the magnitude of the local bee species richness in a nearly original part of the Atlantic Rainforest, of which today only a few percent are left. Concerning the highly eusocial bees, the species discovery curve suggests that all species have been already discovered in this study. The survey of these bees was probably more thorough due to their populous and perennial colonies.

Highly eusocial bees and the plants they visit

At Boracéia, the melittophilous plant species comprise the vast majority of all angiosperms (Wilms 1996). The main food resources of the stingless bees are the many species of Asteraceae, Myrtaceae and Melastomataceae. These three plant families together received from 25% to over 50% of all the flower visits recorded for the workers of the meliponine species. Together with the Orchidaceae, these are also the plant families of extraordinary species richness at Boracéia, with many abundant taxa having a staggered flowering phenology. The resultant ranking of important food sources for stingless bees reflects more or less the local floral composition of this *Mata Atlântica* rainforest, at least the prevailing melittophilous fraction. As a group, the highly eusocial bees seem therefore to have an opportunistic harvesting strategy, which is known for stingless bees in general in the neotropics (Ramalho *et al* 1990).

The relations between the highly eusocial bees and the plants, of which many are pollinated by these bees, is not likely to generate specialized dependences or even oligolecty on the part of the bees. Due to the need of perennial colonies for a permanent nutritional supply, generalistic foraging behaviour may have evolved in eusocial bees, requiring a rich resource base with sufficient flowers available over space and time. The flowering plants themselves are forced to attract numerous foraging bees by offering rich nectar and pollen resources. To increase outcrossing, they can even guide bee movements between single plant specimens by temporary differences in quality or quantity of resources offered (Frankie & Haber 1983). The resulting diffuse coevolution between highly eusocial bees and bee plants may culminate in the syndrome of mass-flowering (Bawa 1983). In the *Mata Atlântica* rainforest of Boracéia, mass-flowering is a common feature of trees which are monopolized by the very abundant stingless bees. Meliponine scout bees are capable of rapidly locating any temporal mass blossom in this highly structured habitat and of effectively harvesting resources from mass blooming trees by means of their social recruitment systems (Lindauer & Kerr 1958; Roubik 1989).

Resource partitioning or competition ?

Partitioning of resources is generally thought to reduce competition and to have a function in community structuring. Studying bees and wasps in Costa Rica, Heithaus (1979) found a positive correlation between the level of specialization by community members and species richness of the community. The generalistic foraging behaviour commonly followed by all meliponines does not permit simple, direct bee-plant relationships. In fact, for these bees the list of resource plants they utilize includes numerous angiosperm species, nearly all of which are shared with other stingless bee species. Nevertheless, the trophic niche overlap between two stingless bee species does not exceed 0.5, and most frequently lies between 0.2 and 0.4. This reflects different degrees of preference for distinct food plants. Generally such varying preferences result in a quantitative rather than a qualitative partitioning of the resources. It remains open as to whether this partitioning is the result of interspecific competition, either historical or current. Regarding this question, the observations of Johnson and Hubbell (1974) and Hubbell and Johnson (1978) suggest a structuring in resource use modulated by direct competition, at least among some trigonine bees. Contrarily, in the *Melipona* bees there seems to be a fixed preference for a particular food plant spectrum (Ramalho *et al* 1989, 1990).

As for the stingless bees, so too the Africanized honey bee does not occupy a distinctly different trophic niche. On the contrary, this introduced species is well integrated within the stingless bee community of Boracéia between the Meliponini and Trigonini. The Africanized honey bee has the largest average niche overlap with all other highly eusocial bee species, and also the niche overlap with *Partamona helleri* represents the largest absolute overlap in this highly eusocial bee community. This may reflect competitive relationships which are stronger than might otherwise be expected between native species. The competitive role of the Africanized honey bee in the highly eusocial bee community of Boracéia is even more evident when considering this bee's abundance and body size (Fig. 7). All stingless bees suffer more competitive pressure from the Africanized honey bee than from any other highly eusocial bee species. To what degree workers of stingless bees try to avoid competition with the workers of the Africanized honey bee is unknown, but due to the rather large niche overlap indices of stingless bees with *Apis mellifera*, avoidance does not seem to be very prominent, at least at the plant species level. In addition, workers of all stingless bee species were observed foraging with numerous workers of Africanized honey bees on the same blossom.

Possible impact of the Africanized honey bee

To be successful in a community, an invader has to be superior in competing with the indigenous inhabitants. For that reason, the positioning of the Africanized honey bee in the Boracéia bee community probably depends more on its own properties than on interactions with native bees. The calculated pro-

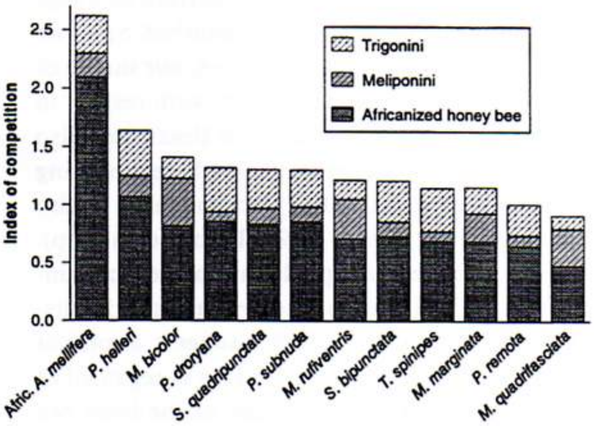

Fig. 7. Profile of the distribution of competitive load (CL) and competitive pressure (CP) in the highly eusocial bee community. Competitive load refers to the categories in the legend and was summed up for the species of Meliponini and Trigonini, respectively. Competitive pressure refers to the species given on the abscissa.

files of competitive load and pressure (Fig. 7) within the Boracéia community of highly eusocial bees support this hypothesis. The Africanized honey bee is the only species for which its intraspecific competitive load is higher than the interspecific competitive pressure from all the other highly eusocial bees.

Known to explore and to exploit rich resources efficiently, the honey bee probably occupies the most profitable position in the Boracéia food market, being well in the centre of the trophic sphere of the native stingless bees. This point of view is supported by the fact that meliponine species showing the most similar floral preferences are the most abundant ones. For the 11 most common species of stingless bees, Spearmans' correlation coefficient between a species' niche overlap with the Africanized honey bee and its abundance is 0.80 ($p < 0.01$). In consequence, competition for food between the Africanized honey bee and native bees should affect primarily the more abundant species, which in turn should make extinction of native community members less probable. However, rare species with small populations might be more susceptible to increased competitive pressure. Considering the rare species at Boracéia the few data on flower visitation do not indicate a more pronounced niche overlap with the Africanized honey bee. *Trigona fulfiventris*, for example, less frequently visited flowers of trees. In Fig. 6, this species would occupy the most peripherical position. However, further analyses of the trophic niche relations of the rare species were not possible due to the scarcity of data.

A preliminary qualification of the degree to which populations of stingless bees have possibly declined already as a result of the introduction of the Africanized honey bee may be dealt with by another approach.

Population decline of stingless bees ?

The carrying capacity of the floral resources in a certain ecosystem may be given by the biomass of all its particular users. Based on the average body weight of the worker bees and their abundance, the total biomass of the Africanized honey bee population in the Boracéia forest exceeds that of all stingless bees by a factor of 1.4. Because only a small fraction of floral resources is exploited exclusively by the Africanized honey bee but not by any stingless bee, over 98% of the actual biomass of the introduced species may be assumed as equivalent to the biomass of replaced meliponines. If this assumption were correct, a decline of over 50% in the stingless bee population could be calculated, varying for individual species from 45% to 65% (Table 3).

Table 3. Calculated hypothetical decline of stingless bee populations due to the impact of competition by introduced Africanized honey bees. The values indicate how much the assumed original population of a particular species might have been reduced to present day values.

Stingless bee species	Calculated population decline in %
Melipona bicolor	55.0
Melipona marginata	59.5
Melipona quadrifasciata	45.9
Melipona rufiventris	57.8
Paratrigona subnuda	62.1
Partamona helleri	63.7
Plebeia droryana	62.3
Plebeia remota	62.1
Scaptotrigona bipunctata	58.6
Schwarziana quadripunctata	65.4
Trigona spinipes	52.8
mean	58.7

However, such a scenario depends on the assumption of effective competition in the past between invading Africanized honey bees and native stingless bees. For several reasons, the calculated values are more likely to represent a worst case scenario rather than the real competitive impact of the Africanized honey bee.

In our calculations, the numerous species of solitary bees were neglected. In fact, for flowers visited by both meliponines and Africanized honey bees, stingless bees were on an average 1.6 times more abundant than solitary bees. The distribution of body sizes of flower-visiting solitary and stingless bees was nearly the same. Therefore, approximately 40% of the competitive impact of Africanized honey bees might in fact concern solitary bees. Of course, there are also several non-bee flower visitors. Population decline of these due to competition with Africanized honey bees might even increase the resources available to stingless bees.

Resource magnitude, exploitation and bee carrying capacity

A central point in the discussion of the impact of competition by the Africanized honey bee is the assumption that food is the limiting factor for bee populations. The calculations of the possible population decline of stingless bees were carried out under the assumption that the biomass of bees is directly correlated with the availability of flower resources. However, this dependence is more assumed than evidenced by field data. The question arises: can and do stingless bees avoid competition with Africanized honey bees by changing their food resources? As discussed earlier, the results of our analyses of trophic niche overlap do not indicate a switch by stingless bees to qualitative different plant resources. However, there seems to be a good possibility that avoidance occurs at the plant specimen or flower patch level.

Since most of the food plants in the Boracéia forest important for the nutritional input of highly eusocial bees show a mass-flowering syndrome, simultaneous exploitation to depletion of these rich and synchronously offered resources seems rather improbable, and foraging stingless bees should be easily able to avoid competition with honey bees. Moreover, under Boracéia weather conditions, rain often terminates the resource harvest of bees rather than there being total depletion of the nectar and pollen supply. Therefore, the effect of increased competition on changes in population growth seems to be buffered by the excess of food supplied under mass-flowering conditions.

According to these considerations, the carrying capacity of the tropical rainforest of Boracéia for highly eusocial bees is not linearly correlated with the existing biomass of its community members. Perhaps during troughs in resource supply, such a correlation may be valid. However, eusocial bees may be well buffered against a temporary shortage of resource availability by their storage of honey and pollen within their nests.

Case studies like our bee-flower field survey at Boracéia are only snapshots in the dynamics of population ecology. Extrapolations into past and future scenarios will always remain hypothetical. In reality, the future development of the bee community at Boracéia will depend on an open question: has the establishment of an Africanized honey bee population already reached an equilibrium ? If not, it would be interesting to observe whether eventual changes in the abundance of the native stingless bees will follow the suggested scenario.

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