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Pollination biology in a palm swamp community in the Venezuelan Central Plains

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RAMIREZ, N. & BRITO, Y., 1992. **Pollination biology in a palm swamp community in the Venezuelan central plains.** In a palm swamp community that differs strongly from the surrounding savanna in the Venezuelan central plains, the pollination and floral biology of 33 plant species were studied during three years: 1983, 1984 and 1989. The most frequent flower colours were white, pink, yellow, and in a lesser proportion green, brown, purple and red. Floral symmetry was found in roughly equal proportion for actinomorphic and zygomorphic flowers. Most flowers were short-lived (6–12 hours); in monoecious species the female flowers were longer-lived than the male flowers. The most frequent rewards were pollen and nectar (36.4%) and pollen (30.3%). At the community level, bee- and wasp-pollination prevailed in 57.1% of plant species studies, followed by wind- (14.3%), fly- (11.4%), butterfly- (8.6%), bird- (5.7%) and beetle-pollination (2.9%). Between one and five plant species were simultaneously visited by the visitor species. The vast majority of the pollinating species displayed a high degree of load specificity: 26 pollinator species (65.0%) carried pollen from only one plant species, eight (20.0%) carried pollen from two plant species, three (7.5%) carried pollen from three plant species and one (2.5%) carried pollen from five plant species. Visitor specificity and pollen transportation were similar amongst the visiting agents. Plant pollination-system specificity and pollen transportation were statistically significant among plant species with different pollinator types, but plant pollination system and pollen transportation were not different among floral symmetry, floral longevity, reward type, plant sexuality, breeding system and plant life form. The visitor species/plant species ratio was 1.6, and the pollinator species/plant species ratio was 1.3. Among different guilds, birds, Coleoptera and Lepidoptera showed the highest pollinator species/plant species ratio, and wind pollination exhibited the lowest.

ADDITIONAL KEY WORDS:—Floral biology.

CONTENTS

INTRODUCTION

Geographic trends in the features of species making up communities interest ecologists because they may suggest factors underlying the organization of communities and the characteristics of their species (Regal, 1982). Surveys of

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pollination biology at the community level allow the characterization of the reproductive structure, function and organization of communities. However, the number of studies of pollination biology evaluated at the community level in tropical communities is relatively scarce (Percival, 1974; Bawa *et al.*, 1985; Bawa, 1990; Ramirez, 1989; Ramirez *et al.*, 1990; Seres & Ramirez, personal communications). These studies allow the comparison of the communities related to those specific characteristics of the community. A further level of analysis evaluating the relative effectiveness of various flower visitors in achieving pollen dispersal and pollen deposition are lacking (Bawa, 1990), but recent studies on pollination specificity and pollen load transportation at the community level, indicated that the effectiveness of visiting agents as pollinators may be increased through differential pollen load transportation (Ramirez, 1992).

A tropical palm swamp community, dominated by *Mauritia flexuosa* and known locally as 'morichal', exhibits characteristics which provided information in the global understanding of the natural communities. During the initial phase of this study, we found that: (1) The 'morichales' are composed of well defined vegetation units that differ in species composition from the surrounding savanna vegetation (Brito & Ramirez, 1988). In this context, the 'morichales' are discrete communities, isolated from each other. Gene flow among small habitats via pollen (and seed) may be curtailed (Janzen, 1987). (2) Flowering phenology shows a large overlapping behaviour in most of the plant species studied in the 'morichal' community (Ramirez & Brito, 1987); this pattern increased the probability of sharing pollinator species. (3) The 'morichal' is characterized by a low number of plant species with obligate cross-pollination; self-compatibility is the rule among short-lived plant species (Ramirez & Brito, 1990). According to these characteristics, pollen flow could be limited within each 'morichal', enforcing intra-population pollen flow. Under such circumstances, pollinator specificity might have evolved in response to isolation and flowering conditions overlapping, promoting diffuse plant-pollinator interaction, and hence self-compatibility in that plant species of the 'morichal' community.

This research characterizes the floral biology and pollination spectrum of the 'morichal' community, and tests whether pollination systems and unspecialized pollen transportation are in accord with the high proportion of self-compatibility found in the 'morichal' (Ramirez & Brito, 1990). Alternative features in pollination specificity may be found based on the fact that flowers of sympatric species sharing pollinators differ in the placement of their sexual structures and each species may be able to use a unique part of the body of the pollinator for transfer of gametes (Waser, 1983). In addition, we propose to answer the following questions: do floral traits affect pollination specificity and pollen transportation within the 'morichal'?; are the pollinators of the 'morichal' able to travel long distances?; does the plant and animal diversity promote diffuse relationship between plant and pollinator?

Study site

This study was conducted in a 'morichal' community dominated by *Mauritia flexuosa* in the central plains (Altos Llanos Centrales) of Venezuela, located in Guárico State, *c.* 17 km SW of Calabozo (8°56′N; 67°25′W) at an altitude of 74 m.

The 'morichales' originate at the water heads and tributaries of rivers (Sarmiento & Monasterio, 1968). The climate of the 'morichal' coincides with the macro-climate of the area; the temperature is significantly isothermic, with annual values between 24°C and 28°C. Precipitation varies throughout the year, with a marked biseasonality, characteristic of the Venezuelan central plains, consisting of definite rainy and dry periods. The rainy season lasts 6 months (May to October) with the maximum precipitation in August and four months with less than 20 mm of rain. April and November are considered periods of transition (Sarmiento & Monasterio, 1968; Walter & Medina, 1971). Although there is a significant reduction in precipitation during the dry season, the 'morichales' remain almost totally flooded due to the presence of natural water affluents.

The habitat can be divided into three strata: a discontinuous arboreal level, represented principally by *Mauritia flexuosa* (Palmae) at 25 m; an intermediate level at 3 to 7 m in which *Ludwigia nervosa* (Onagraceae), *Miconia stephananthera* (Melastomataceae) and other species are present, and the lowest level represented by several species of the following families: Cyperaceae, Gentianaceae, Lythraceae, Rubiaceae, Euphorbiaceae and others (Aristeguieta, 1968). These communities were described by Beard (1944) as palm swamp communities and Pires & Prance (1985) in Amazonia as 'Buritizal'.

METHODS

During 1983, 1984 and 1989, field observations were made to describe the pollination and floral biology of 33 plant species of a 'morichal' in the Altos Llanos Centrales in Venezuela. We recorded floral longevity (time from anthesis to withering of flowers), morphology (symmetry of flower and/or inflorescence, according pollination unit) and colour, and determinated type and abundance of reward (nectar, pollen, both together, and floral parts) offered to the visitors. In addition, the life form, plant sexuality and breeding system were listed according to Ramirez & Brito (1990).

The activity of the visitors was monitored daily during the period of floral activity (from 16–20 h per plant species) in different months of the year, during the period of maximum blooming. We captured as many visitors as possible. The presence and qualitative abundance of pollen, and the part of the body where it was transported were determined. Pollinators were distinguished from visitors using three criteria: (1) the presence of pollen; (2) the part of the body where pollen was transported, and (3) if the pollen on the body of an animal was available for transfer to stigmas (the pollen load made contact with the stigma during a visit).

To compare the relative levels of pollinator specificity we used four indices (Ramirez, 1988). These indices represent a general feature of pollination ecology as an approach to estimate community pollination in the species-visit context and vary from zero to one; higher values indicate a greater degree of specificity or pollen transportation and were calculated using previously reported flowering phenology (Ramirez & Brito, 1987).

The pollen specificity load index (SPLI) evaluates the number of sites where the pollinator carries pollen (n) divided by the total number of pollen loads ($N =$ plant species) carried. In this case, the sites of pollen transportation were given by the number of different pollen loads and different sites. For example, the pollen of two plant species located on the thorax, abdomen and leg of an insect simultaneously, was considered as only one site (SPLI = 0.5). However, pollen of two plant species distributed so that one was on the thorax and the other on the abdomen, was considered as two sites (SPLI = 1.0).

The pollinator specificity index (SPI) (given by $1/N$, where N is the number of plant species visited) is independent of the presence of pollen load (specificity visitor index) and measures the visiting capacity of a particular visiting agent.

The community pollination index (CPI) is given by the number of pollinators of one plant species divided by the sum of plant species visited by each one of the pollinators: $CPI = N_a/\Sigma\ X_i$, where, N_a = total number of pollinator species recorded on plant species a, and X_i = number of plant species visited by pollinator i. The CPI evaluates the proportion in which the pollinators are shared.

Pollen transportation specificity (PTS): the number of pollen loads localized on the same site can be associated with the efficiency of pollination. The PTS is given by $1/N$, where N is the number of different pollen loads at the same site.

The first two indices, SPI and PSLI, evaluate the specificity and the capacity of pollen transportation of pollinators and visitors. In contrast, the second two indices, CPI and PTS, evaluate the specificity of pollination system and pollen transportation of plant species.

Statistical analysis

Each index was subjected to an arcsine transformation before analysis. The indices were analysed with one-way analysis of variance (among pollinator types, floral symmetry, floral longevity, reward type and life form), and t tests between sexual system (monoecious vs hermaphrodite species) and breeding system (self-compatibility vs self-incompatibility) (Sokal & Rohlf, 1981).

RESULTS

Floral morphology

The most frequent flower colours were white ($N = 10$, 30.3%), pink ($N = 7$, 21.2%) and yellow ($N = 7$, 21.2%), and in a lesser proportion, green ($N = 3$, 9.1%), brown ($N = 3$, 9.1%), purple ($N = 2$, 6.1%) and red ($N = 1$, 3.0%). Actinomorphic and zygomorphic floral symmetries were found in roughly equal proportions 42.4% and 39.4% respectively. Irregular flowers or pollination units occurred in 18.2% of the 33 plant species considered.

Floral longevity

Most flowers were short-lived, from 6 to 12 hours. Of the 36 individual floral longevities recorded, 8 (22.2%) lasted 6 h, 14 (38.8%) lasted 12 h, 7 (19.4%) lasted 24 h, 5 (13.9%) lasted 48 h and 2 (5.6%) lasted more than 48 h.

In monoecious species, the male flowers had a relative short period of life compared with the female flower. The longevity of female flowers was three times longer than male flowers in Euphorbiaceae, four times longer in Cyperaceae and six times longer in Araceae (Appendix 1). Floral longevity in *Sinningia* sp. was higher than other hermaphrodite and monoecious plant species. In those species in which the floral activity lasted more than 24 hours, the flowers survived the early morning hours, when the activity of pollinators reaches its maximum (e.g. *Sinningia* sp. and *Clidemia capetillata)*.

Reward

The frequencies of species with different rewards in the sample of 33 species were as follows: nectar and pollen, 36.4%; pollen, 30.3%; nectar, 15.2%; staminodes, 3.0%; and without reward, 15.2% (wing pollinated).

Visitor diversity

The complete list of visiting agents is found in Appendix 2. Hymenoptera were the most common visitors in the 'morichal' community (8 families and 26 genera). Halictidae and Apidae were the most abundant families of bees, and Vespidae was the most diverse among wasp families (Table 1). Diptera and Lepidoptera included 4 and 3 families, and 9 and 7 genera respectively (Table 1). The most diverse families of dipterans were Sarcophagidae and Syrphidae. In contrast, Hesperiidae was the most numerous lepidopteran family in the

TABLE 1. Systematic position of the anthophylous fauna represented as the number and percentage of genera and species

Major group Order Family	Genera N (%)	Species N (%)	Total N (%)
Birds			
Apodiformes			
Trochilidae	1 (2.2)	2 (3.7)	2 (3.7)
Insects			
Coleoptera			
Scarabaeidae	1 (2.2)	1 (1.9)	1 (1.9)
Diptera			
Calliphoridae	1 (2.2)	1 (1.9)	
Empididae	1 (2.2)	1 (1.9)	
Sarcophagidae	4 (8.9)	4 (7.5)	
Sirphidae	3 (6.7)	4 (7.5)	
Tabanidae	1 (2.2)	1 (1.9)	11 (20.7)
Hymenoptera			
Anthophoridae	3 (6.7)	3 (5.6)	
Apidae	5 (11.1)	5 (9.4)	
Halictidae	4 (8.9)	8 (15.1)	
Megachilidae	3 (6.7)	3 (5.6)	
Bees			19 (35.8)
Pompilidae	1 (2.2)	1 (1.9)	
Scoliidae	1 (2.2)	1 (1.9)	
Sphecidae	3 (6.7)	3 (5.6)	
Vespidae	6 (13.3)	7 (13.2)	
Wasps			12 (22.6)
Hymenopterans			31 (58.5)
Lepidoptera			
Hesperiidae	5 (11.1)	6 (11.3)	
Nymphalidae	1 (2.2)	1 (1.9)	
Pieridae	1 (2.2)	1 (1.9)	
Butterflies			8 (15.1)
Total	45	53	

TABLE 2. Average pollinator indices and visitor species/plant species and pollinator species/plant ratios for visitor types

Pollinator Indices	Visitor types														
	Bird		Coleoptera		Diptera		Hymenoptera				Lepidoptera		Wind*		
							Bee		Wasp						
	N	X (SD)	N	X (SD)	N	X (SD)	N	X (SD)	N	X (SD)	N	X (SD)	N	X (SD)	F statistic **($P <$)
PSI	2	0.50 (0.00)	1	1.00 (–)	11	0.86 (0.26)	20	0.74 (0.32)	11	0.73 (0.32)	8	0.86 (0.19)	5	0.35 (0.11)	$F_{4,46} = 1.00$ (N.S.)
SPLI	2	0.50 (0.00)	1	1.00 (–)	9	0.94 (0.16)	19	0.76 (0.29)	6	1.00 (0.00)	4	1.00 (0.00)		—	$F_{4,34} = 1.98$ (N.S.)
Ratios															
Visitor species / Plant species		1.00		1.00		0.78		0.83		1.37		1.00		—	—
Pollinator species / Plant species		1.00		1.00		1.50		0.86		1.20		1.00		0.20	—

*According to Appendix 1.
**Excluding wind and coleopteran pollinator types.
N.S., Not significant.

'morichal' (Table 1). The birds and beetles were represented by only one family and only one genera each (see Appendix 2).

Visitors and pollinators

Pollinator activity was basically diurnal, with the greatest frequency of visits occurring between 0800 and 1200 hours. Later in the day, the biotic activity diminished considerably. From the 53 visitor species recorded (no wind considered), 30 (56.6%) visited one plant species, 14 (26.4) visited two plants species, four (7.4%) visited three plant species, and five (9.6%) visited more than four plant species simultaneously. Of the 54 visiting agents recorded in the 'morichal' community (considering wind as a pollinating agent), 42 (77.7%) were pollinators and 12 (22.2%) were visitors. The last group included a large proportion of monolectic species ($N = 9$, 16.7%), indicating that the proportion of monolectic pollinator species was 38.9%.

At the community level, bee- and wasp-pollination prevailed in 57.1% of the 'morichal' plant species. The other 43% of the species were pollinated by wind, flies, butterflies, birds and beetles (Table 2).

The visitor species/plant species ratio was 1.6, and the pollinator species/plant species ratio was 1.3. Visitor species/plant species ratios and pollinator species/plant species ratios showed values of one for bird, coleopteran and lepidopteran groups. The visitor species/plant species ratio was higher than pollinator species/plant species ratio for wasp groups; the opposite occurred for fly and bee groups (Table 2). The group of wind-pollinated plant species exhibited the lowest ratio (Table 2).

Visitor specificity

The number of plant species visited and the abundance of pollen transported varied according to visitor type. The vast majority of the visiting species displayed a high degree of pollen load specificity; 26 pollinator species (65.0%) carried pollen from only one species, 8 (20.0%) carried pollen from two plant species, 3 (7.5%) carried pollen from three plant species, 2 (5.0%) carried pollen from four plant species and 1 (2.5%) carried pollen from five plant species. Two analyses of variances showed that visitor specificity (SPI) and specificity pollen load index (SPLI) were not statistically significant among visitor types (Table 2).

Birds visited two plants species simultaneously (SPI = 0.5), but they were very specific in pollen transportation (SPLT = 1.0). Coleopterans visited and pollinated only one plant species (SPI and SPLI = 1.0). Many of the dipterans visited one plant species (SPI = 1.0), but *Palpada pusio* and *Taxomerus* aff. *floralis* visited four and five plants species respectively. Dipterans transported very little pollen, and the pollen load was often on ventral positions on the various specimens examined (Appendix 2). However, flies were very specific in pollen transportation (SPLI varied from 0.5 to 1.0).

The most numerous and heterogeneous group of insects was represented by the hymenopterans in the 'morichal' community. The visiting capacity varied from one to four (*Polybia occidentalis*, SPI = 0.20), or seven plants species visited simultaneously (*Apis mellifera, Augochloropsis callichroa*). These last two insect species showed the lowest values of SPI (Appendix 2). SPI values were less than 0.5 for *Melipona favosa, Pereirapis* sp.$_2$ and *Polistes subsericeus*. The other hymenopterans recorded were specific visitors (SPI ranged from 0.5 to 1.0). The specificities of pollen loads (SPLI) were similar or slightly superior than SPI in bees; the pollen loads were localized in the same sites of the pollinator body (Appendix 2). In contrast, when wasps visited more than one plant species, the SPLI were greater than SPI. Wasp species pollinated only one plant species (Appendix 2).

Butterflies were very specific (SPI = 0.5–1.0); they visited one or three plants species simultaneously (Appendix 2), but they only carried pollen of one plant species (SPLI). The wind showed the lowest values of SPI (Appendix 2).

Plant pollination specificity

Pollination community index (PCI) and specificity pollen load index (SPLI) were significantly different among plants with different modes of pollination. Wind-pollinated species showed the lowest value of PCI, and butterflies showed the highest value (Table 2). Butterfly-pollinated species displayed the highest value of pollination community index (PCI), and wind-pollinated species the lowest value of PCI; bee-, wasp-, bird- and fly-pollinated species showed similar values of PCI (Table 3). In contrast, pollen transportation specificity (PTS) was higher in bird- and butterfly-pollinated species compared with bee-, wasp- and fly-pollinated species (Table 3). Pollination specificity indices were not affected by life form, plant sexuality, breeding system, floral symmetry and floral longevity (Table 4), but pollination system and pollen transportation specificity were statistically different among the types of rewards and pollination types (Table 4). Pollination community index (PCI) was higher in nectar- and nectar- and pollen-rewarded species than in pollen- and without-rewarded species (Table 4). In contrast, pollen transportation specificity (PTS) was significantly higher in nectar-rewarded species than in pollen- and pollen- and nectar-rewarded species (Table 4).

The values of community pollination index (CPI) indicated higher specificity in *Clidemia capetillata, Diodia multiflora, Montrichardia arborescens, Thalia geniculatra, Melochia villosa* and *Miconia stephananthera* (only one pollinator) and in *Aeschynomene pratensis* and *Cuphea o'donnelli*, with two and three unshared pollinators respectively (Appendix 1). Values between 0.50 and 0.90 corresponded to species of plants which share pollinators with two or more plant

TABLE 3. Mean values for pollination system of plant pollination indices and frequences of pollination system for the 'morichal' community

Pollination indices	Pollination system: Bee and wasp	Beetle	Fly	Bird	Butterfly	Wind	
	X (SD)	X (SD)	X (SD)	X (SD)	X (SD)	X (SD)	F statistic ($P <$)
PCI	0.58 (0.28)	1.00 (−)	0.55 (0.21)	0.50 (0.00)	1.00 (0.00)	0.32 (0.06)	$F_{4,30} = 10.53$* (0.001)
PTS	0.67 (0.25)	1.00 (−)	0.64 (0.21)	1.00 (0.00)	1.00 (0.00)	—	$F_{3,26} = 4.83$** (0.01)
N (%)	20 (57.14)	1 (2.86)	4 (11.43)	2 (5.71)	3 (8.57)	5 (14.29)	35***

*Excluding Coleoptera.

**Excluding Coleoptera and wind.

***The number of species exceeds the total of 33 because three species were pollinated by more than one group of pollinators.

TABLE 4. Mean values for floral symmetry, floral longevity, reward type, plant sexuality, breeding system, and life form of pollination indices and statistical results

	Pollination indices	
Variable	PCI X (SD)	PTS X (SD)
Floral symmetry		
Actinomorphic	0.67 (0.26)	0.75 (0.22)
Zygomorphic	0.60 (0.29)	0.81 (0.24)
Irregular	0.42 (0.29)	0.53 (0.41)
F Statistic ($P <$)	$F_{2,29} = 1.06$ (N.S.)	$F_{2,25} = 1.17$ (N.S.)
Floral longevity		
≥ 6 h	0.54 (0.27)	0.61 (0.26)
≥ 12 h	0.67 (0.31)	0.80 (0.25)
24–48 h	0.66 (0.28)	0.90 (0.13)
F Statistic ($P <$)	$F_{2,27} = 0.65$ (N.S.)	$F_{2,25} = 2.67$ (N.S.)
Reward		
Nectar	0.76 (0.25)	0.97 (0.06)
Pollen	0.55 (0.32)	0.61 (0.30)
Pollen-nectar	0.67 (0.25)	0.67 (0.19)
Without	0.32 (0.07)	—
F Statistic ($P <$)	$F_{3,28} = 3.58$ (0.05)	$F_{2,24} = 3.93$ (0.05)
Plant sexuality		
Hermaphrodite	0.63 (0.29)	0.78 (0.25)
Monoecious	0.51 (0.26)	0.64 (0.26)
Student's t-test ($P <$)	0.55 (N.S.)	0.63 (N.S.)
Breeding system		
Self-compatible	0.66 (0.24)	0.77 (0.22)
Self-incompatible	0.57 (0.32)	0.75 (0.28)
Student's t-test ($P <$)	0.23 (N.S.)	0.19 (N.S.)
Life form		
Annual herb	0.63 (0.24)	0.77 (0.28)
Perennial herb	0.53 (0.27)	0.72 (0.26)
Shrub	0.88 (0.15)	0.92 (0.10)
F Statistic ($P <$)	$F_{2,30} = 2.47$ (N.S.)	$F_{2,25} = 0.75$ (N.S.)

species. For example, *Saggitaria guyanensis, Caperonia pallustris, Croton hirtus, Hyptis delatata, Desmodium barbatum* and *Heliconia psittacorum* had two or three common pollinators. The CPI varied from 0.20 to 0.45 in plant species with pollinators of low specificity as in *Mimosa camporum, Rhynchanthera serrulata* and *Xyris laxifolia* with one pollinator, and with two very promiscuous ones as in *Hyptis conferta* (*Apis mellifera*), and three pollinators with low or high specificity as in *Syngonanthus caulescens, Schultesia brachyptera* and *Xyris savanensis* (Appendix 2).The lowest specificity value of the pollination system was found in *Xyris laxifolia* with one promiscuous pollinator (*Augochloropsis callichroa*) (Appendix 2).

The values of pollen transportation specificity (PTS) were higher or similar than that of CPI (Appendix 1). PTS was from 0.25 to 0.50 times greater than CPT in *Schultesia brachyptera, Sinningia* sp., *Hyptis conferta, Hyptis dilatata* and *Heliconia psittacorum.* In contrast, the lowest values of PTS were similar or superior than that of CPI. For example, *Mimosa camposum, Rhynchantera serrulata* and *Xyris laxifolia* had the same values for CPI and PTS, and in *Syngonanthus caulescens* and *Xyris savanensis,* PTS values were slightly greater than that of CPI (Appendix 1).

DISCUSSION

Floral symmetry

The symmetry, form and size of the flower determine two fundamental mechanisms in foraging behaviour on zygomorphic flowers: on bilabiate flowers, pollen collection takes place on the dorsal part of the visitor's body, and pollen collection takes place on the ventral part of the visitor's body, frequently associated to zygomorphic flowers (Macior, 1974). Among plant species recorded in the 'morichal' community, there is no correlation between symmetry and pollination specificity. The high frequency of unspecialized and generalist visitors probably promote this pattern. Thus, more specialized zygomorphic flowers do not increase pollination specificity nor pollen load transportation compared with actinomorphic and irregular symmetries.

Colour

It has frequently been observed that the range of floral colour present in a local flora is not uniform among geographic regions or phytosociological communities (Scogin, 1983). High-altitude alpine floras are rich in white and yellow flowers (Kevan, 1972, in Scogin, 1983), whereas the tropics are rich in brightly coloured, red and orange flowers (Scogin, 1983). The 'morichal' community, as well as a previously recorded tropical shrubland community in the Venezuelan Guayana (Ramirez *et al.*, 1990), displayed a great diversity of colours. Both communities exhibited high proportion of white flowers, but differed in the proportion of the other floral colours. Yellow and white flowers, mostly frequent in the 'morichal' community, are widely visited by a large variety of insects, including unspecialized flies and parasitic hymenoptera (Kevan, 1983 and references herein). Thus, the predominances of white and yellow flowers in the 'morichal' is associated with the attraction of specialized and unspecialized hymenopterans, lepidopterans and dipterans.

The traditional explanation for a geographical non-harmonious distribution of floral colour has been that pollinators are also non-uniformly distributed. This model proposes that natural selection has operated to increase the frequency of floral colouration to match the colour preferences of the local pollinator spectrum (Scogin, 1983). The frequency distribution of pollination types between the 'morichal' and the shrubland community previously studied (Ramirez *et al.*, 1990) showed high similarity, but floral colour differed. This comparison is not in agreement with the model of Scogin (1983), and suggests that pollinator and colour spectra are only partially correlated.

Floral longevity

The proportion of short-lived flowers recorded in the 'morichal' community (67.1%) was higher than that recorded at the community level (Percival, 1974; Ramirez *et al.*, 1990). The short-lived flower pattern in the 'morichal' community is consistent with those reported in tropical lowland forests (Frankie *et al.*, 1983; Primack, 1985), but is inconsistent with the longer floral longevity recorded in herbaceous cloud forest species (Stratton, 1989; Seres & Ramirez, unpublished data). As most of the plant species studied in the 'morichal' are herbs and shrubs, then the comparative shorter floral longevity in the 'morichal' community is not given by the life form but by the environmental condition.

Short-lived flowers have been associated with breeding systems: selfing species tend to have shorter floral longevities than outcrossing species (Primack, 1985). The high frequency of one-day flowers is correlated with the elevated incidence of self-compatibility and agamospermy reported in the 'morichal' community (Ramirez & Brito, 1990).

The length of flower life has been positively linked with visitors. The majority of flowers that last all day received most visits by all classes of animals compared with species with shorter floral longevity (Percival, 1974). However, differences in floral longevity affect neither pollination system nor pollen specificity load transportation in the 'morichal' community. The extensive floral longevity in a small fraction of the sample examined is in many cases related to dichogamy and pollination predictability. The longest floral longevity increases the probability of visitation (Primack, 1985; Seres & Ramirez, unpublished data). The longer floral longevity of female flowers of monoecious species may lead to increased chances of pollination in greenish, very inconspicuous flowers, and fly- and wind-pollinated species in the 'morichal'. In addition, the extensive floral longevity in female flowers of monoecious and andromonoecious species is consistent with the hypothesis that the evolution of flora longevity in these species resulted from maximization of female reproductive success (Stratton, 1989).

Reward

The high proportion of plants producing nectar alone and combined with pollen in the 'morichal' community is similar to those recorded in the coastal scrubs of Jamaica (Percival, 1974), and in a shrubland in the Venezuelan Guayana (Ramiraz *et al.*, 1990). The high proportion of plant species producing nectar in the three communities points to a dependence on nectar-seeking animals as pollinators, a requirement satisfied by the preponderance of these types of visitors.

The type of reward determines differences in pollination system and pollen transportation specificity. The lowest specificity pollination system is mainly associated with plant species without reward—wind-pollinated species—which use only the wind as a pollen vector. In contrast, where only nectar occurs as a reward, then pollen load transportion is higher than in plant species with pollen and pollen-nectar as reward. The high pollen transportation specificity in nectar-rewarded species may be due to pollinator specialization in nectar composition or nectar deterrents, selecting specific pollinators, and flowers with long corolla tubes. Among these species are hummingbirds and Euglosinae.

Visitor diversity

The spectrum of visitor species in the 'morichal' community is very similar to that found in the shrubland community in the Venezuelan Guayana (Ramirez, 1989). The two communities differ in environmental conditions, but are similar in plant species number and vegetation structure. In contrast, the spectrum of visitor species recorded on monocotyledon plant species in a Venezuelan cloud forest (Seres & Ramirez, unpublished data) is clearly different. Therefore, the anthophylous fauna among neotropical communities is strongly correlated with vegetation structure and diversity, as well as their floristic composition. For example, in a more diverse community, the two most dominant bee-families with respect to the number of species were Anthophoridae and Megachilidae in a seasonal neotropical habitat (Heithaus, 1979), while in the 'morichal' community the most diverse bee-families were Apidae and Halictidae. In addition, the anthophylous fauna recorded in the 'morichal' community, suggests that only a few pollinator species, such large bees, may be considered as long distance pollinators; the largest proportion of pollinating agents are small insects. Under such figure, flow of genes via pollen is limited; the average distance among 'morichal' communities is 25.9 km $\pm$ 18.2 km (calculated from Blydenstein, 1962).

Frequency distribution of pollination types

The frequency distribution of pollination modes in the 'morichal' is very similar to that found in the Venezuelan shrubland community (Ramirez, 1989); both differ from the coastal scrub pollination spectrum in Jamaica, namely butterfly, solitary bee, and hummingbird flowers (Percival, 1974), and from the neotropical lowland rain forest pollination spectrum (Bawa *et al.*, 1985; Bawa, 1990). The proportion of pollination modes in the lowland tropical rain forest is characterized by a dominance of bee-pollinated species (Bawa *et al.*, 1985; Bawa, 1990), but this group of pollinators occurred in a lower proportion than the 'morichal' studied here, and in the Venezuelan shrubland community (Ramirez, 1989). In a similar way, the diversity of pollination systems was higher in the lowland tropical rain forest (Bawa *et al.*, 1985; Bawa, 1990) than the shrubland community (Ramirez, 1989) and the 'morichal' community. This trend indicates that the diversity of pollination systems increases with plant community diversity and vegetational structure.

Klein (1989) indicated that insect abundance, as well as diversity, decreases with the size of habitat. 'morichal' communities are well-defined vegetational units, isolated from one another (Brito & Ramirez, 1988), as well as from the Venezuelan shrubland community (Ramirez, 1989). The low pollination system diversity found in both communities compared with tropical lowland rain forest (Bawa *et al.*, 1985; Bawa, 1990) is determined by the plant diversity, relative isolation, and vegetation structure.

Visitor and pollinator specificity

The observations that pollination system specificity and pollen load transportation differ amongst the different pollination types but visitor specificity does not differ among major groups of visitor needs explanation. Visitor indices evaluated specificity irrespective of pollen load and many visitors were only visiting one plant species; in a similar way, the specificity pollen load index, as defined here, estimated the number or parts where pollen load is transported. Differential pollen transportation on different parts of the pollinator body enhance high levels of pollination specificity in the 'morichal' community. For example, the specificity pollen load index increases noteworthily compared with the pollination community index for bird-pollinated species. In contrast, wind-pollinated species exhibit the lowest pollination community index, because wind is used by a large proportion of plant species as a pollinating agent, and specificity can only be reached through reproductive differences in temporal and spatial distribution.

Plant diversification in visitor systems such as major groups of potential pollinating agents might have arisen as a consequence of plant diversity and/or limitation in the number of potential pollinator species. Note that visitor species/plant species and pollination species/plant species ratios of visiting groups are close to one in those less numerous groups (birds lepidopterans, and beetles), and less than one for more numerous groups (bees, wasps and wind). It is not clear whether the higher floral abundance is due to higher visitor abundance or vice versa (Pleasant, 1983); each animal can have a ranking of preferred plant food, and each plant a similar ranking of animal forager (Howe, 1984). However, limited or saturated groups may be biasing the richness of different groups in the community. This seems possible if the other groups are potentially available. Hiethaus (1974) showed a clear correlation between the diversity of consumer and resource availability.

A pollination species/plant species ratio close to one, correlated with low specificity visitor indices, in some of the groups, and at the community level, suggests that plant-animal interactions are symmetrical and diffuse in the 'morichal' community. Similar results in another low plant diversity community in the Venezuelan Guayana (Ramirez, 1992), indicate that in tropical low plant diversity communities exhibit diffuse plant-pollination interaction, and are nearly symmetrical according to the number of interacting species. Under symmetrical species diversity, diffuse plant-pollinator interactions may be considered to be a convenient community pollination structure because the number of potential pollinators per plant species is increased. Obligate mutualism, such as monolectic insects (e.g. species-species fig agonid wasp, Ramirez, 1970) are rare, and make such a community prone to instability (Futuyama, 1973, May, 1973).

Pollination specificity systems, species ratios, and the frequency distribution of pollination systems are not completely associated. Only the lowest values of pollination specificity in wind-pollinated species correspond to the lowest pollinator species/plant species ratio. Pollination specificity systems evaluated by pollination community index and specificity pollen load index show that there is a large proportion of species with pollination system overlapped, associated with diffuse plant-pollination interactions in the 'morichal' community. The similarity in pollination specificity, according to plant life forms, sexual systems, and breeding system shows that the level of specificity of the pollination system does not explain the reproductive feature of the plant species in the 'morichal' community. Isolated conditions appear the best explanation for all the reproductive traits found in the 'morichal' community.

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APPENDIX 1

Plant and floral characteristics, visiting agents and pollination indices for 33 plant species

Species	Life form*	Sexuality*	Flower colour	Floral symmetry	Floral longevity (hours)	Rewards	No. total visitors	No. of effective pollinators	PCI $\bar{X}$	PTS $\bar{X}$	Visitors	Pollination system
ALISMATACEAE												
1. *Saggitaria quyanensis* Kunth.	h	M	Yellow and white	Actinomorphic (1)	6	P	3	2	0.50	0.67	Diptera Syrphidae *Toxomerus* aff. *floralis*† Hymenoptera Halictidae *Dialictus* sp.7 *Pereirapis* sp.2	Bees
ARRACEAE												
2. *Montrichardia arborescens* (L.) Schott.	h	M	Cream	Actinomorphic (1) Zygomorphic (2)	3♀ 24♂	E	1	1	1.00	1.00	Coleoptera Scarabaeidae *Cyclocephala gravis*	Beetle
CYPERACEAE												
3. *Rhynchospora barbata* (Vahl.) Kunth.	h	M	Brown-greenish	Zygomorphic (3)	48♀ 12♂	—	1	1	0.30	—	Wind	Wind
4. *Rhynchospora velutina* (Kunth.) Boeck.	h	M	Brown-greenish	Zygomorphic (3)	48♀ 12♂	—	1	1	0.29	—	Wind	Wind
ERIOCAULACEAE												
5. *Syngonanthus caulescens* (Poir.) Ruhl.	h	M	Cream	Actinomorphic (1, 2)	12	P	4	4	0.30	0.36	Diptera Empididae *Euhibus* sp. Syrphidae *Toxomerus* aff. *floralis*	Bee and Fly

APPENDIX 1—*continued*

Species	Life form*	Sexuality*	Flower colour	Floral symmetry	Floral longevity (hours)	Rewards	No. total visitors	No. of effective pollinators	PCI X	PTS X	Visitors	Pollination system
											Hymenoptera Apidae *Apis mellifera* Halictadae *Pereirapis* sp. 2	
EUPHORBIACEAE												
6. *Caperonia pallustris* (L.) St. Hil.	h	M	Cream-greenish	Actinomorphic (1)	36♀ 12♂	N+, P	3	3	0.75	0.83	Diptera Sarcophagidae *Sarcophagula occidua* Hymenoptera Halictidae *Augochloropsis vesta* Vespidae *Polybia occidentalis*	Bee and Wasp
7. *Croton hirtus* L'Hér.	h	M	Cream-greenish	Actinomorphic (1)	36♀ 12♂	N+,P	3	3	0.60	0.67	Diptera Syrphidae *Ornidia obesa* Syrphydae *Palpada pusio* Hymenoptera Halictidae *Augochloropsis vesta*	Fly
GENTIANACEAE												
8. *Schultesia brachyptera* Cham.	h	H	Pink	Actinomorphic (1)	12	N+,P	3	3	0.43	0.75	Hymenoptera Apidae *Apis mellifera* Vespidae *Eumenes* sp. *Polybia ignobilis*	Bee and Wasp

GESNERIACEAE 9. *Sinningia* sp.	h	H	Red	Zygomorphic (1)	48–72	N	2	2	0.50	1.00	Apodiformes Trochilidae *Amazilia fimbriata* *Amazilia tovasi*	Bird
LAMIACEAE 10. *Hyptis conferta* Pohl ex Benth. var. *angustifolia* Benth.	h	H	White	Zygomorphic (1)	≤ 12	N,P	5	2	0.33	0.62	Hymenptera Anthophoridae *Ceratina* (Crewella) sp. Apidae *Apis mellifera* Sphecidae *Cerceris* sp.† Vespidae *Omicron ruficolle*† *Polistes subsericeus*†	Bee
11. *Hyptis dilatata* Benth.	h	H	Purple	Zygomorphic(1)	≤ 12	N+,P	10	3	0.50	0.75	Diptera Syrphidae *Palpada pusio*† Hymenoptera Halictidae Augochloropsis *callichroa* Pompilidae *Pepsis* sp.† Sphecidae *Cerceris* sp.† *Ectemnius* sp. *Sphex melanopus*† Vespidae *Parancistrocerus* sp. *Polistes subsericeus*† *Polybia ignobilis*† Lepidoptera Hesperiidae *Pyrgus oileus orcus*†	Bee and Wasp

APPENDIX 1—*continued*

Species	Life form*	Sexuality*	Flower colour	Floral symmetry	Floral longevity (hours)	Rewards	No. total visitors	No. of effective pollinators	PCI X	PTS X	Visitors	Pollination system
LEGUMINOSAE, MIMOSOIDEAE												
12. *Mimosa camporum* Benth.	h	M	Pink	Actinomorphic (1, 2)	≤ 12	N,P	3	1	0.33	0.33	Hymenoptera Apidae *Apis mellifera*† *Mellipona favosa* Vespidae *Polybia occidentalis*†	Bee
LEGUMINOSAE, PAPILIONOIDEAE												
13. *Aeschynomene pratensis* var. *caribaea* Rudd.	h	H	Yellow	Zygomorphic (1)	≤ 12	N,P	4	2	1.00	1.00	Hymenoptera Anthophoridae *Exomalopsis* sp. Megachilidae *Megachile* sp. Vespidae *Eumenes* sp.† *Polybia occidentalis*†	Bee
14. *Desmodium barbatum* (L.) Benth. & Oerst.	h	H	Pink	Zygomorphic (1)	8	N,P	3	3	0.60	0.67	Hymenoptera Halictidae *Augochloropsis vesta* Megachilidae *Anthidiellum* sp. Scoliidae *Campsomeris dorsata*	Bee
LYTHRACEAE												
15. *Cuphea o'donellii* Lourt.	h	H	Purple	Zygomorphic (1)	≤ 12	P+,N	6	3	1.00	1.00	Hymenoptera Scoliidae *Campsomeris dorsata*†	Butterfly

										Lepidoptera Hesperiidae *Cogia calchas* *Pyrgus olieus orcus* *Urbanus dorantes dorantes*† Nymphalidae *Junonia evarete*† Pieridae *Eurema nise*	
MARANTHACEAE											
16. *Thalia geniculata* L.	h	H	White	Irregular (1)	8	N	1	1	1.00	1.00 Hymenoptera Apidae *Eulaema nigrita*	Bee
MELASTOMATACEAE											
17. *Clidemia capitellata* (Bompl.) D. Don var. *depends* (D. Don.) Machr.	S	H	White	Zygomorphic (1)	30	P	2	1	1.00	1.00 Diptera Calliphoridae *Phaenicia* sp.† Hymenoptera Halictidae *Angochloropsis* sp. *Melipona favosa*	Bee
18. *Besmoscelis* villosa (Aubl.) Naud.	h	H	Pink	Actinomorphic (1)	6	P	6	3	0.50	0.61 Diptera Syrphidae *Palpada pusio*† Hymenoptera Apidae *Apis mellifera*† *Euglossa cordata* Halictidae *Augochlora* sp. *Augochloropsis callichroa*†	Bee
19. *Miconia stephananthera* Ule	S	H	White	Actinomorphic (1)	12	P	2	1	1.00	1.00 Hymenoptera Halictidae *Augochloropsis vesta*	Bee

APPENDIX 1—*continued*

Species	Life form*	Sexuality*	Flower colour	Floral symmetry	Floral longevity (hours)	Rewards	No. total visitors	No. of effective pollinators	PCI X	PTS X	Visitors	Pollination system
											Lepidoptera Hesperiidae *Urbanus simplicius*†	
20. *Pterolepis glomerata* (Rottb.) Miq.	h	H	Pink	Zygomorphic (1)	6	P	5	3	0.43	0.58	Diptera Syrphidae *Toxomerus marginatus*† Hymenoptera Apidae *Euglossa cordata* Halictidae *Augochloropsis callichroa* *Dialictus* sp. Vespidae *Pachyoderynus brevithorax*†	Bee
21. *Rhynchanthera serrulata* (L.C. Rich.) DC.	h	H	Pink	Zygomorphic (1)	6	P	3	1	0.33	0.33	Diptera Syrphidae *Palpada pusio*† Hymenoptera Apidae *Melipona favosa* Lepidoptera Hesperiidae *Pompeius amblyspila*†	Bee
MUSACEAE (Heliconiaceae)												
22. *Heliconia psittacorum* L. f.	h	H	Yellow Orange	Zygomorphic (1)	12	N+	2	2	0.50	1.00	Apodiformes Trochilidae *Amazilia fimbriata* *Amazilia tovasi*	Bird

OCHNACEAE											
23. *Sauvagesia rubiginosa* St. Hil.	h	H	White	Actinomorphic (1)	12	P	4	1	1.00	1.00	Diptera Syrphidae *Toxomerus* aff. *floralis*† Hymenoptera Halictidae *Dialictus* sp. Lepidoptera Hesperiidae *Helipetes arsalte arsalte*† *Pyrqus oileus orcus*†	Bee
ONAGRACEAE											
24. *Ludwigia decurrens* Walters	h	H	Yellow	Actinoimorphic (1)	≥ 8	P+N	3	2	0.50	0.67	Diptera Sarcophagidae *Chrysagria duodecimpuntata* Syrphidae *Toxomerus marginatus*† Hymenoptera Halictidae *Pereirapis* sp. 2	Bee and Fly
25. *Ludwigia nervosa* (Poir.) Hara	S	H	Yellow	Actinomorphic (1)	12	P,N	16	5	0.71	0.80	Diptera Sarcophagidae *Helicobia morionella*† *Oxysarcoderia peltata*† Syrphidae *Ornidia obesa* Tabanidae *Tabanus* sp.† Hymenoptera Anthophoridae *Xylocopa fimbriata* Apidae *Apis mellifera*† *Trigona anqustula*	Bee

APPENDIX 1—*continued*

Species	Life form*	Sexuality*	Flower colour	Floral symmetry	Floral longevity (hours)	Rewards	No. total visitors	No. of effective pollinators	PCI X	PTS X	Visitors	Pollination system
											Halictidae *Augochlora* sp. † *Augochloropsis callichroa*† *Dialictus* sp.† Megachilidcae *Anthidium* sp. Sphecidae *Sphex melanopus* Vespidae *Polistes subsericues*† *Polybia occidentalis*† Lepidoptera Hesperiidae *Urbanus dorantes dorantes*† Pieridae *Eurema nise*†	
POACEAE (Gramineae)												
26. *Aristida* capillacea Lam.	h	H	Greenish	Irregular (3)	NA	—	1	1	0.42	—	Wind	Wind
27. *Panicuam laxum* Swartz	h	H	Greenish	Irregular (3)	NA	—	1	1	0.35	—	Wind	Wind
28. *Paspalum pilosum* Lam.	h	H	Greenish	Irregular (3)	NA	—	1	1	0.25	—	Wind	Wind
RUBIACEAE												
29. *Diodia multiflora* DC.	h	H	White	Actinomorphic (1)	12	N	2	1	1.00	1.00	Hymenoptera Apidae *Apis mellifera*† Lepidoptera Hesperiidae *Urbanus dorantes dorantes*	Butterfly

STERCULIACEAE												
30. *Byttnera scabra* Loefl.	S	H	Purple-brownish	Actinomorphic (1)	⩾ 48	N	4	4	0.80	0.87	Diptera Sarcophagidae *Helicobia morionella* *Oxysarcodexia peltata* Syrphidae *Toromerus* aff. *floralis* *Toxomerus marginatus*	Fly
31. *Melochia villosa* (Mill.) Fauzett & Rendle. var. *villosa*	h	H	Pink	Actinomorphic	6	N+P	3	2	1.00	1.00	Hymenoptera Halictidae *Augochloropsis callichroa*† Lepidoptera Hesperiidae *Heliopetes arsalte arsalte* *Urbanus dorantes dorantes*	Butterfly
XYRIDACEAE												
32. *Xyris laxifolia* Martius var. *delta*	h	H	Yellow	Irregular	6	P	2	1	0.25	0.25	Diptera Syrphidae *Toxomerus* aff. *floralis*† Hymenoptera Halictidea *Augochloropsis callichroa*	Bee
33. *Xyris savanensis* Miq.	h	H	Yellow	Irregular	6	P	4	3	0.27	0.34	Diptera Syrphidae *Toxomerus* aff. *floralis*† Hymenoptera Apidae *Apis mellifera* Halictidae *Augochloropsis callichroa* Megachilidae *Anthidium* sp.	Bee

*According to Ramirez and Brito (1990): h = herb, S = shrub; H = hermaphrodite; M = monoecious. (1) = Floral symmetry; (2) = inflorescence symmetry (= symmetry of pollination unit); (3) = spikelet. NA = Not available; P = Pollen; N = nectar; E = staminodes; + = main reward.

†Without pollen. PCI = Pollination Community Index. PTS = Pollen Transportation Specificity.

APPENDIX 2

Visiting agents, plant species visited, pollinator indices and pollen load characteristics for 53 visiting agents recorded at the 'morichal' community

Visiting agents	Plant species visited†	Plant species simultaneously visited‡	Total number of plant simultaneously pollinated	SPI $\bar{X}$	Pollen load§ Abundance	Pollen load§ Position of the body	SPLI $\bar{X}$
Birds							
Apodiformes							
Trochilidae							
Amazilia fimbriata	9; 22	(9; 22)	2	0.50	A; A	B(S, i); hs, Bs	0.50
Amazilia tovasi	9; 22	(9; 22)	2	0.50	A; A	B(S, i); hs, Bs	0.50
Insects							
Coleoptera							
Scarabaeidae							
Cyclocephala gravis Bates	2	2	1	1.00	A	V(ab, t, e)	1.00
Diptera							
Calliophoridae							
Phaenica sp.	17*	17*	0	1.00	—	—	—
Empididae							
Euhibus sp.	5	5	1	1.00	A	V(t, e)	1.00
Sarcophagidae							
Chrysagria duodecimpuntata Townsend	24	24	1	1.00	S	V(t, e)	1.00
Helicobia morionella (Aldrich)	25*; 30	25*; 30	1	1.00	*; S	*; V(t, e)	1.00
Oxysarcodexia peltata (Aldrich)	25*; 30	25*; 30	1	1.00	*; S	*; V(t, e)	1.00
Sarcophagula occidua (Fabricius)	6	6	1	1.00	S	Vt	1.00
Syrphidae							
Ornidia obesa (Fabricius)	7; 25	7; 25	1	1.00	A; S	V(h, P, t); V(t, e)	1.00
Palpada pusio (Wiedemann)	7; 11*; 18*; 21*	(7; 11; 18; 21); (7; 21)	1; 1	0.37	S; *; *; *	Vh; *; *; *	1.00
Toxomerus aff. *floralis* (Fabricius)	(1*; 5; 23*; 30; 32*; 33*)	(1; 5; 23; 30; 33); (32; 33)	2; 0	0.35	*; S; *; S; *; *	*; V(h, ab, t, e)P; *; V(h); P; *; *	0.50
Toxomerus marginatus (Say)	20*; 24*; 30	(20; 24); 30	0; 1	0.75	*; *; A	*; *; V(h); P	1.00
Tabanidae							
Tabanus sp.	25*	25	0	1.00	*	*	—

Hymenoptera							
Anthophoridae							
Ceratina (Crewella) sp.	10	10	1	1.00	A	V(ab, e)	1.00
Exomalopsis sp.	13	13	1	1.00	A	V(t, ab, e)	1.00
Xylocopa fibriata Fabricius	25	25	1	1.00	A	V(t, ab, e)	1.00
Apidae							
Apis mellifera L.	5; 8; 10; 12; 18*; 25*; 29*; 33	(5; 8; 10; 12; 18; 25; 33); (5; 12; 29; 33)	5; 3	0.19	S; A; S A; *; *; *; S	V(t, ab, e); V(t, e); V(t, ab); V(t, e); *; *; *; V(ab, e)	0.27
Euglossa cordata (L.)	18; 20	(18; 20)	2	0.50	A; A	V(ab, e); V(ab, e)	0.50
Eulaema nigrita (Lepeletier)	16	16	1	1.00	A	P	1.00
Melipona favosa (Fabriciis)	(12; 18; 21)	(12; 18; 21)	3	0.33	A; S; A	V(ab, e); Vt; V(t, e)	0.50
Trigona angustula	25	25	1	1.00	A	e	1.00
Halictidae							
Augochlora sp.	18	18	1	1.00	S	V(t, e)	1.00
Augochlora sp.3	25*	25	0	1.00	*	*	—
Augochloropsis callichroa (Cockerell)	11; 18*;20; 25; 31*; 32; 33;	(11; 18; 20; 25; 31; 32; 33); (11; 18; 20; 31; 32; 33)	4; 4	0.25	A; *; A; *; *; S; A	V(t, ab); *; V(ab, e); *; *; V(t, ab, e); V(t. ab, e)	0.25
Auchochloropsis vesta (Smith)	6; 7; 14; 19	(6; 7); (6; 14); 19	2; 2; 1	0.67	A; A; S; S	V(t, e); V(t, e); V(t, ab, e); V(t, ab, e)	0.67
Augochloropsis sp.	17	17	1	1.00	A	V(t, e)	1.00
Dialictus sp.	20; 23; 25*	(20; 25); 23	1; 1	0.75	S; A; *	V(t, e); V(t, e); *	1.00
Dialictus sp.7	1	1	1	1.00	A	V(t, ab, e)	1.00
Pereirapis sp.2	1; 5; 24	(1; 5; 24)	3	0.33	A; S; S	V(t, ab, e); V(t, ab); V(t, ab, e)	0.33
Megachilidae							
Anthidiellum sp.	14	14	1	1.00	A	V ab	1.00
Anthidium sp.	25; 33	(25; 33)	2	0.50	S; S	V(t, e); V(ab, e)	0.50
Megachile sp.	13	13	1	1.00	A	V(t, ab)	1.00
Pompilidae							
Pepsis sp.	11*	11	0	1.00	*	*	—
Scoliidae							
Campsomeris dorsata (Fabricius)	14; 15*	(14; 15)	1	1.00	A; *	V(ab, e); *	1.00
Sphecidae							
Cerceris sp.	10*; 11*	(10; 11)	0	0.50	*; *	*; *	—
Ectemnius sp.	11	11	1	1.00	S	V ab	1.00
Sphex melanopus Dahlbon	11*; 25	(11; 25)	1	1.00	*; S	*; V(ab, h)	1.00

APPENDIX 2—*continued*

Visiting agents	Plant species visited†	Plant species simultaneously visited‡	Total number of plant simultaneously pollinated	SPI X	Pollen load§ Abundance	Pollen load§ Position of the body	SPLI X
Vespidae							
Eumenes sp.	8; 13*	(8; 13)	1	0.50	S; *	Vt; *	1.00
Omicrom ruficolle (Zavettari)	10*	10	0	1.00	*	*	—
Pachodynerus brevithorax (Saussure)	20*	20	0	1.00	*	*	—
Parancistrocerus sp.	11	11	1	1.00	S	V(t, ab, e)	1.00
Polistes subsericeus Saussure	10*; 11*; 25*	(10; 11; 25)	0	0.33	*; *; *	*; *; *	—
Polybia ignobilis (Haliday)	8; 11*	(8; 11)	1	0.50	A; *	Vt; *	1.00
Polybia occidentalis (Olivier)	6; 12*; 13*; 25*	(6; 12; 13; 25)	1	0.20	S; *; *; *	V(ab, e); *; *; *	1.00
Lepidoptera							
Hesperiidae							
Cogia calchas (Herrich-Schaeffer)	15	15	1	1.00	S	P	1.00
Heliopetes arsalte arsalte L.	23*; 31	23; 31	1	1.00	*; S	*; P	1.00
Pompeius amblyspoila (Mabille)	21*	21	0	1.00	*	*	—
Pyrgus oileus orcus (Stoll)	11*; 15; 23*	(11; 15); 23	1	0, 75	*; S; *	*; P; *	1.00
Urbanus dorantes dorantes (Stoll)	15*; 25*; 29; 31	(15; 25; 31); 29	1; 1	0.67	*; *; ,A; A	*; *; V(h); P; P	1.00
Urbanus simplicius (Stoll)	19*	19	0	1.00	*	*	—
Nymphalidae							
Junonia evarete Cramer	15*	15	0	1.00	*	*	—
Pieridae							
Eurema nise Cramer	15; 25*	(15; 25)	1	0.50	S; *	P; *	1.00
Wind	3; 4; 26; 27; 28	(3; 26; 27); (26; 27); (3; 4; 27); (3; 4; 27; 28)	3; 2; 3; 4	0.35	—	—	—

*Without pollen load, visitor.
†Plant species number according to Appendix 1.
‡Parentheses indicate groups of species visited simultaneously (calculated from phenological report of Ramirez & Brito (1987) and personal observation of N. Ramirez).
§Following sequence of first column. Abbreviations: V, Ventral; S, superior; i, inferior; h, head; P, proboscis; t, thorax; e, extremities; ab, abdomen; B, beak; A, abundant; S, scarcity.