Chapter 14
Temporal Patterns of Pollination and Seed Dispersal in *Capões* of the Southern Pantanal

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14.1 Introduction

Reproductive phenology involves temporal patterns of resource availability throughout the year, these patterns being regulated by both environmental and biotic factors, including herbivores, pollinators and seed dispersers (Rathcke and Lacey 1985; Morellato et al. 2016; see also the chapter on "Synthesis of the Present Knowledge on Plant Phenology of the Pantanal" Chap. 13). Pollination and seed dispersal are two key processes in the reproductive ecology of most plants, which depend on a myriad of different pollen and seed vectors (Hansen and Muller 2009). The concept of syndromes comprises a set of characteristics of plant species commonly adjusted to a particular biotic group or abiotic agent as a result of providing pollination and seed dispersal services (Faegri and van der Pijl 1979; van der Pijl 1982). Floral attributes, such as shape, size, colour of corolla, period of anthesis and presence and type of odour, as well as offered resources, frequently vary among types of pollen vectors. Similarly, fruit traits like shape, size, weight, consistency, colour, dehiscence, pulp composition and seed size are variable according to different seed vectors.

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G. A. Damasceno-Junior, A. Pott (eds.), *Flora and Vegetation of the Pantanal Wetland*, Plant and Vegetation 18, https://doi.org/10.1007/978-3-030-83375-6_14

Most tropical plant species greatly depend on biotic vectors for reproduction, being invertebrates the commonest pollinators (van der Pijl 1982; Bawa 1990; Fleming and Kress 2013; Rech et al. 2016). Bees represent the most important group of pollinators, since they pollinate a vast number of Neotropical species (Bawa 1990; Aoki and Sigrist 2006; Lopes et al. 2007; Souza et al. 2016). Birds and bats pollinate ca. 15% to 28% of the plant species in a given community, being the most important groups of pollen vectors among vertebrates (Borges 2000; Oliveira and Gibbs 2000; Machado and Lopes 2004; Fischer et al. 2014; Quirino and Machado 2014). Likewise, animal-mediated seed dispersal is the main strategy among tropical plants, representing 50–90% of the species in local forest communities (Howe and Smallwood 1982; Jordano 2000; Tabarelli and Peres 2002). In wet forests, many plants produce fleshy fruits adapted to animal consumption, whereas anemochoric species or those dispersed by other abiotic modes prevail in dry environments with marked seasonality (Machado et al. 1997; Griz and Machado 2001; Jara-Guerrero et al. 2011; Carvalho and Sartori 2014).

Different groups of pollinators and seed dispersers can present seasonal variation in the use of flower and fruit resources (Koptur et al. 1988; Fischer et al. 2018). In addition, these groups may use different strata of the forests, as each stratum presents microclimatic conditions and availability of resources associated with a specific fauna (Bawa et al. 1985; Almeida-Neto et al. 2008). Since animal communities are stratified and seasonally variable in relation to their requirements and to their frequency of occurrence, the vertical distribution in the vegetation and seasonality are expected to affect plant-animal interactions (Koptur et al. 1988; Bawa 1990; Araujo and Sazima 2003; Souza et al. 2018).

The concept of pollination syndrome by Faegri and van der Pijl (1979) has been controversial because it assumes specialization of animal-plant interactions though specialized pollination systems are uncommon (Waser et al. 1996; Ollerton et al. 2009; Jordano 2010). Nonetheless, the concept of syndrome allows to objectively classify plant species according to their main pollinator types, being useful for addressing plant reproductive ecology at the community level and for comparisons among vegetation types (Machado and Lopes 2004). Results on seed dispersal syndromes are likewise useful in the same contexts, and they have indeed been used for such studies (Griz and Machado 2001). Overall, results of pollination and seed dispersal syndromes can raise broad ecological issues and provide valuable information for finer studies on plant reproductive biology (Dafni and O'Toole 1994; Parra-Tabla and Bullock 2002; Muchhala and Jarrín 2002).

Studies on pollination in the Pantanal have mainly focused on particular plant species in open physiognomies and riparian forests (e.g. Sazima et al. 2001; Longo and Fischer 2006; Paulino-Neto 2007; Fava et al. 2011; Silva et al. 2013; Cunha et al. 2014; Fadini et al. 2018), likewise studies on seed dispersal, which are notably related to mammals or fishes (Teixeira et al. 2009; Costa-Pereira et al. 2011; Donatti et al. 2011; Wang et al. 2011; Munin et al. 2012; Correa et al. 2016; Correa and

Fischer 2017; Fischer et al. 2018). Araujo and Sazima (2003) evaluated the year-round flower availability for hummingbirds and the species pollinated by them in the capões of the Pantanal, i.e. natural semideciduous forest patches (0.5 to 5 ha) surrounded by seasonally floodable grasslands. Since the capões form a patchy-forested landscape, the knowledge on phenology, pollination and dispersal modes in this physiognomy can offer a comparative basis and provide guidelines for understanding plant reproductive biology in fragmented forests.

In this chapter, we provide an overview on flowering and fruiting phenology, as well as on the pollination and seed dispersal syndromes of species occurring in capões. In addition, we describe patterns of occurrence of syndromes among microhabitats and the seasonal occurrence of syndromes throughout the year, thus also assessing resource availability for flower visitors and fruit eaters. Overall, this study reports how the pollination and seed dispersal syndromes of the plant community are arranged in time and in the vertical space in capões of the southern Pantanal.

14.2 Methods

14.2.1 Study Site

Fieldwork was carried out in 52 capões ranging from 0.2 to 3.8 ha (0.99 ± 0.75 ha) in the Miranda subregion, southern Pantanal (14° to 22° S and 53° to 66° W), yielding a total sample area of about 51.6 ha. These forest patches are commonly circular or elliptical in shape and 1–3 m more elevated than the natural grasslands surrounding them (Fig. 14.1). They are important elements of the landscape by sheltering flood-intolerant plant species and terrestrial animals during the flood pulses. Their origin has been attributed to abiotic and biotic factors associated with local geomorphology and differential erosion. Floristically, the interior of capões is mainly composed of species typical of semideciduous alluvial forests and their edges composed of plants characteristic of gallery forests and Chaco (Prance and Schaller 1982; Damasceno-Junior et al. 1999).

The climate in the southern Pantanal is tropical and markedly seasonal, with hot and wet summers and dry winters with cold fronts. The average annual rainfall ranges between 800 and 1400 mm, 80% being concentrated from November to March (Silva et al. 2000). During the period of data collection (1999–2000), the average annual rainfall and temperature were 1058 mm and 24.9 °C, respectively (data obtained from a local station, available in CEMTEC, the Monitoring Center for Weather, Climate and Water Resources of the State of Mato Grosso do Sul, Brazil).

Fig. 14.1 Overview of a capão in the southern Pantanal, Mato Grosso do Sul state, Brazil

14.2.2 Reproductive Phenology

Flowering and fruiting phenology were studied for all plant species in the 52 capões between May 1999 and May 2000. Each forest patch was entirely sampled for flowering and fruiting individuals once during the study period, and we haphazardly selected three to five different patches each month (at least 1 km apart from each other). We recorded all reproductive individuals for habit and numbers of open flowers, unripe and ripe fruits. Data, including all plants' life-forms (tree, shrub, herb, hemiparasite and climber), were noted in the field and confirmed in the literature (Pott and Pott 1994; Damasceno-Junior et al. 1999; Pott et al. 2011). The duration of flowering and fruiting periods was calculated for each syndrome, and the phenological patterns were classified as brief (1 month), intermediate (2–5 months) or extended (more than 5 months) (sensu Newstrom et al. 1994).

14.2.3 Pollination and Seed Dispersal Syndromes

Plants were classified into pollination and seed dispersal syndromes according to their flower and fruit characteristics, respectively (sensu Faegri and van der Pijl 1979; van der Pijl 1982). We collected flowers and fruits from different individual plants and preserved them in ethanol 70% for complementary morphological measurements in the laboratory. For flowers, we recorded colour, presence of odour, period of anthesis and floral rewards. Flower types were classified as open, tube, gullet, flag, bell, brush or inconspicuous (Faegri and van der Pijl 1979). We occasionally recorded flower visitors for 87 plant species and systematically recorded the visitors of 44 species, summing 131 species (53%) with records of floral visitors. Focal observations lasted 1–15 h ($\bar{x}$ = 3.7 ± 3.35 h) for each plant species and summed 151 h 29 min (143 h 19 min during daylight and 8 h 10 min at night). Data on flower visitors and the literature helped to check for species pollination syndromes, inferred based on floral biology and morphological attributes. Pollination syndrome classes were melittophily (bees), sphingophily (moths), cantharophily (beetles), myophily (flies), psychophily (butterflies), ornithophily (birds), chiropterophily (bats) and anemophily (wind) (sensu Faegri and van der Pijl 1979). Species whose flowers appeared to be pollinated by more than one group of insects were classified as generalist-entomophilous. Six species were classified as undetermined pollination syndromes, and they were not included in the analyses. Seed dispersal syndromes were classified based on the evaluation of morphological attributes of fruits or infructescences, as well as on the literature. We considered colour, size, weight, consistence (dry, fleshy), dehiscence, seed size and number. Fruit types followed the classification of Spjut (1994). Seed dispersal syndromes were then classified as zoochory, either when diaspores presented tissues consumed by animals or adhesive structures as hooks or viscous substances to adhere to animals' bodies (epizoochory); anemochory, when diaspores were winged or plumed; and autochory, when diaspores primarily depend on the parent plant for dispersal through explosion or dropping by gravity (van der Pijl 1982).

14.3 Results

We recorded 284 plant species belonging to 65 families in the 52 capões of the Miranda subregion. The richest family was Fabaceae (N = 51 species), followed by Malvaceae (N = 26), Asteraceae (N = 14), Rubiaceae (N = 14) and Euphorbiaceae (N = 12). The other families contributed with one to nine species (Table 14.1). We recorded 248 flowering species and 111 fruiting species in the capões. Based on pollination and seed dispersal syndromes, most plant species were associated with animal vectors (Table 14.1; Fig. 14.2).

Pollination syndromes ranked as follows: melittophilous (47.2%), generalist-entomophilous (34.7%), myophilous (6.1%), psychophilous (3.1%), ornithophilous (2.4%), sphingophilous (1.4%), cantharophilous and chiropterophilous (both with 1%). Anemophily was recorded for 3.1% of the species (Fig. 14.2a). Concerning seed dispersal syndromes, zoochory was predominant (63.7%), followed by anemochory (19.1%) and autochory (17.2%) (Fig. 14.2b). Diaspores with tissues consumed by animals prevailed among zoochoric species (95%; N = 67), whereas epizoochory was recorded for only 5% of them (N = 4).

Table 14.1 Pollination and seed dispersal syndromes (sensu Faegri and van der Pijl 1979 and van der Pijl 1982, respectively) of 248 flowering species and 111 fruiting species recorded in 52 capões of the southern Pantanal, Miranda subregion. Nomenclature follows REFLORA (http://floradobrasil.jbrj.gov.br)

Family Species	Life-form	Pollination syndrome	Seed dispersal syndrome
Acanthaceae			
Ruellia erythropus (Nees) Lindau	Shrub	Melittophily	–
Ruellia geminiflora Kunth	Herb	Melittophily	–
Ruellia simplex Wright	Herb	Melittophily	–
Alismataceae			
Echinodorus grandiflorus (Cham. & Schltr.) Micheli	Herb	Melittophily	–
Echinodorus lanceolatus Rataj	Herb	Melittophily	–
Echinodorus macrophyllus (Kunth) Micheli	Herb	Melittophily	–
Amaranthaceae			
Pfaffia glomerata (Spreng.) Pedersen	Herb	Entomophily	–
Amaryllidaceae			
Hippeastrum puniceum (Lam.) Kuntze	Herb	Ornithophily	–
Anacardiaceae			
Astronium fraxinifolium Schott	Tree	Melittophily	Anemochory
Astronium urundeuva (M. Allemão) Engl.	Tree	–	Anemochory
Mangifera indica L.	Tree	Entomophily	Zoochory
Annonaceae			
Annona cornifolia A.St.-Hil.	Shrub	Cantharophily	Zoochory
Annona emarginata (Schltdl.) H.Rainer	Tree	Cantharophily	Zoochory
Unonopsis guatterioides (A.DC.) R.E.Fr.	Tree	Melittophily	Zoochory
Apiaceae			
Eryngium elegans Cham. & Schltdl.	Herb	Psychophily	–
Apocynaceae			
Aspidosperma australe Müll. Arg.	Tree	Myophily	Anemochory
Forsteronia pubescens A. DC.	Climber	Melittophily	–
Funastrum clausum (Jacq.) Schltr.	Climber	–	Anemochory
Prestonia quinquangularis (Jacq.) Spreng.	Climber	Melittophily	–
Prestonia coalita (Vell.) Woodson	Climber	Melittophily	–
Rauvolfia ligustrina Willd.	Shrub	Melittophily	–
Rhabdadenia madida (Vell.) Miers	Climber	Melittophily	Anemochory
Tabernaemontana siphilitica (L.f.) Leeuwenb.	Shrub	Psychophily	–
Thevetia bicornuta Müll. Arg.	Shrub	Melittophily	–
Arecaceae			

(continued)

Table 14.1 (continued)

Family Species	Life-form	Pollination syndrome	Seed dispersal syndrome
Acrocomia aculeata (Jacq.) Lodd. ex Mart.	Tree	–	Zoochory
Attalea phalerata Mart. ex Spreng.	Tree	Melittophily	Zoochory
Bactris glaucescens Drude	Shrub	Entomophily	–
Copernicia alba Morong ex Morong & Britton	Tree	Entomophily	Zoochory
Desmoncus horridus subsp. *prostratus* (Lindman) Henderson	Tree	–	Zoochory
Praxelis diffusa (Rich.) Pruski	Herb	Entomophily	–
Aristolochiaceae			
Aristolochia esperanzae Kuntze	Climber	Myophily	Anemochory
Asteraceae			
Ageratum conyzoides L.	Herb	Entomophily	–
Aspilia latissima Malme	Herb	Entomophily	–
Baccharis glutinosa Pers.	Shrub	Entomophily	–
Bidens gardneri Baker	Shrub	Entomophily	Epizoochory
Centratherum punctatum Cass.	Shrub	Melittophily	–
Chromolaena maximilianii (Schrad. ex DC.) R.M.King & H. Rob.	Shrub	Entomophily	–
Chromolaena odorata (L.) R.M. King & H. Rob.	Shrub	Entomophily	Anemochory
Lessingianthus rubricaulis (Humb. & Bonpl.) H. Rob.	Shrub	Entomophily	–
Mikania capricorni B.L. Rob.	Climber	Entomophily	Anemochory
Mikania micrantha Kunth	Climber	Entomophily	–
Mikania sp.1	Climber	Entomophily	–
Orthopappus angustifolius (Sw.) Gleason	Herb	Entomophily	–
Sphagneticola brachycarpa (Baker) Pruski	Herb	Entomophily	–
Stilpnopappus pantanalensis H. Rob.	Herb	Entomophily	–
Vernonia sp.1	Shrub	Entomophily	Anemochory
Bignoniaceae			
Amphilophium crucigerum (L.) L.G. Lohmann	Climber	Melittophily	–
Bignoniaceae sp.1	Climber	Melittophily	–
Cuspidaria lateriflora (Mart.) DC.	Climber	–	Anemochory
Dolichandra uncata (Andrews) L.G. Lohmann	Climber	Melittophily	–
Fridericia pubescens (L.) L.G. Lohmann	Climber	Melittophily	Anemochory
Handroanthus heptaphyllus (Vell.) Mattos	Tree	–	Anemochory

(continued)

Table 14.1 (continued)

Family Species	Life-form	Pollination syndrome	Seed dispersal syndrome
Tabebuia aurea (Silva Manso) Benth. & Hook.f. ex S. Moore	Tree	Melittophily	Anemochory
Tanaecium neobrasiliense L.G. Lohmann	Climber	Melittophily	–
Tanaecium pyramidatum (Rich.) L.G. Lohmann	Climber	Melittophily	Anemochory
Boraginaceae			
Cordia glabrata (Mart.) A. DC.	Tree	Melittophily	Anemochory
Euploca filiformis (Lehm.) J.I.M.Melo & Semir	Shrub	Melittophily	–
Heliotropium indicum L.	Shrub	Melittophily	–
Varronia curassavica Jacq.	Shrub	Melittophily	–
Bromeliaceae			
Bromelia balansae Mez	Herb	Ornithophily	–
Cannabaceae			
Celtis iguanaea (Jacq.) Sarg.	Shrub	–	Zoochory
Trema micrantha (L.) Blume	Tree	Anemophily	Zoochory
Celastraceae			
Hippocratea volubilis L.	Climber	Entomophily	Anemochory
Salacia elliptica (Mart. ex Schult.) G. Don	Tree	Entomophily	Zoochory
Chrysobalanaceae			
Couepia uiti (Mart. & Zucc.) Benth. ex Hook.f.	Tree	Melittophily	Zoochory
Leptobalanus parvifolius (Huber) Sothers & Prance	Shrub	Melittophily	–
Combretaceae			
Combretum lanceolatum Pohl ex Eichler	Shrub	–	Anemochory
Combretum laxum Jacq.	Shrub	Entomophily	Anemochory
Combretum leprosum Mart.	Tree	Melittophily	–
Commelinaceae			
Murdannia nudiflora (L.) Brenan	Herb	Melittophily	–
Convolvulaceae			
Aniseia martinicensis (Jacq.) Choisy	Climber	Melittophily	–
Camonea umbellata (L.) A.R.Simões & Staples.	Climber	Melittophily	Autochory
Ipomoea rubens Choisy	Climber	Melittophily	–
Ipomoea subtomentosa (Chodat & Hassl.) O'Donell	Climber	Melittophily	–
Ipomoea sp.	Climber	–	Autochory
Jacquemontia densiflora (Meisn.) Hallier f.	Climber	Melittophily	–

(continued)

Table 14.1 (continued)

Family Species	Life-form	Pollination syndrome	Seed dispersal syndrome
Cucurbitaceae			
Cayaponia podantha Cogn.	Climber	–	Zoochory
Momordica charantia L.	Climber	Melittophily	–
Dilleniaceae			
Doliocarpus dentatus (Aubl.) Standl.	Shrub	–	Zoochory
Ebenaceae			
Diospyros sp.1	Tree	–	Zoochory
Erythroxylaceae			
Erythroxylum anguifugum Mart.	Shrub	Melittophily	Zoochory
Euphorbiaceae			
Acalypha communis Müll. Arg.	Shrub	Anemophily	–
Alchornea discolor Poepp.	Shrub	Melittophily	–
Astraea lobata (L.) Klotzsch	Herb	Entomophily	–
Croton corumbensis S. Moore	Shrub	Entomophily	Zoochory
Croton glandulosus L.	Shrub	Melittophily	–
Croton montevidensis Spreng.	Shrub	Melittophily	–
Croton sarcopetaloides S. Moore	Shrub	Entomophily	–
Croton urucurana Baill.	Shrub	Entomophily	–
Manihot carthagenensis (Jacq.) Müll. Arg.	Shrub	Melittophily	–
Microstachys hispida (Mart. & Zucc.) Govaerts	Shrub	Myophily	–
Sapium haematospermum Müll. Arg.	Tree	Entomophily	Zoochory
Sebastiania sp.1	Shrub	Myophily	–
Fabaceae			
Anadenanthera colubrina (Vell.) Brenan	Shrub	Melittophily	–
Ancistrotropis peduncularis (Kunth) A. Delgado	Climber	Melittophily	–
Andira inermis (W.Wright) DC.	Tree	–	Zoochory
Bauhinia mollis (Bong.) Dietr.	Shrub	Sphingophily	Autochory
Bauhinia pentandra (Bong.) D. Dietr.	Shrub	–	Autochory
Calopogonium caeruleum (Benth.) C.Wright	Climber	–	Autochory
Camptosema ellipticum (Desv.) Burk.	Shrub	Ornithophily	Autochory
Canavalia mattogrossensis (Barb. Rodr.) Malme	Climber	Melittophily	–
Canavalia piperi Killip & J.F. Macbr.	Climber	Melittophily	–
Canavalia rosea (Sw.) DC.	Climber	Melittophily	–
Canavalia sp.1	Climber	–	Autochory
Centrosema brasilianum (L.) Benth.	Climber	Melittophily	Autochory
Centrosema vexillatum Benth.	Climber	Melittophily	–

(continued)

Table 14.1 (continued)

Family Species	Life-form	Pollination syndrome	Seed dispersal syndrome
Chaetocalyx brasiliensis (Vogel) Benth.	Climber	Melittophily	Epizoochory
Chamaecrista nictitans (L.) Moench	Shrub	Melittophily	–
Crotalaria incana L.	Shrub	Melittophily	–
Crotalaria micans Link	Shrub	Melittophily	–
Crotalaria stipularia Desv.	Shrub	Melittophily	–
Ctenodon histrix (Poir.) D.B.O.S. Cardoso, P.L.R. Morales	Shrub	Entomophily	Epizoochory
Desmodium barbatum (L.) Benth.	Shrub	Entomophily	–
Desmodium cuneatum Hook. & Arn.	Shrub	Melittophily	–
Desmodium incanum (Sw.) DC.	Shrub	Melittophily	–
Desmodium tortuosum (Sw.) DC.	Shrub	Melittophily	–
Dioclea burkartii R. H. Maxwell	Climber	–	Autochory
Dioclea glabra Benth.	Climber	–	Autochory
Discolobium pulchellum Benth.	Shrub	Melittophily	–
Enterolobium contortisiliquum (Vell.) Morong	Tree	Melittophily	Zoochory
Eriosema platycarpon Micheli	Shrub	Entomophily	–
Indigofera lespedezioides Kunth	Climber	Melittophily	Autochory
Indigofera suffruticosa Mill.	Shrub	–	Autochory
Indigofera sabulicola Benth.	Herb	Melittophily	–
Inga vera Willd.	Tree	–	Zoochory
Inga vera subsp. *affinis* (DC.) T.D.Penn.	Tree	Entomophily	–
Lachesiodendronviridiflorum (Kunth) P.G. Ribeiro, L.P. Queiroz & Luckow	Tree	–	Autochory
Machaerium amplum Benth.	Shrub	Melittophily	–
Macroptilium lathyroides (L.) Urb.	Climber	Melittophily	–
Mimosa debilis Humb. & Bonpl. ex Willd.	Shrub	Entomophily	–
Mimosa pellita Humb. & Bonpl. ex Willd.	Shrub	Entomophily	–
Mimosa polycarpa Kunth	Shrub	Entomophily	–
Mimosa pudica L.	Shrub	–	Autochory
Mimosa sp.1	Shrub	–	Autochory
Senegalia tenuifolia (L.) Britton & Rose	Tree	Melittophily	Autochory
Senna aculeata (Pohl ex Benth.) H.S.Irwin & Barneby	Shrub	Melittophily	–
Senna occidentalis (L.) Link	Shrub	Melittophily	–
Senna pilifera (Vogel) H.S.Irwin & Barneby	Shrub	Melittophily	–

(continued)

Table 14.1 (continued)

Family Species	Life-form	Pollination syndrome	Seed dispersal syndrome
Senna splendida (Vogel) H.S.Irwin & Barneby	Shrub	Melittophily	–
Sesbania virgata (Cav.) Pers.	Shrub	Melittophily	Autochory
Stylosanthes acuminata M.B.Ferreira & Sousa Costa	Shrub	Melittophily	–
Vigna longifolia (Benth.) Verdc.	Climber	Melittophily	–
Zornia crinita (Mohlenbr.) Vanni	Shrub	Entomophily	–
Gentianaceae			
Coutoubea ramosa Aubl.	Shrub	Entomophily	–
Iridaceae			
Cipura paludosa Aubl.	Herb	Melittophily	–
Lamiaceae			
Aegiphila vitelliniflora Walp.	Shrub	Psychophily	Zoochory
Hyptis campestris Harley & J.F.B. Pastore	Herb	Melittophily	–
Hyptis sp.1	Herb	Melittophily	–
Hyptis sp.2	Herb	Melittophily	–
Mesosphaerum suaveolens (L.) Kuntze	Shrub	Melittophily	–
Vitex cymosa Bertero ex Spreng.	Tree	Melittophily	Zoochory
Lauraceae			
Ocotea diospyrifolia (Meisn.) Mez	Tree	Melittophily	Zoochory
Loranthaceae			
Psittacanthus acinarius (Mart.) Mart.	Hemiparasite	Chiropterophily	Zoochory
Psittacanthus cordatus (Hoffmanns.) G. Don	Hemiparasite	Ornithophily	Zoochory
Lythraceae			
Adenaria floribunda Kunth	Shrub	Melittophily	Zoochory
Cuphea antisyphilitica Kunth	Shrub	Melittophily	–
Cuphea melvilla Lindl.	Shrub	Ornithophily	–
Malpighiaceae			
Amorimia pubiflora (A.Juss.) W.R. Anderson	Climber	Melittophily	–
Byrsonima cydoniifolia A. Juss.	Shrub	Melittophily	Zoochory
Heteropterys hypericifolia A. Juss.	Climber	Melittophily	Anemochory
Mascagnia sepium (A. Juss.) Griseb.	Climber	Melittophily	–
Malvaceae			
Abutilon sp. 1	Herb	Entomophily	–
Abutilon sp. 2	Herb	Entomophily	–
Byttneria rhamnifolia Benth.	Tree	Myophily	–
Corchorus hirtus L.	Shrub	Melittophily	–
Corchorus argutus Kunth	Shrub	Melittophily	–
Guazuma ulmifolia Lam.	Tree	Entomophily	Zoochory

(continued)

Table 14.1 (continued)

Family Species	Life-form	Pollination syndrome	Seed dispersal syndrome
Helicteres guazumifolia Kunth	Shrub	Ornithophily	Autochory
Helicteres lhotzkyana (Schott & Endl.) K.Schum.	Shrub	Chiropterophily	Autochory
Herissantia nemoralis (A.St.-Hil.) Brizicky	Herb	Entomophily	–
Malvaceae sp.1	Herb	Entomophily	–
Malvaceae sp.2	Shrub	Entomophily	–
Malvastrum americanum (L.) Torr.	Shrub	Entomophily	–
Melochia parvifolia Kunth	Shrub	Entomophily	–
Melochia pyramidata L.	Herb	Entomophily	–
Melochia simplex A.St.-Hil.	Shrub	Entomophily	–
Melochia villosa (Mill.) Fawc. & Rendle	Shrub	Entomophily	–
Pavonia sidifolia Kunth	Shrub	Entomophily	–
Pseudabutilon aristulosum (K. Schum.) Krapov.	Shrub	Entomophily	–
Sterculia apetala (Jacq.) H. Karst.	Tree	Entomophily	Zoochory
Sida cerradoensis Krapov.	Shrub	Entomophily	–
Sida linifolia Cav.	Shrub	Entomophily	–
Sida rhombifolia L.	Herb	Entomophily	–
Sida santaremensis Mont.	Shrub	Entomophily	–
Waltheria indica L.	Shrub	Melittophily	–
Wissadula amplissima (L.) R.E.Fr.	Shrub	–	Autochory
Wissadula hernandioides (L.Hér.) Garcke	Shrub	Entomophily	–
Meliaceae			
Trichilia elegans A. Juss.	Tree	Melittophily	–
Menispermaceae			
Cissampelos pareira L.	Climber	Myophily	Zoochory
Cissampelos sp.1	Climber	Myophily	–
Hyperbaena hassleri Diels	Climber	Myophily	–
Odontocarya tamoides (DC.) Miers	Climber	Myophily	Zoochory
Moraceae			
Ficus insipida Willd.	Tree	–	Zoochory
Ficus luschnathiana (Miq.) Miq.	Tree	Melittophily	–
Ficus obtusifolia Kunth	Tree	–	Zoochory
Ficus pertusa L.F.	Tree	–	Zoochory
Molluginaceae			
Mollugo verticillata L.	Herb	Entomophily	–
Myrtaceae			
Eugenia egensis DC.	Shrub	Melittophily	Zoochory
Eugenia florida DC.	Tree	Melittophily	–

(continued)

Table 14.1 (continued)

Family Species	Life-form	Pollination syndrome	Seed dispersal syndrome
Eugenia sp.1	Shrub	–	Zoochory
Eugenia sp.2	Shrub	–	Zoochory
Myrtaceae sp.1	Shrub	Melittophily	–
Psidium guajava L.	Shrub	Melittophily	Zoochory
Psidium guineense Sw.	Shrub	Melittophily	Zoochory
Psidium nutans O. Berg	Shrub	Melittophily	–
Nyctaginaceae			
Neea hermaphrodita S. Moore	Shrub	Entomophily	Zoochory
Ochnaceae			
Ouratea purpuripes S. Moore	Tree	Melittophily	–
Sauvagesia erecta L.	Herb	Melittophily	–
Onagraceae			
Ludwigia grandiflora (Michx.) Greuter & Burdet	Herb	Melittophily	–
Ludwigia irwinii Ramamoorthy	Shrub	Melittophily	–
Ludwigia octovalvis (Jacq.) P.H. Raven	Shrub	Melittophily	–
Ludwigia sp.1	Herb	Melittophily	–
Orobanchaceae			
Buchnera longifolia Kunth	Shrub	Melittophily	–
Passifloraceae			
Passiflora foetida L.	Climber	Melittophily	Zoochory
Passiflora pohlii Mast.	Climber	Melittophily	Zoochory
Phyllanthaceae			
Phyllanthus orbiculatus Rich.	Shrub	Entomophily	–
Piperaceae			
Piper aduncum L.	Shrub	Myophily	Zoochory
Piper tuberculatum Jacq.	Tree	Myophily	–
Plantaginaceae			
Angelonia salicariifolia Bonpl.	Shrub	Melittophily	–
Bacopa scabra (Benth.) Descole & Borsini	Herb	Melittophily	–
Scoparia montevidensis (Spreng.) R.E.Fr.	Herb	Melittophily	–
Poaceae			
Axonopus leptostachyus (Flüggé) Hitchc.	Herb	Anemophily	–
Panicum sp.1	Herb	Anemophily	–
Setaria vulpiseta (Lam.) Roem. & Schult.	Herb	Anemophily	–
Sorghastrum setosum (Griseb.) Hitchc.	Herb	Anemophily	–
Trachypogon spicatus (L.f.) Kuntze	Herb	Anemophily	Epizoochory
Polygalaceae			

(continued)

Table 14.1 (continued)

Family Species	Life-form	Pollination syndrome	Seed dispersal syndrome
Asemeia violacea (Aubl.) J.F.B.Pastore & J.R.Abbott	Herb	Melittophily	–
Polygala timoutoides Chodat	Herb	Melittophily	–
Polygonaceae			
Coccoloba cujabensis Wedd.	Shrub	–	Zoochory
Coccoloba parimensis Benth.	Shrub	Entomophily	Zoochory
Portulacaceae			
Portulaca fluvialis D. Legrand	Herb	Melittophily	–
Rhamnaceae			
Gouania lupuloides (L.) Urb.	Climber	Myophily	Anemochory
Rhamnidium elaeocarpum Reissek	Tree	Myophily	Zoochory
Rubiaceae			
Borreria quadrifaria E.L.Cabral	Herb	Entomophily	–
Borreria verticillata (L.) G.Mey.	Herb	Entomophily	–
Borreria sp.1	Herb	Entomophily	–
Cordiera sessilis (Vell.) Kuntze	Shrub	–	Zoochory
Genipa americana L.	Tree	Entomophily	Zoochory
Guettarda sp.	Shrub	–	Zoochory
Psychotria carthagenensis Jacq.	Shrub	Entomophily	Zoochory
Randia armata (Sw.) DC.	Shrub	–	Zoochory
Richardia grandiflora (Cham. & Schltdl.) Steud.	Shrub	Entomophily	–
Sabicea aspera Aubl.	Climber	Melittophily	–
Spermacoce eryngioides (Cham. & Schltdl.) Kuntze	Shrub	Entomophily	–
Spermacoce exilis (L.O.Williams) C.D. Adams	Herb	Entomophily	–
Staelia thymoides Cham. & Schltdl.	Shrub	Entomophily	–
Tocoyena formosa (Cham. & Schltdl.) K. Schum.	Shrub	Sphingophily	Zoochory
Rutaceae			
Zanthoxylum rigidum Humb. & Bonpl. ex Willd.	Tree	Entomophily	Zoochory
Salicaceae			Zoochory
Casearia aculeata Jacq.	Shrub	Entomophily	Zoochory
Casearia sylvestris Sw.	Tree	–	Zoochory
Xylosma venosa N.E.Br.	Shrub	Entomophily	Zoochory
Sapindaceae			
Cardiospermum grandiflorum Sw.	Climber	Entomophily	Anemochory
Cardiospermum halicacabum L.	Climber	–	Anemochory
Dilodendron bipinnatum Radlk.	Tree	Entomophily	–
Melicoccus lepidopetalus Radlk.	Tree	Entomophily	Zoochory

(continued)

Table 14.1 (continued)

Family Species	Life-form	Pollination syndrome	Seed dispersal syndrome
Paullinia elegans Cambess	Climber	Entomophily	Zoochory
Paullinia pinnata L.	Climber	Entomophily	Zoochory
Sapindus saponaria L.	Tree	Entomophily	Zoochory
Serjania caracasana (Jacq.) Willd.	Climber	Entomophily	Anemochory
Serjania erecta Radlk.	Shrub	Entomophily	Anemochory
Smilacaceae			
Smilax campestris Griseb.	Climber	Myophily	–
Smilax sp.1	Climber	Myophily	–
Solanaceae			
Cestrum obovatum Sendtn.	Shrub	Sphingophily	Zoochory
Cestrum strigilatum Ruiz & Pav.	Shrub	Sphingophily	–
Nicotiana plumbaginifolia Viv.	Herb	Entomophily	–
Solanum aculeatissimum Jacq.	Shrub	Melittophily	–
Solanum americanum Mill.	Shrub	–	Zoochory
Solanum viarum Dunal	Shrub	Melittophily	–
Solanum sp.1	Herb	Melittophily	–
Talinaceae			
Talinum fruticosum (L.) Juss.	Herb	Melittophily	–
Turneraceae			
Turnera melochioides Cambess.	Shrub	Melittophily	–
Urticaceae			
Cecropia pachystachya Trécul	Tree	Myophily	Zoochory
Verbenaceae			
Lantana camara L.	Shrub	Psychophily	–
Lantana canescens Kunth	Shrub	Psychophily	–
Lantana trifolia L.	Shrub	Psychophily	–
Lippia alba (Mill.) N.E.Br. ex P. Wilson	Shrub	Psychophily	–
Stachytarpheta cayennensis (Rich.) Vahl	Shrub	Psychophily	–
Violaceae			
Pombalia communis (A.St.-Hil.) Paula-Souza	Shrub	Melittophily	–
Vitaceae			
Cissus erosa Rich.	Climber	Entomophily	Zoochory
Cissus spinosa Cambess.	Climber	Entomophily	Zoochory
Cissus verticillata (L.) Nicolson & Jarvis	Climber	Entomophily	Zoochory
Vochysiaceae			
Vochysia divergens Pohl	Shrub	Melittophily	–

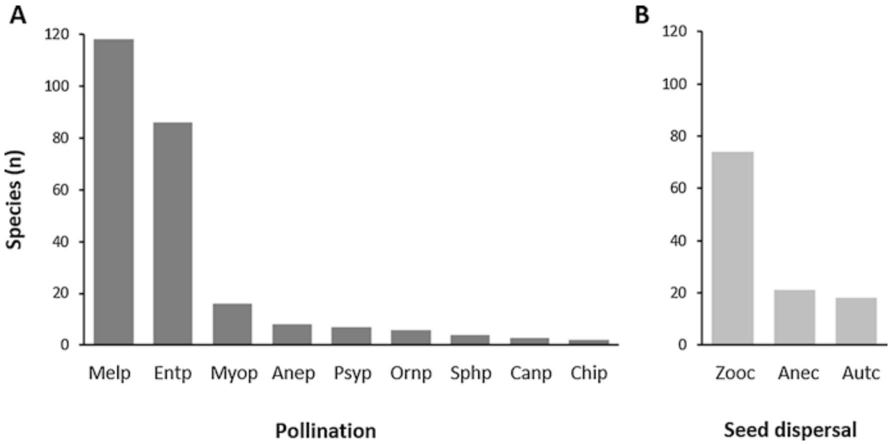

Fig. 14.2 Number of species within pollination (**a**) and seed dispersal (**b**) syndromes recorded in 52 capões in the southern Pantanal, Miranda subregion. Melp, melittophily; Entp, entomophily; Myop, myophily; Anep, anemophily; Psyp, psychophily; Ornp, ornithophily; Sphp, sphingophily; Canp, cantharophily; Chip, chiropterophily; Zooc, zoochory; Anec, anemochory; Autc, autochory

We recorded predominance of white and yellow-coloured flowers. Among different floral types reported, open or tube flowers were related to different pollination syndromes, whereas gullet flowers predominated among melittophilous species. On the other hand, inconspicuous flowers were mainly anemophilous, whereas flag and brush flowers were related to pollination by bees, bats or hummingbirds (Fig. 14.3). Fleshy fruits were found in 64% of the fruiting species, and 36% presented dry fruits. Berries were the most abundant fruit type, followed by legumes, drupes, capsules and samaras (Fig. 14.3).

The pollination syndromes had representatives among all different life-forms. Melittophily, generalist-entomophily and ornithophily occurred in the greatest variety of life-forms, whereas sphingophily exclusively occurred in shrub species (Fig. 14.4a). Myophilous and anemophilous species were predominantly climbers and herbs, respectively (Fig. 14.4a). Regarding seed dispersal syndromes, zoochoric species showed the greater variety of life-forms, with a predominance of trees and shrubs. Autochory predominated among shrub species and anemochory among herbs (Fig. 14.4b).

Flower and fruit sources peaked during the rainy season (December to March), although they were available for pollinators and seed dispersers throughout the year. The richness of blooming species in each pollination syndrome varied monthly during the study, and it peaked during the rainy season (Fig. 14.5). All pollination syndromes were represented in March, and at least four of them were represented in the other months. Melittophily and generalist-entomophily were the syndromes with more species blooming each month (Fig. 14.5).

Duration of flowering seasons was intermediate or brief for most species. Generalist-entomophilous, psychophilous, ornithophilous and cantarophilous

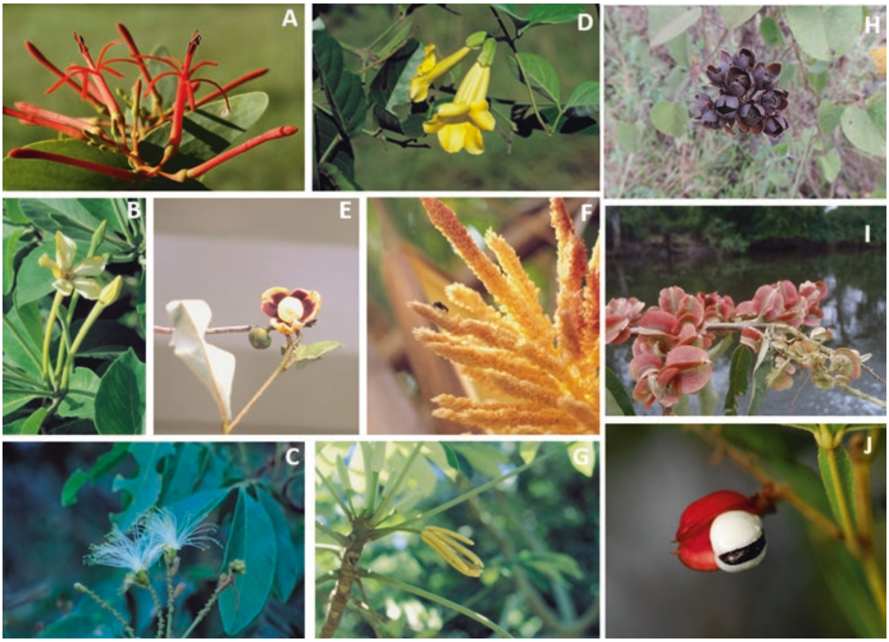

Fig. 14.3 Flowers and fruits of species recorded in capões of the southern Pantanal, Miranda subregion. (**a**) *Psittacanthus cordatus* (Loranthaceae) – ornithophily; (**b**) *Tocoyena formosa* (Rubiaceae) – sphingophily; (**c**) *Inga vera* subsp. *affinis* (Fabaceae) – generalist-entomophily; (**d**) *Dolichandra uncata* (Bignoniaceae) – melittophily; (**e**) *Annona cornifolia* (Annonaceae) – cantharophily; (**f**) *Attalea phalerata* (Arecaceae) – melittophily; (**g**) *Cecropia pachystachya* (Urticaceae) – myophily; (**h**) *Merremia umbellata* (Convolvulaceae) – autochory; (**i**) *Combretum lanceolatum* (Combretaceae) – anemochory; (**j**) *Paullinia pinnata* (Sapindaceae) – zoochory. Credits for images: (**h**) Camila Silveira Souza; (**i** and **j**) Paulo Robson de Souza

species frequently presented flowering seasons of intermediate duration; anemophilous species showed mainly brief flowering periods; whereas flowering seasons of myophilous, chiropterophilous, sphingophilous and melittophilous species were brief or intermediate. Extended flowering seasons occurred for melittophilous, generalist-entomophilous, myophilous and ornithophilous species. Ornithophilous species were those with longer flowering seasons.

The density of flowering individuals was also greater in the rainy season, between November and March, for most pollination syndromes (Fig. 14.6). Generalist-entomophilous species presented the highest density of individuals peaking in February. Sphingophilous species presented two flowering peaks, one in the dry season (August) and another one in the rainy season (January) (Fig. 14.6). Melittophilous species presented greater density of flowering individuals in February, and anemophilous species peaked in October, both in the rainy season. On the other hand, the highest density of chiropterophilous flowers was recorded in April, during the dry period (Fig. 14.6).

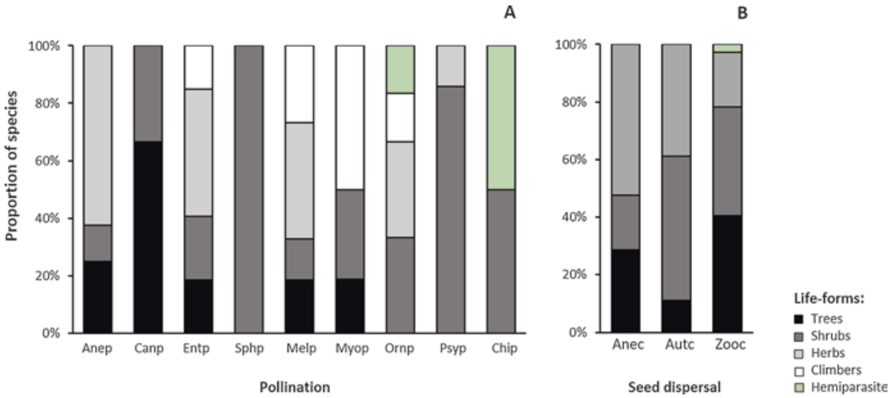

Fig. 14.4 Pollination (**a**) and seed dispersal (**b**) syndromes recorded for different life-forms in capões of the southern Pantanal, Miranda subregion. Melp, melittophily; Entp, entomophily; Myop, myophily; Anep, anemophily; Psyp, psychophily; Ornp, ornithophily; Sphp, sphingophily; Canp, cantharophily; Chip, chiropterophily; Zooc, zoochory; Anec, anemochory; Autc, autochory

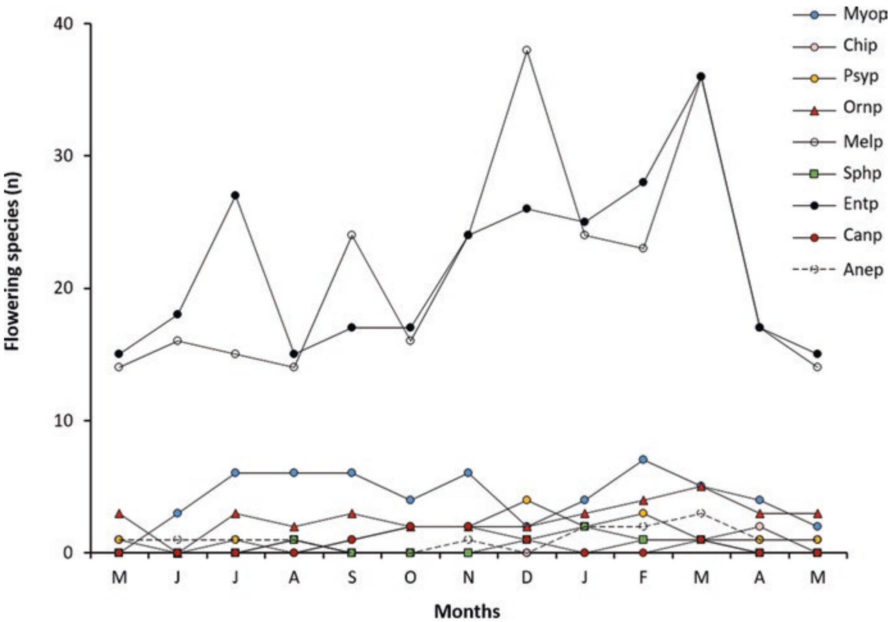

Fig. 14.5 Number of flowering species bearing different pollination syndromes throughout the year in 52 capões of the southern Pantanal, Miranda subregion. Melp, melittophily; Entp, entomophily; Myop, myophily; Anep, anemophily; Psyp, psychophily; Ornp, ornithophily; Sphp, sphingophily; Canp, cantharophily; Chip, chiropterophily

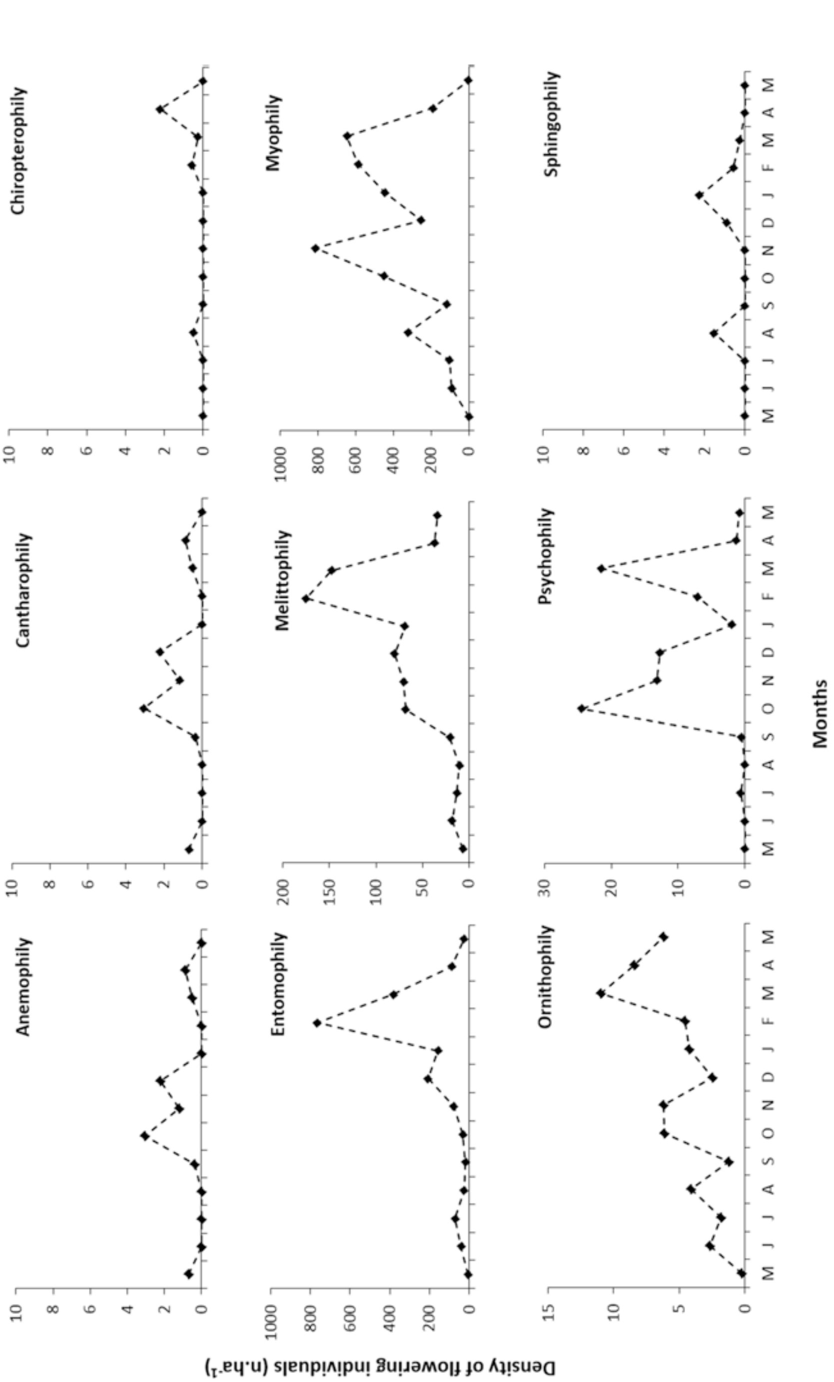

Fig. 14.6 Density of flowering individuals bearing different pollination syndromes throughout the year in 52 capões of the southern Pantanal, Miranda subregion

Fruiting of the different syndromes in the capões varied throughout the year with different patterns. Most zoochoric species fruited during the rainy season, between November and January, whereas the highest diversity of autochoric and anemochoric species occurred in the dry season, in July–August and August–September, respectively (Fig. 14.7a). The duration of fruiting periods for most of the species was intermediate. Zoochoric species presented periods of intermediate and extended fruiting duration, whereas autochoric and anemochoric species showed mainly brief fruiting seasons.

The highest density of fruiting individuals was recorded among zoochoric species, followed by anemochoric and autochoric. Zoochoric fruits were available throughout the year with a peak in January, in the rainy season (Fig. 14.7b). Anemochoric fruits peaked from September to November, corresponding to the

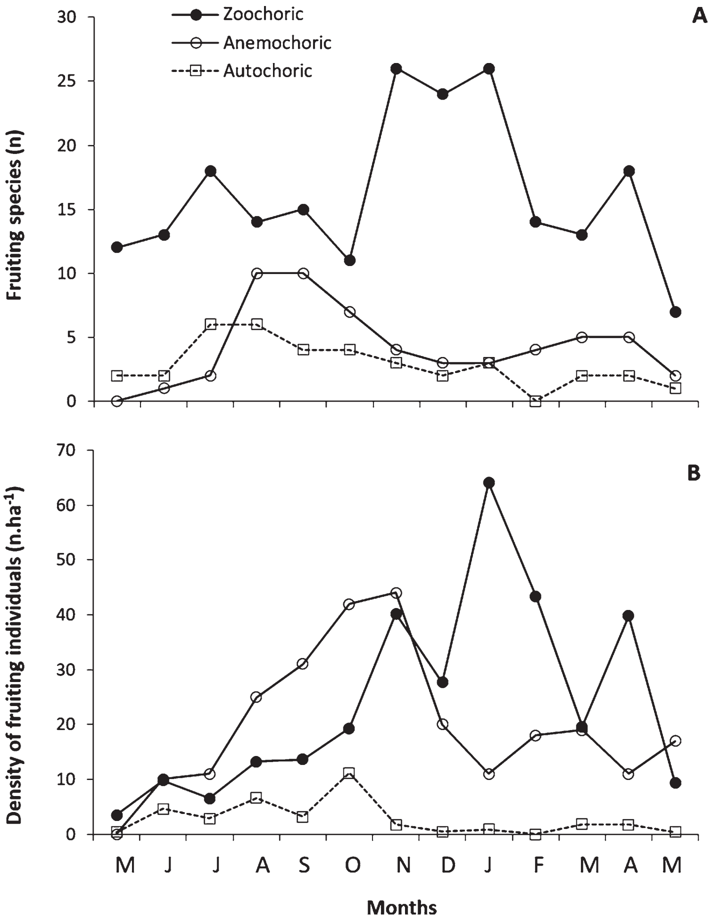

Fig. 14.7 Number of fruiting species and density of fruiting individuals in each seed dispersal syndrome throughout the year in 52 capões of the southern Pantanal, Miranda subregion

transition from the dry to the wet season (Fig. 14.7b). Autochoric species presented greater density of fruiting individuals between June and October, corresponding to the dry period, with few fruiting individuals in the rainy season (Fig. 14.7b).

14.4 Discussion

Our results show that animals, rather than wind or gravity, greatly mediate pollination and seed dispersal throughout the year in capões of the southern Pantanal, as expected for Neotropical forests in general (Griz and Machado 2001; Machado and Lopes 2004; Ramírez 2004; Quirino and Machado 2014; Carvalho and Sartori 2014; Souza et al. 2016; Rech et al. 2016). The high resource availability for pollinators and seed dispersers in the capões throughout the year highlights the importance of these forested patches in providing resources to local fauna. A total of 97% of the species are zoophilous, 93% are pollinated by invertebrates and 4% by vertebrates, whereas the abiotic syndrome was recorded for only 3% of the species. Likewise, 60.4% of the fruiting species offer resources for fruit-eating animals, while 39.6% are epizoochoric or depend on abiotic agents for seed dispersal. The predominance of plant species that rely upon animals for pollen and diaspore dispersion, and the dependence of these animals on floral and fruit sources, makes tropical forests the setting for complex interactions that influence species distributions and the structure and diversity of local communities (Jordano et al. 2006; Fleming and Kress 2013; Rech et al. 2016). In the capões of the Pantanal, though most plant species are associated with mutualist animals, their pollination and seed dispersal systems appear to be rather generalists, a situation likely related with the severe and markedly seasonal floods and droughts.

Melittophily and generalist-entomophily were the most frequent pollination syndromes in the capões (81% of species). This result is similar to those recorded in other tropical environments, including humid and dry forests (Silberbauer-Gottsberger and Gottsberger 1988; Oliveira and Gibbs 2000; Machado and Lopes 2004; Quirino and Machado 2014; Souza et al. 2016). Most melittophilous and generalist-entomophilous flowers were the open type and offered nectar and pollen as reward to flower visitors, what indicates a high predominance of generalist pollination systems because resources from such flowers are easily accessible by different visitors varying in time and space (Ollerton et al. 2007). Furthermore, several melittophilous and generalist-entomophilous species are also important sources of nectar for hummingbirds inhabiting the capões of the Pantanal (Araujo and Sazima 2003).

The proportions of ornithophilous and chiropterophilous species in the capões (2.4% and 1%, respectively) were similar to those reported in sites in the Cerrado (Silberbauer-Gottsberger and Gottsberger 1988; Oliveira and Gibbs 2000) and lower than those in the Brazilian Caatinga (Machado and Lopes 2004; Quirino and Machado 2014). The marked seasonality with a severe dry season and the patchy distribution of capões in a vast matrix of open grasslands are both factors likely to contribute to a low richness and abundance of hummingbirds and hummingbird-pollinated flowers (Araujo and Sazima 2003).

Chiropterophily is still rarer than ornithophily in the capões of the southern Pantanal, and it does not occur among tree species (but just for one shrub and one hemiparasite), contrasting with other Neotropical forests where bat-pollinated trees are relatively common (Atlantic Forest, Sazima et al. 1999; Caatinga, Machado and Lopes 2004; Quirino and Machado 2014; Nhecolândia subregion of the Pantanal, Munin et al. 2012). When compared with the Caatinga's community, these values are contrasting, since Machado and Lopes (2004) and Quirino and Machado (2014) reported a high proportion of chiropterophilous species, corresponding to 13.1% and 11%, respectively. In the Caatinga, there is an elevated diversity of trees and columnar cacti that are bat-pollinated (Queiroz 2014). Additionally, the low proportion of pollination by bats compared with the other pollination syndromes in the capões seems to be related with the low representativity of specialized nectarivorous bats in the Pantanal (Fischer et al. 2018). Moreover, the same features that limit the richness of hummingbirds may be associated with the low diversity of nectarivorous bats, as both are long-lived vertebrates.

The percentage (3%) of anemophily in the capões was close to that reported for tropical humid forests and the semiarid Caatinga. Approximately 2.5% of the flora of tropical forests and 3–4% of the Caatinga flora have been reported to be wind-pollinated (Bawa et al. 1985; Kress and Beach 1994; Machado and Lopes 2004; Quirino and Machado 2014). In the Cerrado, however, anemophily can reach 14% of species in the local flora, mainly represented by grasses (Silberbauer-Gottsberger and Gottsberger 1988; but see Oliveira and Gibbs 2000).

Melittophilous, generalist-entomophilous, myophilous and ornithophilous flowers occurred in all vertical strata of the vegetation, anemophilous species occurred mostly in the herbaceous stratum, and cantharophilous, psychophilous and sphingophilous species occurred only in the lowest stratum (herbaceous and shrubby) of the capões (Fig. 14.4a). The stratification of the pollination syndromes recorded in the capões was similar to those found in other studied communities and should be related to the vertical distribution of the anthophilous fauna (Machado and Lopes 2004; Quirino and Machado 2014; Souza et al. 2016).

Zoochory has been reported as the predominant seed dispersal syndrome in tropical regions, where it may reach more than 80% of the local species in humid forests, with a decreasing frequency towards less humid or dry environments (Gentry 1983; Carvalho and Sartori 2014). Seed dispersal by animals is a determinant step for plant reproductive success, since it increases the probability of colonization of new areas and reduces the density of dispersed seeds, thus decreasing predation on seeds and intraspecific competition among seedlings in the vicinity of the mother plants (Jordano 2017). Therefore, zoochory seems to be especially important for plants inhabiting small forest patches such as the capões of the Pantanal.

We observed that zoochory was predominant among tree and shrub species, as reported by Griz and Machado (2001) in the Brazilian Caatinga and by Freitas et al. (2013) and Carvalho and Sartori (2014) in the Brazilian Chaco. On the other hand, for the herbaceous species prevailed anemochory followed by autochory syndromes.

Stratification of the vegetation may affect the distribution of resources to dispersers (Morellato and Leitão-Filho 1992). Generally, zoochory is well represented along the vertical strata among trees, shrubs and climbers, and their seed dispersers can move both horizontally and vertically, thus increasing the efficiency of seed dispersal (Fenner 1985; Jordano 2000). Therefore, the different proportions of fleshy fruits produced by plants with different life-forms (and therefore occupying different strata) in the capões (Fig. 14.4b) can reduce the overlap of niches among animals that depend on these resources.

Most species and individuals flowered in the rainy season in the capões, similarly to those recorded in other tropical environments, especially in communities with a pronounced dry season (Machado and Lopes 2004; Quirino and Machado 2014; Souza et al. 2016; see also the chapter on "Synthesis of the Present Knowledge on Plant Phenology of the Pantanal" Chap. 13). Zoochorous species showed a fruiting peak during the rainy season, whereas anemochoric species peaked in the transition between the dry and the rainy periods, and autochoric species in the dry period. These results follow a general pattern among tropical forests (Machado et al. 1997; Griz and Machado 2001; Freitas et al. 2013; Carvalho and Sartori 2014).

Our study highlights that animal-mediated pollination and seed dispersal are common and crucial for the dynamics of the capões in the southern Pantanal. The disruption of pollination and seed dispersal interactions, together with their benefits, directly results in the impairment of the reproductive success of the partnership and reduction of the likelihood of individuals remaining in the habitat (Bascompte and Jordano 2014). The loss of ecological interactions may occur before species disappearance, affecting species functionality and ecosystems services at a faster rate than species extinctions (Valiente-Banuet et al. 2015). Therefore, conserving pollination and seed dispersal, including the animals that provide these services to plants, should become a priority in forest conservation efforts globally (Neuschulz et al. 2016).

As the capões of the Pantanal are small and sparse forest patches in an open landscape, local plant population genetic structures depend upon the ability of pollinators or seed dispersers to move between them. The presence of scattered shrubs and trees in the grassland matrix likely provides additional resources for flower visitors and seed dispersers (Silveira et al. 2018), thus stimulating movements of animal vectors among different capões. Therefore, detailed field studies addressing mechanisms of pollen and seed dispersal by different animal groups (invertebrates and vertebrates) are necessary for a better understanding of how their foraging activities across the landscape may affect gene flow among these forested patches in the southern Pantanal. These natural forest patches and their plant and animal assemblages were established throughout long-term ecological processes of successful colonization and establishment, rather than by contemporaneous disturbances caused by forest fragmentation and land modifications for human use. In this sense, further studies on pollination and seed dispersal dynamics in the capões of the Pantanal, and on the composition of the surrounding open matrix, can raise important issues on the species assembly and sustainability in situations of forest loss and fragmentation.

Acknowledgements We thank A. Brun (in memoriam), P.A.A. Cara and L. Ramos for field assistance; G. Damasceno-Júnior and U. Rezende for plant identification; and the staff of the Base de Estudos do Pantanal (UFMS) for logistical support. Funds were provided by Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (CAPES) fellowship grant to VGNG; Fundação de Apoio ao Desenvolvimento do Ensino, Ciência e Tecnologia de MS (FUNDECT), Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq) for financial support through the project "Padrões de diversidade da fauna e flora no Pantanal Sul Matogrossense" (521746/97); CNPq also provided research productivity fellowships to ACA (310999/2018-9), EF (484808/2013-3) and MS (302781/2016-1).

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