Pollination and seed dispersal modes of woody species of 12-year-old secondary forest in the Atlantic Forest region of Pernambuco, NE Brazil

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ABSTRACT

The ability of degraded areas to recover secondary vegetation and the degree of integrity of plant–animal interactions of the resulting vegetation is getting increasingly important for biodiversity and landscape conservation. We studied the seed dispersal and pollination modes of woody species of two 12-year-old secondary forest patches, beforehand used for sugarcane cultivation. Sixty plots were installed with a total area of 0.6 ha. A total of 61 woody species were encountered. Although the study sites were isolated from old-growth forests by the matrix of sugarcane, the array of dispersal modes was the same as in old-growth forest fragments and the percentage of animal-dispersed species was similar (89.8%). The percentage of large-seeded species was even larger than expected (18%), despite the local extinction of large-bodied mammals and birds. Besides the dispersal of large seeds mainly by rodents and bats, more than half of the large-seeded species are consumed by humans and may have reached the study areas this way. Most pollination modes found in forest fragments in the region were also present in the secondary forests; however, no pollination mediated by vertebrates was found among the studied species, neither by birds nor by bats, and a high percentage of species showed an unspecialized pollination mode (55.7%). Due to the high abundance of a few species pollination by hawkmoths was very common among canopy individuals (42.7%), and many sub-canopy individuals were pollinated by large bees (39.8%). The study exemplifies the resilience of sites degraded by intense agriculture, which may still lead to a forest, simplified in plant–animal interactions. Such secondary forest is likely to serve for protection against erosion, and increasing connectivity between forest fragments.

Introduction

The Atlantic Forest (Mata Atlantica) stretches over 27° of latitude along the Brazilian coastline and covered 1,363,000 km^2 in pre-Columbian times (Hirota, 2003). It is one of the global biodiversity hotspots (Myers et al., 2000). However, over 92% of its original area has been logged for agriculture, livestock farming, mining and other uses and the remaining forest patches are highly fragmented (CPRH, 2001; Frickmann Young, 2003; Hirota, 2003). The area has also the highest population density of the country, since about 106 million people are living in the region (Hirota, 2003).

The forests north of the São Francisco River form a specific endemism area called Pernambuco Endemism Center (PEC) (Silva and Casteleti, 2003). Here, the rates of habitat fragmentation are the highest and only about 5% of the original forest cover is left (Silva and Casteleti, 2003). The remaining forest fragments are interspersed like an archipelago in a sea of monoculture sugarcane plantations, which is an inhospitable matrix for forest species (Ranta et al., 1998). Beside these forest fragments, an area of an approximately similar size is covered with secondary vegetation in early or suppressed stages of succession (Ribeiro et al., 2009).

The sugarcane plantation owners protect their forest fragments against fire and logging to ensure watershed protection and water supply for sugar production (Girão et al., 2007). During the last decades, these corporations intensified and improved their cultivation, harvest, and sugar and ethanol production methods (Kimmel et al., 2008). During the time of governmental subsidy between 1980 and 1990 little adapted sites were cultivated, but abandoned as this support stopped (Ranta et al., 1998). Furthermore, the promoted migration of rural people from

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settlement on the corporations' property into coastal conurbations led to abandoned areas as well (Andrade, 2001). Depending on time, disturbance intensity, use-history, edaphic, and other biotic and abiotic conditions, the following secondary succession led to different secondary vegetation physiognomies ranging from open grass and shrub dominated to close secondary forest sites (Kimmel, 2006). Such secondary vegetation is controversially discussed for conservation strategies as being buffer zones around old-growth forest fragments, stepping stones, corridors for forest species between forest patches, or even as refuges for forest species (Ranta et al., 1998; Sanderson et al., 2003; Laurance, 2007; Bihn et al., 2008; Santos et al., 2008; Lopes et al., 2009).

A crucial point for landscape conservation is the resilience of degraded areas, i.e., the possibility of natural succession to take place via vegetative means or dispersal of diaspores (Rodrigues et al., 2009). In a recently published practical guidebook, to promote reforestation in the region, it is assumed that natural regeneration cannot occur where the seed bank is eliminated, or only if sites are situated directly besides existing forests (Alves-Costa et al., 2008). Seeds larger than 15 mm are thought to be hardly dispersed at all (Silva and Tabarelli, 2000). Another important point is the functional diversity of the resulting vegetation, especially in terms of plant–seed-disperser and plant–pollinator interactions, since an increase in diversity of one partner leads to an increase of diversity of the other as it was shown for the latter plant–animal interaction (Fontaine et al., 2006). Santos et al. (2008) found that forest fragments and secondary forest patches, compared to continuous forest, were inhabited by fewer large-seeded species that are dispersed by vertebrates and instead by many more pioneer plant species. A loss of functional diversity of these interactions in secondary forest compared to old-growth forest was reported for Costa Rica (Chazdon et al., 2003) and recently for the PEC (Santos et al., 2008; Lopes et al., 2009). Lopes et al. (2009) compared secondary forest with small forest fragments and with continuous forest and confirmed that secondary forest and small forest fragments are inhabited by fewer vertebrate-pollinated species and individuals, and have a higher abundance and diversity of species that are pollinated by diverse small insects.

In this study, we analyzed the dispersal and pollination modes of woody plant species in 12-year-old secondary forests, including the undergrowth, to exemplify the resilience and degree of integrity of plant–animal interactions of an area beforehand used for the cultivation of sugarcane and to evaluate its conservational value.

Material and methods

Study site

The study was conducted at the sugarcane plantation São José, in the municipalities of Igarassu and Araçoiaba, within the PEC.

Mean annual precipitation is 1520 mm, and mean average temperature is 25 °C (Schessl et al., 2008). There is a rainy season from January to August, and a pronounced dry season from September to December, with monthly precipitation below 100 mm (Schessl et al., 2008). The red–yellow podzolic soil is sandy to loamy (Schessl et al., 2008), the content of clay varies from 8 to 32% and that of sand from 91 to 55% (Freitas et al., pers. comm.). The original vegetation is dense lowland rainforest (Veloso et al., 1991).

On the plantation, 206 mature forest fragments and secondary forest patches remain, covering 28% of the plantation (Trindade et al., 2008). The fragments have a mean size of 61 ha, varying from 0.12 to 498 ha, and differ in age and history (Trindade et al., 2008). Most of them are very irregularly shaped and extend along steep hills and rivers, at 30 to 110 m a.s.l. (Schessl et al., 2008; Trindade et al., 2008). The four most important forest tree species in these fragments of old-growth forests are *Thyrsodium schomburgkianum* Benth. (Anacardiaceae), *Eschweilera ovata* (Camb.) Miers. (Lecythidaceae), *Tapirira guianensis* Aubl. (Anacardiaceae), and *Pogonophora schomburgkiana* Miers. ex Benth. (Euphorbiaceae) (Rocha et al., 2008; Silva A.G. et al., 2008; Silva H.C.H. et al., 2008).

Two sites of secondary forest (hereafter also called "capoeira") of sufficient size for the installation of plots and of known age of about 12 years of regeneration were chosen: Capoeira 1: latitude 7°48′55″S; longitude 35°02′15″W, 130 ha, at Engenho Campinas; and Capoeira 2: latitude 7°48′05″S; longitude 35°02′15″W, 20 ha, at Engenho Cumbe de Baixo (Fig. 1). The soil is relatively rich in clay (20%) and silt (17%), but the sand content clearly dominates (63%) (Freitas et al., pers. comm.). The vegetation patches cover mainly steep slopes, and a central river valley in Capoeira 1 is partially flooded due to a dam construction. The minimum distance to the next older forest fragment is 50 m. The sites were used as pastures at least since 1969 and were completely cleared between 1975 and 1981 for sugarcane cultivation according to aerial photographs from 1969, 1975 and 1981 and interviews with local inhabitants. Cultivation ceased at these sites only a few years later and the areas were used as pasture again. In 1995, these sites were finally taken out of usage, after a proprietor change. Only the river valley in capoeira 1 is sometimes used as temporary pasture, which, combined with the flooding led to the establishment of grassland dominated by exotic *Urochloa mutica* (Forsk.) Nguyen (Poaceae). The valley slopes are mainly covered with secondary forest, with a canopy height of 12 m, and interspersed open sites that are probably the result of fires spreading from the surrounding sugarcane fields.

Data collection and analysis

Fieldwork was conducted during 24 months from January 2007 to December 2008. Thirty 10×10 m plots were installed in each of the two sites, summing up to a total area of 0.6 ha.

Fig. 1. On the left view of a secondary forest patch from the outside, surrounded by the sugarcane matrix; on the right a group of *Albizzia saman* trees, which shed their leaves during the dry season.

The distance between the plots was 10 m. In these plots, 5×5 m^2 subplots were established. All tree individuals with a diameter of or greater than 5 cm at a height of 1.3 m (dbh) (hereafter called canopy trees) were marked and measured in the plots; individuals of 1–5 cm dbh (hereafter called sub-canopy) were marked and measured in the subplots. Plant species were identified by comparison of collected fertile and sterile material with specimens of the herbarium IPA (Instituto Agronômico de Pernambuco), the herbarium PEUFR (Universidade Federal Rural de Pernambuco) and ULM (Ulm University). The collected specimens are deposited at the same herbaria. From the number of individuals found in the 0.6 ha, the number of individuals per hectare was calculated. For the calculation of pollination and seed dispersal modes, only fertile individuals were considered, juvenile infertile ones being excluded. The flowers and fruits of all studied species were collected and classified.

The classification of dispersal modes were based on the diaspore structure. Anemochory was characterized by wing- or plume-like structures of the dispersal unit and exozoochory by hooks to cling to fur or feathers of animals. In the case of endozoochory, the dispersal units often bear fleshy or other nutrient-rich tissues, others than the seeds themselves. Synzoochory was assumed when the dispersal unit was bare of fruit parts and hence the scatter-hoarding animals usually consume the seeds themselves, or the dispersal unit bears such tissues but the seed or pyrene (in the following simply "seed") was too large to be swallowed, considering that very large-sized animals like tapirs are extinct in the study area (Lobova and Mori, 2007; van der Pijl, 1982; Silva and Pontes, 2008). The dispersal by rodents, bats and birds might overlap, e.g., in Lecythidaceae (Prance and Mori, 1979). Myrmecochory was treated separately; it was diagnosed when the diaspores were very small, shiny and had elaiosomes (van der Pijl, 1982). Autochory was characterized by an explosive opening of capsules, the absence of any of the above-mentioned attributes, and small-sized seeds, which makes scatter-hoarding unlikely, at least by larger rodents like agoutis.

Species with seeds up to 15 mm long were considered small seeded, while large-seeded species had seeds above this threshold. This limit is commonly used in literature (Santos et al., 2008).

The classification of pollination modes was based upon floral structure, time of floral activity (diurnal/nocturnal), and in most cases on flower visitor observations and literature review (Table 1). Flower visitors were recorded and their behavior was observed. Probable effective pollinators, i.e., animals that contacted pollen and stigma, were distinguished from flower visitors that could not act as pollinators. The expected pollination modes were the same as in Girão et al. (2007). The only exception is that we included wasp pollination in melittophily. The pollination modes were as follows: pollination by bats (chiropterophily), non-flying mammals, bees (small and large; melittophily), beetles (cantharophily), birds (ornithophily), diverse small insects (DSI), flies (myiophily), moths (settling while flower visiting; phalenophily), hawkmoths (sphingids; hovering while visiting flowers; sphingophily), butterflies (psychophily) and wind (anemophily).

Results

Altogether, 61 species were identified in the investigated plots, 21 of them being canopy-only species (considering only fertile adults) and 22 sub-canopy-only species. Sixteen species were found fertile in both groups and two species, Ocotea glomerata and Xylopia frutescens, were found only infertile. The three most abundant canopy species were Inga ingoides, Albizzia saman and Casearia sylvestris. The most abundant sub-canopy species were Gustavia augusta, Senna georgica and Casearia sylvestris.

The density of the canopy trees was 1828 individuals/ha, that of the fertile sub-canopy was 2433 individuals/ha and 2140 individuals/ha were infertile juveniles. Only fertile individuals were included in the analysis.

The majority of canopy and sub-canopy species (94.6% and 86.8%, respectively) was primarily vertebrate-dispersed: only 5.4% and 10.5% were wind-dispersed or autochorous, and only one sub-canopy species (2.6%), represented by seven individuals (Pera ferruginea), was dispersed by ants (Table 1). Of the 51 vertebrate-dispersed species, 45 were endozoochorous. More than half of these (30 species) had shiny, red, orange, yellow, black or red, and black-combined diaspores that typically attract birds (an exemption is Elaeis guianensis, which has shiny orange-red fruits, and large seeds that are synzoochorous). In addition, seven species had small seeds with pulp attached and hence can be dispersed by birds as well, besides by bats and other small mammals, and reptiles. The diaspores of three species were rather likely to attract mainly mammals and reptiles: Annona sp., Inga ingoides, Talisia esculenta, and five species are known to be dispersed by cattle or are used as fodder: Albizzia saman, Apeiba tibourbou, Guazuma ulmifolia, Senna georgica and Albizzia polycephala (Janzen and Martin, 1982; Lorenzi, 2002; Sampaio and Gamarra-Rojas, 2002). Fruits of A. tibourbou were always encountered parasitized by larvae and hence were never found ripe. Seven species were probably scatter-hoarded or carried by bats and Triumfetta althaeoides fruits have hooks to cling to fur or feathers of bypassing animals.

The majority of canopy and sub-canopy species had small seeds (73.0% and 86.8%). Approximately similar percentages of all individuals, namely 74.4% of the canopy and 71.8% of the sub-canopy, had small seeds (Table 2). Of the 11 large-seeded species, six had fruits that are also consumed by humans: Annona sp. (common name: Araticum), Acrocomia intumescens (Macaiba), Elaeis guineensis (Dendê), Inga ingoides (Ingá beira do rio), Pouteria grandiflora (Oití trubá) and Talisia esculenta (Pitomba). The infructescences of E. guineensis were also frequently found to be used as baits for hunting. Eschweilera ovata, Gustavia augusta, Swartzia pickelii, Strychnos parvifolia and Rauvolfia grandiflora were the other five large-seeded species.

The pollination modes melittophily (large and small bees), cantharophily, phalenophily and pollination by various small insects (DSI) were encountered among canopy and sub-canopy species. The only psychophilous species, Hirtella racemosa, was part of the sub-canopy, while the sphingophilous species Inga ingoides, Albizzia saman, Albizzia polycephala and Himatanthus phagaedanicus and the only myiophilous species Guazuma ulmifolia were only encountered fertile in the canopy stratum. Only infertile individuals were found of the single thrips-pollinated species, Xylopia frutescens. Ornithophily and chiropterophily, were not encountered (Fig. 2). The largest number of species, both, in the canopy and sub-canopy stratum, as well as most individuals in the sub-canopy had generalist flowers. Among canopy individuals, sphingophily was the most common syndrome (40.2%). This was mainly due to the abundance of Inga ingoides and Albizzia saman. Altogether, four canopy species (10.8%) were pollinated by sphingids (Fig. 2). A large number of sub-canopy individuals were pollinated by large bees (39.8%), compared to only 15.4% of the species. This asymmetry was due to the abundance of Gustavia augusta and Senna georgica.

Discussion

The studied secondary forest is a good example of how the mutual interactions between plants and animals look like after

Table 1
Total number of fertile and infertile individuals, diameter groups, pollination and dispersal modes of woody species occurring in two capoeiras, Usina São José, Zona da Mata, state of Pernambuco.

Family/species	Ind	Diam	Poll	Disp	Seed	Ref
ANACARDIACEAE						
Tapirira guianensis Aubl.	97	3*	gen (11)	endo	s	11
ANNONACEAE						
Annona sp.	3	2	can (8)	endo (8)	l	8
Xylopia frutescens Aubl.	40	1*	thrips (8)	endo	s	8
APOCYNACEAE						
Allamanda blanchetii A. DC.	100	1	mela	anem	s	
Himatanthus phagedaenicus (Mart.) Woodson	2	2	sphi	anem	s	
Rauvolfia grandiflora Mart. ex A. DC.	22	3	mela	endo	l	
ARALIACEAE						
Schefflera morototoni (Aubl.) Maguire, Steyerm. and Frodin	52	3*	gen	endo	s	
ARECACEAE						
Acrocomia intumescens Drude	35	3*	can (3,10)	syn	l	3,10
Desmoncus sp.	20	1	can	endo	s	
Elaeis guineensis Jacq.	2	2	can (4)	syn	l	4
ASTERACEAE						
Tilesia baccata (L.) Pruski	7	1	gen	endo	s	
Erechtites hieraciifolius (L.) Raf. ex DC.	7	1	gen	anem	s	
CAESALPINIACEAE						
Apuleia leiocarpa (Vogel) J.F. Macbr.	13	1	gen	anem	s	
Senna georgica Irwin and Barneby	202	3	mela (2)	endo (6,7)	s	2,6,7
CECROPIACEAE						
Cecropia palmata Willd.	107	2	gen	endo	s	
CHRYSOBALANACEAE						
Hirtella racemosa Lam.	27	1	psych (5)	endo	s	5
CLUSIACEAE						
Vismia guianensis (Aubl.) Pers.	97	3	gen	endo	s	
CORDIACEAE						
Cordia nodosa Lam.	73	1	gen	endo	s	
Cordia polycephala (Lam.) I.M. Johnst.	7	1	gen	endo	s	
Cordia sellowiana Cham.	8	3*	gen	endo	s	
EUPHORBIACEAE						
Pera ferruginea (Schott) M.	7	1	gen	myr	s	
FABACEAE						
Machaerium hirtum (Vell.) Stellfeld	225	3*	mesma	anem	s	
Swartzia pickelii Killip ex Ducke	167	3	mela (2)	syn	l	2
FLACOURTIACEAE						
Casearia sylvestris Sw.	390	3	gen (8)	endo	s	8
Casearia hirsuta Sw.	127	3	gen	endo	s	
Casearia cf. *javitensis* (Kunth)	150	3	gen	endo	s	
HERNANDIACEAE						
Sparattanthelium botocudorum Mart.	27	1	gen (13)	endo	s	13
LAURACEAE						
Ocotea glomerata Benth. & Hook.f.	7	1*	myio (11)	endo	s	11
LECYTHIDACEAE						
Eschweilera ovata (Cambess.) Miers	62	3*	mela (11)	syn (11)	l	11
Gustavia augusta L.	530	3	mela	syn	l	
LOGANIACEAE						
Strychnos parvifolia A. DC.	20	1	phal	endo	l	
MELASTOMATACEAE						
Clidemia capitellata (Bonpl.) D. Don	47	1	mesma	endo	s	
Miconia hipoleuca (Bonpl.) DC.	27	1	mesma	endo	s	
Miconia minutiflora (Bonpl.) DC.	70	3	mesma	endo	s	
MIMOSACEAE						
Albizzia polycephala Benth.	233	3*	sphi	endo (7)	s	7
Albizzia saman (Jack.) F. Müll.	710	3*	sphi	endo (1,6,7)	s	1,6,7
Inga ingoides (Rich.) Willd.	490	3*	sphi	endo	l	
MORACEAE						
Brosimum sp.	60	3	gen	endo		
MYRTACEAE						
Campomanesia dichotoma (O.Berg) Mattos	92	3	gen	endo	s	
Psidium guianense Pers.	157	3	gen	endo	s	
Eugenia sp.	13	1	gen	endo	s	
Myrtaceae sp. 4	62	3	gen	endo	s	
Myrtaceae sp. 5	13	1	gen	endo	s	
NYCTAGINACEAE						
Guapira laxiflora (Choisi) Lundell	30	3	gen	endo	s	
PIPERACEAE						
Piper arboreum Aubl.	13	1	gen	endo	s	
Piper marginatum Jacq.	140	1	gen (13)	endo	s	13
POLYGONACEAE						
Coccoloba mollis Casar	268	3*	gen	endo	s	
RUBIACEAE						
Alseis pickelii Pilger & Schmale	27	1	gen	anem	s	

Table 1 (*continued*)

Family/species	Ind	Diam	Poll	Disp	Seed	Ref
Genipa americana L.	2	2	mela	endo	s	
Psychotria capitata Ruiz & Pav.	13	1	gen	endo	s	
Psychotria bracteata DC.	13	1	gen	endo	s	
SAPOTACEAE						
Pouteria grandiflora (A. DC.) Baehni	15	3	phal	syn	l	
SAPINDACEAE						
Cupania cf. *oblongifolia* Mart.	808	3*	gen	endo	s	
Cupania paniculata Cambess.	62	3*	gen	endo	s	
Cupania revoluta Rolfe	50	3*	gen	endo	s	
Talisia esculenta (St.-Hil.) Radlk.	10	3*	gen	syn	l	
STERCULIACEAE						
Guazuma ulmifolia L.	92	2	myio (9)	endo (1)	s	9,1
TILIACEAE						
Apeiba tibourbou Aubl.	197	3*	mela (13)	endo (1)	s	13,1
Triumfetta althaeoides Lam.	20	1	gen	exo	s	
VERBENACEAE						
Aegiphila pernambucensis Moldenke	15	3	gen	endo	s	
VIOLACEAE						
Amphirrhox cf. *longifolia* (St.-Hil) Spreng.	20	1	mela (12)	aut	s	12

Ind=number of individuals; Diam=diameter group: 1=sub-canopy, 1*=juvenile (infertile), 2=canopy, 3=sub-canopy and canopy, 3*=fertile only in the canopy; Poll – pollination modes: ane=anemophily, can=cantharophily, gen=generalist pollination, mela=melittophily (large bees), mesma=melittophily (small bees), myio=myiophily, phal=phalenophily; psych=psychophily; sphi=sphingophily; thrips=pollination by thrips; Disp=dispersal modes: anem=anemochory, aut=autochory, endo=endozoochory, exo=exozoochory, myr=myrmecochory, syn=synzoochory; Seed=Seed and/or pyrene size class: s=small (1–15 mm), l=large (> 15 mm); Ref=References: 1= Janzen and Martin (1982), 2= Buchmann (1983), 3= Henderson (1995), 4= Proctor et al. (1996), 5= Arista et al. (1997), 6= Lorenzi (2002), 7= Sampaio and Gamarra-Rojas (2002), 8= Gottsberger and Silberbauer-Gottsberger (2006), 9= Westerkamp et al. (2006), 10= Moore (2001), 11= Krause (2008), 12= M. Braun (pers. comm.), 13=M. Ulbricht (2006).

Table 2
Dispersal modes and seed-size classes in percent, of fertile woody species and fertile individuals of the canopy and sub-canopy, collected in two capoeiras, Usina São José, Zona da Mata, state of Pernambuco. Small seeded=seeds up to 15 mm, large seeded=seeds greater than 15 mm.

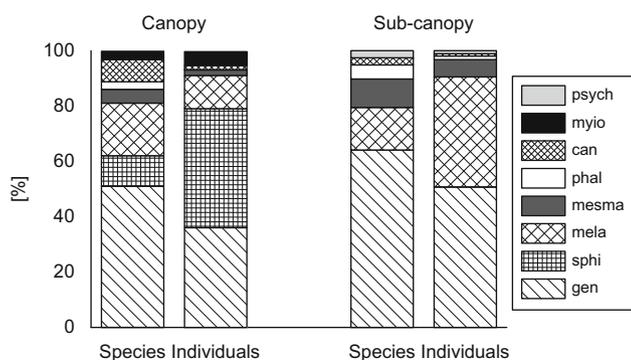| Dispersal mode	Canopy		Sub-canopy	
	Species	Individuals	Species	Individuals
Endozoochory	70.3	84.3	71.1	57.2
Synzoochory	19.4	6.2	10.5	26.6
Exozoochory	0.0	0.0	2.6	0.8
Myrmecochory	0.0	0.0	2.6	0.3
Anemochory	5.6	2.2	10.5	6.0
Autochory	5.4	4.8	5.3	9.0
Small seeded	73.0	74.4	86.8	71.8
Large seeded	27.0	25.6	13.2	28.2

Fig. 2. Pollination modes in percent, of woody species and fertile individuals of the canopy and sub-canopy, in two capoeiras, Usina São José, Zona da Mata, state of Pernambuco. gen=generalist pollination, sphi=sphingophily (sphingids), mela=melittophily (large bees), mesma=melittophily (small bees), phal=phalenophily (moths), can=cantharophily (beetles), myio=myiophily (flies), psych=psychophily (butterflies).

recuperation of sites that were intensively used for agriculture. During the 1980s, the studied sites were cleared of any original vegetation except a few shrubs and used for sugarcane cultiva-

tion. Hence, all tree species must have reached these sites, crossing at least the 50 m that separate Capoeira 1 from the next old growth forest fragment. In spite of that, canopy and sub-canopy vertebrate-dispersed species accounted for more than 80%, just as in an old-growth forest in the region (Santos et al., 2008). These values are only slightly below those Chazdon (2003) found for Costa Rican secondary and old-growth forests. Furthermore, relatively more canopy species had large seeds than in forest edge tree communities or other secondary forests inside the largest fragment of the region (Santos et al., 2008). This is surprising considering the unprecedented local mass extinction of large-bodied mammals and large frugivorous birds in the region and that many surviving species have ranges limited to particular forest fragments (Farias et al., 2007; Silva and Pontes, 2008) and exemplifies the resilience of the highly degraded area. The main dispersers at the study site were supposedly agouti (*Dasyprocta agouti*), fox (*Cerdocyon thous*), raccoon (*Procyon cancrivorus*) and lizard (*Tupinambis teguixim*), besides bats, various small- to medium-sized bird species, small rodents and marsupial species. These animals or their footprints were frequently observed and they are well-known fruit dispersers (Castro and Galetti, 2004; Lobova and Mori, 2007; Lobova et al., 2003; Nelio, 2006; van der Pijl, 1982). Relatively large animals are of importance with regard to the dispersal of the large seeds embedded in fruit pulp of *Annona* sp., *Inga ingoides*, *Rauvolfia grandiflora* and *Strychnos parvifolia*. The diaspores of *Swartzia pickelii*, *Gustavia augusta* and *Eschweilera ovata* are almost bare of any fleshy pulp, therefore we assume that they must have been scatter-hoarded by *D. agouti*; however, the latter might well be dispersed by bats (Prance and Mori, 1979). Some fruit trees with large seeds, such as *Acrocomia intumescens*, *Elaeis guineensis*, *Pouteria grandiflora* and *Talisia esculenta*, were probably not only dispersed by wildlife but also by humans and domestic animals that foraged at the sites when they were used as pastures. The second most important tree species, *Albizzia saman*, the second most important sub-canopy species *Senna georgica*, *Albizzia polycephala*, *Apeiba tibourbou* and *Guazuma ulmifolia* are likely to have reached the sites with cattle and horses as its fruits serve as fodder (Janzen and Martin, 1982; Lorenzi, 2002; Sampaio and Gamarra-Rojas, 2002). However,

diaspores adapted to particular animals might not reach the sites due to dispersal limitation. For example, the seeds of the chiropterophilous tree *Parkia pendula*, a common species of the Atlantic Forest fragments nearby (Piechowski and Gottsberger, 2008), were observed to be consumed and hence probably also dispersed by *Cebus flavius* monkeys, which are restricted to one single forest fragment at the São José plantation. Due to this disperser limitation, these seeds did not reach the capoeiras (Vlasaková and Piechowski, unpublished). Seeds of this species, directly sawn into the studied secondary forest, germinated and the saplings developed normally (Kimmel, unpublished).

Myrmecochorous small seeds with elaiosomes were only found in the shrub *Pera ferruginea*. Species dispersed by ants are likely to be hampered in colonizing sites cleared from stumps from which vegetative regeneration can take place, if no seed bank has remained and without any connection to existing forests, because ants do not carry seeds across long distances, and those that do as leaf-cutting ants, cut emerging seedlings (Costa et al., 2007; Horvitz and Schemske, 1986; Silva et al., 2007).

We found almost all expected pollination modes: canthar-ophily, phalenophily, psychophily, myiophily and sphingophily; pollination by thrips was not encountered among fertile indivi-duals, but juveniles of the thrips-pollinated *Xylopia frutescens* were found. However, we did not find any flowers adapted to vertebrates, neither birds, non-flying mammals, nor bats. This reflects the degradation of the analyzed vegetation, since in more intact vegetation of analyzed South American vegetation types pollination by bats and birds does occur (Dulmen, 2001; Girão et al., 2007; Gottsberger and Silberbauer-Gottsberger, 2006; Lopes et al., 2009; Machado and Lopes, 2004; Ramírez, 2004; Yamamoto et al., 2007). There is a parallel to the results of Lopes et al. (2009) who found much less bat-, non-flying mammal- and bird-pollinated species and individuals in secondary forest plots, and altogether less species and individuals pollinated by vertebrates. Chazdon et al. (2003) found less bat-pollinated species but more hummingbird-pollinated species in secondary forests, compared to old-growth forests. The ornithophilous herb *Heliconia psitta-corum* L.f. (Heliconiaceae), the ornithophilous liana *Lundia cordata* (Bignoniaceae) and two chiropterophilous lianas, *Mucuna pruriens* (L.) DC. and *M. urens* (L.) Medik. (Fabaceae), occurred in young secondary vegetation (T. Kimmel, unpublished), but were not part of our analysis due to their growth form.

Both canopy and sub-canopy of the analyzed capoeiras had more species with generalist than with bee flowers. This is exceptional since melittophily was the main pollination mode in all other studies conducted elsewhere in Neotropical biomes (Borges et al., 2009; Dulmen, 2001; Girão et al., 2007; Gottsberger and Silberbauer-Gottsberger, 2006; Lopes et al., 2009; Machado and Lopes, 2004; Ramírez, 2004; Yamamoto et al., 2007). Comparing secondary forest with old-growth forest, Chazdon et al. (2003) and Lopes et al. (2009) observed relatively more tree species pollinated by diverse small insects in secondary forest and small forest fragments than in continuous old-growth forest. These comparisons lead to the assumption that the earlier the succession stage is, or the smaller the forest fragments are, the more species are pollinated by various small insects and show a generalist pollination mode.

In opposition to the results of Girão et al. (2007), who assumed that hawkmoth pollination decreases with increasing disturbance, and Lopes et al. (2009), who found no typical pioneer species to be hawkmoth-, or beetle-pollinated, a relatively large number of sphingophilous species and individuals were found in the canopy of the studied capoeiras. Among canopy individuals, sphingophily was even the most common pollination mode. This can be explained by the high abundance of the tree species *Inga ingoides* and *Albizzia saman*. In addition, beetle-pollinated *Annona* sp.,

Elaeis guineensis, *Acrocomia intumescens* and *Desmoncus* sp. were found and, considering their habitat, are definitely characterized as pioneers. A shift from a moderate percentage of species pollinated by large bees to much higher percentage of individuals with this pollination mode, in the sub-canopy, can also be explained by the uneven abundance of species, which is a typical feature of young secondary vegetation (Harper et al., 1996). Wind-pollination is not totally absent in the studied vegetation: however, the only wind-pollinated species, *Cecropia palmata*, was categorized as generalist because it was also pollinated by diverse small insects.

Classification is one major source for bias in analyzing a plant community's pollination modes. First, flowers are not always specialized to specific pollinators (see e.g., Johnson and Steiner, 2000). Second, different observers may come to different results, e.g., *Inga edulis* and *I. thibaudiana* were classified to be bird-pollinated by Chazdon et al. (2003), and to be bat-pollinated by Lopes et al. (2009). According to Vogel (1968)*Inga sessilis* is probably the only member of the genus clearly adapted to bats and none is adapted to bird pollination. Third, in some cases the way of calculating the scores of pollination modes differ from each other. In some studies, single species account for more than one pollination mode (e.g., Dulmen, 2001; Ramírez, 2004; Yamamoto et al., 2007), while in others one species can only have one mode of pollination (Chazdon, 2003; Gottsberger and Silberbauer-Gottsberger, 2006, this study; Machado and Lopes, 2004). Forth, careful literature analysis and correct data extraction from literature are crucial. Girão et al. (2007) and Lopes et al. (2009) both quote Steiner (1983) when writing that *Mabea occidentalis* is non-flying mammal-pollinated, however, Steiner (1983) described this species to be clearly bat-pollinated, and only occasionally visited by non-flying mammals. Fifth, the case of *Ocotea glomerata*, which occurred in the capoeiras, is an example for the need of detailed ecological studies of single species. It has open unisexual flowers, visited by a wide range of insects, and it was possible only through a laborious study to render evidence that exclusively fly species effectively pollinate them (Krause, 2008). Sixth, flower visitors may profit from floral resources independent from pollination mode or success. This is often of importance for animal populations, including endangered or rare mammals, especially in times of scarcity of other resources (Garber, 1988; Janson et al., 1981; Marín-Gómez, 2008). The two most common canopy species *Inga ingoides* and *Samanea saman* bear easily accessible flowers with relatively large amounts of nectar (Kimmel, unpublished). Hummingbirds were observed to feed also on melittophilous flowers of *Genipa americana* and *Rauvolfia grandiflora* and many others.

The study took place in one of the world's most endangered hotspots of biodiversity (Myers et al., 2000) and indeed there are several implications for nature conservation and restoration that can be drawn from our findings. The fact that regeneration of secondary forest took place after complete clearing, including the elimination of the seed bank by sugarcane cultivation, and spatial isolation from diaspores sources exists, gives hope that the much-discussed reforestation is feasible without high costs. According to Brazilian legislation (Código Florestal Brasileiro, 2001), river banks, slopes with an inclination above 45°, and 100 m broad strips along the borders of tablelands must be reforested, so that erosion is prevented and a re-connection of fragments via corridors and stepping stones is facilitated – necessary measures to preserve the biodiversity of existing fragments (SECTMA, 2002). We think that most sites would only have to be taken out of cultivation and protected against fire that can spread from neighboring sugarcane fields and regeneration would occur by itself. Most animal groups that mutually interact with plants and are therefore of high importance for ecosystem functioning, will

find suitable partners in the secondary vegetation and are hence supposed to be able to use it as habitat or for migration. The encountered gaps in the composition of pollination modes, especially the absence of bat pollination and the lack of seeds typically dispersed by large birds or monkeys, and species dispersed by ants, should be bridged by active reforestation.

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