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Pollination and Dispersal Systems in a Cerrado Remnant (Brazilian Savanna) in Southeastern Brazil

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ABSTRACT

The aim of this work was to identify the pollination and dispersal systems among the species in a disjunct marginal cerrado area and to compare the frequency of these systems to those found in other Neotropical vegetation. The floral and diaspore traits and the pollination and dispersal systems of 176 species were analysed in a cerrado remnant in Southeastern Brazil. The most frequent pollination system was melittophily (63% of the studied species) with the remaining 37% distributed among diverse pollination systems. Zoochory was the predominant system of dispersal (44.9%). The frequencies of melittophily and zoochory observed in diverse tropical areas were the main feature that allowed the formation of distinct groups in the dendrograms generated by cluster analysis.

Key words: dispersal syndrome, melittophily, pollination syndrome, similarity, zoochory

INTRODUCTION

The Cerrado Biome, a major Brazilian savanna-like ecosystem, is currently one of the most threatened biomes of South America, mainly due to the rapid expansion of agriculture (Oliveira and Marquis, 2002). The cerrado vegetation encompasses several physiognomies ranging from the grassland to tall woodland (Coutinho, 2002). Because of the rich biodiversity of this ecosystem and the threats that are constantly imposed, attempts to describe the plant species composition and reproductive biology is becoming essential for the understanding and preservation of the cerrado remnant areas.

Pollination and dispersal are critical stages in plant reproduction and can influence the community structure by affecting the plant reproductive success, which is essential for the maintenance of species (Bawa, 1985; Oliveira and Gibbs, 2000; Machado and Lopes, 2004). Considering this, efforts have been made to describe the dispersal and pollination biology at community level in the Neotropics (see Bawa et al., 1985; Oliveira and Gibbs, 2002; Ramírez, 2004; Gottsberger and Silberbauer-Gottsberger, 2006). The pollination and reproductive biology of cerrado plant communities have been studied in some areas (Silberbauer-Gottsberger and Gottsberger, 1988; Oliveira and Gibbs, 2000; Gottsberger and Silberbauer-Gottsberger, 2006; Martins and Batalha, 2006; Barbosa and Sazima, 2008). From these studies, some trends could be drawn such as the occurrence of a great diversity of pollination systems but with bees as the main pollinators and the predominance of diurnal flowers and zoochory as the main dispersal mode.

However, cerrado vegetation has great floristic-structural heterogeneity among distant and even proximate geographic areas (Castro et al., 1999;

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Bridgewater et al., 2004). This is an evidence of the occurrence of regional patterns in cerrado vegetation which are influenced by the regional climate, soil fertility, and other ecological features (Durigan et al., 2003a). It is well known that São Paulo State holds one of the cerrado centers of diversity whose floristic composition is different from the other cerrado diversity centers in Brazil (Ratter et al., 1996; Durigan et al., 2003a). Considering this, it seemed important to know if a cerrado remnant located in a disjunct marginal cerrado area in São Paulo State, far from the "core" cerrado area located at Central Brazil, could exhibit similar features regarding the pollination and dispersal systems previously described in other cerrado areas. The characterization and maintenance of cerrado remnants are nowadays essential, mainly if we consider its role in the connection with other fragments, allowing pollen flow and seed dispersion among the close areas.

This work was developed aiming to answer the following questions: What were the pollination and dispersal systems among the species in a disjunct marginal cerrado area? What was the frequency of these systems? What were the predominant systems in each growth form in this vegetation? Was the frequency of these systems similar to those found in other Neotropical vegetation? It was considered that the answers to these questions would bring evidences about the interactions among the vegetation community, flower visitors and seed dispersers which could emphasize the need to preserve the fragmented vegetation.

MATERIALS AND METHODS

Field work was conducted in a 1 ha study plot on a private cerrado fragment (approximately 5 ha in total) at 830 m altitude (22º57'34"S, 48º31'20"W), located in Botucatu, central-south region of São Paulo State, Southeastern Brazil. The climate of the region is Cfa type (hot climate with rain in the summer, drought in the winter and hottest month average temperature superior to 22^{o}C), according to Koeppen classification (Cunha and Martins, 2009), and the soil in the area is Red-Yellow Latosol according to the Brazilian System of Soil Classification (EMBRAPA, 1999). The physiognomy of the studied vegetation is classified as cerrado *sensu stricto* which is characterized by the presence of trees and shrubs as dominants but with a fair amount of herbaceous vegetation (Coutinho, 2002).

Field trips were performed weekly from March 2004 to April 2005 during which the plants of all growth forms in reproductive phase were collected and identified. The voucher specimens were deposited in the Herbarium BOTU. The species and families were arranged according to Angiosperm Phylogeny Group II (APG, 2003). A preliminary floristic survey in the same area has been previously performed (Ishara et al., 2008).

For each plant species, the floral attributes (form, size, colour and floral rewards) were analyzed and the pollination system was inferred and classified according to Faegri and Pijl (1979) and Wyatt (1983) definitions. Then, the conclusion about the main pollination systems were confronted with the field observations made previously and obtained from the literature.

The species diaspores characteristics were also analyzed and their dispersal systems were inferred according to Pijl (1982), which were based on fruit type, mesocarp, colour, size and morphology of the diaspores. These classifications were also checked by an extensive search of the literature. In cases when more than one pollinator/disperser was quoted in the literature, only the main pollinator or disperser was considered for the analyses. Data of pollination mode frequencies from the present study and other comparable eight tropical studied areas [Oliveira and Gibbs (2000), Gottsberger and Silberbauer-Gottsberger (2006) and Barbosa and Sazima (2008) for cerrado, Machado and Lopes (2004) for caatinga, Kinoshita et al. (2006), Yamamoto et al. (2007) and Bawa et al. (1985) for tropical forests and Ramírez (2004) for Venezuelan savanna] were evaluated using the cluster analysis.

The same analysis was performed for the dispersal frequencies comparing the present study and another four tropical areas (Gottsberger and Silberbauer-Gottsberger (2006) for cerrado, Griz and Machado (2001) for caatinga, Kinoshita et al. (2006) and Yamamoto et al. (2007) for tropical forests). The connection among clusters was measured using the Ward's method and the distances between the clusters were measured as Euclidean distances (Ludwig and Reynolds, 1988).

RESULTS

In the study area, 176 plant species belonging to 52 families were registered (Table 1). The richest family was Asteraceae (26 species), followed by Fabaceae-Faboideae (11 species), Myrtaceae (11 species), Fabaceae-Caesalpinioideae (eight species), Bignoniaceae, Rubiaceae and Solanaceae (seven species each), Apocynaceae, Euphorbiaceae, Malpighiaceae and Melastomataceae (six species each). Together, they accounted for 57% of the surveyed species.

Insects were the most frequent pollinators related to approx. 92% of the studied species (Tables 1 and 2). The other pollination systems were considered less frequent since only 3.4% of the species were classified as anemophilous, 2.3% were ornithophilous and 2.3% were chiropterophilous. In the assemblage of entomophilous species, 63% were considered to be melittophilous, with the remaining 29% distributed among the diverse small insects (18.2%), moths (4.0%), butterflies (2.3%), wasps (2.3%), flies (1.7%) and beetles (0.5%).

Table 1 - Pollination and dispersal systems of species in a cerrado remnant in Botucatu, SP, Southeastern Brazil. Gf: growth form (tr: tree, sh: shrub, he: herb, vi: vine, ep: epiphyte), Pol: pollination systems (bat: bats, bee: bees, bet: beetles, but: butterflies, fli: flies, hum: hummingbirds, ins: diverse small insects, mot: moths, was: wasps, win: wind), Disp: dispersal systems (ane: anemochory, aut: autochory, endozoo: endozoochory, epizoo: epizoochory).

Species	Gf	Pol	Source	Disp	Source
ANNONACEAE					
Duguetia furfuracea (A. St.-Hil.) Saff.	sh	bet	3, 10, 15	endozoo	8, 15
APOCYNACEAE					
Aspidosperma tomentosum Mart.	tr	mot	15, 27, 29	ane	15, 29
Blepharodon bicuspidatum E. Fourn.	vi	bee	15	ane	15
Ditassa obcordata Mart.	vi	bee	§	ane	§
Mandevilla illustris (Vell.) Woodson	he	bee	§	ane	23
M. velutina K. Schum.	he	bee	3	ane	8, 23
Temnadenia violacea (Vell.) Miers.	vi	bee	15	ane	8, 15
ARALIACEAE					
Schefflera vinosa (Cham. and Schltdl.) Frodin and Fiaschi	tr	bee	15	endozoo	8, 15
ARECACEAE					
Allagoptera campestris (Mart.) Kuntze	he	bee	15	endozoo	§
ASTERACEAE					
Acanthospermum australe (Loefl.) Kuntze	he	bee	15	epizoo	8, 15
Achyrocline satureoides (Lam.) DC.	he	bee, was, fli	3, 13, 15	aut, ane	8, 15, 23
Baccharis dracunculifolia DC.	sh	bee, was, fli	3, 13, 15	ane	8, 15
B. pseudotenuifolia Malag.	sh	bee	§	ane	§
B. trimera (Less.) DC.	sh	ins	28	ane	23, 28
Bidens gardneri Baker	he	bee, ins	1, 3, 15	epizoo	8, 15
Chresta sphaerocephala DC.	sh	bee	§	ane	25
Eupatorium debeauxii B.L. Rob.	he	ins	§	ane	§
E. intermedium DC.	sh	ins	28	ane	23, 28
E. odoratum L.	sh	bee, ins	1, 15	ane	15
E. vauthierianum DC.	sh	ins	28	ane	28
Gochnatia barrosii Cabrera	sh	ins	§	ane	30
G. pulchra Cabrera	sh	ins	§	ane	8, 23
Mikania strobilifera Gardner	sh	ins	§	ane	§
Piptocarpha axillaris (Less.) Baker	tr	ins	24	ane	24
P. macropoda (DC.) Baker	tr	ins	28	ane	28, 31
P. rotundifolia (Less.) Baker	tr	but, ins	15, 29	ane	8, 15, 29
Trixis divaricata (Kunth) Spreng.	sh	ins	§	ane	§
Vernonia bardanoides Less.	sh	bee	3, 15	ane	8, 15, 25
V. chamissonis Less.	sh	ins	§	ane	§

(Cont. ...)

(Cont. Table 1)

Species	Gf	Pol	Source	Disp	Source
V. cognata Less.	sh	ins	§	ane	9
V. elegans Gardner	sh	ins	§	ane	§
V. geminata Kunth.	sh	ins	§	ane	§
V. platensis (Spreng.) Less.	sh	ins	§	ane	§
V. polyanthes Less.	sh	bee	3, 15	ane	8, 31
V. tweediana Baker	sh	ins	28	ane	28
BIGNONIACEAE					
Anemopaegma glaucum Mart. ex DC.	sh	bee	15	ane	§
Arrabidaea pulchella Bureau	vi	bee	§	ane	30
A. samydoides (Cham.) Sandwith	vi	bee	32	ane	§
Jacaranda oxyphylla Cham.	sh	bee	15, 32	ane	15, 23
Memora axillaris K. Schum.	sh	bee	§	ane	23
Pyrostegia venusta (Ker Gawl.) Miers	vi	hum	15	ane	8, 23
Tabebuia ochracea (Cham.) Standl.	tr	bee	7, 15, 29, 31	ane	8, 15, 23, 29, 31
BORAGINACEAE					
Cordia monosperma (Jacq.) Roem. and Schult.	sh	ins	28	endozoo	28
Tournefortia paniculata Vent.	sh	bee	18	endozoo	18
BROMELIACEAE					
Aechmea bromeliifolia (Rudge) Baker	ep	hum	15	endozoo	15
CARYOCARACEAE					
Caryocar brasiliense Cambess.	sh	bat, mot	10, 15, 17, 27, 29	endozoo	8, 10, 15, 29
CELASTRACEAE					
Plenckia populnea Reissek	tr	bee, ins	15, 29	ane	8, 15, 29
Tontelea micrantha A.C. Sm.	sh	fli	15	endozoo	8, 15
CHRYSOBALANACEAE					
Couepia grandiflora (Mart. and Zucc.) Benth. ex Hook. f.	tr	bee, mot	15, 27, 29	endozoo	8, 15, 29
CLUSIACEAE					
Kielmeyera rubriflora Cambess.	tr	bee	15	ane	8, 15
K. variabilis Mart. and Zucc.	sh	bee	5, 15	ane	8, 30
COMMELINACEAE					
Commelina erecta L.	he	bee, fli	15	aut	8, 15
CONVOLVULACEAE					
Evolvulus nummularius (L.) L.	he	bee	§	aut	§
Ipomoea delphinioides Choisy	he	bee	15	aut	§
Merremia digitata (Spreng.) Hallier f.	he	bee	15	aut	9, 15
M. macrocalyx (Ruiz and Pav.) O´Donell	vi	bee	15	ane	24
CUCURBITACEAE					
Cayaponia espelina (Silva Manso) Cogn.	vi	bee	§	endozoo	8, 9
Momordica charantia L.	vi	bee, bet, but	1, 18, 20	endozoo	18, 24
DILLENIACEAE					
Davilla elliptica A. St.-Hil.	sh	bee	3, 10, 15, 29	endozoo, aut	8, 9, 15, 29
EBENACEAE					
Diospyros hispida A. DC.	tr	mot	15	endozoo	8, 15
ERYTHROXYLACEAE					
Erythroxylum campestre A. St.-Hil.	sh	was, bee	3, 6, 15	endozoo	8, 15
E. cuneifolium (Mart.) O.E. Schulz	sh	was	15	endozoo	8, 9
E. suberosum A. St.-Hil.	sh	was, bee	6, 15	endozoo	8, 10, 15, 29
E. tortuosum Mart.	sh	bee, was, but	6, 15, 29	endozoo	8, 15, 29

(Cont. ...)

(Cont. Table 1)

Species	Gf	Pol	Source	Disp	Source
EUPHORBIACEAE					
Croton glandulosus L.	sh	bee, ins	1, 18	aut	9
Dalechampia triphylla Lam.	vi	bee	24	aut	18, 24, 28
Manihot caerulescens Pohl	sh	bee	§	aut	8
M. hilariana Baill.	he	ins	§	aut	§
Sebastiania commersoniana (Baill.) L.B. Sm. and Downs	tr	ins	§	aut	§
S. serrulata (Mart.) Mullenders	he	win	3	aut	8
FABACEAE - CAESALPINIOIDEAE					
Bauhinia rufa (Bong.) Steud.	tr	bat	20, 24	aut	8, 24
Chamaecrista desvauxii var. *brevipes* (Benth.) H.S. Irwin and Barneby	sh	bee	3, 15	aut	8, 15
C. desvauxii var. *langsdorffii* (Kunth ex Vogel) H.S. Irwin and Barneby	sh	bee	3, 15	aut	8, 15
C. flexuosa (L.) Greene	sh	bee	15	aut	8, 15
Hymenaea stigonocarpa Mart. ex Hayne	tr	bat	10, 15, 27, 29	endozoo	8, 10, 15, 29
Senna bicapsularis (L.) Roxb.	sh	bee	15	endozoo	22
S. occidentalis (L.) Link	sh	bee	1, 15	aut	28
S. rugosa (G. Don.) H.S. Irwin and Barneby	sh	bee	15	aut	3, 8, 15
FABACEAE - FABOIDEAE					
Acosmium subelegans (Mohlenbr.) Yakovlev	tr	bee	10, 15	ane	8, 10, 15
Crotalaria unifoliolata Benth.	sh	bee	§	aut	§
Dalbergia miscolobium Benth.	tr	bee	15, 29	ane	8, 29
Desmodium discolor Vogel	sh	bee	§	epizoo	§
Eriosema longifolium Benth.	he	bee	§	aut	9
Glycine wightii (Graham ex Wight and Arn.) Verdc.	vi	bee	§	aut	§
Machaerium acutifolium Vogel	tr	bee	15, 29	ane	8, 15, 29
Platypodium elegans Vogel	tr	bee	10	ane	8, 10
Rhynchosia melanocarpa Grear	vi	bee	§	endozoo	8, 9
Stylosanthes acuminata M.B. Ferreira and Souza Costa	he	bee	1	aut	§
Zornia reticulata Sm.	he	bee, was	3, 15	epizoo	15
FABACEAE - MIMOSOIDEAE					
Anadenanthera falcata (Benth.) Speg.	tr	bee	15	aut	8, 15
Mimosa bimucronata (DC.) Kuntze	sh	bee	§	aut	28
M. dolens subsp. *acerba* (Benth.) Barneby	sh	bee	15	epizoo	9
M. dolens subsp. *rigida* (Benth.) Barneby	sh	bee	15	epizoo	9
Stryphnodendron adstringens (Mart.) Coville	tr	bee, fli	11, 15, 29	endozoo, aut	11, 15
IRIDACEAE					
Trimezia juncifolia Klatt	he	bee	§	aut	8, 23
LAMIACEAE					
Aegiphila lhotszkyana Cham.	sh	ins, bee	29	endozoo	8, 29
Eriope crassipes Benth.	he	bee	15	aut	15, 25
Hypenia macrantha (A. St.-Hil. ex Benth.) Harley	he	bee	§	aut	§
Hyptis villosa Pohl ex Benth.	sh	bee	15	aut	§
Peltodon tomentosus Pohl	he	bee, was	1, 15	aut	1, 3, 8, 9, 15

(Cont. ...)

(Cont. Table 1)

Species	Gf	Pol	Source	Disp	Source
LAURACEAE					
Ocotea corymbosa (Meisn.) Mez	tr	ins	§	endozoo	8, 9
O. pulchella (Nees) Mez	tr	ins	28	endozoo	8, 9, 28
LYTHRACEAE					
Lafoensia pacari A. St.-Hil.	tr	bat, mot	10, 15, 27, 29	ane, aut	8, 9, 29
MALPIGHIACEAE					
Banisteriopsis campestris (A. Juss.) Little	sh	bee	3, 15	ane	8, 15
B. oxyclada (A. Juss.) B. Gates	vi	bee	§	ane	15
Byrsonima coccolobifolia Kunth	sh	bee	4, 10, 15, 29	endozoo	8, 10, 15, 29
B. intermedia A. Juss.	sh	bee	3, 15	endozoo	8, 15
B. verbascifolia (L.) DC.	tr	bee	4, 15, 29	endozoo	8, 15, 29
Heteropterys umbellata A. Juss.	sh	bee	§	ane	8
MALVACEAE					
Eriotheca gracilipes (K. Schum.) A. Robyns	tr	bee	15	ane	8, 15
Peltaea speciosa (Kunth) Standl.	sh	bee	15	aut	9
Sida glaziovii K. Schum.	he	bee	15	aut	8
Waltheria indica L.	sh	but, bee	1, 15	aut	15
MELASTOMATACEAE					
Leandra aurea (Cham.) Cogn.	sh	bee	§	endozoo	22
Miconia albicans (Sw.) Triana	sh	bee	15	endozoo	8, 14, 15, 22
M. langsdorffii Cogn.	sh	bee	14, 15, 31	endozoo	14, 15, 31
M. ligustroides (DC.) Naudin	sh	bee	14, 15	endozoo	8, 14, 15, 22
Tibouchina gracilis (Bonpl.) Cogn.	sh	bee	§	ane	9
T. stenocarpa (DC.) Cogn.	tr	bee	14	ane	8, 14
MYRSINACEAE					
Rapanea guianensis Aubl.	tr	ins, bee	§, 15	endozoo	9, 29
R. umbellata (Mart.) Mez	tr	ins, win	15, 28	endozoo	22, 28, 31
MYRTACEAE					
Blepharocalyx salicifolius (Kunth) O. Berg	tr	bee, ins	16, 29	endozoo	15, 16, 29
Campomanesia pubescens (DC.) O. Berg	sh	bee	3, 15, 16	endozoo	8, 15, 16,
Eugenia bimarginata DC.	sh	bee	15	endozoo	8, 15, 16
E. obversa O. Berg	sh	bee	§	endozoo	23
Myrcia bella Cambess.	tr	bee	15	endozoo	8, 15
M. guianensis (Aubl.) DC.	tr	bee	§	endozoo	16
M. lingua (O. Berg.) Mattos and D. Legrand	tr	bee	§	endozoo	8
M. multiflora (Lam.) DC.	tr	bee	16	endozoo	16
Psidium cinereum Mart. ex DC.	sh	bee	16	endozoo	8, 16
P. incanescens Mart. ex DC.	sh	bee	15	endozoo	15
P. pohlianum O. Berg	tr	bee	§	endozoo	16
NYCTAGINACEAE					
Guapira noxia (Netto) Lundell	tr	ins, bee	15, 29	endozoo	8, 15, 22, 29
G. opposita (Vell.) Reitz.	tr	mot	24	endozoo	24, 31
OCHNACEAE					
Ouratea spectabilis (Mart. ex Engl.) Engl.	tr	bee	15	endozoo	8, 15
ORCHIDACEAE					
Epidendrum elongatum Jacq.	he	bee	§	ane	§
Rodriguezia decora Rchb. f.	he	bee	§	ane	§

(Cont. ...)

(Cont. Table 1)

Species	Gf	Pol	Source	Disp	Source
OROBANCHACEAE					
Esterhazya splendida J.C. Mikan	sh	hum	15	ane	23
PASSIFLORACEAE					
Passiflora alata Curtis	vi	bee	19	endozoo	30
P. suberosa L.	vi	was	19	endozoo	30
PERACEAE					
Pera glabrata (Schott) Poepp. ex Baill.	tr	ins	28	endozoo, aut	24, 28, 30, 31
POACEAE					
Andropogon leucostachyus Kunth	he	win	25	aut, ane	8, 23, 28
Eragrostis maypurensis (Kunth) Steud.	he	win	15	epizoo	15
Lasiacis ligulata Hitchc. and Chase	he	win	§	aut	§
Melinis minutiflora P. Beauv.	he	win	15, 28	ane	8, 23, 28
Tristachya leiostachya Nees	he	win	3, 15	epizoo	8, 15, 23
ROSACEAE					
Rubus brasiliensis Mart.	sh	bee	§	endozoo	§
RUBIACEAE					
Alibertia concolor (Cham.) K. Schum.	sh	mot, ins	28, 31	endozoo	28, 31
Borreria alata (Aubl.) DC.	he	fli	21	aut	§
Coccocypselum lanceolatum (Ruiz and Pav.) Pers.	he	ins	28	endozoo	8, 28
Declieuxia fruticosa (Willd. ex Roem. and Schult.) Kuntze	he	bee, was, fli	3, 15	endozoo	8, 15
Palicourea rigida Kunth	sh	hum, bee	3, 15, 29	endozoo	8, 15, 29
Psychotria sessilis Vell.	sh	ins	§	endozoo	§
Tocoyena formosa (Cham. and Schltdl.) K. Schum.	sh	mot	1, 10, 15, 27, 29	endozoo	8, 10, 15, 29
RUTACEAE					
Zanthoxylum rhoifolium Lam.	tr	ins	24, 28, 29	endozoo	9, 24, 28, 29, 30
SAPINDACEAE					
Serjania erecta Radlk.	sh	bee, was	3, 15	ane	8, 9, 15
S. laroutteana D. Dietr.	vi	bee	18	ane	§
SAPOTACEAE					
Pouteria torta (Mart.) Radlk.	tr	mot, bee	15, 29	endozoo	8, 15, 29
SMILACACEAE					
Smilax polyantha Griseb.	vi	ins	§	endozoo	30
SOLANACEAE					
Solanum aculeatissimum Jacq.	sh	bee	1, 2, 13	endozoo	§
S. americanum Mill.	sh	bee	13, 18	endozoo	28
S. erianthum D. Don.	sh	bee	§	endozoo	§
S. lacerdae Dusén	sh	bee	§	endozoo	§
S. lycocarpum A. St.-Hil.	sh	bee	15, 29	endozoo, aut	8, 15, 29
S. paniculatum L.	sh	bee	12	endozoo	23
S. variabile Mart.	sh	bee	2, 28, 31	endozoo	28, 31
STYRACACEAE					
Styrax ferrugineus Nees and Mart.	tr	bee, was	15, 29	endozoo	8, 15, 29
SYMPLOCACEAE					
Symplocos lanceolata A. DC.	tr	ins	§	endozoo	§
THYMELAEACEAE					
Daphnopsis utilis Warm.	tr	ins	§	endozoo	30
TURNERACEAE					

(Cont. ...)

(Cont. Table 1)

Species	Gf	Pol	Source	Disp	Source
Turnera hilaireana Urb.	he	bee	§	aut	§
VERBENACEAE					
Lippia lupulina Cham.	he	but, bee	15	aut	9, 15
L. velutina Schauer	sh	but	§	aut	§
VITACEAE					
Cissus erosa Rich.	vi	fli, was	3, 15	endozoo	8, 15
VOCHYSIACEAE					
Qualea grandiflora Mart.	tr	mot	10, 15, 27, 29	ane	8, 15, 29
Q. multiflora Mart.	tr	bee	15, 29	ane	8, 10, 15, 29
Vochysia tucanorum Mart.	tr	bee, mot	15, 26, 31	ane	8, 15, 31

1: Araujo (2001), 2: Avanzi and Campos (1997), 3: Barbosa and Sazima (2008), 4: Barros (1992), 5: Barros (2002), 6: Barros (1998), 7: Barros (2001), 8: Batalha and Mantovani (2000), 9: Batalha et al. (1997), 10: Borges (2000), 11: Felfili et al. (1999), 12: Forni-Martins et al. (1998), 13: Freitas (2002), 14: Goldenberg and Shepherd (1998), 15: Gottsberger and Silberbauer-Gottsberger (2006), 16: Gressler et al. (2006), 17: Gribel and Hay (1993), 18: Kinoshita et al. (2006), 19: Koschnitzke and Sazima (1997), 20: Lenzi et al. (2005), 21: Machado and Loiola (2000), 22: Manhães (2003), 23: Mantovani and Martins (1993), 24: Morellato (1991), 25: Munhoz and Felfili (2007), 26: Oliveira and Gibbs (1994), 27: Oliveira et al. (2004), 28: Paraná (2002), 29: Silva Júnior (2005), 30: Weiser (2007), 31: Yamamoto et al. (2007), 32: Yanagizawa and Maimoni-Rodella (2007). § System defined after morphological analysis and comparison with congener species whose pollination/dispersal systems are known.

Melittophily was registered in all growth forms but epiphytes (Table 2). All pollination systems but anemophily occurred among the shrubs. Trees were considered as pollinated by bees, small insects, moths, butterflies and bats.

Ornithophily was only registered in the shrubs (Orobanchaceae and Rubiaceae), one vine (Bignoniaceae) and one epiphyte (Bromeliaceae). Cantharophily occurred only in one shrub of Annonaceae family. Anemophily occurred only in the herbs of Euphorbiaceae and Poaceae families. Chiropterophily was related only in one shrub (Caryocaraceae) and three trees (Fabaceae-Caesalpinioideae and Lythraceae). Moths were considered for the trees (Apocynaceae, Ebenaceae, Nyctaginaceae and Sapotaceae) and shrubs (Rubiaceae), and butterflies occurred in the trees (Asteraceae), shrubs (Malvaceae and Verbenaceae) and herbs (Verbenaceae).

Table 2 - Pollination and dispersal systems for plants of all growth forms in a cerrado remnant in Botucatu, SP, Southeastern Brazil.

	Tree	Shrub	Herb	Vine	Epiphyte	Total
N. spp.	45	79	33	18	1	176
Wind	-	-	6	-	-	6
Diverse small insects	12	16	3	1	-	32
Flies	-	1	1	1	-	3
Bees	24	51	22	14	-	111
Wasps	-	3	-	1	-	4
Beetles	-	1	-	-	-	1
Moths	5	2	-	-	-	7
Butterflies	1	2	1	-	-	4
Hummingbirds	-	2	-	1	1	4
Bats	3	1	-	-	-	4
Autochory	3	13	19	2	-	37
Anemochory	17	28	6	9	-	60
Zoochory	25	38	8	7	1	79

In some of the richest families, i.e., Melastomataceae, Malpighiaceae, Solanaceae, Myrtaceae and Fabaceae-Faboideae, melittophily was the unique pollination system and also prevailed in Apocynaceae, Euphorbiaceae, Bignoniaceae and Fabaceae-Caesalpinioideae. Diverse small insects were important pollinators in Asteraceae, Rubiaceae and Euphorbiaceae. The families exhibiting the most diverse assemblage of pollinators were Rubiaceae, Euphorbiaceae and Asteraceae.

The principal pollination systems registered in the cerrado of Botucatu, i.e., melittophily and pollination by small insects were the same found in some studies performed in other cerrado areas as described in Table 3. Melittophily was also prevalent in other communities such as cerrado in Minas Gerais State, cerrado in São Paulo State, caatinga, semideciduous forest, rain forest and savanna (Table 3). The dendrogram generated by the cluster analysis showed segregation in two large groups, one including two areas of cerrado and another including the studied area plus the other compared sites (Fig. 1).

Table 3 - Total number and frequency, into parenthesis, of pollination systems in the present study and other tropical studied areas. Pollination systems (bat: bats, bee: bees, bet: beetles, but: butterflies, fli: flies, hum: hummingbirds, ins: diverse small insects, mot: moths, was: wasps, win: wind).

	Pollination systems									
	win	**ins**	**fli**	**bee**	**was**	**bet**	**mot**	**but**	**hum**	**bat**
Cerrado[1]	6 (3.4)	32 (18.2)	3 (1.7)	111 (63.0)	4 (2.3)	1 (0.5)	7 (4.0)	4 (2.3)	4 (2.3)	4 (2.3)
Cerrado[2]	-	29 (49.0)	♦	19 (32.0)	♦	1 (2.0)	7 (12.0)	-	1 (2.0)	2 (3.0)
Cerrado[3]	40 (13.0)	111 (37.0)	4 (1.0)	114 (38.0)	♦♦	8 (3.0)	6 (4.0)	3 (1.0)	5 (3.0)	3 (1.0)
Cerrado[4]†	18.8	8.3	6.8	49.6	10.5	1.5	-	-	3.0	1.5
Caatinga[5]	3 (2.0)	19 (12.4)	-	66 (43.1)	2 (1.3)	1 (0.7)	2 (8.5)	6 (3.9)	23 (15.0)	20 (13.1)
Seasonal semideciduous forest[6]†	14.0	-	11.0	73.0	♦♦	-	3.0	5.0	4.0	2.0
Semideciduous montane forest[7]	3 (1.7)	36 (20.9)	11 (6.4)	87 (50.6)	♦♦	4 (2.3)	11 (6.4)	7 (4.1)	6 (3.5)	7 (4.1)
Tropical rain forest[8]	4 (2.5)	26 (15.8)	-	68 (41.5)	7 (4.3)	12 (7.3)	26 (15.9)	8 (4.9)	7 (4.3)	5 (3.0)
Venezuelan savanna[9]	8 (10.7)	-	7 (9.3)	35 (46.7)	9 (12.0)	-	1 (1.3)	12 (16.0)	3 (4.0)	-

[1]This study, [2]Oliveira and Gibbs (2000), [3]Gottsberger and Silberbauer-Gottsberger (2006), [4]Barbosa and Sazima (2008), [5]Machado and Lopes (2004), [6]Kinoshita et al. (2006), [7]Yamamoto et al. (2007), [8]Bawa et al. (1985), [9]Ramírez (2004), † only % available, ♦ included within diverse small insects, ♦♦ included within bees.

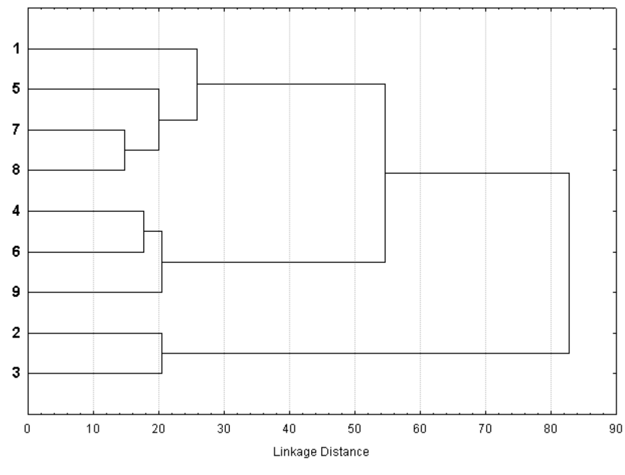

Figure 1 - Cluster analysis dendrogram using frequency of pollination systems. 1: This study; 2: Oliveira and Gibbs (2000), cerrado; 3: Gottsberger and Silberbauer-Gottsberger (2006), cerrado; 4: Barbosa and Sazima (2008), cerrado; 5: Machado and Lopes (2004), caatinga; 6: Kinoshita et al. (2006), seasonal semideciduous forest; 7: Yamamoto et al. (2007), semideciduous montane forest; 8: Bawa et al. (1985), tropical rain forest; 9: Ramírez (2004), Venezuelan savanna.

Zoochory was the predominant system of dispersal, occurring in 44.9% of the species (Table 2) and endozoochory was the most frequent system, since it was registered for 41% of the species. Anemochory (34.1%) and autochory (21.0%) were also well represented in the studied vegetation. Zoochory was registered in all the growth forms. Anemochory and autochory were absent only in the epiphytes (Table 2). Among the richest families, the three dispersal systems were observed only in Asteraceae and Fabaceae-Faboideae species. Some families exhibited only one system: Myrtaceae and Solanaceae were endozoochorous, Apocynaceae and Bignoniaceae were only anemochorous and Eupohorbiaceae was only autochorous. The dispersal systems frequency registered in the cerrado of Botucatu was similar to another cerrado area, differing from other vegetation types (Table 4). The dendrogram generated by the cluster analysis showed that the studied area was more similar to cerrado and caatinga areas, whereas the other group included only the forest areas (Fig. 2).

Table 4 - Total number and frequency, into parenthesis, of dispersal systems in the present study and other tropical studied areas.

	Dispersal systems		
	autochory	**anemochory**	**zoochory**
Cerrado[1]	37 (21.0)	60 (34.1)	79 (44.9)
Cerrado[2]	78 (25.0)	88 (30.0)	135 (45.0)
Caatinga[3]	13 (31.0)	14 (33.0)	15 (36.0)
Seasonal semideciduous forest[4]†	18.0	21.0	63.0
Semideciduous montane forest[5]	17 (11.3)	41 (27.1)	93 (61.6)

[1]This study, [2]Gottsberger and Silberbauer-Gottsberger (2006), [3]Griz and Machado (2001), [4]Kinoshita et al. (2006), [5]Yamamoto et al. (2007), † only % available.

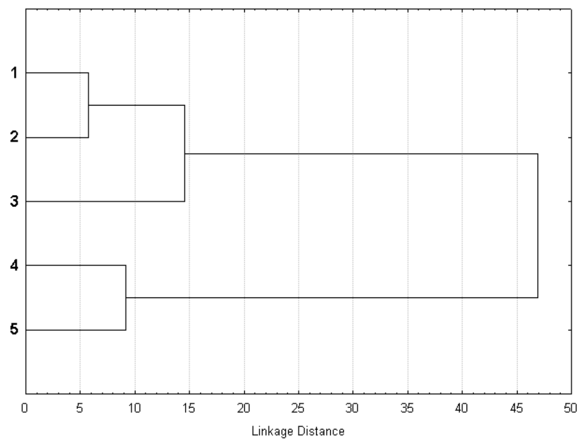

Figure 2 - Cluster analysis dendrogram using frequency of dispersal systems. 1: This study; 2: Gottsberger and Silberbauer-Gottsberger (2006), cerrado; 3: Griz and Machado (2001), caatinga; 4: Kinoshita et al. (2006), seasonal semideciduous forest; 5: Yamamoto et al. (2007), semideciduous montane forest.

DISCUSSION

The restrictions to the kind of analysis performed in the present study have been pointed out by Mitchell et al. (2009) and Ollerton et al. (2009). Nevertheless, they were overcome by an extensive search of the literature concerning pollination biology of cerrado plants, many of them performed on the same geographic region. Besides, this methodology was adopted in order to allow comparisons with other investigations made at the same geographic region using the same methodology (e.g. Kinoshita et al., 2006; Yamamoto et al., 2007).

Several pollination systems were found in the cerrado of Botucatu, suggesting the occurrence of a significant amount of interactions among the plants and diverse groups of animals, as previously reported by Silberbauer-Gottsberger and Gottsberger (1988), Oliveira and Gibbs (2000; 2002), Gottsberger and Silberbauer-Gottsberger (2006) and Barbosa and Sazima (2008). The frequency of pollination modes in the studied area was dominated by bee pollination (63%) and the other pollination modes accounted for smaller percentages. The predominance of melittophily was also observed in several tropical vegetations such as tropical rain forest (Bawa et al., 1985), Venezuelan savanna (Ramírez, 2004), caatinga (Machado and Lopes, 2004), cerrado (Gottsberger and Silberbauer-Gottsberger, 2006; Barbosa and Sazima, 2008) and semideciduous forests (Kinoshita et al., 2006; Yamamoto et al., 2007). Many bees are versatile and extremely active pollinators, being able to obtain the resources from several plant species exhibiting a great variety of floral characteristics (Faegri and Pijl, 1979).

Pollination by the diverse small insects was well represented in the area (18.2%). Similar proportion of this system were found in other tropical areas (Bawa et al., 1985; Borges, 2000; Machado and Lopes, 2004). These flowers represent an important resource to many insects since the lack of morphological specialization makes the floral rewards accessible to a wide variety of insects (Bawa et al., 1985).

Among the other pollination systems found in the studied area, humming birds and bats were restricted to few plant species and this seemed to be a very common feature of cerrado vegetation. These findings led to the conclusion that cerrado vegetation was a poor nourishment source for these animals. However, Gottsberger and Silberbauer-Gottsberger (2006) reported that there was a continual migration of birds, bats and also some insects, from the cerrado to the surrounding gallery forest and other close-by vegetation types, on a daily bases, and this would complement the diet of these animals. Furthermore, some birds forage flowers that do not have attributes for the ornithophily syndrome (Machado and Lopes, 2004) and some ornithophilous plants can also be pollinated by the bees, and *vice versa* (Kinoshita et al., 2006). Ramírez (2004) observed that the incidence of species pollinated by the bats occurred predominantly among the tree species and tended to decrease from the closed areas (forests) to more open areas (savanna and disturbed sites). However, species pollinated by the humming birds occurred predominantly in the areas of savanna and forest-savanna transition, where there were more herbs and shrubs.

The frequency of flowers pollinated by the flies, wasps, beetles, moths and butterflies was low and this seemed to be a common feature in the cerrado areas (Gottsberger and Silberbauer-Gottsberger, 2006; Barbosa and Sazima, 2008). All the anemophilous species were herbs corroborating the observations of Ramírez (2004), Gottsberger and Silberbauer-Gottsberger (2006) and Barbosa and Sazima (2008) that the frequency of wind pollinated species was higher in the open vegetation types where there was higher incidence of herbaceous plants.

The higher frequency of bee pollinated species observed in the tropical forests, Venezuelan savanna, caatinga, cerrado in Minas Gerais State and in the studied Botucatu cerrado, was the main feature that allowed the formation of a distinct group in relation to distribution of pollination modes (Fig. 1). The Venezuelan savanna, the seasonal forest and the cerrado of Minas Gerais State were more similar due the occurrence of a larger proportion of species pollinated by the wind and flies, which differentiated them from other areas. The other cerrado areas were very distinct from this group mainly due to the high frequency of plants pollinated by the diverse small insects. Similarity in the pollination spectrum may be considered as a spatio-temporal form of community convergence (Ramírez, 2004), which can be defined as the condition when one or more communities reach the same “state” in terms of identities, absolute and relative abundances of constituent species, including similar variation features (Grover and Lawton, 1994).

It was somewhat surprising that the studied Botucatu cerrado had not joined the cerrado group. This result led to the observation that although the richest families in study area were among the most important families in the cerrado biome (Mendonça et al., 1998) and in several cerrado fragments in São Paulo State (Cavassan, 2002), many plant species also occurred in the seasonal semideciduous forest. Among the identified species, 18 (10%) were not found in the main listings from the flora of the cerrado (Mendonça et al., 1998; Castro et al., 1999) and several other species also occurred in semideciduous forest fragments in Botucatu region. It is undeniable that the study area can be easily distinguished from the forest formations by its physiognomy which is characteristic of cerrado vegetation. However, its floristic composition indicated that the area might be considered a transition from the cerrado to seasonal semideciduous forest, as pointed out by Ishara et al. (2008), since there were many species that have been previously reported in the seasonal semideciduous forest in Botucatu region, such as *Alibertia concolor*, *Guapira opposita*, *Lafoensia* *pacari, Miconia ligustroides, Ocotea corymbosa, Ocotea pulchella, Pera glabrata, Platypodium elegans, Qualea multiflora, Rapanea umbellata, Solanum variabile, Tibouchina stenocarpa* and *Vochysia tucanorum* (Grombone-Guaratini and Maimoni-Rodella, 1995). Two other species, *Leandra aurea* and *Piptocarpha macropoda* are considered only as forest components (Barbosa and Martins, 2008). In relation to this point, Durigan et al. (2003b) reported that in many areas there was a floristic gradient from cerrado to seasonal forest, with different proportions of ecotone species. Hence, the study area could represent an ecotone, considering its proximity to a fragment of seasonal forest and the presence of unusual species of the cerrado vegetation. In fact, the floristic analysis of the study area performed by Ishara et al. (2008) revealed low similarity in relation to other cerrado areas, even among those geographically near cerrado areas.

The zoochory system was predominant in Botucatu cerrado and was also reported as the most frequent in the tropical vegetation (Pijl, 1982; Bollen et al., 2004). Similar proportions for this and the other dispersal systems were observed in another cerrado located in Botucatu region (Gottsberger and Silberbauer-Gottsberger, 2006). The presence of 34% anemochorous species was expressive, and this dispersion syndrome was generally associated with vegetation types of dry habitats (Howe and Smallwood, 1982) and open areas (Opler et al., 1980; Griz and Machado, 2001), which was the case of the cerrado. The importance of anemochorous species in the colonization of savannic areas was emphasized by Vieira et al. (2002). Autochory was also related with open vegetation (Howe and Smallwood, 1982; Griz and Machado, 2001).

In other vegetation types, the distribution of dispersal systems was somehow different (Table 4). In semideciduous forest in São Paulo State, zoochory species were more frequent and occurred in approx. 60% of the species (Kinoshita et al., 2006; Yamamoto et al., 2007). On the other hand, in caatinga, the dispersal system distribution was more equilibrate since zoochory was observed in 36% of the species while anemochory (33%) and autochory (31%) almost reached the same proportion (Griz and Machado, 2001). The cerrado in Botucatu, concerning the dispersal systems, seemed to occupy an intermediary position between the semideciduous forest and caatinga since it had a higher proportion of zoochorous species but not reaching the magnitude of the forest, and a large proportion of anemochorous species, slightly superior to that observed in the caatinga. Additionally, cerrado and caatinga, more open and dry vegetations, were reunited in a distinct group with similar distribution of dispersal modes, while semideciduous forests constituted another group, very dissimilar in relation to the first one because the dispersal modes were dominated by zoochory (Fig. 2).

The high proportion of species pollinated and dispersed by the animals in the studied cerrado area emphasized the role of these mutualistic interactions in the maintenance of natural ecosystems, even though the results obtained in the present study may be limited in some extent. These features demonstrated that small fragments of vegetation could also be of critical importance in the urgent task of conservation.

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