

Fruiting phenology of palms and trees in an Atlantic rainforest land-bridge island

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Abstract

Tropical forests show periods of scarcity and high fruit production in the same year and/or between years. Palms are an important component of Neotropical rainforests and a significant food resource for several frugivores. Therefore, their role as keystone resource may be exacerbated in highly impoverished areas. In Anchieta Island, São Paulo/Brazil, human settlements have modified and impoverished the forest, mainly through overharvesting and the introduction of exotic plants and several mammal species. We assessed the offer of fruits consumed by vertebrate frugivores at this island, the vegetation of which is belonging to the Brazilian Atlantic rainforest. We compared whether the fruiting patterns and fruit fall differ between palms and trees, and discuss the importance of palms as a food resource for frugivores and the implications for Anchieta Island conservation. Phenological patterns were seasonal for both trees and palms; however, the times of fruiting occurrence differed. Fruit fall biomass was at least twice lower than reported for other Atlantic rain forests and was also different between trees and palms. Palms contributed more than 80% of the overall fruit fall biomass. Palms may constitute an alternative food resource in periods of low fruit availability, although they do not provide resources for the entire assemblage of vertebrate frugivores. Energy-rich fruits, such as those produced by palms, may play an important role in the maintenance of frugivore populations in isolated, disturbed environments with a high density of vertebrate frugivores, low diversity of fruiting species and fruit biomass such as those found on Anchieta Island.

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Introduction

Tropical rainforests are considered one of the world's most productive habitats, where fruit biomass ranges between 180 and 1000 kg ha⁻¹ yr⁻¹ (Jordano, 1992). Of this biomass, about 70–94% is produced by woody species, and the seeds and fruits are dispersed by vertebrates (Howe and Smallwood, 1982; Jordano,

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1992). Despite this high fruit production, phenology patterns display both, temporal and spatial fluctuations in well-preserved tropical rain forests (Castro et al., 2007; Frankie et al., 1974; Morellato et al., 2000; Wright et al., 1999). Although seasonal reproduction patterns are frequently found in most tropical rain forests, weak or non-seasonal fruiting patterns have been also reported for some communities (Hilty, 1980; Koptur et al., 1988; Morellato et al., 2000). Phenological patterns are also influenced by the successional status of the forest and secondary forests might present more extended fruiting patterns and larger crop sizes per area than primary forests (Fleming, 1985; Levey, 1988a, b).

Palms are an important food resource for a wide assemblage of vertebrate frugivores (Forget et al., 1994; Galetti et al., 1999; Kiltie, 1981; Peres, 1994a; Zona and Henderson, 1989), and have been regarded as a “keystone resource” for frugivores in tropical forests (Kinnaird, 1992; Terborgh, 1986a). The Arecaceae family presents a wide distribution in tropical and subtropical areas of the world with approximately 189 genera and 3000 species (Henderson et al., 1995). Neotropical forests comprise 60 genera and 550 species of palms, with at least 10 genera and 40 species occurring in the Brazilian Atlantic forest, many of which are endemic (Henderson et al., 1995).

Reproductive phenological studies on palms are frequently based on a single species (Borchsenius, 2002; Castro et al., 2007; Galetti et al., 1999; Henderson et al., 2000; Scariot and Lleras, 1995), and less frequently on several species or communities (Borchsenius, 1997; De Steven et al., 1987; Henderson et al., 2000; Ibarra-Manríquez, 1992; Peres, 1994b). As far as we know, this is the first study to compare palm fruiting phenology patterns with the wider tree community.

Insular environments have long been used by biologists to test basic principles of ecology, evolution and biogeography (Vitousek et al., 1995; Whitaker, 1998). More recently, insular environments have played a prominent role in conservation ecology, where the aim has usually been to conserve species or assemblages unique to isolated habitats (Drake et al., 2002). Islands, because of their peculiar attributes (isolation, small populations, community “impoverishment”, absence of entire taxonomic groups and high levels of endemism) (Whitaker, 1998), are more susceptible than continental habitats and have historically been disturbed due to human intervention mostly through the introduction of invasive plants and feral animals that are conducive to the disruption of mutualism (Courchamp et al., 2003; Fernandez Palacios and Morici, 2002; Maunder et al., 2002).

In the coastal area of Brazil, land-bridge and oceanic islands have been highly disturbed by the introduction of exotic species (Bovendorp and Galetti, 2007). One of these islands is Anchieta Island (Parque Estadual Ilha

Anchieta), located 530 m off the coast of the state of São Paulo, southeast Brazil. In 1983, Anchieta Island suffered from the introduction of several mammal species such as agoutis, coatis, capybaras, deer and armadillos (Bovendorp and Galetti, 2007). The establishment of human settlements in the area resulted in the modification and impoverishment of the forest, mainly through overharvesting and the introduction of exotic plants species (Guillaumon et al., 1989). Therefore, common vertebrate-dispersed families of Atlantic rain-forest trees such as Lauraceae, Myricaceae and Myrtaceae are rare and most of the natural vegetation has been altered (Guillaumon et al., 1989). Nine palms with seeds dispersed by vertebrates occur on the island, of which six are native and three are exotic.

We evaluated the temporal variation in the offer of fruit species consumed by vertebrate frugivores on Anchieta Island from a comparative perspective. We contrast the fruiting patterns and fruit fall between palms and trees and discuss the importance of palms as a food resource for frugivores in this disturbed habitat. We expected to find longer fruiting patterns for palms in relation to that presented by trees, therefore emphasizing the importance of palms as a reliable and high-quality food resource (De Steven et al., 1987; Peres, 1994b) for introduced and native vertebrate frugivores in the impoverished environment of Anchieta Island. We suggest that palms may represent a keystone resource, supporting vertebrate frugivores on highly disturbed, isolated environments.

Materials and Methods

Study site

The study was carried out at Anchieta Island, a land-bridge island of 806 ha located in Ubatuba, Northeast of São Paulo State, Brazil (45°02'W, 23°31'S) (Fig. 1).

By the middle of the 19th century, the original indigenous settlements of Anchieta Island were supplanted by Europeans, who subsisted through activities such as fishing, and coffee, sugarcane, corn and potato cultures (Guillaumon et al., 1989). In 1904, the residents of the island were transferred to the continent due to the establishment of a State Prison in the area (Guillaumon et al., 1989). During the prison period, activities such as plantations, cattle ranching and the harvesting of wood for both fuel and the fabrication of broomsticks were carried out on the island (Guillaumon et al., 1989). In 1977 Anchieta Island was established as a São Paulo State Park and, currently, there are no residents in the Island, which is one of the largest tourist attractions in the São Paulo state (Robim, 1999).

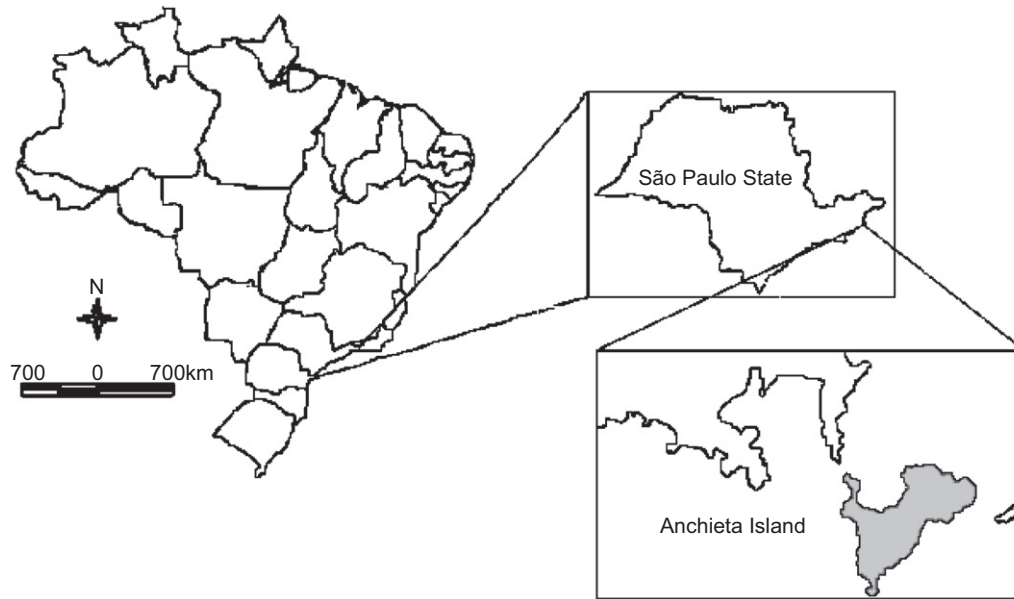


Fig. 1. Location of Anchieta Island (gray) in the Northeast of São Paulo State, Brazil.

The climate of Anchieta Island is tropical rainy (Köppen, 1948) with substantial rain occurring every month. Rainfall and temperature data for the 1956–1985 period indicate the presence of two distinct periods within a year, one super-humid from September to May with rainfalls above 100 mm per month, and the other less humid from June to August when rainfall is below 100 mm per month (Walter, 1986; Fig. 2a). There is no rainfall deficit in the study site. The mean temperature was 24 °C, the total annual rainfall was 2104 mm (Fig. 2b) and the annual mean relative humidity was 84%. Climate and photoperiod data for the study site were provided by the Instituto Agronômico de Campinas (IAC) and Pereira et al. (2001) respectively.

Anchieta Island is covered by secondary lowland Atlantic rainforest dominated by *Nectandra* spp., *Tabebuia cassinoides* (Lam.) DC., *Simarouba* spp., *Clarisia racemosa* Ruiz & Pav., *Cedrela fissilis* Vell., *Dalbergia nigra* Vell., *Plathymenia* spp. and *Myrcarpus frondosus* Allemão (Guillaumon et al., 1989). Among native palms species are *Astrocaryum aculeatissimum*, *Attalea humilis*, *Syagrus pseudococos*, *Syagrus romanzoffiana*, *Bactris setosa* and *Euterpe edulis* (Guillaumon et al., 1989; see Appendix A for authors of scientific names). Three introduced palm species occur in the island, the invasive Chinese palm *Livistona chinensis* and the ornamental *Cocos nucifera*, which is restricted to the settlement areas along the beach (Guillaumon et al., 1989) and one individual of *Euterpe oleracea*. The coconut palms and *E. oleracea* were not considered in our present study because their fruits are not eaten by vertebrate frugivores or they are rare in the island. In addition to the introduced palms species, we found individuals of the introduced species *Anacardium*

occidentale L., *Artocarpus heterophyllus* Lam., *Bambusa vulgaris* Schrad. ex J.C. Wendl., *Carica papaya* L., *Casuarina* sp., *Cycas circinalis*, *Citrus aurantium* L., *Hibiscus* spp., *Coffea arabica* L., *Eucalyptus* sp., *Eugenia jambolana* Lam., *Hovenia dulcis* Thunb. and *Mangifera indica* L., which are restricted to the administration area of the Park or to the abandoned settlements of the prison period. We do not have access to a complete floristic list of species since the only study conducted in the Island up till now is restricted to the dune vegetation (Reis-Duarte, 2004).

Palms studied

A. aculeatissimum has simple or multiple stems of 4–8 m height, the fruits are light brown ranging from 3 to 4.5 cm in length and 3 to 3.5 cm in diameter (Henderson et al., 1995; Lorenzi et al., 1996, 2004), and are consumed by scatter-hoarding rodents (Donatti, 2004; Galetti et al., 2006).

A. humilis has a subterranean or simple stem of 1 m height. Its fruits are light brown and range from 6 to 9 cm in length and 4 to 8 cm in width; it is also dispersed by scatter-hoarding rodents (Lorenzi et al., 1996, 2004) as found also for congeneric species with similar fruits (Almeida and Galetti, 2007).

S. pseudococos has a simple 10–15 m high stem and yellow colored fruits, 6–7 cm in length and 4 cm in width. It is also dispersed by rodents (Lorenzi et al., 1996, 2004; C. Donatti, unpublished data). *S. romanzoffiana* has a solitary stem of 7–15 m height, yellow-orange fruits, 2–3 cm in length and 1–2 cm in diameter. Its seeds are consumed by primates,

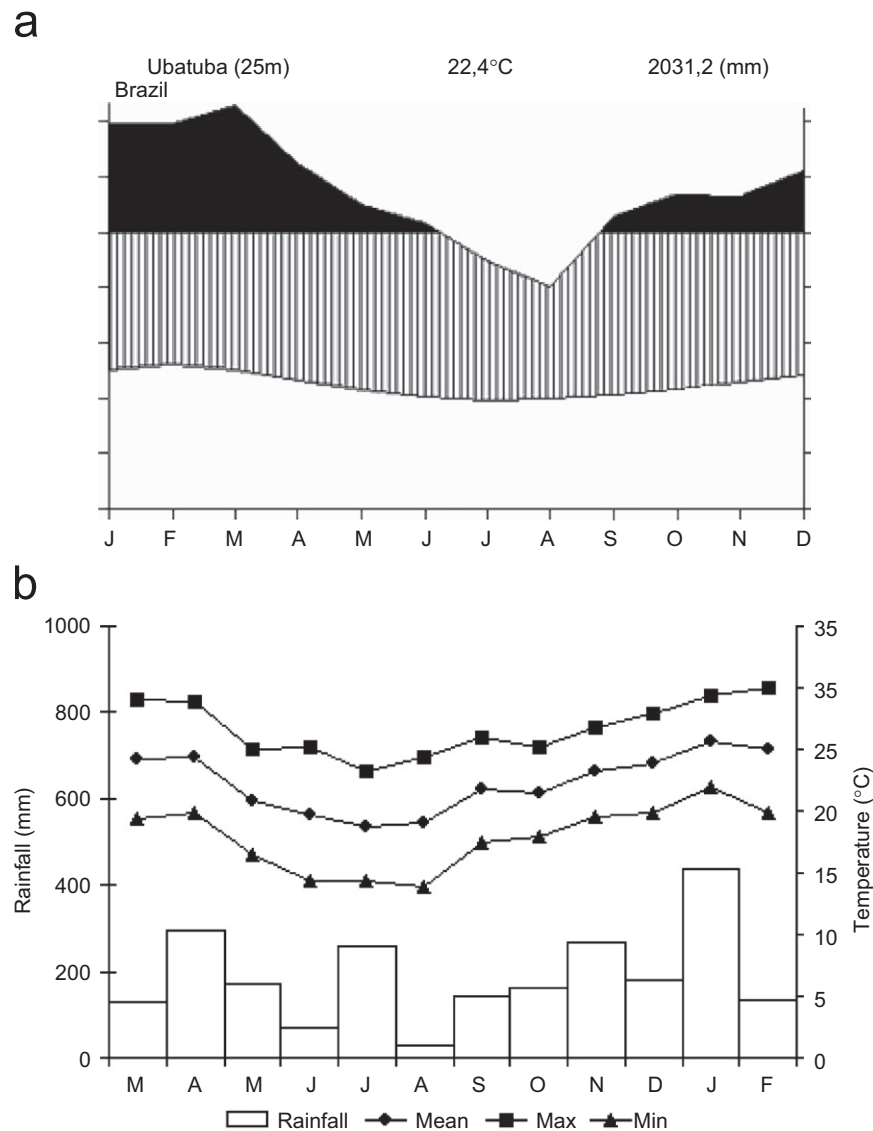


Fig. 2. (a) Climatic diagram according to Walter (1986) displaying the mean rainfall and temperature for a 30 years period (1956–1985) in the Ubatuba region (45°07'W and 23°30'S), and (b) Distribution of rainfall and mean temperature during the study period in Ubatuba, Brazil. Data from Instituto Agrônomico de Campinas (IAC).

carnivores, ungulates, birds and squirrels (Galetti et al., 1992; Henderson et al., 1995; Lorenzi et al., 1996, 2004).

B. setosa has multiple stems of 6 m height, fruits of a dark-purple color ranging from 1 to 1.5 cm in length and 1.5 to 2 cm in diameter. It is dispersed by carnivores (Lorenzi et al., 1996, 2004; Marques, 2004).

E. edulis has solitary stems of 5–12 m height, black-purple drupes of 1–1.4 cm in length and it is dispersed by birds, squirrels, bats and primates (Galetti et al., 1999; Henderson et al., 1995; Lorenzi et al., 1996, 2004).

L. chinensis also has solitary stems of 5–15 m height and dark green fruits, which are dispersed mainly by birds, but also eaten by foxes, tapirs, deers and rodents (Galetti et al., 1999).

Information about the mammal fauna on the island prior to human occupation is limited, although Bovendorp and Galetti (2007) suggest it might be similar to that present on the mainland. Fifteen mammal species were introduced to Anchieta Island in 1983, and nowadays they represent the highest density of mammals in the forest (Bovendorp and Galetti, 2007). The avifauna of Anchieta Island is highly impoverished with only 72 forest dwelling species and suffered severe modifications due to poaching, forest logging and the introduction of exotic species, especially nest predators (Alvarez and Galetti, unpublished). Tanagers, thrushes and flycatchers are the most important frugivores on the island (Fadini, 2005). Larger species, such as toucans, the dusky-legged guans and jacutingas are absent on

Table 1. List of vertebrate frugivores that eat palm fruits at Anchieta Island, Ubatuba, SP, Brazil, indicating whether fruits are consumed in the canopy or if they feed on fallen fruits

Frugivores		Fruit consumption		Palms eaten	Reference
Group	Species	Fallen fruits	Canopy		
Reptiles	<i>Tupinambis meriane</i>	x		Sr, Sp	Castro and Galetti (2004)
Birds	<i>Turdus flavipes</i>		x	Ee, Lc	Fadini (2005)
	<i>Turdus albicollis</i>		x	Ee, Lc	Fadini (2005)
	<i>Saltator similis</i>		x	Ee, Lc	Fadini (2005)
Mammals					
Marsupialia	<i>Didelphis aurita</i>	x	x	Sr	M Galetti, unpublished data
Carnivora	<i>Nasua nasua</i>	x	x	Sr	Alves-Costa
Primates	<i>Callicthrix penicillata</i>		x	Sr	
	<i>Cebus nigrurus</i>		x	Sr, Sp	M Galetti, unpublished data
Rodentia	<i>Dasyprocta leporina</i>	x		Sr, Sp, Ee, Lc, Ah, Aa, Bs	C. Donatti, unpublished data
Rodentia	<i>Cuniculus paca</i>	x		Sr, Sp, Ee, Lc, So, Ah, Aa, Bs	
Rodentia	<i>Trynomis</i> spp.	x		Sr, Ee, Lc	R. Bodendorp and C. Neves, unpublished data

Sr = *Syagrus romanzoffiana*, Sp = *Syagrus pseudococos*, Ah = *Attalea humilis*, Bs = *Bactris setosa*, Lc = *Livistronia chinensis*, Aa = *Astrocaryum aculeatissimum*.

Anchieta Island (Fadini, 2005). The Anchieta Island has one of the most impoverished frugivore fauna of the whole Atlantic rain forest and most of the available frugivores feed on palm fruits in some periods of the year (Table 1).

Phenological data

Phenological observations on flowering and fruiting patterns were carried out monthly, from May 2004 to May 2005 along three trails of approximately 1 km in length. Since we intended to study only tree species, all trees with DBH (diameter at breast height) ≥ 15 cm and within a 2 m distance from the trails were marked with aluminum tags (Morellato et al., 2000). All individuals of palms with evidence of reproductive activity such as reproductive scars or old inflorescences/infructescences were marked along the trails (Henderson et al., 2000). We did not use the same methodology for palms and trees because it is difficult to establish a DBH that indicates reproductive stage within palm species and they display different growth strategies (Henderson, 2002). Therefore, we used a method that guaranteed sampling of reproductive individuals in both groups: A minimum sample size of 10 palm individuals per species was established since they are the focus of this study and a minimum sample size is required in order to describe the species phenology (Fournier and Charpantier, 1975). Thus, a total of 272 trees and 116 palms were monitored monthly for the presence or absence of flower buds,

open flowers, unripe and ripe fruits (Bencke and Morellato, 2002). In Appendix A we present a list of the plant species with the number of sampled individuals per species, phenological data and dispersal modes described on the basis of our own observations and the literature. The voucher material is deposited in the Herbarium Rioclarense (HRCB) at Universidade Estadual Paulista (UNESP).

Fruit biomass

To estimate the fruit fall trends of palms and trees, 10 points along the three trails were randomly selected each month, and all the animal-dispersed fruits and seeds were collected, oven-dried at 50 °C for 1 week and then weighed (Charles-Dominique et al., 1981). The values were transformed into $\text{kg ha}^{-1} \text{ month}^{-1}$ for each group. The area sampled at each point was limited by tags measuring 1 m to either side of the trail, beginning at the center, and was 10 m long, covering a total area of 20 m² (10 m \times 2 m). The total area sampled to quantify fruit production each month was 0.06 ha. The collection of the fruits and seeds was carried out according to Castro et al. (2007).

We chose the raked trail survey because it is a practical and rapid method for assessing fruiting phenology (Zhang and Wang, 1995). It also provides more comparable results than other methods, and has the advantage of efficiently censoring a relatively large area of the forest avoiding the effect of plant species

concentration and maximizing the spatial variation in each site (Barlow and Peres, 2006). These advantages compensate the fact that the method overlooks the consumption of fruits by arboreal mammals and does not account for the fruits consumed by terrestrial frugivores, which can rapidly remove fruits from the ground (Zhang and Wang, 1995), particularly in the Anchieta Island where the density of frugivores is high. The elevated densities of rodents that may prey upon palm fruits may also lead to an even lower estimate of the fruit fall on Anchieta Island.

Data analysis and statistics

For the statistical analyses, individuals were separated into two groups, palms and animal-dispersed trees. Four phenological reproductive variables were calculated for each individual of each group, following Morellato et al. (2000). These variables were: (a) date of first unripe fruit, (b) date of first ripe fruit, (c) date of unripe fruit peak and (d) date of ripe fruit peak. Flowering was described qualitatively only to clarify fruiting patterns.

Circular statistics were used to look for seasonality, as proposed by Morellato et al. (2000), calculating the mean angle for data of each of the phenological variables mentioned above. The angle indicates the date or month of flowering or fruiting events, with 0° representing the first month of observation (Morellato et al., 2000). When the peak date occurred in two consecutive months, the average was used (Morellato et al., 2000). The frequency of species in each phenological variable within each angle was calculated and the following parameters were estimated: the mean angle a , the angular dispersal confidence limit of the frequency distribution, and the length of the vector r which is a measure of concentration around the mean angle. It ranges from zero when an equal number of phenological records occur in each angle to one when all records occur in one single angle or month. The significance of the mean angle was estimated by the Rayleigh (z) test. The mean date corresponding to the mean angle for each phenophase was determined by converting the mean angular directions to corresponding mean dates. Analyses followed Zar (1996) and were performed with ORIANA software (Kovach, 1984); Watson's U (von Mises) test was carried out to check the normal distribution of the data.

The seasonality hypothesis tests also followed Morellato et al., (2000), defining status H_0 as phenological variables being distributed uniformly all year round, and hence there is no seasonality. If H_0 is rejected, phenological variables are not uniformly distributed, and thus there is a significant mean angle or date for the phenological variable or seasonal pattern. The intensity of concentration around the mean

angle, denoted by r , can be considered a measure of the degree of seasonality (Morellato et al., 2000). When the mean angle was significant, a two sample Watson–Williams test (F) was performed to compare the mean dates between palms and trees.

Results

We observed the phenology of 57 species, where 67% were vertebrate-dispersed species, 12% were wind dispersed, 5% were autochoric and 16% were undetermined (see Appendix A). Of the 272 trees sampled, 29.8% did not show any reproductive event, 51.1% just flowered and 19.1% flowered and fruited. We observed 50 tree species from which 8% did not show reproductive activity, 12% just flowered and 80% flowered and fruited. From the 116 palms sampled, 16.4% did not show any reproductive event, 10.3% just flowered and 73.3% flowered and fruited. We used only vertebrate-dispersed species ($N = 38$) in the statistic analyses and in the graphic comparisons between palms and trees.

Comparative phenology of palms and trees

Flowering of trees occurred between September and November, with a peak in November (Fig. 3a). Palms presented a more irregular pattern with individuals flowering in all months, increasing in the rainy season (Fig. 3b). The period of higher fruiting activity for animal-dispersed trees occurred from November to February with a peak for unripe fruits in January (19.2% of individuals), and in February for ripe fruits (19% of individuals; Fig. 3a). Palm individuals fruited all the year round, with a reduction in the percentage from January to April, which coincided with the period of higher activity in trees (Fig. 3b). Palms presented a fruiting peak in November for unripe fruits (47.41% of individuals) and in December for ripe fruits (29% of individuals) (Fig. 3b).

Fruiting was seasonal for both trees and palms (Table 2), and the seasonal patterns were significantly different between trees and palms both for the first date ($F = 10.53$, $p = 0.001$) and the peak date ($F = 7.430$, $p = 0.007$) of ripe fruits. Unripe fruits did not show significant differences among palms and trees.

Fruiting activity of trees was concentrated in the wettest season, from November to February, while palms constantly showed more than 10% of individuals fruiting in all months (Fig. 4a). Only from December to February did trees present a higher percentage of individuals fruiting than palms, while from March to October palms exhibited a notably higher percentage of individuals fruiting (Fig. 4a).

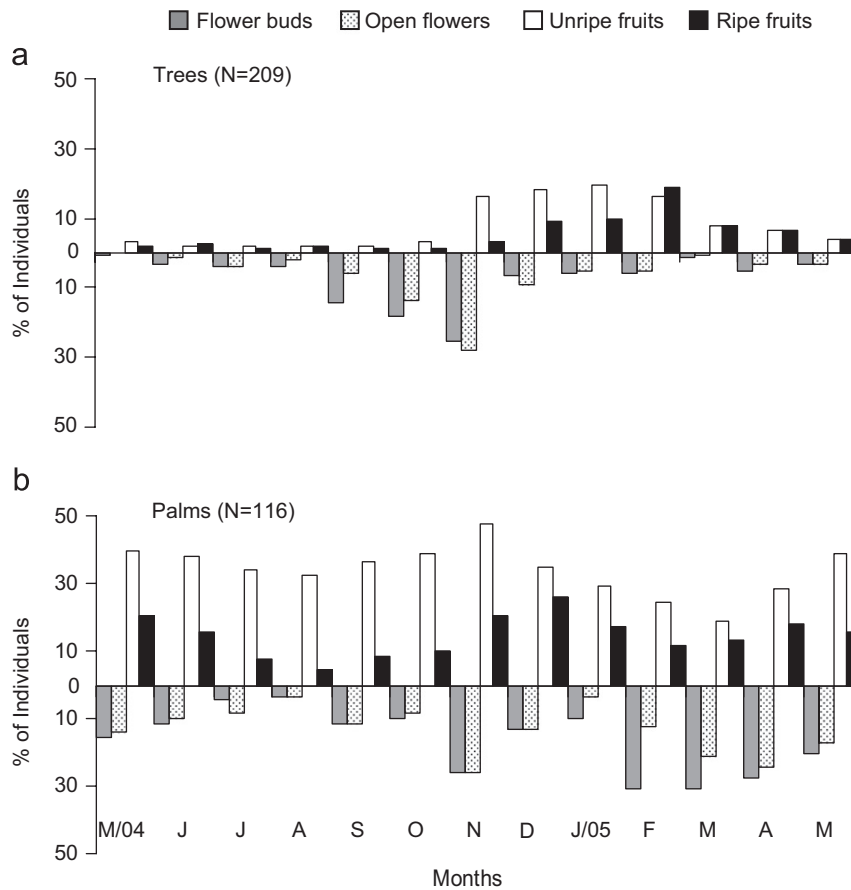


Fig. 3. Percentages of individuals of (a) trees and (b) palms flowering and fruiting on Anchieta Island, Ubatuba, Brazil.

Table 2. Circular statistical analysis of the occurrence of seasonality for palms (seven species) and trees (38 species) on Anchieta Island, Ubatuba, Brazil

	Phenological variables			
	Unripe fruits		Ripe fruits	
	First date	Peak date	First date	Peak date
Palms				
Observations (<i>N</i>)	32	31	52	52
Mean angle (<i>a</i>)	185.64°	220.94°	202.09°	214.97°
Mean date	30/Nov	6/Jan	17/Dec	30/Dec
Circular deviation	68.79°	59.44°	74.30°	69.59°
Length of mean vector (<i>r</i>)	0.48	0.58	0.43	0.48
Rayleigh test (<i>p</i>)	<0.01	<0.01	<0.01	<0.01
Trees				
Observations (<i>N</i>)	95	95	100	100
Mean angle (<i>a</i>)	202.707°	219.12°	241.429°	247.595°
Mean date	17 Dec	5/Jan	28/Jan	3/Feb
Circular deviation	53.108°	53.75°	57.943°	62.871°
Length of mean vector (<i>r</i>)	0.651	0.644	0.6	0.548
Rayleigh test (<i>p</i>)	<0.01	<0.01	<0.01	<0.01

Significant values $p < 0.05$.

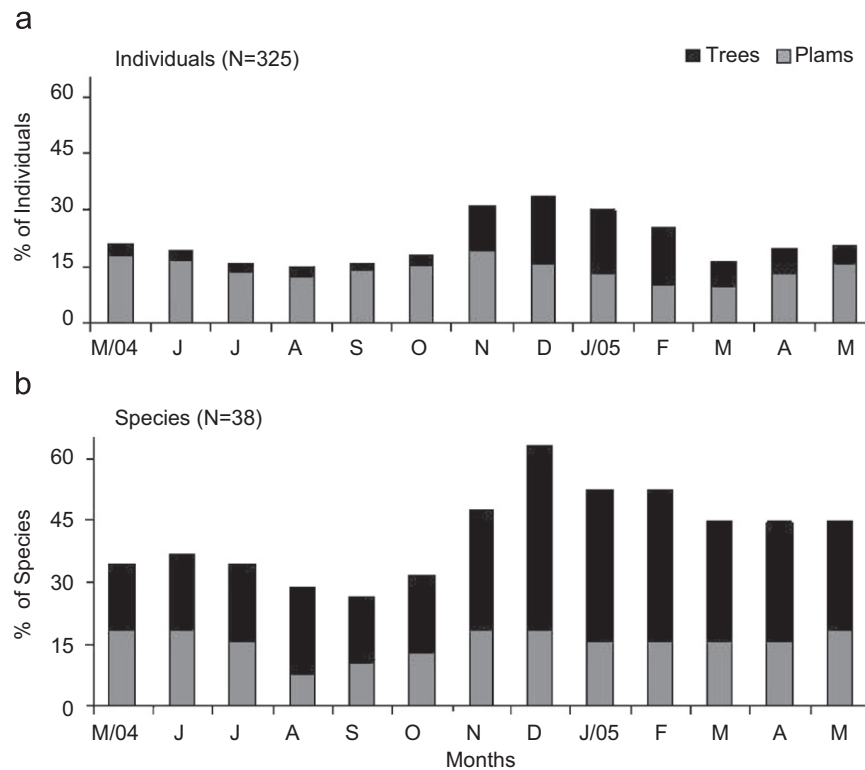


Fig. 4. Relative percentage of (a) individuals and (b) species of trees and palms fruiting on Anchieta Island, Ubatuba, Brazil.

Trees showed a higher percentage of species fruiting in the wettest season that overlapped with the period with higher percentage of trees fruiting (November–February) (Fig. 4b). Palms presented a constant number of species fruiting almost all year, generally ranging from 5% to 12% of species, with a similar but less pronounced trend than that observed for the proportion of individuals fruiting (Fig. 4b).

Fruit biomass

Palms showed a high peak of fruit biomass in April while for trees a less pronounced fruit peak occurred in December (Fig. 5a). Palms also showed two minor peaks, one in October–November and the other in January. Both peaks were higher than the peak for tree fruit biomass (Fig. 5a). From July to September fruit fall biomass was almost nil for both groups. The overall fruit fall biomass was $119 \text{ kg ha}^{-1} \text{ yr}^{-1}$, $103.2 \text{ kg ha}^{-1} \text{ yr}^{-1}$ of this value – 83.7% – corresponded to palm fruits. Among palms, the higher contribution to fruit fall biomass was contributed by *S. pseudococos* ($50 \text{ kg ha}^{-1} \text{ yr}^{-1}$, 42%), *S. romanzoffiana* ($36.6 \text{ kg ha}^{-1} \text{ yr}^{-1}$, 30.76%) and *E. edulis* ($13.8 \text{ kg ha}^{-1} \text{ yr}^{-1}$, 11.6%) (Fig. 5b). *B. setosa* showed no contribution at all, in accordance with its restricted distribution and low abundance in the Anchieta Island.

Palm species phenology

Astrocaryum aculeatissimum

Flowering occurred from January to June. Fruiting took place almost all the year round, from March to December, with a peak in July and August for unripe fruits (8% of individuals) and in November for ripe fruits (6% of individuals) (Fig. 6a).

Attalea humilis

The flowering and fruiting of *A. humilis* was highly irregular, with low proportions of individuals in flower and fruit almost every month (Fig. 6b).

Syagrus pseudococos

This species showed the highest percentage of individuals flowering and fruiting. Flowering occurred all the year round, with more than 15% of individuals in flower from February to April and peaking in April (Fig. 6c). Fruiting occurred all the year round too, with up to 24% of individuals having unripe fruits during a prominent peak from August to October. A lower peak in December was registered for ripe fruits, comprising 15% of the individuals (Fig. 6c).

Syagrus romanzoffiana

Flowering was concentrated from September to December but fruiting was observed all the year round

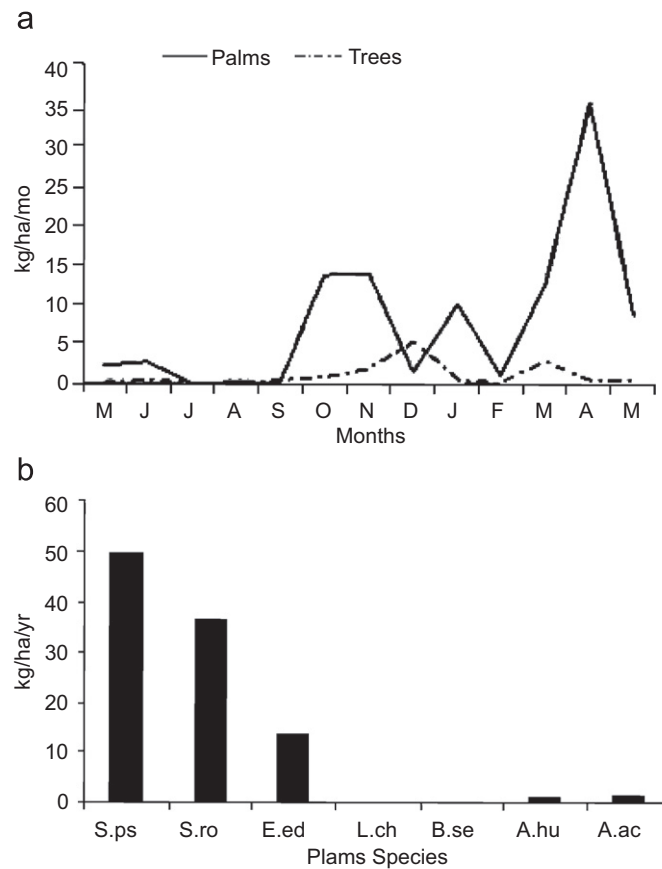


Fig. 5. Patterns of fruit fall on Anchieta Island, Ubatuba, Brazil. (a) Fruit fall biomass trends ($\text{kg ha}^{-1} \text{ months}^{-1}$) of trees and palms, and (b) total fruit fall biomass ($\text{kg ha}^{-1} \text{ yr}^{-1}$) of the palm species *S.ps*, *Syagrus pseudococos*; *S.ro*, *Syagrus romanzoffiana*; *E.ed*, *Euterpe edulis*; *L.ch*, *Livistona chinensis*; *B. se*, *B. setosa*; *A. hu*, *Attalea humilis*; *A.ac*, *Astrocaryum aculeatissimum*.

(Fig. 6d). The highest percentage of fruiting individuals was found in May, with 7% and 8% of the individuals bearing unripe and ripe fruits, respectively (Fig. 6d).

Bactris setosa

This species showed the shortest flowering and fruiting period of all species (Fig. 6e). Flowering occurred from November to December, peaking in November, and fruiting was observed from November to January, showing an unripe fruit peak in November with 7% of the individuals and a ripe fruit peak in December for 5% of the individuals.

Euterpe edulis

Flowering occurred from September to January, while fruiting was observed from November to July, peaking from December to February (8% of individuals) for unripe fruits, and in March and April for ripe fruits (7% of individuals) (Fig. 6f).

Livistona chinensis

Flowering occurred from September to April with less than 5% of the individuals flowering (Fig. 6g). Fruiting was observed in all months except August. Unripe fruits

occurred all the year round, peaking from October to February and from April to May (4% of individuals). Ripe fruits were found from February to July, peaking in May and June (5% of individuals) (Fig. 6g).

Discussion

Contrary to our expectations palms, similar to trees, presented seasonal fruiting patterns on Anchieta Island. However, the divergent timing of occurrence of ripe fruits between palms and trees suggests a complementary ripe fruiting pattern, thereby providing food resources for frugivores throughout the year, as expected. Seasonal and non-seasonal fruiting patterns have been reported for tropical rain forest trees (Hilty, 1980; Koptur et al., 1988; Morellato et al., 2000; Williams-Linera, 1997). The seasonal fruiting pattern of Anchieta Island trees differs from the non-seasonal fruiting patterns for trees from community in the mainland (Morellato et al., 2000). The differences might be related to the secondary status of the studied forest, as suggested by comparison with studies of other

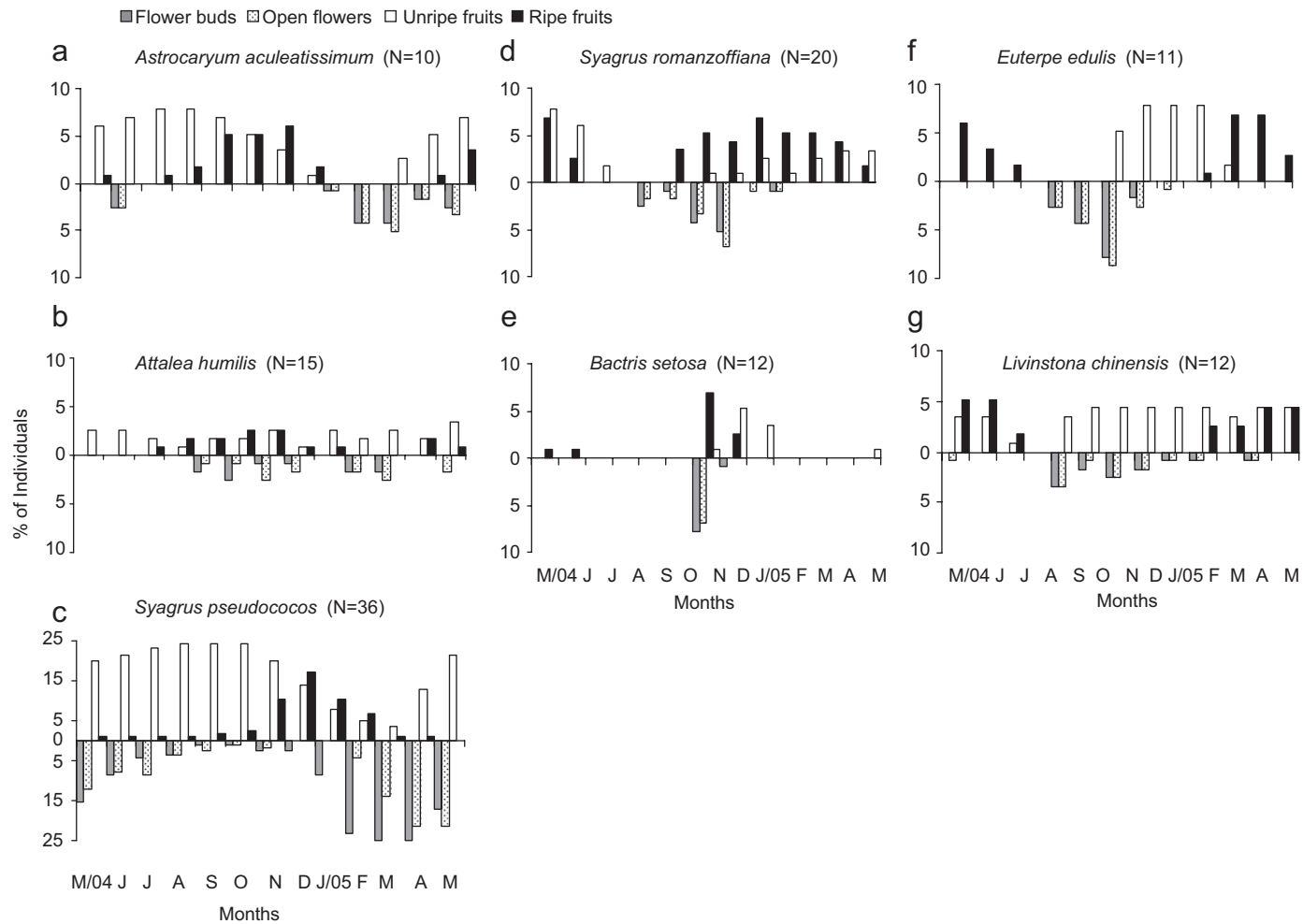


Fig. 6. Relative percentage of individuals flowering and fruiting from seven palm species on Anchieta Island, Ubatuba, Brazil, grouped by main vertebrate seed dispersal agent: (a–c) rodent; (d, e) mixed (dispersed by general species) and (f, g) bird dispersed species. Note the different scale for *Syagrus pseudococos*.

Table 3. Flowering and fruiting patterns of palm communities in several neotropical rain forest sites

Country	Season		Rainfall (mm)
	Flowering	Fruiting	
México ^a	Dry season (Apr–May)	All year	4725
Panama ^b	Rainy season (May to mid-Dec)	All year	2400
Brazil ^c	Dry season (July–Sept)	***	2186
French Guiana ^d	Dry season (Aug–Sept)	Wet season (Dec–Jan)	3108
Brazil ^e	***	All year	3256

***Not evaluated.

^aIbarra-Manríquez (1992).

^bDe Steven et al. (1987).

^cHenderson et al. (2000).

^dSist (1989).

^ePeres (1994b).

Table 4. Comparison of estimates of fruit fall biomass ($\text{kg ha}^{-1} \text{yr}^{-1}$) of animal-dispersed species using different methods in neotropical rain forests

Country	Field station	Fruit fall ($\text{kg ha}^{-1} \text{year}^{-1}$)	Methods	Reference
Brazil	Saibadela	370	Fruit traps	Galetti (1996)
Brazil	Serra do Mar	228	Trail census	Marques (2004)
Brazil	Cardoso Island	127	Trail census	Castro, unpublished data
Brazil	Ilha Anchieta	119	Trail census	Present study

*Data corresponding only to *Euterpe edulis* fruit biomass.

neotropical forests (Bawa and Ng, 1990; Opler et al., 1980). With regard to the palms, several studies have shown that reproductive phenological behavior is extremely variable (Henderson, 2002); flowering can be restricted to a particular season, and fruiting is frequently non-seasonal (Table 3).

Fruit fall on Anchieta Island also differed between palms and trees, as predicted, and was extremely low when compared to other well-preserved Atlantic forest sites (see Table 4). The overall low fruit fall biomass on Anchieta Island may be related to the absence of large-seeded plant species, such as some taxa from Sapotaceae, Myristicaceae and Lauraceae, probably due to logging before the park was created. Additionally, most of the remaining secondary forest tree species produce small fruits: The best represented fruits in the studied plots originate from families with mostly small fruits (Sapindaceae, Melastomataceae, Myrsinaceae and Nyctaginaceae). Although disturbed forests are expected to produce higher fruit fall biomass than well-preserved areas, elevated levels of disturbance may lead to a low fruit fall biomass (Ganzhorn, 1995; Khan et al., 2005; Levey, 1988a, b), as it is the case also in Anchieta Island.

Palms constituted more than 80% of the total fruit fall biomass at Anchieta Island, with *S. pseudococos*, which is the dominant palm in the study site, summing up to 42% of the overall fruit production, while *E. edulis* fruit fall corresponded to only 12%. Both species are an

important food resource for different vertebrate frugivores (Galetti et al., 1999). From June to August estimated fruit fall was nil for palms and trees, although 30% of palm individuals were bearing ripe fruits, suggesting high removal rates of fruits in that period, and stressing the importance of palms as a food resource for vertebrate frugivores in times of low fruit availability on Anchieta Island.

The overall low fruit fall on Anchieta Island may have critical consequences if the elevated densities of mammal species there are considered, especially because the species cannot move to other sites to exploit alternative food resources. In consequence, maintaining groups of species such as palms constitute a primary task if other groups of species that depend on them shall be conserved. Although palms do not provide resources for all the assemblage of vertebrate frugivores on Anchieta Island all the year round, their importance as a major resource in such an impoverished environment is supported by the divergent patterns of production of ripe fruits in different trees, and by the high fruit fall biomass.

Terborgh (1986a, b) proposed that in neotropical forests some plant parts, such as palm nuts, nectar and figs, sustain a large proportion of the vertebrate animal community during annual seasons of food scarcity. Kinnaird (1992) also stressed the importance of groups of species that present fruiting times slightly shifted from

one another or from the community peak in providing food resources during months of generally low production.

Extremely disturbed environmental conditions in combination with high populations of exotics species are not an exclusive condition of Anchieta Island. Many sites, especially islands, suffer from the anthropogenic effects described for Anchieta Island. In that context, the identification and maintenance of key resources as palms, which may support other species and interactions, should constitute a primary effort in the conservation biology of such sites.

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Appendix A

See Table A1.

Table A1. List of palms and tree species observed on Anchieta Island

Family/species	N	Syndrome	Phenology	
			Flowering	Fruiting
Annonaceae				
<i>Annona cacans</i> Warm.	1	Mammals	Dec	Dec–Jan
Arecaceae				
<i>Astrocaryum aculeatissimum</i> (Schott) Burret	10	Mammals	Jan–June	March–Dec
<i>Attalea humilis</i> Mart. Ex Sprengel	15	Mammals	–	–
<i>Bactris setosa</i> Mart.	12	Mammals	Nov	Nov–Feb
<i>Euterpe edulis</i> Mart.	11	Birds	Sept–Jan	Nov–June
<i>Livistona chinensis</i> (Jacq.) R. Br.	12	Birds	Sept–April	Sept–July
<i>Syagrus pseudococos</i> (Raddi) Glassman	36	Mammals	All year	All year
<i>Syagrus romanzoffiana</i> (Chamm.) Glassman	20	Mammals	Sept–Dec	Oct–June
Apocynaceae				
<i>Tabernaemontana laevis</i> Vell. cf	1	Birds	Sept–Nov	Dec–April
Aquifoliaceae				
<i>Ilex theezans</i> Mart. cf	8	Birds	Nov, Feb	Nov–June
Araliaceae				
<i>Schefflera mortotoni</i> (Aubl.)	4	Birds	Sept–Nov, May–June, Jan	Nov–Aug
Asteraceae				
<i>Gochmatia polymorpha</i> (Less.) Cabrera	2	Wind	May–Nov	*****
Bignoniaceae				
<i>Cybistax antisyphilitica</i> (Mart.) Mart	13	Wind	Oct–Jan	Dec–Feb
Clethraceae				
<i>Clethra scabra</i> Pers. cf	1	Wind	Dec	May–July, Jan
Cecropiaceae				
<i>Cecropia glaziovii</i> Snehli.	6	Mixed	Oct–June	Dec–May
Clusiaceae				
<i>Clusia criuva</i> Cambess.	3	Birds	Sept–Nov	Nov–Jan
Erythroxylaceae				
<i>Erythroxylum pulchrum</i> A. St.-Hill	18	Birds	Aug–Oct, Dec–Jan	Nov–Feb
Euphorbiaceae				
<i>Croton floribundus</i> Sprengel	14	Ants	June, Nov–Dec	May–July, Dec–Jan, April
<i>Croton</i> sp. 1	12	Auto	May–Sept, Dec–Feb	Dec–May, Aug
<i>Pera glabrata</i> (Schott.) Poepp.ex Baill. cf	17	Birds	Aug–April	Dec–May
<i>Sapium glandulosum</i> (L.) Morong	1	Birds	Dec	*****

Table A1. (continued)

Family/species	N	Syndrome	Phenology	
			Flowering	Fruiting
Fabaceae (incl. Caesalpinaceae and Mimosaceae)				
<i>Andira fraxinifolia</i>	4	Bats	*****	*****
<i>Bauhinia</i> sp.	2	Auto	*****	*****
<i>Inga luschnathiana</i> (cf.) Benth.	28	Mammals	July–Feb, April	Oct–May
<i>Machaerium nicticans</i> (Vell.) Benth.	2	Wind	Feb	Feb–March
Fabaceae sp. 1	1	Animals	Jan–Feb	*****
Fabaceae sp. 2	1	Animals	*****	*****
Flacourtiaceae				
<i>Casearia decandra</i> Jacquin	3	Birds	May–Sept	Aug–Nov
Lauraceae				
<i>Lauraceae</i> sp.1	1	Birds	Dec	Dec–April
<i>Nectandra oppositifolia</i>	2	Birds	*****	*****
Melastomataceae				
<i>Miconia cinnamomifolia</i> (DC.) Naudin	13	Birds	Sept–Nov	Nov–April,
<i>Tibouchina mutabilis</i> (Vell.) Cogn.	5	Wind	Sept–Feb	Oct–July
Meliaceae				
<i>Guarea macrophylla</i> Vahl.	1	Birds	Jan–Feb	*****
Moraceae				
<i>Ficus</i> sp. 1	4	Mixed	–	–
Myrsinaceae				
<i>Rapanea ferruginea</i> (Ruiz&Pav.) Mez	1	Birds	May–July	Aug–Oct
<i>Rapanea umbellata</i> (Mart.) Mez	13	Birds	April–May, July, Sept, Feb	July, April–Dec
Myrtaceae				
<i>Eugenia</i> sp.	1	Mixed	July	*****
<i>Myrtaceae</i> sp 1	1	Mixed	*****	*****
Nyctaginaceae				
<i>Guapira opposita</i> (Vell.) Reitz	54	Birds	Jul–Dec, Feb, April–May	Jul–Aug, Oct–May
<i>Guapira</i> sp.	7	Birds	Nov–Dec	Dec–Feb
Rubiaceae				
<i>Rubiaceae</i> sp. 1	1	Birds	Dec–Jan, May	Feb–Jun
Rutaceae				
<i>Dictyoloma vandellianum</i> A. Juss.	2	Wind	July–Nov	Nov–Aug
Sapindaceae				
<i>Matayba guianensis</i> Aublet	4	Birds	June, Sept–Nov	All year
Solanaceae				
<i>Aureliana fasciculata</i> (Vell.) Sendtn.	2	Mammals	Nov	Dec–Jun
<i>Solanum</i> sp.	1	Bats	May–June	July–Aug
Verbenaceae				
<i>Aegiphila sellowiana</i> Cham.	1	Birds	Nov	Nov–Jan
<i>Citharexylum myrianthum</i> Cham.	5	Birds	Nov–Dec	Nov–Feb
Undetermined				
Undetermined 1	1	und	Aug–Sept	*****
Undetermined 2	1	und	Sept	*****
Undetermined 3	1	und	July–Sept	Oct–Nov
Undetermined 4	1	und	Dec	Jan–Feb
Undetermined 5	1	und	Oct	Oct–Nov
Undetermined 6	2	und	Feb–March	Feb–April
Undetermined 7	1	und	Dec	Dec
Undetermined 8	1	und	July	July
Undetermined 9	1	Wind	Dec	Dec
Undetermined 10	1	und	Sept, March–April	Feb–April

N = number of individuals, seed dispersal syndrome (animal, wind, auto = autochory and und = undetermined syndrome), and phenology (— irregular **** without event).

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