Structure of bee-flower system in the coastal sand dune of Abaeté, northeastern Brazil

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ABSTRACT. Structure of bee-flower system in the coastal sand dune of Abaeté, northeastern Brazil. For twelve months (from January to December of 1996) we investigated bee-flower interactions in a sea coastal ecosystem in Bahia, Brazil. Samples were taken three times each month. 3983 individuals belonging to 49 bee species, grouped in 13 morph-functional categories, visited 66 plant species belonging to 39 botanic families. It was observed 310 interactions between bees and plants at species level. The use of floral resources by bees was not homogeneous; most of the plant species received a low number of visitors. No restricted plant-bee species relationship in resource use concerning the subset of analyzed interactions was detected. In Abaeté the generalist relationships predominated.

KEYWORDS. Apoidea, Bahia, floral resources, sandbank.

RESUMO. Estrutura do Sistema Abelha-Flor nas Dunas Litorâneas de Abaeté, Nordeste do Brasil. As interações entre abelhas e flores foram investigadas três vezes por mês, durante doze meses (entre janeiro a dezembro de 1996) em um ambiente de dunas litorâneas com vegetação de restinga no Nordeste do Brasil. Foram amostrados 3983 indivíduos de abelhas pertencentes a 49 espécies, agrupadas em 13 categorias morfo-funcionais. Essas visitaram 66 espécies de plantas pertencentes a 39 famílias vegetais. Trezentos e dez (310) interações entre abelhas e plantas, em nível de espécie foram observadas. O uso de recursos florais por abelhas não foi homogêneo, a maioria das espécies de plantas recebeu um baixo número de visitantes. Não foi notada nenhuma relação especializada, em nível de espécie, entre plantas e abelhas no subconjunto de interações analisadas. Em Abaeté, houve predominância de relações de generalistas.

PALAVRAS-CHAVE. Apoidea, Bahia, recursos florais, restinga.

Bee-flower interaction constitutes a relationship of "balanced mutual exploration", where flowers offer rewards to attract visitors, potential pollinators, which in exchange pollinate them accidentally while visiting them in search of offered benefits (Westerkamp 1996).

It is a risky relationship for the flower, since visitors not always are their effective pollinators, just using the resources in an opportunistic manner (Laroca 1970; Renner 1983; Westerkamp 1991).

Some flowers developed characteristics that make the rewards accessible only to the legitimate pollinators (Fabaceae, Malpighiaceae, Bignoniaceae, Orchidaceae etc.). According to the Darwinist approach, these characteristics are interpreted as adaptations to pollinator agents that exercise selective pressure on them. Floral characteristics as a whole have been used as a base for the establishment of the concept of pollination syndrome (Faegri & Van Der Pijl 1979; Proctor *et al.* 1996).

However, for Herrera (1995), floral characteristics do not need to represent adaptations to their pollinators, and the interactions between animals and plants for plant reproduction can continue in the absence of mutual adaptations.

Wasser *et al.* (1996) consider the generalist interactions between bees and flowers as a rule, and not an exception, in ecological communities. To the opposite, empiric data obtained by Petanidou & Ellis (1996) revealed that most species were oligotrophic in a shrub Mediterranean ecosystem, in Greece.

In this context, Dicks *et al.* (2002) obtained results that suggest that plant and insect species are organized in compartments and that these compartments reflect the classic pollination syndromes in two plant communities in England.

More recently, Dupont *et al.* (2003) concluded that interactions were "structured by the abundance", in other words, more common plants were visited by many visitors and the most common animals used a larger spectrum of plants as food resources.

From this, we can conclude that the relationship between plants and their floral visitors is much richer and complex than until then it was imagined.

The great majority of plant-pollinator interactions is submerged in a complex net of interactions (Memmott 1999), where as much generalization as compartmentalization can be observed, just depending on the different scales used in those interaction analysis.

In the Neotropical area, most of the analysis of floral plant-visitor system was based on Apoidea surveys on flowers, with standardized methodology (Sakagami *et al.* 1967; Heithaus 1979a, 1979b; Laroca *et al.* 1982; Camargo & Mazucato 1984; Bortoli & Laroca 1990; Carvalho & Bego 1997; among others). In general, those surveys suggest that specialization is rare in tropical ecosystems. It is common the use of several plant species by a bee species, as well as a wide spectrum of bee species to visit one plant species, as observed by Dupont *et al.* (*op. cit.*).

However, it is frequent the so called preferential relationships. Some plants are more intensively visited by one or more bee species, or guilds. Those preferential relationships by bees not always result in reproductive success for the plants, although they suggest a tendency to compartmentalization.

In most surveys, the group of bees that visited the largest number of plant species was considered as the most important pollinator. Gottsberger *et al.* (1988), for instance, observed that *Centris leprieuri* Spinola 1841, the only resident bee in the beach dune ecosystem of São Luís, visited six of the ten studied plant species. They considered this bee as their potential pollinator.

In this study, we investigated the structure of the bee-flower system in a coastal dune community, with sandbank vegetation, in Abaeté, Salvador, Bahia. We intended to answer the following questions:

How is the bee-flower system characterized, as for its composition and relationships?

Does the structure of the bee-flower system in this environment present tendency to a certain pattern? In affirmative case, which are the possible factors that would be related to the identified pattern?

Which would be the implications of the bee-flower interactions in the context of the conservation of local landscape?

MATERIAL AND METHODS

Study area. Field study was conducted in a restricted area (8.2ha) of coastal dunes with sandbank vegetation, belonging to the Environmental Protection Area of Abaeté Ponds and Dunes (12º56'S, 38º21'W), in Salvador, Bahia. According to Köppen classification, the local climate is tropical hot and humid, with annual average temperature of 25.8ºC, relative humidity of 81% and monthly rainfall of 175.03mm.

Sampling procedure. Samplings were accomplished three times a month, during 12 months, from January to December, 1996. The floral visitors' sampling was made by two collectors according to Sakagami *et al.* (1967). Each sampling lasted 12 hours, from 6:00h to 18:00h, totaling 840 hours, 420 hours per collector.

Plants in flower were collected and pressed in the field. Estimations of the total number of flowers per species were made in the following way: a) in species with individual flowers, the total number of individuals was multiplied by the mean number of flowers per individual; b) in species with inflorescences, the total number of individuals was multiplied by the mean number of inflorescences per individual and by the mean number of flowers per inflorescence; c) in shrubs or arboreal species we evaluated the mean number of flowers and/or inflorescences per branch, the mean number of flowers per inflorescence and the mean number of branches per individual; the mean number of flowers obtained per individual was multiplied by the total number of individuals of the species.

The exsiccates are deposited in the herbaria of RADAM BRASIL (IBGE-Salvador), HUEFS (State University of Feira de Santana, Feira de Santana) and HALCB (Federal University of Bahia, Salvador) and bees in the reference collection of the Laboratory of Bee Biology and Ecology-LABEA, from Bioscience Institute, Federal University of Bahia (UFBA). The specimens were identified by specialists (see acknowledgments).

Other data regarding plant species were taken in the field: flower color, shape, symmetry and habit. For complementally exams, flowers were collected and fixed in alcohol 70%. In laboratory, measurements of the corolla length and diameter were made.

Data analysis. Specimens were grouped into morph-functional categories in order to analyze interactions between bee fauna and flora (Viana & Kleinert 2005). The identification of morph-functional bee categories is quite useful in understanding the bee-flower relationship in biotic communities. Bees form alimentary guilds that, in general, include species characterized by a lot of similarities, including body size, social structures, foraging strategies, taxonomy and food preferences (Heithaus 1979b).

The floral syndromes were determined by some secondary criteria from Faegri & Van Der Pijl (1979), as flower morphology, complemented with literature data, behavior observations and visitors' frequency.

We adopted the same nomenclature proposed by Faria (1994), where: melittophilous (Melit) are the plants whose resources can be explored by Apoidea and sometimes by other groups of insects (Diptera, Lepidoptera, Coleoptera, other Hymenoptera, among others); primarily melittophilous (Melit+) are the plants in which the resources are accessible especially to Apoidea and they are the main visitors; strictly melittophilous (Melit *) are those in which the resources are accessible exclusively to Apoidea, being hardly explored by other insects without flower's damage.

To verify the relationship between bees' body length and the diameter of the corolla and between the size of the glossa and the depth of the corolla we applied the χ^2 test of ordinal correlation.

For determination of the plant species predominantly visited by bees in the study area we used the method of probability of Kato *et al*. 1952 *apud* Laroca 1995.

The number of interactions (I) was calculated from the number of intersections in the matrix bee (A) x plants (P).

Two niche dimensions were analyzed: the trophic niche (H'Pl), which is represented by the number of plant species visited by the bees and their frequencies on the flowers, and the temporal niche (H'O), which is indicated by the number of samplings in which the bee species were captured and their frequencies in each sampling. These values were expressed by the diversity index of Shannon-Wiener (H ') (Ludwig & Reynolds 1988).

To determine the relationships between flowering intensity and bees' flight activity, and among the two analyzed dimensions of the niche, we used simple linear regression and to evaluate similarity in the use of the floral resources by the bees and the attractivity of the pollinators for the plants we applied the grouping method UPGMA. The similarity coefficients were: Sorensen

(Southwood & Henderson 2000) and the Euclidian Relative Distance (Ludwig & Reynolds 1988). The similarity matrices and the dendograms were calculated by SAS System program.

RESULTS

In Abaeté, 3983 individuals of Apoidea visited 66 plant species (55 genera, 39 families) (Table I). They belonged to 49 species and 5 families (*sensu* Michener 1965), (Table II).

To analyze the relationships between bees and plants these species were grouped in 13 morph-functional categories. In most cases, taxonomic agreement was found at genera level (Table II).

We observed 310 interactions between bees and plants at species level. The use of floral resources by bees was not homogeneous; most of the plant species received a low number of visitors. Of the 66 species of plants, 12 were predominantly visited (77.43% of the total number of visits). In decreasing order: *Cuphea brachiata* (Lythraceae), *Waltheria cinerescens* (Sterculiaceae), *Humiria balsamifera* (Humiriaceae), *Acosmium bijugum* (Fabaceae), *Eriope blanchetii* (Lamiaceae), *Manilkara salmannii* (Sapotaceae), *Tapirira guianensis* (Anacardiaceae), *Chamaecrista ramosa* (Caesalpiniaceae), *Byrsonima microphylla* (Malpighiaceae), *Coccoloba cordifolia* (Polygonaceae), *Borreria cymosa* (Rubiaceae) and *Struthanthus polyrrhizua* (Loranthaceae).

Cuphea brachiata, *Acosmium bijugum* and *Eriope blanchetii* were visited by the most visitors diversity: 9 bee morpho functional categories (22 species), 7 categories (22 species) and 10 categories (21 species), respectively (Table I).

The predominant categories in number of individuals were *Xylocopa*, *Trigona spinipes*, others Trigonini/*Apis mellifera* and Centridini. Augochlorini and *Dichrantidium/Pseudocentrum* were also well represented in the area; *Ceratinula, Colletes, Dialictus, Mesoplia/Mesonychium littoreum, Chilicola* and *Florilegus* were represented by few individuals (Table II).

Xylocopa and *Trigona spinipes* also visited the largest number of plant species, 44 and 40 respectively, followed by *Apis mellifera* (24 spp), Centridini (22 spp) and Augochlorini (21 spp).

Throughout the year, correlation between floral abundance and number of bee individuals was positive and statistically significant ($r=0.68$; $p<0.05$) in Abaeté. The number of flowering individuals per plant species varied from 1 to more than 400 along the year. Many plant species presented great flower abundance gathered in dense inflorescences, as *Tapirira guianensis*, *Coccoloba cordifolia*, *Humiria balsamifera*, *Byrsonima sericea*, *Acosmium bijugum*, *Protium icicariba* and *Protium bahianum.* The mean number of flowers per individual varied from 10,000 in the first two species to more than 50,000 in the others.

The plants predominantly visited by the categories present melittophilous, strictly melittophilous or primarily melittophilous flowers (Table III).

In Abaeté, although it has been identified a relationship between bees's body size and the diameter of the corolla (÷2 of correlation = 338.717 p = 0.001), the association was not linear (÷2 of correlation = 0.04 p = 0.841).

On the other hand, the relationship between glossa's size and the depth of the corolla was highly significant (÷2 of correlation = 465.223 p = 0.001), meaning that as larger the depth of the corolla the largest the length of the visitor's glossa.

In general, the predominant categories (*Trigona spinipes, Xylocopa*, other Trigonini / *Apis mellifera*, Augochlorini, Centridini and *Dicranthidium/Pseudocentrum*) were also those that presented the highest values in the two dimensions of the niche (Fig. 1).

When we analyzed the two dimensions of the niche (trophic and temporal) and the morpho-functional categories of Apoidea were correlated the ($r=0.76$; $p<0.05$).

Except for *Dialictus*, in all other categories the values of temporal diversity were higher than the values of the trophic ones, indicating that, although those categories present generalistic habits, they concentrate their visits in certain preferential resources.

The plant species predominantly visited were also analyzed in relation to the values of bees diversity collected in each species, and of the diversity of samples in which each plant species was visited by bees.

Temporal diversity (number of samples in which the plant was visited), along the sampling period (H'O), and visitors' diversity (H'Ab) in the plants predominantly visited did not present correlation ($r = 0.37$; $p>0.05$), perhaps because although most of the plant species have been available for the bees, along almost the whole sampling period, they were not visited in a homogeneous way by them (Fig. 2). There was a concentration of individuals of few species on their flowers.

Eriope blanchetii was the plant species with the largest values of temporary diversity and visitors' diversity being therefore more "generalist in its use" of potential pollinators.

The species with the smallest values of H'O were *Coccoloba cordifolia*, *Borreria cymosa* and *Manilkara salzmanni.* These species have seasonal blooming, alternating them along the study year.

Although *Waltheria cinerescens* and *Cuphea brachiata* have presented high H'O, meaning that their flowers have been visited by bees during the whole sampling year, the visitors' diversity (H'Ab) was low, mostly by the influence of the high number of individuals of *Xylocopa* (*Neoxylocopa*) *cearensis* collected in their flowers. Similar situation happened to *Struthanthus polyrrhizua,* which was intensively visited by *Trigona spinipes.*

In *Acosmium bijugum* and *Tapirira guianensis*, the values of visitors' diversity were influenced by the high numbers of *Trigona spinipes* and *Xylocopa* (*Neoxylocopa*) *cearensis* and of *Trigona spinipes* and *Apis mellifera,* respectively.

Byrsonima microphylla, a plant species which produce floral oils, was visited just by, Centridini category, specialized in the collection of this resource.

Bees grouping similarity related to the use of certain floral sources, and plants grouping similarity in relation to the number of species and the number of individual visitors, are presented in dendograms (Figs. 3 and 4, respectively).

In Figure 3a we can observe 3 groups: the first formed by *Mesoplia/Mesonychium littoeium* (MMl), *Chilicola (*Ch) and *Florilegus (*Fg); the second formed by *Trigona spinipes* (Ts), *Xylocopa* (Xy) Other Trigonini/Apis *mellifera* (TAm) and

Table I. Plant species visited by morpho-functional categories of Apoidea in Abaeté, Salvador, BA (codes as in Table II).

Family	Plant species	Plant code	Morpho-functional categories in each plant species (number of individuals)	Total number of species (nº of individuals)
Anacardiaceae	*Tapirira guianensis* Aubl.	Tg	Xy(20); Ag(2); TAm(68); Ts(68); DP(1)	6 (159)
Apocynaceae	*Mandevilla funiformis* (Vell.) K. Schum.	Mf	Ts(1)	1 (1)
Araceae	*Anthurium longipes* N.E. Br.	Al	Ts(4)	1 (4)
Arecaceae	*Allagoptera brevicalyx* Moraes	Ag	Ts(3)	1 (3)
Asclepiadaceae	*Ditassa blanchetii* Decne.	Db	TAm(1)	1 (1)
Asteraceae	*Prolobus nitidus** (Baker) R.M. King & H. Rob.	Cn	Xy(8); Ct(1); Dp(2); Dl(1); Ag(1)	6 (13)
	*Litothamus nitidus** (DC.) W.C. Holmes	Mn	Xy(15); Ag(11); TAm(4); Ts(4)	8 (34)
	*Stilpnopappus scaposus** DC.	St	Xy(1)	1 (1)
	*Lepidaploa arenaria** (Mart. ex DC.) H. Rob.	Va	Xy(43); Ct(6); DP(11); Ag(1);	7 (61)
	L. edmundoi (G. M. Barroso)* H. Rob.	Ved	Ct(1); Ag(2)	2 (3)
Bignoniaceae	*Tabebuia elliptica* (DC.) Sandwith	Te	Xy(2); Ct(1); Ag(2); EBm(4); Ts(23)	7 (32)
Bromeliaceae	*Aechmea* sp	Ai	Ebm(1)	1 (1)
Burceraceae	*Protium bahianum* Daly	Pb	Xy(7); Ag(1); TAm(8); Ts(17);	5 (33)
	P. icicariba (DC.) Marchant	Pi	Xy(22); Ag(1); Am(33); Ts(9)	4 (65)
Caesalpiniaceae	*Chamaecrista ramosa* var. *ramosa* (Vogel) H.S. Irwin & Barneby.	Cr	Xy(108); TAm(1); Ct(14); EBm(11); Ts(24)	15 (158)
Capparaceae	*Dactylaena microphylla* Eichler.	Dm	Xy(2); Ts(1); DP(8)	4 (11)
Clusiaceae	*Kielmeyera argentea* Choisy	Ka	Xy(4); EBm(2); Ts(13)	5 (19)
Convolvulaceae	*Evolvulus maximiliani* (Mart. ex Choisy)	Esp	Xy(1); Ag(2); Ts(1);DP(1)	4 (5)
Ericaceae	*Agarista revoluta* (Spreng.) Hook. f. ex Nied.	Ar	Xy(1); TAm(5); Ts(5)	3 (11)
Euphorbiaceae	*Euphorbia gymnoclada* Boiss.	Eg	DP(1)	1 (1)
Fabaceae	*Acosmium bijugum* (Vogel) Yakovlev	Ab	Dl(1); Xy(180); Ct(1); Ag(9); EBm(1); TAm(40); Ts(110)	22 (342)
	Centrosema brasilianum (L.) Benth.	Ctb	Xy(8); Ct(4); EBm(5)	7 (17)
	C. coriaceum Benth.	Ctc	Xy(2); Ts(1)	2 (3)
	Moldenhawera nutans L.P. Queiroz, G.P. Lewis & Allkin.	Mw	Xy(1); Ct(2); Ts(1)	4 (4)
	Poecilanthe itapuana G. P. Lewis	Pt	Tam (1)	1(1)
	Stilosanthes viscosa (L.) Sw.	Sv	Xy(9); DP(7); Ct(4)	5 (20)
	Swartzia apetala var. *subcordata* R.S. Cowan	Sw	Xy (1)	1 (1)
	Vigna halophila (Piper) Maréchal, Mascherpa & Stainier	Vh	Xy(63); Ct(6); MMl(1); EBm(1)	7 (71)
Humiriaceae	*Humiria balsamifera* var. *parvifolia* (A. Juss.) Cuatrec.	Hb	Xy(171); Ct(1); Ag(11); TAm(169); Ts(12);	9 (364)
Icacinaceae	*Emmotum affine* Miers	Ea	Xy(1); Ag(1); TAm(5)	3 (7)
Krameriaceae	*Krameria bahiana* B. B. Simpson	Kb	Ct(47)	7 (47)
Lamiaceae	*Eriope blanchetii* (Benth.) R. M. Harley	Eb	Cl(23); Cr(36); Dl(1); Xy(59); Ct(11); EBm(3); Ag(50); TAm(4); Ts(64); DP(64)	21 (315)
Lauraceae	*Ocotea notata* (Nees & C. Martius ex Nees) Mez	On	Ts(8)	1 (8)
Loranthaceae	*Struthanthus polyrrhizua* (Mart. ex Roem. & Schult.) Martius ex G. Don.	Sp	Xy(9); TAm(6); Ag(2); Ts(59); DP(3)	6 (79)
	S. flexilis (Rusby) Kuijt	Sf	Xy(2); TAm(1)	2 (3)
Lythraceae	*Cuphea brachiata* (Mart.) Koehne	Cb	Ch(2); Xy(497); Ct(128); Fg(1); MMl(9); EBm(4); Ag(2); Ts(1); DP(2)	22 (646)
Malpighiaceae	*Byrsonima sericea* DC.	Bs	Ct(57)	8 (57)
	B. coccolobaefolia Kunth	Byc	Ct(2)	1 (2)
	B. microphylla A. Juss.	Bm	Ct(143)	12 (143)
	Stigmaphyllon paralias A. Juss.	Sg	Ct(1)	1 (1)

Table I. Cont.

Family	Plant species	Plant code	Morpho-functional categories in each plant species (number of individuals)	Total number of species (nº of individuals)
Melastomataceae	*Comolia ovalifolia* (DC.) Triana	Co	Xy(13); EBm(1); Ag(1)	3 (15)
	*Tibouchina bradeana** Renner	Pe	Xy(11); Ct(2)	5 (13)
Mimosaceae	*Abarema filamentosa* (Benth.) Pittier	Af	TAm(3)	1 (3)
Myrtaceae	*Calycolpus legrandii* Mattos	Cl	Xy(1); Ag(2); EBm(2); DP(1); Ts(3)	6 (9)
	Eugenia pistaciifolia DC.	Ep	Ts(1)	1 (1)
	Myrcia melanosepala Kiaersk.	Msp1	Ts(6)	1 (6)
	Myrcia guianensis (Aubl.) DC.	Msp2	Xy(3); TAm(15); Ts(17);	3 (35)
Ochnaceae	*Ouratea rotundifolia* (Gardner) Engl.	Or	Ct(1); TAm(1); Ts(6)	3 (8)
Passifloraceae	*Passiflora edulis* Sims	Pa	Xy(9); Ct(1)	5 (10)
Polygalaceae	*Polygala trichosperma* Chod. & Hub.	Pp	Xy(5); DP(1); Ts(1)	4 (7)
	Polygala violacea Aubl.	Psp	Xy(1)	1 (1)
Polygonaceae	*Coccoloba cordifolia* Meisn.	Cc	Xy(28); Ts(97)	3 (125)
	C. ramosissima Wedd.	Cor	Xy(6); TAm(23);Ts(22)	3 (51)
Rubiaceae	*Borreria cymosa* (Spreng.) Cham. & Schltdl.	Bc	Dl(2); Xy(11); TAm(73); Ts(1)	4 (87)
	Mitracarpus frigidus var. *discolor** (Miq.) K. Schum	Bsp	Xy(5); Dl(2); Ag(1); TAm(4); Ts(3); Ct(1)	6 (16)
	B. verticillata (L) G. Mey.	Bv	Dl(2); Xy(2); TAm(1); Ts(5);	4 (10)
	Guettarda platypoda DC.	Gp	Ts(8)	1 (8)
	*Rudgea crassifólia** Zappi & E. Lucas	Asp	EBm(1); Ts(19)	2 (20)
Sapindaceae	*Cardiospermum integerrimum* Radlk.	Ci	Xy(3); Ag(1);TAm(1); Ts(9)	4 (14)
Sapotaceae	*Manilkara salzmannii* (DC.) H. J. Lam.	Ms	Xy(29); TAm(135); Ts(1)	3 (165)
Solanaceae	*Solanum stagnale* Moric.	Ss	EBm(11); TS(3)	3 (14)
Sterculiaceae	*Waltheria cinerescens* St. Hilaire	Wc	Xy(489); Ct(18); DP(4); Ag(46); TAm(10); Ts(13);	16 (580)
Theaceae	*Ternstroemia* sp	Tsp	EBm(1)	1 (1)
Velloziaceae	*Vellozia dasypus Seub.*	Vd	Xy(4)	1 (4)
Verbenaceae	*Lantana camara L.*	Lc	Xy(5)	1 (5)
	Vitex cymosa ex. Berter ex Spreng.	Vc	Xy(11); Ag(1); EBm(1); Ts(15)	4 (28)
Number of visitors			13 categories	(49 spp) 3983 ind.

(* These plants species have changed names)

Augochlorini (Ag) and the third one by *Ceratinula (*Cr) and *Colletes* (Cl).

The pairs formed by *Ceratinula (*Cr) and *Colletes* (Cl) and by *Chilicola (*Ch) and *Florilegus (*Fg) shared a single resource, *Eriope blanchetii* and *Cuphea brachiata*, respectively.

The use of the Euclidian Relative Distance (Figure 3b) indicates that the same three groups are practically repeated. There was a displacement of *Dicranthidium/Pseudocentrum* (DP) to the third group, with an association with Cr and Cl. This happened due to the high frequency of DP in *Eriope blanchetii*, the single plant species visited by Cr and Cl.

In the second group, we can identify subsets formed by TAm, Ts, Dl and Xy , Ag. Except for Dl, the categories in this grouping are the most abundant and generalist. The pairs formed by these categories presented low similarity levels. These categories remain grouped mainly for the high number of visited plants and for their abundances.

In relation to plant species, Fig. 4a shows the formation of two more similar groups. The first formed by *Acosmium bijugum* (Ab)*, Humiria balsamifera* (Hb) and *Waltheria cinerescens* (Wc), more generalist species as for the number of visitors' species. The second formed by *Coccoloba cordifolia (Cc), Manilkara salzmanni (Bad), Borreria cymosa (Bc), Tapirira guianensis (Tg) and Struthanthus polyrrhizua (Sp). Manilkara salzmanni (Bad*) and *Borreria cymosa (Bc)* was the pair with the highest similarity.

As for bees' analysis, the two employed indexes also resulted in very similar plant groupings.

Using the Euclidian Relative Distance (Fig. 4b) the similarity dendogram shows 3 major groupings. In those, it is noteworthy three pairs with the smallest mean distances, in other words, with the highest affinities. The close association between *Cuphea brachiata* (Cb) and *Waltheria cinerescens* (Wc) was due mainly to the high frequencies of *Xylocopa* (Xy) in their flowers, while *Coccoloba cordifolia* (Cc) and *Struthanthus polyrrhizua* (Sp) were grouped due to the high proportions of visits of *Trigona spinipes* (Ts).

The pair with the highest similarity, formed by *Manilkara*

Table II. Bees collected and plant species visited (code as in Table I), in Abaeté, Salvador, BA.

Family	Morph-functional category (code)	Apoidea species	Plant species visited by bees (nº of individuals)	Total nº of plants visited (nº of bees)
Colletidae	*Chilicola* (Ch)	*Chilicola (*Stenocelis*)* sp 1	Cb(2)	1(2)
	Colletes (Cl)	*Colletes petropolitanus* Delatorre, 1896	Eb(23)	1(23)
Halictidae	*Dialictus* (Dl)	*Dialictus (*Chloralictus*) opacus* Moure,1940	Ab(1); Bc(2); Bsp (2); Bv(2); Cn(1); Eb(1);	6(9)
	Augochlorini (Ag)	*Augochlora* sp 1 *Augochlora* sp 2 *Augochloropsis callichroa* (Cockerell, 1900) *Augochloropsis* sp 1 *Pseudoaugochloropsis pandora* (Smith, 1853)	Ab(9); Bc(2); Bsp(2); Bv(2); Cb(2); Ci(1); Cl(1); Co(1); Cn(2); Ea(1); Eb(50); Esp(2); Hb(11); Mn(11); Pb(1);Pi(1); Sp(2); Te(2); Tg(2); Va(1); Vc(1); Ved(2); Wc(46)	21 (150)
Megachilidae	*Dicranthidium/ Pseudocentrum* (DP)	*Dicranthidium arenarium* Ducke, 1907 *Dicranthidium luciae* Urban, 1992 *Pseudocentrum* (*Pseudocentrum*) sp 1 *Pseudocentrum* (*Pseudocentrum*) sp 2 *Pseudocentrum* (*Pseudocentrum*) sp 3	Cb(2); Cl(1); Cn(1); Dm(8); Eb(64); Eg(1); Esp(1); Pp(1); Sp(3); Sv(7); Tg(1); Va(11); Wc(4)	13(105)
Anthophoridae	Centridini (Ct)	*Centris* (*Centris*) *aenea* Lepeletier, 1841 *Centris* (*Centris*) *caxiensis* Ducke, 1907 *Centris* (*Centris*) *flavifrons* Fabricius, 1775 *Centris* (*Centris*) *leprieuri* Spinola, 1841 *Centris* (*Centris*) *nitens* Lepeletier, 1841 *Centris* (*Centris*) *spilopoda* Moure, 1969 *Centris* (*Hemisiella*) *tarsata* Smith, 1874 *Centris* (*Hemisiella*) *trigonoides* Lepeletier, 1841 *Centris* (*Paremisia*) *fuscata* Lepeletier, 1841 *Centris* (*Paremisia*) *pulchra* Moure *et al,* 2003 *Centris* (*Ptilotopus*) *sponsa* Smith, 1854 *Centris* (*Xanthemisia*) *lutea* Friese, 1899 *Epicharis* (*Xanthepicharis*) *bicolor* Smith, 1854 *Epicharis* (*Xanthepicharis*) *nigrita* Friese, 1900	Ab(1); Bm(143); Bs(57); Byc(2); Cb(128); Cn(1); Cr(14); Ctb(4); Eb(11); Hb(1); Kb(47); Mw(2); Or(1); Pa(1); Pe(2); Sg(1); Sv(4); Te(1); Va(6); Ved(1); Vh(6); Wc(18)	22(452)
	Ceratinula (Cr)	*Ceratinula* sp 1 *Ceratinula* sp 2	Eb(36)	1(36)
	Florilegus (Fg)	*Florilegus similis* Urban, 1970	Cb(1)	1(1)
	Mesoplia/ Mesonichium litoreum (MMl)	*Mesonychium littoreum* Moure, 1944 *Mesoplia* sp 1 *Mesoplia* sp 2	Cb(9); Vh(1)	2(10)
	Xylocopa (Xy)	*Xylocopa* (*Megaxylocopa*) *frontalis* Olivier, 1789 *Xylocopa* (*Neoxylocopa*) *cearensis* Ducke, 1910 *Xylocopa* (*Neoxylocopa*) *grisescens* Lepeletier, 1841 *Xylocopa* (*Neoxylocopa*) *nigrocincta* Smith, 1854 *Xylocopa* (*Schoenherria*) *prov. subcyanea* Pérez, 1901 *Xylocopa* (*Neoxylocopa*) *suspecta* Moure & Camargo, 1988	Ab(180); Ar(1); Bc(11); Bsp(6); Bv(2); Cb(497); Cc(28); Ci(3); Cl(2); Cn(8); Co(13); Cor(6); Cr(108);Ctb(8); Ctc(2); Dm(2); Ea(1); Eb(59); Esp(1); Hb(171); Ka(4); Lc(5); Mn(15); Ms(29); Msp2(3); Mw(1); Pa(9);Pb(7); Pe(11); Pi(22); Pp(5); Psp(1); Sa(1);	44(1874)
Apidae	Other Trigonini/ *Apis mellifera* (Tam)	*Apis mellifera* Linnaeus, 1758 *Frieseomellita doederlini* (Friese, 1900) *Frieseomellita silvestri languida* Moure, 1989 *Trigonisca* sp 1	Ab(40); Ar(5); Af(3); Bc (73); Bsp(4); Bv(1); Ci(1); Cor(23); Cr(1); Db(1); Ea(5); Eb(4); Hb(169); Mn(4); Ms(135); Msp2(15); Or(1); Pb(8); Pi(33); Pt(1);Sf(1); Sp(6); Tg(68); Wc(10);	24(612)
	Euglossini/ Bombini (EBm)	*Bombus morio* (Swederus, 1787) *Euglossa cordata* (Linnaeus, 1758) *Eulaema meriana flavescens* Friese, 1899 *Eulaema nigrita* Lepeletier, 1841 *Euplusia mussitans* Fabricius, 1787	Ab(1); Ai(1); Asp(1); Cb(4); Cl(2); Co(1); Cr(11); Ctb(5); Eb(3); Ka(2); Ss(11); Te(4); Tsp(1); Vc(1); Vh(1)	15(49)
	Trigona spinipes (Ts)	*Trigona spinipes* (Fabricius, 1793)	Ab(110); Ag(3); Al(4); Ar(5); Asp(19); Bc(1); Bsp(3); Bv(5); Cb(1); Cc(97); Ci(9); Cl(3); Cn(1); Cor(22); Cr(24); Ctc(1); Dm(1); Eb(64); Ep(1); Esp(1); Gp(8); Hb(12); Ka(13); Mf(1); Mn(4); Ms(1); Msp1(6); Msp2(17); Mw(1); On(8); Or(6); Pb(17); Pi(9); Psp(	40(660)

Table III. Characteristics of the most predominant visited plant species (=3084 individuals, 77.43% from the total number of visitors) by the morpho-functional categories in Abaeté, Bahia, from January to December 1996.

Family	Species (code)	Syndrome	Color	Blosson arrangement	Resourse	Anther dehiscence	Sexuality	Life form	Symmetry
Anacardiaceae	*Tapirira guianensis (Tg)*	Melit	Br	Inflorescence	Nectar	Long.	Hermaphrodite	Tree	Radial
Caesalpiniaceae	*Chamaecrista ramosa (Cr)*	Melit*	Am	Isolated	Pollen	Apical pore	Hermaphrodite	Sub-shrub	Zigomorphic
Fabaceae	*Acosmium bijugum (Ab)*	Melit	Cr	Inflorescence	Nectar/Pollen	Long.	Hermaphrodite	Shrub	Radial
Humiriaceae	*Humiria balsamifera (Hb)*	Melit	Cr	Inflorescence	Nectar	Long.	Hermaphrodite	Shrub	Radial
Lamiaceae	*Eriope blanchetti (Eb)*	Melit*	Li	Inflorescence	Nectar	Long.	Hermaphrodite	Shrub	Zigomorphic
Loranthaceae	*Struthanthus polyrrhizua (Sp)*	Melit	Cr	Inflorescence	Nectar	Long.	Hermaphrodite	Hemiparasite	Radial
Lythraceae	*Cuphea brachiata (Cb)*	Melit+	Am	Isolated	Nectar	Long.	Hermaphrodite	Sub-shrub	Zigomorphic
Malpighiaceae	*Byrsonima microphylla (Bm)*	Melit*	Ro	Inflorescence	Oil/Pollen	Long.	Hermaphrodite	Shrub	Zigomorphic
Polygonaceae	*Coccoloba cordifolia (Cc)*	Melit	Br	Inflorescence	Nectar/Pollen	Long.	Dioic	Shrub	Radial
Rubiaceae	*Borreria cymosa (Bc)*	Melit	Cr	Inflorescence	Nectar	Long.	Hermaphrodite	Sub-shrub	Radial
Sapotaceae	*Manilkara salzmannii (Ms)*	Melit	Cr	Inflorescence	Nectar	Long.	Hermaphrodite	Shrub	Radial
Sterculiaceae	*Waltheria cinerescens (Wc)*	Melit	Am	Inflorescence	Nectar/Pollen	Long.	Hermaphrodite	Shrub	Radial

Color: Li= Lilac, Br= White, Cr= Cream, Am= Yellow, Ro= Pink; Syndrome: Melit= Melittophilous, Melit+= primarily Melittophilous, Melit*= Strictly Melittophilous; Anther dehiscence: Long= Longitudinal

salzmanni (Ms) and *Borreria cymosa* (Bc), was almost exclusively visited by *Apis mellifera*.

Byrsonima microphylla appears isolated (Figs. 4a and b), due to the fact that it was visited by a single category (Centridini).

DISCUSSION

Structure of the bee-flower system in Abaeté: composition and relationships. The large solitary bees, *Xylocopa* and Centridini, and the eusocial species, *Apis mellifera* and *Trigona spinipes*, prevailed.

Xylocopa and Centridini are resident bees in the dunes. Nests of *Xylocopa* were found in branches of *Agarista revoluta* (Spr) DC (Silva & Viana 2002), while some of Centridini were found in pre-existent cavities (Viana *et al.* 2001) in the sandy soil of the dunes. These species are multivoltines, presenting high values of temporal niche width.

Apis mellifera is an introduced bee species, widely distributed in the Brazilian ecosystems, except in humid forests. It is found in high frequencies on flowers. No nest of this species was found in the area. Taking also into account the low value of temporal niche, it suggests that the individuals of this species have been attracted to the dunes by attractive flowerings. Due to their long-lived colonies, these bees do not specialize in determined floral types, using any flower for which they are recruited. Floral preference can change from one season to the other. This characteristic makes *Apis mellifera* a low efficient pollinator (Westerkamp 1991).

Trigona spinipes, a native bee species, was also a sporadic visitor in the dunes. This species builds aerial nests which are in general very populous. However, in spite of its high abundance in the study area, no nest was seen during the sampling period.

Cortopassi-Laurino & Ramalho (1988) and Wilms *et al. (*1996) also found a high value of the trophic niche width (H ') for *Trigona spinipes* (Ts). These authors suggest that these bees have H' values, because they make many "illegitimate" visits to non melittophilous flowers, or to those specialized in big bees, that are not usually visited by other Apoidea in the community. In this case, they don't act as pollinators's agents for the plant, because they do not touch the female parts of the flower.

Nectar robbery by *Trigona spinipes* was observed in the conspicuous flowers of *Tabebuia elliptica* (Bignoniaceae), of *Agarista revoluta* (Ericaceae) and of *Mandevilla funiformis* (Apocynaceae), adapted to other pollinators. These bees perforated the corolla in the height of the nectary introducing their glossa for "illicit" nectar collection.

Pollen robbery behavior by *Trigona spinipes* was more evident in flowers of *Chamaecrista ramosa* (Caesalpiniaceae) and of *Solanum stagnale* (Solanaceae). After 2 hours of observations, 13 in 100 flowers of *Chamaecrista ramosa* had their stamens cutted.

Laroca (1970) was the first to describe this pollen robbery cut technique by bees of the genus *Trigona* in 4 species of Melastomataceae. This behavior leads to a reproductive loss for the plant, since the big vibrating bees, like *Xylocopa* and Centridini, potential pollinators, avoid the flowers visited earlier by this bee.

Although the great majority of the species presented melittophilous characteristics, we did not observe any specific relationships between bee species and plant species. The plant species with the highest floral densities were the most visited by most of bee species and the more abundant bee species concentrated their visits in few plant species.

Only two categories (*Colletes* and *Ceratinula*) fed on just a single plant species. However, the plant species (*Eriope blanchetii*) used by these bees was visited also by most of the other categories.

Similar pattern was observed by Dupont *et al.* (2003) in the Canaries islands, indicating that the use of several species of plants by a pollinator and of several pollinators species by a plant is more likely a rule and not an exception in different ecological communities (Waser *et al.* 1996).

Although generalization has prevailed, plant species presented different degrees of importance for each one of the visitors' categories. Generally there was a difference in visitors'

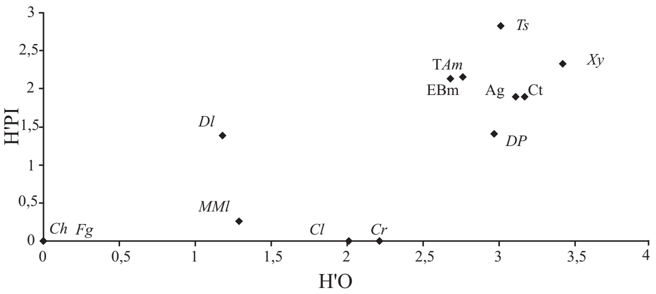

Fig. 1. Relationship between plant species diversity (H'Pl) and occurrence diversity (H'O) (number of samplings in which species was captured; temporal niche) within the morph-functional categories of Apoidea in Abaeté, Salvador, Bahia. Codes: *MMl=Mesoplia* and *Mesonychium litorium;* EBm=Euglossini/Bombini; *Ts=Trigona spinipes;* T*Am*=Other Trigonini and *Apis mellifera; Xy=Xylocopa; Cr=Ceratinula; Fg=Florilegus;* Ag=Augochlorini; *Dl=Dialictus; DP=Dicranthidium e Pseudocentrum; Cl=Colletes; Ch=Chilicola;* Ct=Centridini.

proportion in the different resources. Several preferential associations were evidenced.

Other authors (Cortopassi-Laurino & Ramalho 1988 and Martins 1995, Wilms *et al.* 1996) also observed low values of similarity among polilectic species. Although these bees have visited many plants of the same species, they visited more intensively different species.

Even not linear, we identified associations among categories of big bees, more specialized, and big and conspicuous flowers, such as: Centridini and the oil producing species of the families Malpighiaceae and Krameriaceae and among Euglossini/Bombini (EBm) and the flowers of Bignoniaceae (Te), Caesalpiniaceae (Cr), Fabaceae (Ctb), Solanaceae (Ss) and Lytraceae (Cb). These associations were not linear probably due to the fact that the image of small flowers was incorporated to the inflorescences allowing an increase in its detection by bees, constituting a compensatory strategy for them (Dafni & Kevan 1997). Many smaller flowers that could be less efficiently detected are found in fact in dense and profuse inflorescences.

The relationship between the size of the visitor's glossa and the depth of the corolla was positive and highly significant. As nectar is deliberately hidden depthly inside the flower, it forces the bee to go deeper inside and to reach a more precise position in relation to pollination surface. The depth of the nectary has always to exceed the tongue's length to maintain floral fitness (Westerkamp 1996). The shorter the tongue is and smaller in size the most difficult is the visitor's position.

Small flowers, less conspicuous, that produce low amounts of nectar are not advantageous for big bees, although they can be appropriate for small ones, as *Struthanthus polyrrhizua,* that was intensively visited by *Trigona spinipes*.

If flowers specialize in bees through nectar, the bees on the other hand specialize (oligoleticity) in their host flowers through pollen. Flowers visited for pollen collection are restricted to bees (Westerkamp 1996).

Bees collecting actively pollen usually do not pollinate. This happens as a consequence of the contamination of bee body by pollen. One of the rare exceptions is the flowers with poricide anthers and their visitors capable to vibrate them for pollen retreat: while bees forage actively for pollen collection, they are contaminated with it and they accomplish pollination (Buchmann 1983).

The flowers with poricide anthers favor big bees able to collect pollen by vibration. In Abaeté, the categories of big bees (Xy, Ct and Ebm) concentrated pollen collection on flowers with poricide anthers of the families Caesalpiniaceae (Cr) and Solanaceae (Ss).

Although other small bees, also vibrating bees, like Augochlorini, have also visited flowers with poricide anthers, they acted as robbers because they did not contact the stigma. Their visits decrease the flower pollen supply available to the legitimate pollinators and can increase pollination efficiency will increase since the pollinator will have to visit more flowers in more plants to assure the necessary amount of pollen.

Another preferential relationship happened among the category Centridini and the oil producing flowers of the families Malpighiaceae and Krameriaceae.

The pollination systems involving oil production as floral rewards represent one of the strongest example of dependence of a plant group by a particular bee taxon and vice-versa.

Gottsberger (1986) found nine different species of Centridini visiting and likely pollinating the flowers of *Byrsonima coccolobaefolia*. In Abaeté, the three species predominantly visited for oil collection, *Byrsonima microphylla, Byrsonima sericea* and *Krameria bahiana* were visited, respectively, by 12, 8 and 7 species of Centridini.

The presence of oil producing flowers as floral resources of the families Malpighiaceae and Krameriaceae seems to increase local population abundance of Centridini, which, by other hand, promote their reproductive success.

Identified tendencies and related factors. In general, bees presented generalist food habits and they were active during the whole year. According to the different bloomings the species changed their preferential resources. We did not notice any plant-bee species close relationship in resources use concerning the subset of analyzed interactions.

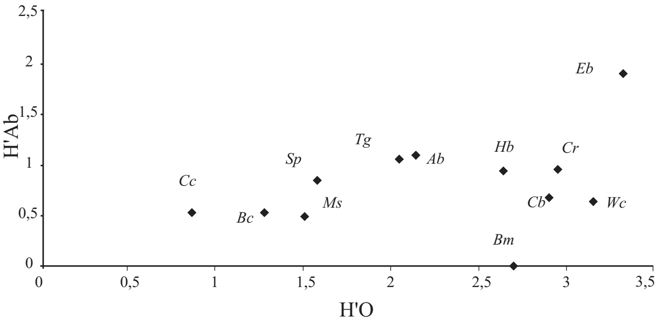

Fig. 2. Relationship between bee diversity (by categories) (H'Ab) and visits diversity (H'O) (number of samplings in which species was visited) within the predominant visited plant species in Abaeté, Salvador, Bahia. Codes: *Cc=Coccoloba cordifolia; Bc=Borreria cymosa; Ms=Manilkara salmanni; Sp=Struthanthus polyrrhizua; Tg=Tapirira guianensis; Ab=Acosmium bijugum; Hb=Humiria balsamifera; Cb=Cuphea brachiata; Cr=Chamaecrista ramosa; Wc=Waltheria cinerescens; Eb=Eriope blanchetii*

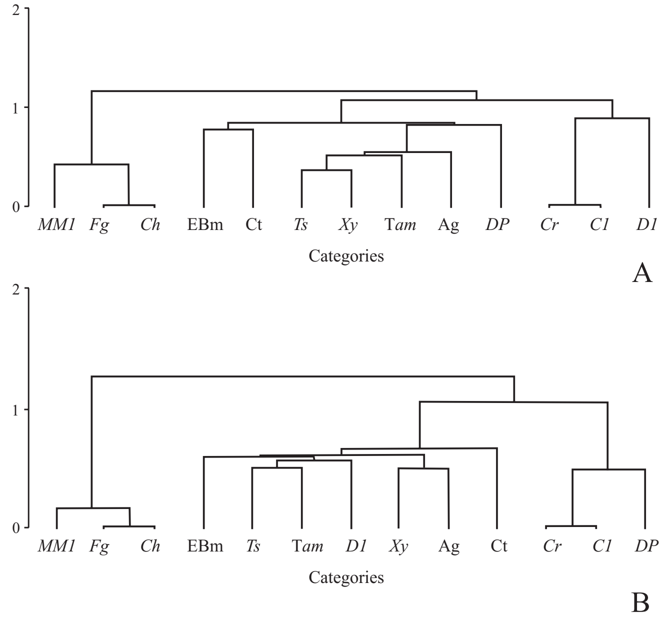

Fig. 3. Similarity dendograms among the morph-functional categories of Apoidea in relation to visited plant species in Abaeté dunes, Salvador, Bahia, between January and December, 1996. Species were grouped according to UPGMA using Sorensen's index (A) and Relative Euclidian Distance (B). Codes: *MMl=Mesoplia* and *Mesonychium litorium;* EBm=Euglossini/Bombini; *Ts=Trigona spinipes;* T*Am*=Other *Trigonini* and *Apis mellifera; Xy=Xylocopa; Cr=Ceratinula; Fg=Florilegus;* Ag=Augochlorini; *Dl=Dialictus; DP=Dicranthidium* and *Pseudocentrum; Cl=Colletes; Ch=Chilicola;* Ct=Centridini.

In this environment generalist plants with long flowering periods also prevail. Although predominantly melittophilous their flowers are little specialized, opening up for a great spectrum of opportunistic visitors that do not contribute to their reproductive success. The lack of mechanical restrictions imposed by floral morphology, which facilitate the nectar access for the visitors, allied to the previsibility of the resource, would be the responsible factors for the intensive visits of some predominant species (Silva *et al.* 2005).

Similar systems, where most of the plants are visited by a great number of visitors and many visitors use a great number of plants seems to prevail in several ecological communities (Memmott 1999; Dupont *et al.* 2003), unlike what was thought in the past.

The predominant morph-functional categories in number of individuals were also the ones that presented the largest number of interactions with the local flora, in spite of having concentrated their visits in few preferential resources, taking into account mainly floral abundance. These bees seem to choose the sources from which they can obtain the largest amounts of food and they concentrate on them.

The plants in which those categories concentrated their visits presented a high density (number of individuals/hectare), as *Waltheria cinerescens, Cuphea brachiata, Chamaecrista ramosa* and *Borreria cymosa*, or abundant blooming ("mass flowering"), as *Acosmium bijugum, Coccoloba cordifolia, Tapirira guianensis, Manilkara salzmanni and Humiria balsamifera.*

Other authors also observed this pattern of intense exploration of few resources when they analyzed the trophic diversity (H ') of some species of eusocial bees in several neotropical habitats (Ramalho *et al.* 1985; Kleinert-Giovannini & Imperatriz-Fonseca 1987; Cortopassi-Laurino & Ramalho 1988; Imperatriz-Fonseca *et al.* 1989; Wilms *et al.* 1996).

Besides floral abundance, other factors can contribute to local structuring of the bee-flower system in Abaeté, as for instance, the predominance of species with flowers with melittophilous characteristics that could exclude other floral visitors favoring bees. For instance, the predominance of species as *Cuphea brachiata* and *Eriope blanchetii,* that produce nectar in a constant manner and in low concentration (Silva *et al.* 2005), and of *Chamaecrista ramosa,* that presents poricide anthers, besides the presence of oil producing species of the families Malphigiaceae and Krameriaceae.

Thus, we can infer that the observed pattern in the bee-flower system seems to be structured by abundance as by resource quality.

Implications of bee-flower interactions in the context of the local landscape conservation. In Abaeté, we observed the existence of multiple interactions between bees and flowers, with predominance of generalist relationships. In this environment, submitted to strong climatic pressures (high speed winds, high temperatures and light intensity), the generalist species, with

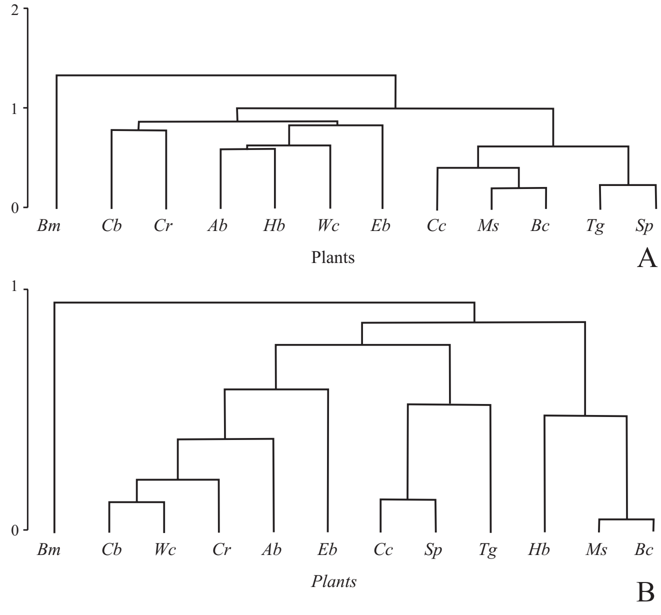

Fig. 4. Similarity dendograms among plant species predominantly visited by in relation to the morph-functional categories of Apoidea in Abaeté dunes, Salvador, Bahia, between January and December, 1996. Species were grouped according to UPGMA using Sorensen's index (A) and Relative Euclidian Distance (B). Codes: *Cc=Coccoloba cordifolia; Bc=Borreria cymosa; Ms=Manilkara salmanni; Sp=Struthanthus polyrrhizua; Tg=Tapirira guianensis; Ab=Acosmium bijugum; Hb=Humiria balsamifera; Cb=Cuphea brachiata; Cr=Chamaecrista ramosa; Wc=Waltheria cinerescens; Eb=Eriope blanchetii.*

larger plasticity in the use of floral resources, are more able to survive when their preferential resources are not more available, going then in search of alternative sources.

In a place with low specialization as the coastal dunes, it is probable that groups of big and more abundant bees, like Centridini and *Xylocopa*, have larger impact on the floral fitness, for they move the largest amount of pollen in the community.

The presence of abundant plants, "generalists" and with long flowering periods, as *Cuphea brachiata* and *Eriope blancheti,* represents a source of resources for an enormous guild of generalist floral visitors, potential pollinators of other local plant species. The uninterrupted production of flowers by these species maintains the pollen flow and the natural pollinator populations, especially in periods of resources shortage.

The aggregated distribution of these plants concentrates the trophic resources, and although small their flowers work as visual incentive for attraction from long distance. The floral density has positive effect on the number and on diversity of visitors (Silva *et al.* 2005).

These bee species and common plant species must be responsible for the maintenance of many rare species in the area, being considered key species by their effect in the persistence of other species in the community (Bond 1994). The loss of these species can put in risk the dependent species and can cause changes in the local landscape and in the ecosystem operation (Gilbert 1980).

Thus, the effort for landscape conservation, in Abaeté, should be emphasized on the whole complex of the local fauna and flora, not just including the rare species, but also the common species, responsible for the survival of the first and consequent maintenance of the local landscape.

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