

REPRODUCTIVE PHENOLOGY  
AND FRUIT PRODUCTION  
ON A LAND BRIDGE ISLAND  
IN THE BRAZILIAN ATLANTIC FOREST

JULIETA GENINI

**Dissertação apresentada ao Instituto de  
Biotecnologia da Universidade Estadual  
Paulista “Julio de Mesquita Filho”,  
Campus de Rio Claro, para a obtenção  
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Biológicas (Área de Concentração:  
Biologia Vegetal)**

Rio Claro  
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## **Resumo**

As florestas tropicais estão entre os ambientes mais produtivos do planeta, sendo que a quantidade de frutos kg/ha pode chegar a 180-1000 kg/ha. Apesar dessa alta produtividade, a fenologia é altamente sazonal, ocorrendo períodos de escassez de recursos e alta produtividade no mesmo ano e/ou entre anos. Os frugívoros exibem uma ampla variedade de adaptações comportamentais e ecológicas para superar esses períodos de escassez. O presente trabalho avaliou as variações temporais na disponibilidade de frutos consumidos por vertebrados frugívoros na Ilha Anchieta, São Paulo, Brasil. Nós procuramos responder às seguintes questões: Os padrões de frutificação e disponibilidade de frutos diferem entre arbóreas e palmeiras? e Os padrões fenológicos de frutificação diferem entre grupos de palmeiras com diferentes síndromes de dispersão?. Os padrões fenológicos foram sazonais para ambos os grupos, no entanto, as datas de ocorrência dos eventos de frutificação foram diferentes. A produção de frutos também foi diferente entre palmeiras e arbóreas, sendo que as palmeiras constituíram mais de 80 por cento do total da biomassa coletada. Os padrões fenológicos foram diferentes entre as palmeiras com diferentes sub-síndromes de dispersão (dispersas por roedores, mistas e aves) fornecendo recursos alimentares para diferentes grupos de frugívoros ao longo do ano. As palmeiras poderiam constituir um recurso alimentar alternativo em períodos de baixa disponibilidade de frutos embora não forneçam recursos para os diferentes tipos de frugívoros da Ilha Anchieta o ano todo.

**Palavras chave:** frutos, fenologia, palmeiras, sazonalidade, frugívoros.

## **Abstract**

Tropical rainforest is considered one of the world's most productive habitats where fruit biomass ranges between 180-1000 kg/ha/yr. Despite this broad fruit production, phenology is highly seasonal in tropical forests, showing alternate periods of fruit scarcity and high resource production both in the same year and/or between different years. Frugivores exhibit a variety of ecological and behavioral adaptations to overcome these fluctuations. We evaluate the temporal variation in the availability of fruits consumed by vertebrate frugivores on Anchieta Island, in the Brazilian Atlantic Forest, Northeast São Paulo State. We aim to answer the following questions: Do fruiting patterns and the availability of fruits consumed by vertebrate frugivores differ between palms and trees? Do palm fruiting patterns differ among seed dispersed groups (rodent, mixed and bird)? Phenological patterns were seasonal for both trees and palms; however, the times of occurrence of fruiting differed. Fruit fall biomass was also different between trees and palms, and palms constituted more than 80 percent of the overall fruit fall biomass. Phenological patterns differed between the seed dispersed palms groups (rodent, mixed and bird seed dispersed palms) providing food resources in distinct periods for different assemblages of vertebrate frugivores. 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 on Anchieta Island all year.

**Key words:** fruits; phenology; palms; seasonality; frugivores

## INTRODUCTION

Tropical rainforest is considered one of the world's most productive habitats where fruit biomass ranges between 180-1000 kg/ha/yr (Jordano, 1992). Of this biomass, about 70-94 percent of woody species produce vertebrate seed dispersed fruits (Howe and Smallwood, 1982; Jordano, 1992). Despite this broad fruit production, phenology is highly seasonal in tropical forests, showing alternate periods of fruit scarcity and high resource production both in the same year and/or between different years (Frankie et al., 1974; Opler et al., 1980; Lieberman, 1982; Leighton and Leighton, 1983; Hilty, 1980; van Schaik et al., 1993; Wright et al. 1999, Leigh, 1999). Even non-seasonal forests, such as the Brazilian Evergreen Atlantic Rainforest, show non-seasonal phenological patterns (Morellato et al., 2000; Talora and Morellato, 2000).

Fruit crops are also spatially variable, and secondary forests tend to have more extended fruiting periods and larger crop sizes per unit area than primary forests, although they are of less nutritional quality for frugivores (Opler et al., 1980; Fleming, 1985 ; Levey, 1988a, b; Chapman et al., 2005). Frugivores exhibit a variety of ecological and behavioral adaptations to overcome these fluctuations (Smythe, 1970, 1978; Leighton and Leighton, 1983; Terborgh, 1986 b, Terborgh and van Schaik, 1987; van Schaik et al., 1993; Peres, 1994a), which could have repercussions on their reproduction, mortality and population density (Glanz, 1982; Milton, 1982; Smythe et al., 1982).

Plant species fruiting in different periods compared to the community fruit peak may constitute "key resources" for frugivores, and have often

been mentioned as “keystone” species (Gilbert, 1980; Milton, 1982; Terborgh, 1986a; Kinnaird, 1992), or species that support the frugivore vertebrate community in periods of extreme fruit scarcity (Terborgh, 1986a,b; Smythe, 1989). According to Peres (2000) keystone plants produce reliable, low redundancy resources that are consumed by a large proportion of the bird and mammal assemblages with which they coexist.

Palms have been cited as an important food resource for primates, (Terborgh and Van Schaick, 1987; Smythe, 1989; Spironello, 1991; Peres, 1994a; Stevenson, 2001; Galetti, 1994), rodents (Smythe, 1978; Forget et al., 1994; Zona and Henderson, 1989; Galetti and Pedroni, 1992), birds (Zona and Henderson, 1989; Reis, 1995; Galetti et al., 2000) and ungulates (Kiltie, 1981; Galetti et al., 2001). 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 forest supports 60 genera and 550 species of palms, with 10 genera and 40 species occurring in the Atlantic forest, many of which are endemic (Henderson et al., 1995).

Among those which are considered keystone species in the Atlantic forest is the endangered palm species *Euterpe edulis* (palm of the heart) (Galetti et al., 1999; Mikich, 2002; Zipparro, 2004). The production of fruits by *E. edulis* can reach up to 28.4 kg/ha/yr in well-preserved areas (or 15.82% of the overall fruit production) (Castro, 2003), and they are consumed by approximately 30 species of birds and mammals (Galetti et al. 1999; Mikich, 2002; Castro, 2003). However, due to over-harvesting, *E.*

*edulis* has been strongly depleted and its fruit production can be nil in some regions (Galetti and Fernandez, 1998).

Studies on palms are mostly focused on seed predation by bruchids and mammals (Janzen, 1972; Wright, 1983; Forget et al., 1994; Pizo and Vieira, 2004; von Allmen et al., 2004); seed size effects on predation and dispersal (Brewer, 2001); consequences of seed dispersal patterns on seed survival and demography (Pizo and Simão, 2001; Silva and Tabarelli, 2001; Fleury and Galetti, 2006); reproductive aspects (Piñero et al., 1982, Ervick and Feil, 1997); fragmentation effects on populations and their interactions (Scariot, 1998, 2001; Wright and Duber, 2001; Donatti, 2004; Fleury and Galetti, 2004; Pires, 2006); and diversity, structure and spatial distribution of communities (De Steven and Putz, 1985; Clark et al., 1995; Lima et al., 2003; Vormisto et al., 2004).

Reproductive phenological studies are generally based on a single species (Scariot and Lleras, 1995; Galetti et al., 1999; Rosa et al., 1998; Henderson et al., 2000; Castro, 2003; Borchsenius, 2002) and less frequently on several species or communities (De Stevens et al., 1987; Sist, 1989; Ibarra Manríquez, 1992; Peres, 1994b; Henderson et al., 2000b). However, few studies have compared palm phenology patterns with the wider community.

Insular environments, ranging from oceanic islands to fragments of once-contiguous natural systems, have long been used by biologists to test basic principles of ecology, evolution and biogeography (Wallace, 1881; Vitousek et al. 1995; Quammen, 1996). 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 attributes (isolation, small populations or “impoverishment”, absence of entire taxonomic groups and high levels of endemism), 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 (Maunder et al., 2002; Fernandez- Palacios and Morici, 2002; Courchamp et al., 2003).

In Brazil, land-bridge and oceanic islands have been highly disturbed by the introduction of exotic species (Galetti et al., unpublished data). One of these islands is Anchieta Island, which is off the coast of the state of São Paulo, southeast Brazil, which, in 1983 suffered the introduction of several mammal species such as agoutis, coatis, capybaras, deer and armadillos (Guillaumon et al., 1989; Bovendorp and Galetti in press). The establishment of human settlements in the area resulted in the modification and impoverishment of the forest, mainly through over harvesting and the introduction of exotic plants species (Guillaumon et al., 1989).

Therefore, common families such as Lauraceae and Myrtaceae are absent, or constitute a very low fraction of the forest, and most of the natural vegetation has been altered (Guillaumon et al., 1989). Seven vertebrate seed dispersed palm species occur on the island, from which six are native and one is exotic, (Appendix 1). In this scenario, they may constitute an important food resource for introduced and native vertebrate frugivores due to their long fruiting period (De Steven et al., 1987; Ibarra Manríquez, 1992; Peres, 1994b; Ervik and Feil, 1997; Lugo and Frangi,

1993, Mantovani , 1998; Mantovani and Morellato, 2000; Galetti et al., 1999).

On the other hand, morphological features of fruits define syndromes that have been associated with different consumer taxa (Janson, 1983; Charles Dominique et al., 1981). Fruit shared features bring about common ecological constraints and may limit responses in fruiting phenology (Mitani, 1999). Thus, palm species showing the same fruit sub-syndrome may display a similar fruiting pattern.

Thus, the goal of this study is to evaluate temporal variation in the availability of fruits consumed by vertebrates on Anchieta Island, and the importance of the palm species contribution to the fruit production compared to tree species. We aim to answer the following questions: Do fruiting patterns and the availability of fruits consumed by vertebrate frugivores differ between palms and trees? and, Does the palm fruiting patterns differ among seed dispersed groups (rodent, mixed and bird)?.

#### **STUDY SITE AND METHOD**

The study was carried out at Ilha Anchieta (now State Park Ilha Anchieta) Ubatuba, a land-bridge island of 823ha located in the Northeast of São Paulo State (45°02', 45°05' W and 23° 31', 23°34' S) in Ubatuba (Figure 1).

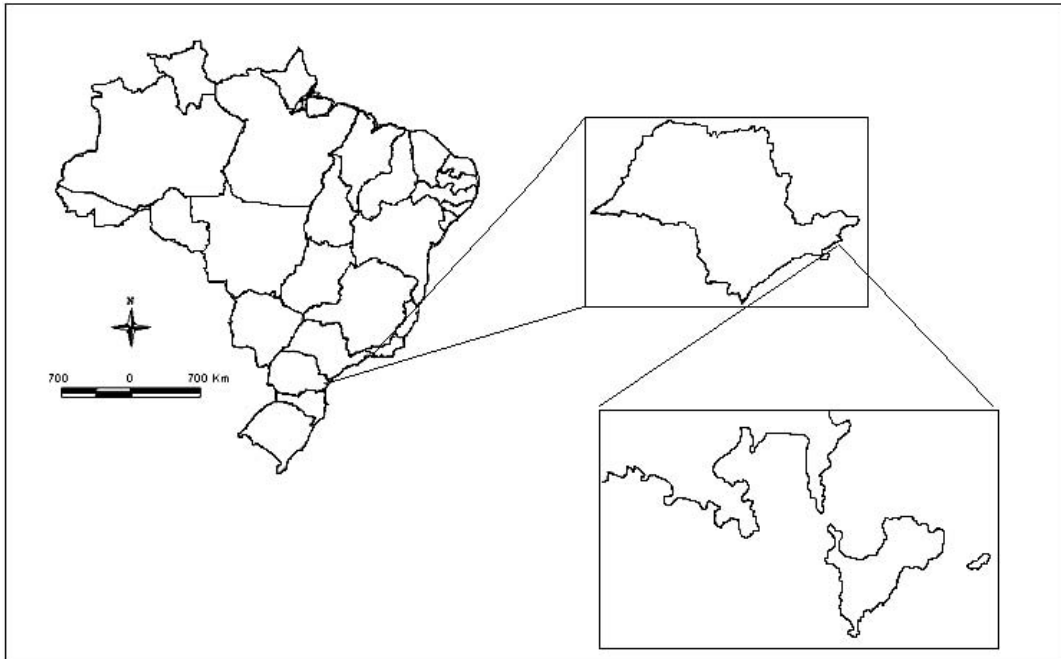


Figure 1. Location of the study site in the Northeast of São Paulo State, Brazil.

The original indigenous settlements of Anchieta Island were supplanted by Europeans by the middle of the 19th century, who subsisted through activities such as fishing, and the cultivation of coffee, sugar cane, corn and potatoes (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 plantation cultivation, 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 1914 the State Prison was abandoned, re-opened in 1928 and then closed in 1955. Finally, in March 1977 Anchieta Island was established as São Paulo State Park (Guillaumon et al., 1989).

The climate of Anchieta Island is tropical rainy according to the Köppen (1948) system, with substantial rain occurring every month. Rainfall

and temperature data for the 1956-1985 period was obtained from the Oceanographic Institute of the University of São Paulo (USP) in Ubatuba, and indicates the presence of two distinct periods, one super-humid from September to May with rainfalls above 100mm/month, and the other less humid from June to September when rainfall is below 100mm/month (Figure 2). There is no rainfall deficit in the study site. Data relating to the study period was obtained from the climatic station in Ubatuba, which belongs to the Institute of Agronomy of Campinas (IAC). The mean temperature was 24°C, the total annual rainfall was 2104mm (Figure 3) and the annual mean relative humidity was 84%. Photoperiod data for the study site, at 23 °S is from Pereira et al. (2001).

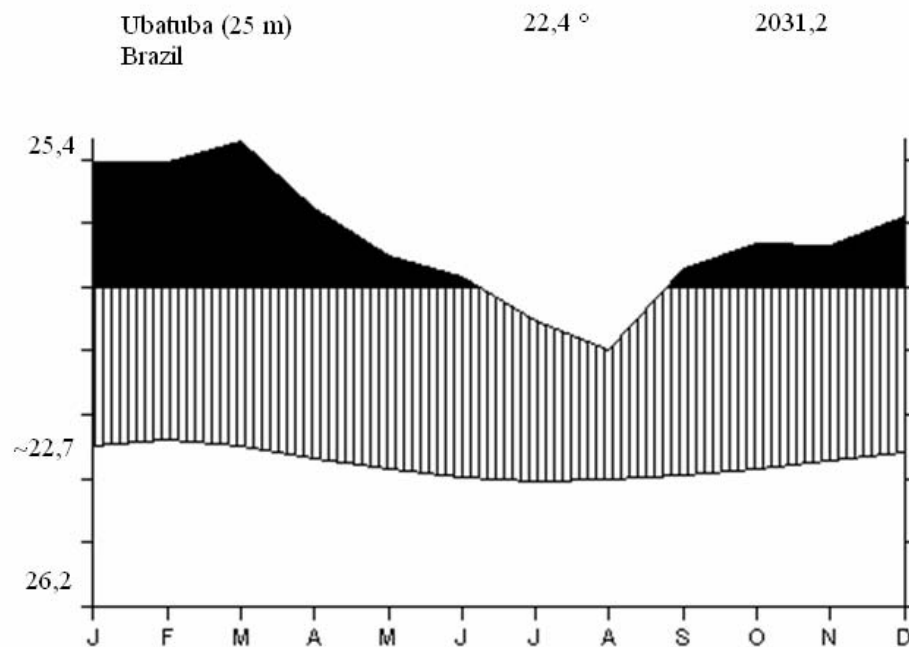


Figure 2. Climatic diagram according with Walter (1986) displaying rainfall and mean temperature for a 30 year period (1956-1985) in the Ubatuba region, SP, Brazil (45 07` W e 23 30`S).

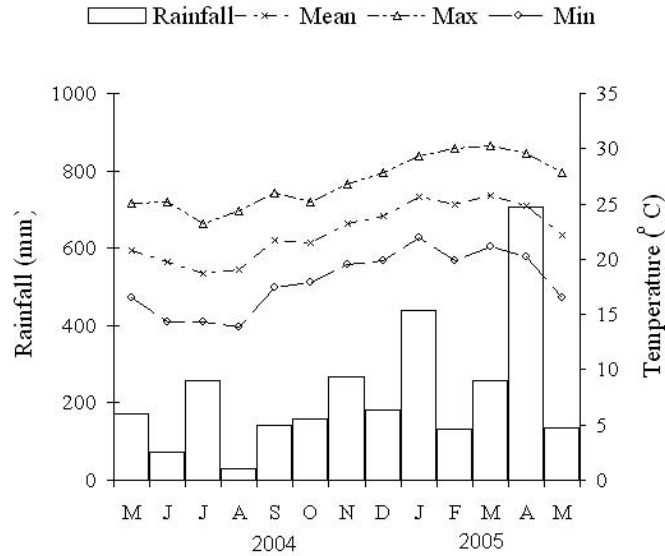


Figure 3. Distribution of rainfall and mean temperature during the study period in the Ubatuba region, SP, Brazil. Data from the Institute of Agronomy of Campinas (IAC)

Anchieta Island is covered by secondary lowland Atlantic forest dominated by *Nectandra* spp., *Tabebuia cassinoides*, *Simaruba* spp., *Clarisia racemosa*, *Cedrella fissilis*, *Dalbergia nigra*, *Mimosops* spp., *Plathymeria* spp., *Myrocarpus frondosus*, *Tabebuia* spp. (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). Among introduced species are the well dispersed Chinese palms *Livistona chinensis* and *Cocos nucifera*, which are restricted to the settlement areas (Guillaumon et al., 1989).

#### Frugivores on palms trees

The palm species consumed by rodents are *Astrocaryum aculeatissimum*, *Attalea humilis* and *Syagrus pseudococos*. *Astrocaryum aculeatissimum* has simple or multiple steams of 4-8 m high, its fruits are

adapted to scatter hoarding mammals, including small rodents, squirrels, and agoutis (Donatti, 2004). Its fruits are light brown and their size ranges from 3 - 4.5 cm in length and 3 – 3.5 cm in diameter (Henderson et al., 1995; Lorenzi et al., 1996, 2004). *Attalea humilis* has a subterranean or simple stem of 1 m high, it is also dispersed by scatter-hoarding species such as rodents, for example agoutis and pacas. Its fruits are light brown and range from 6-9 cm in length and 4 – 8 cm in diameter. Neither of them have fleshy pulp (Henderson et al., 1995; Lorenzi et al., 1996, 2004). *Syagrus pseudococos* has a simple 10-15 m high stem and yellow colored fruits, which range from 6 – 7 cm in length and are 4 cm in diameter. Like the previous species, they are also dispersed by agoutis (Henderson et al., 1995; Lorenzi et al., 1996, 2004; Galetti pers. comm.).

The more generalist seed dispersal species of palms are *Syagrus romanzoffiana* and *Bactris setosa*. The former has a solitary stem of 7-15 m high, yellow-orange fruits, which range from 2 – 3 cm in length and 1 – 2 cm in diameter, and is consumed by primates, ungulates, birds and squirrels (Henderson et al., 1995; Lorenzi et al., 1996, 2004; Galetti et al., 1992). The latter species has multiple stems has fruits of a dark-purple color ranging from 1 – 1.5 cm in length and 1.5 – 2 cm in diameter and is dispersed by birds and carnivores (Marques, R. M. unpublished data).

The other two species of palms on the island, *Euterpe edulis* and *Livistona chinensis*, are mainly dispersed by birds. *E. edulis* solitary stems of 5-12 m high, its fruits are black-purple drupes of 1 – 1.4 cm in length and is also dispersed by squirrels, bats and primates (Henderson et al., 1995; Laps, 1996; Lorenzi et al., 1996, 2004; Galetti et al., 1999). *L.chinensis*

has also solitary stems of 5-15 m high and dark green fruits, which are dispersed by birds (Lorenzi et al., 1996, 2004).

Several mammal species were introduced to the Island in 1983, including coatis (*Nasua nasua*), primates (*Cebus nigrinus* and the exotic *Callicthrix jacchus penicillata*), six banded armadillos (*Euphractus sexcintus*), deer (*Mazama gouazoubira*), southern tamandua (*Tamandua tetradactyla*), native and exotic agoutis (*Dasyprocta punctata* and *D. azarae*, respectively) and capybaras (*Hydrochoerus hydrochoerus*) (Guillaumon et al., 1989). Presently, rodents, coatis and the black-tufted-ear marmosets are found in high densities (Bovendorp and Galetti, in press).

The avifauna of Anchieta Island suffered severe modifications due to over-harvesting and the introduction of exotic species. The Thraupidae family is the best represented, and is particularly important in the seed dispersal of fleshy fruits in habitats suffering from degradation (Fadini and De Marco, 2004). Unfortunately, species of larger body size, such as toucans, the dusky-legged guan, the pipile guan and cotingids are poorly represented on Anchieta Island (Fadini, 2005).

## **METHOD**

Phenological observations on flowering and fruiting patterns were carried out monthly, from May 2004 to May 2005 along three trails of approximately 1km.

All trees with DBH (diameter at breast high) = 15cm and within a 2m distance from the trails were marked with aluminum tags (Zipparro, 2004; Galetti et al., 2004). All individuals of palms with evidence of reproductive activity such as reproductive scars or old inflorescences/infrutescences

were marked along the trails. A minimum sample size of ten palm individuals per species was established (Fournier and Charpentier, 1975). A total of 282 trees and 116 palms were monitored monthly for the presence or absence of flower buds, open flowers, unripe and ripe fruits (Appendix 1) (Bencke and Morellato, 2002). The voucher material is deposited in the Herbarium Rioclarense (HRCB).

Palm species were grouped by dispersal sub-syndrome into: rodent-dispersed palms (*Syagrus pseudococos*, *Astrocaryum aculeatissimum* and *Attalea humilis*); mixed dispersed palms (birds and mammals) (*Syagrus romanzoffiana* and *Bactris setosa*) and bird dispersed palms (*Livistona chinensis* and *Euterpe edulis*). These groups were defined based on literature and personal observations.

#### Fruit Biomass

To estimate the fruit production trends of palms and trees, examinations of 30 plots of 10m X 2m were performed monthly (10 plots per phenology trail) from May 2004 to May 2005. Each trail was marked every 50m and the plots were performed using these marked points, choosing the beginning randomly by using even or odd points. All the fruits present were collected from the ground, dried and weighed and the fruits of tree species were separated from palm fruits (Charles-Dominique, 1981).

#### **DATA ANALYSIS AND STATISTICS**

Graphical analyses were performed using the activity index, which shows the monthly proportion of individuals of palms and trees in each phenophase separately (Bencke and Morellato, 2002). Autochoric and wind dispersed tree species were discharged from statistical analyses and

only zoochorous species were graphically presented, in order to evaluate the fruit availability for vertebrate frugivores. Flowering it is not the scope of this survey therefore general patterns are described.

For the statistical analyses, individuals were separated into two groups, palms and trees. Eight phenological reproductive variables were calculated for each individual of each group, following Morellato et al. (2000). These variables were: a) date of first flower bud, b) date of first open flower, c) date of first unripe fruit, d) date of first ripe fruit, e) date of flower bud peak, f) date of open flower peak, g) date of unripe fruit peak and h) date of ripe fruit peak.

Circular statistics were used to look for seasonality, as proposed by Morellato et al. (2000) and for mean angle data for each of the phenological variables mentioned above. For each variable a number corresponding to the month where the event occurred was assigned. When the peak occurred in two consecutive months, the average was used (Morellato et al., 2000). The angle of a vector on a 360° circle indicates the mean date of flowering or fruiting events, with 0° representing the first month of observation (Morellato et al., 2000). The frequency of occurrence of individuals in each phenophase within each angle was calculated and the following parameters were estimated: the mean angle  $\alpha$ , the angular dispersal confidence limit of the frequency distribution for each phenological variable, and the length of the vector  $r$  which is a measure of concentration around the mean angle. Its value is zero when an equal number of phenology records occur in each month, and its maximum value of one is reached when all records occur in a single calendar month

(Morellato et al., 2000). 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 seek the normal distribution of the data. The significance of the mean angle was estimated by the Rayleigh (z) test.

The seasonality hypothesis tests also followed Morellato et al. (2000), and were  $H_0$ : Phenological records are distributed uniformly all year round, and hence there is no seasonality, and  $H_1$ : Phenological records are not uniformly distributed, and thus there is a mean date for a phenological event or seasonality. If  $H_1$  is accepted, the intensity of concentration around the mean angle, denoted by  $r$ , can be considered a measure of the degree of seasonality. When the mean angle was significant a two sample Watson-Williams test (F) was performed among phenological variables of palms and trees.

Since the Watson's U (von Mises) Test showed a non normal distribution for the data, a Kruskal-Wallis one-way ANOVA was used to test for differences in the time of occurrence of the phenophases for the three seed dispersed palms groups (rodents, mixed, and birds).

## **RESULTS**

The phenology of 57 species was analyzed, where 57.89 percent were zoochorous species, 15.78 percent were wind dispersed and 26.31 percent were undetermined (Appendix 1). From 282 tree individuals, 31.91 percent did not show any reproductive event and of the other 69.09 percent that flowered, only 23.96 percent fruited. From 116 palms, 10.34 percent of

individuals only flowered, 73.29 percent fruited, and 16.37 percent did not show any reproductive event.

Flowering of trees occurred between September - November, with a peak in November (Figure 4A) while palms presented an irregular pattern with individuals flowering in all months (Figure 4B). The period of higher fruiting activity for trees occurred from November to February with a peak for unripe fruits in January (19.2% of individuals), and in February for ripe fruits (18.8% of individuals; Fig. 4A). Palm individuals fruited all year round, with a reduction in the percentage from January to April, which coincided with the period of higher activity in trees (Figure 4B). Palms presented a fruit peak in November for unripe fruits (47.41% of individuals) and in December for ripe fruits (28.86% of individuals) (Figure 4B).

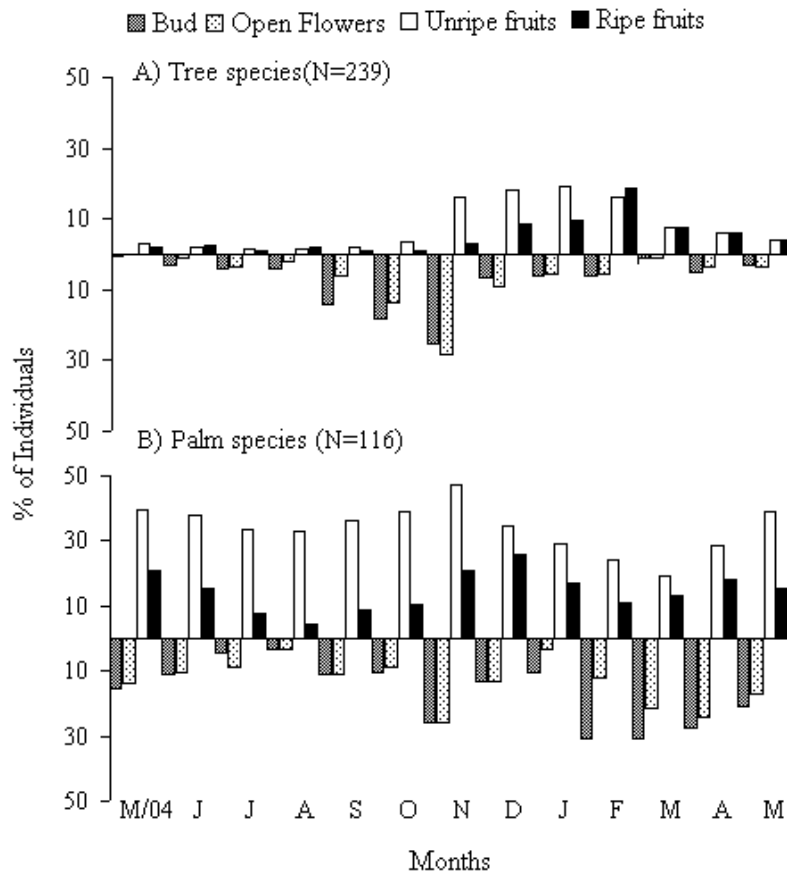


Figure 4. Percentages of individuals of A) trees and B) palms in each phenophase on Anchieta Island, Ubatuba -SP, Brazil.

#### Test for the occurrence of seasonality

All the reproductive phenophases were seasonal both for trees (Table 1A) and palms (Table 1B). Flowering, with exception of the first date of bud for palms, presented lower  $r$  values than was observed for fruiting (Table 1A and 1B). Significant differences were found between palms and trees for bud and ripe fruits for all variables (Table 2).

Table 1. Circular statistical results of the occurrence of seasonality for A) trees (47 species) and B) palms (seven species) on Anchieta Island, Ubatuba - SP. (Significant values  $P < 0.05$ )

	A)							
	Trees				Phenological variables			
	First date	Peak date	First date	Peak date	First date	Peak date	First date	Peak date
	of Bud	of Bud	of Open Flower	of Open Flower	of Unripe Fruits	of Unripe Fruits	of Ripe Fruits	of Ripe Fruits
Observations (N)	174	171	178	169	121	119	125	115
Mean Angle (a)	166.721°	170.985°	181.312°	185.312°	205.218°	219.068°	243.514°	242.725°
Mean date	09.nov	16.nov	24.nov	28.nov	19.dez	01.jan	27.jan	26.jan
Circular deviation	64.408°	65.209°	68.747°	65.209°	53.929°	51.794°	57.74°	54.204°
Length of mean vector (r)	0.532	0.594	0.487	0.523	0.642	0.665	0.602	0.639
Rayleigh Test (P)	0	0	0	0	0	0	0	0
B)								
	Palms				Phenological variables			
	First date	Peak date	First date	Peak date	First date	Peak date	First date	Peak date
	of Bud	of Bud	of Open Flower	of Open Flower	of Unripe Fruits	of Unripe Fruits	of Ripe Fruits	of Ripe Fruits
	of Bud	of Bud	of Open Flower	of Open Flower	of Unripe Fruits	of Unripe Fruits	of Ripe Fruits	of Ripe Fruits

Table 2. Watson-Williams Test (F) results of comparisons between first and peak date variables of palm and trees on Anchieta Island, Ubatuba - SP. NS = not significant values.

Watson-Williams Test (F) for first date flowering					
Bud			Open Flower		
	Palms	Trees		Palms	Trees
Palms	.....	-----	Palms	.....	-----
Trees	7.952**	.....	Trees	NS	.....
Watson-Williams Test (F) for first date fruiting					
Unripe Fruits			Ripe fruits		
	Palms	Trees		Palms	Trees
Palms	.....	-----	Palms	.....	-----
Trees	NS	.....	Trees	12.514**	.....
Watson-Williams Test (F) for peak date flowering					
Bud			Open Flower		
	Palms	Trees		Palms	Trees
Palms	.....	-----	Palms	.....	-----
Trees	10.004**	.....	Trees	NS	.....
Watson-Williams Test (F) for peak date fruiting					
Unripe Fruits			Ripe fruits		
	Palms	Trees		Palms	Trees
Palms	.....	-----	Palms	.....	-----
Trees	NS	.....	Trees	6.529**	.....

\* <0,05, P \*\* <0,001

### Relative Percentages of Tree and Palm Fruiting Patterns

Fruiting activity for trees was concentrated in the wettest season, November to February, while palms constantly showed more than 10 percent of individuals fruiting in all months (Figure 5A). Only from December to February did trees present higher fruiting percentages than

palms, while from March to October palms exhibited a notably higher percentage of individuals fruiting (Figure 5A).

Trees showed a higher number of species percentages than palms. In fact, from November to March they showed higher number of species in fruit than palms (Figure 5B). This higher number of fruiting tree species coincided with the period of more fruiting tree individuals. For palms, the relative species percentage was constant, generally ranging from 5 to 12 percent of species with a similar but less pronounced trend than that observed for the number of individuals (Figure 5B).

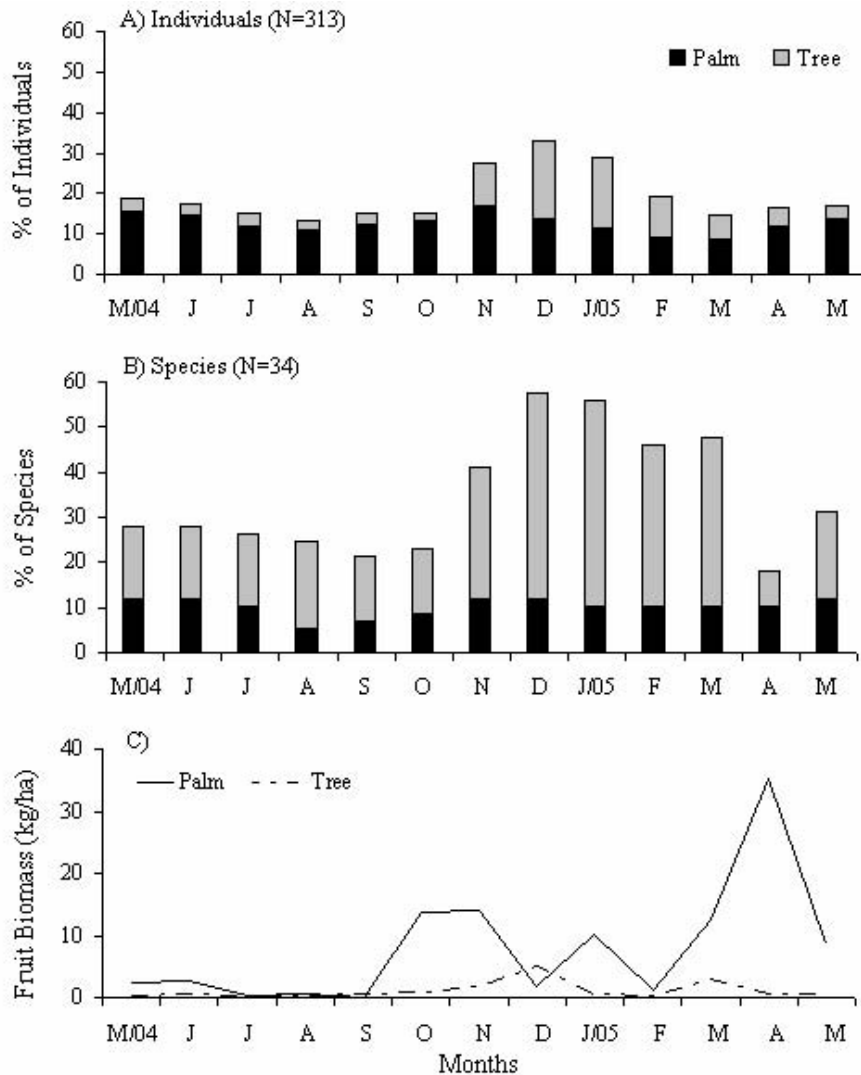


Figure 5. Relative percentage of A) individuals and B) species of trees and palms fruiting and C) Fruit biomass productivity of trees and palms on Anchieta Island, Ubatuba –SP, Brazil.

### Fruit Biomass

Palms showed a high peak of fruit biomass in April while the fruit peak for trees occurred in December and was less pronounced (Figure 5C). Palms also showed two minor peaks, one in October-November and the other in January. Both peaks were higher than the tree biomass peak (Figure 5C). From July to September fruit fall biomass was almost nil for both groups. The overall fruit fall biomass was 119 kg/ha/yr, of this 103.2 kg/ha/yr (83.7%) corresponded to palm fruits (Table 3). Among palms the higher contribution to fruit fall biomass corresponded to *Syagrus pseudococos* (42 %), *Syagrus romanzoffiana* (30.75%) and *Euterpe edulis* (11.6%).

Table 3. Annual fruit fall biomass in kg/ha/yr and its percentage for Trees and seven Palm species compared to overall results on Anchieta Island, Ubatuba , SP, Brazil.

	kg/ha/yr	Total %
Trees	15,8	13,3
<i>Syagrus pseudococos</i>	50	42
<i>Syagrus romanzoffiana</i>	36,6	30,75
<i>Euterpe edulis</i>	13,8	11,6
<i>Livistona chinensis</i>	0,06	0,05
<i>Bactris setosa</i>	0	0
<i>Attalea humilis</i>	1,14	0,96
<i>Astrocaryum aculeatissimum</i>	1,6	1,34

When palms were grouped by seed dispersal sub-syndrome, phenological patterns were more defined, and flowering occurred from September to May for all groups though it was more extended for rodent seed dispersed palms (Figure 6). Fruiting patterns were longer for unripe than for ripe fruits, with the exception of mixed dispersed palms, which showed the same length for both phenophases (Figure 6). For unripe fruits, rodent dispersed palms exhibited a higher percentage of individuals from May to October while birds and mixed dispersed palms presented more activity from November to February. For ripe fruits, rodent dispersed palms overlapped with mixed dispersed palms, although the later presented its major peak in May at the time of the bird dispersed fruit peak, which also offered ripe fruits in March and April. There were differences in the time of occurrence of unripe fruits ( $KW X^2 = 7, 65, df = 2, p > 0.0218$ ) and ripe fruits ( $KW X^2 = 8.9118, df = 2, p > 0.016$ ) among the three palm seed dispersed groups.

For rodent seed dispersed palms flowering and fruiting occurred all year, showing more than 20% of individuals in flower from February to May (Figure 6A). Unripe fruits showed more than 20% of individuals from April to December, peaking from July to September (62.3% of individuals) (Figure 6A). Ripe fruits presented more than 20 % of individuals from November to January peaking in December (Figure 6A).

Mixed dispersed palms had a flowering period concentrated between September and February, peaking in November (Figure 6B). Fruiting was observed from October to July, showing a peak for unripe fruits in

November (43.8 % of individuals) and for ripe fruits in May (28.1 % of individuals) (Figure 6B).

For bird dispersed palms the flowering was observed from September to April, while fruiting occurred almost every month (Figure 6C). Unripe fruits presented more than 20 % of individuals from September to May, showing its peak from December to February (60.9% of individuals). Ripe fruits were observed from February to July, peaking in April and May (56% of individuals) (Figure 6C).

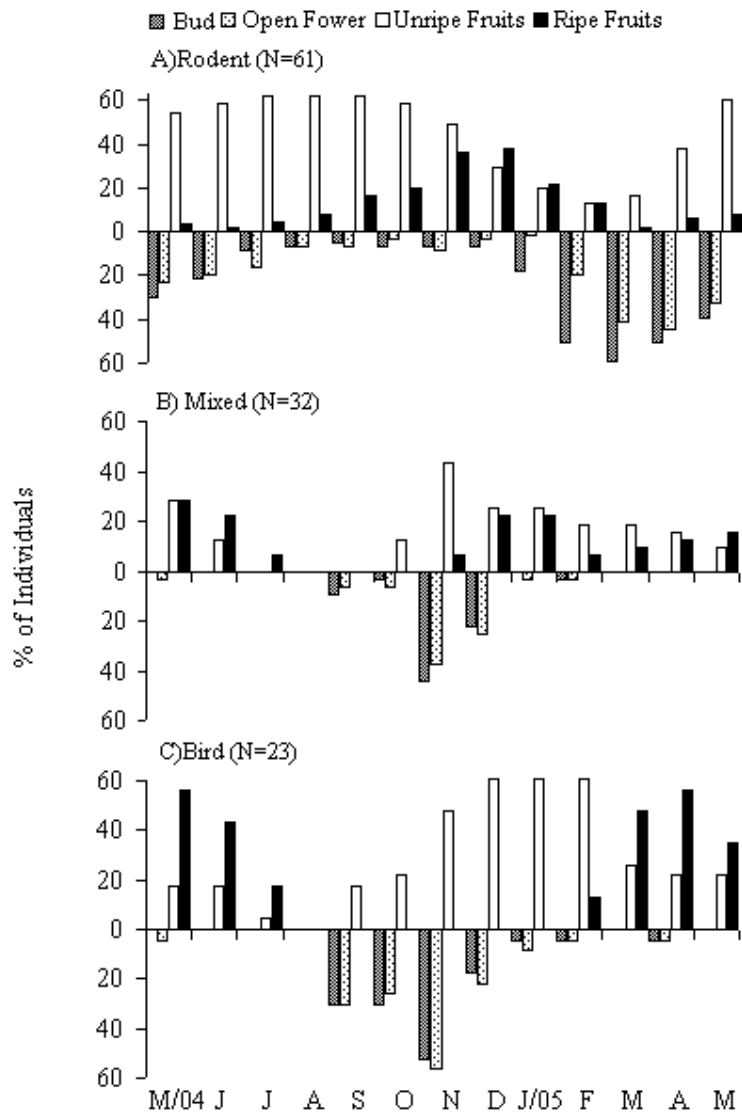


Figure 6. Percentage of A) rodent, B) Mixed and C) bird seed dispersed palms in each phenophase on Anchieta Island, Ubatuba - SP, Brazil. Number of individuals (N) between parentheses.

*Astrocaryum aculeatissimum*: The flowering period occurred from January to June. Fruiting occurred almost all year, from March to December, with a peak in July and August for unripe fruits (7.8 % of individuals) and in November for ripe fruits (6 % of individuals) (Figure 7A).

*Attalea humilis*: The flowering and fruiting behavior of *Attalea humilis* was highly irregular, with low proportions of individuals in flower and fruit almost every month (Figure 7B).

*Syagrus pseudococos*: This species showed the highest percentages of individuals. Flowering occurred all year with more than 3% of individuals in flower from December to April peaking in April (Figure 7C). Fruiting occurred all year round, with higher proportions of individuals in unripe fruits than in ripe fruits. The peak for unripe fruits occurred from August to October (24.13 % of individuals) and in December for ripe fruits (17.24 % of individuals) (Figure 7C).

*Syagrus romanzoffiana*: Flowering was concentrated from September to October. Fruiting percentages were highest from October to June with a peak in May (6.9% and 7.8% of the individuals for unripe and ripe fruits respectively) (Figure 7D).

*Bactris setosa*: This species showed a short flowering and fruiting period (Figure 7E). Flowering occurred from November to January, peaking in November and fruiting from November to January, showing an unripe

fruit peak in November (6.9% of the individuals) and in December for ripe fruit (5.2% of individuals) (Figure 7E).

*Euterpe edulis*: Flowering occurred from September to January, while fruiting was concentrated from November to July with a peak for unripe fruits from November to February (7.8% of individuals) and in March and April for ripe fruits (6.9% of individuals) (Figure 7F).

*Livistona chinensis*: Flowering occurred from September to April with less than 5 per cent of the individuals in flower. Fruiting occurred all months with exception of August. The period of higher activity for unripe fruits was from October to February and from April to May (4.3% of individuals). Ripe fruits occurred from February to July peaking from May to June (5.2% of individuals) (Figure 7G).

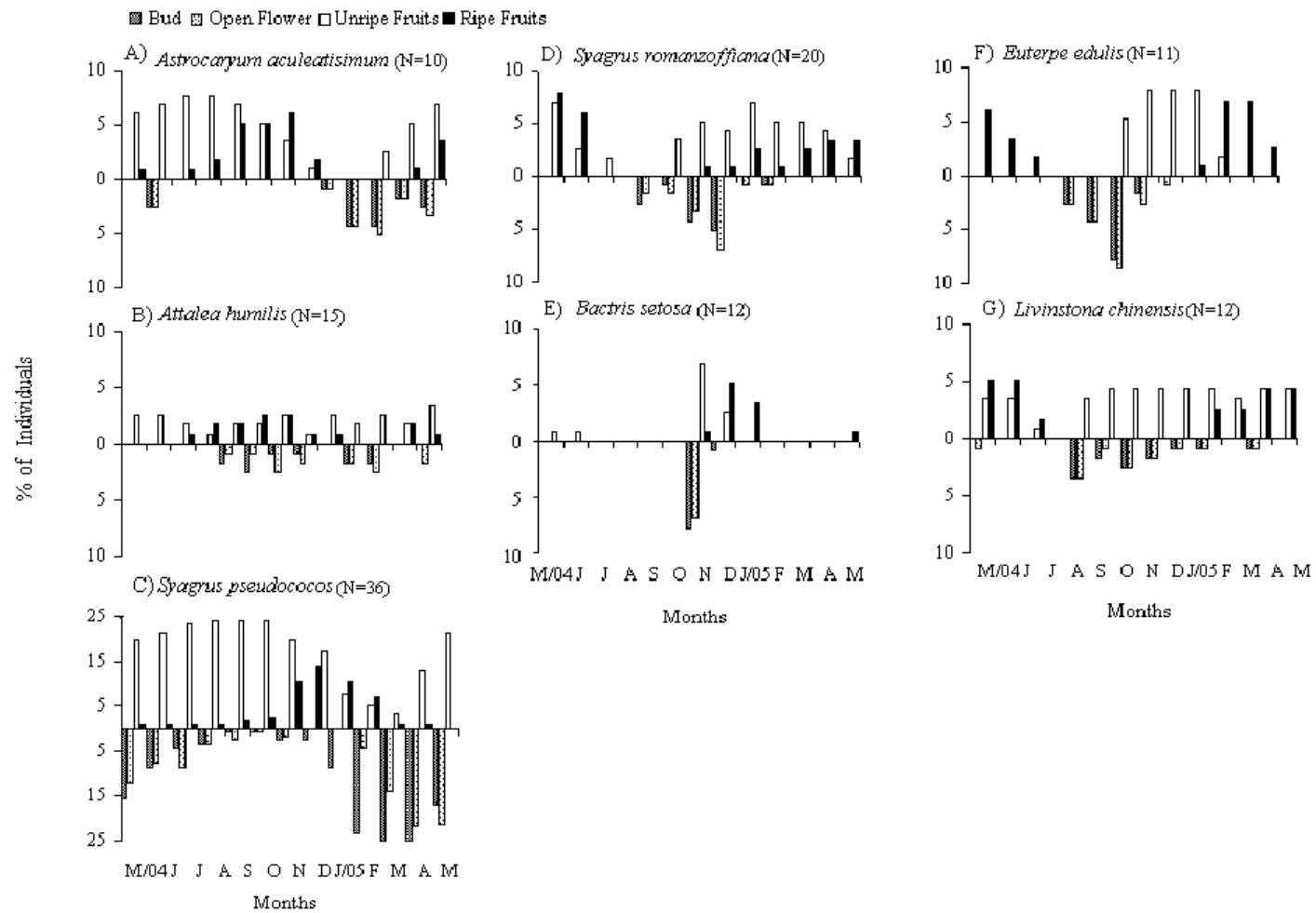


Figure 10. Relative Percentage of individuals flowering and fruiting on seven palm species by: A), B) and C) Rodent; D) and E) Mixed and F) and G) Bird dispersed species on Anchieta Island, Ubatuba, SP, Brazil. Note the different scale for *Syagrus pseudococos*.

## Discussion

This study has revealed that palms as well as trees show seasonal phenological patterns on Anchieta Island. Also, that the time of occurrence of ripe fruits differed suggests a complementary ripe fruiting pattern, thereby providing food resources for frugivores in distinct periods throughout the year.

Contrary to this survey, other phenological studies have reported non-seasonal fruiting patterns in the Atlantic rainforest (Morellato et al., 2000, Talora and Morellato, 2000). Phenological patterns are likely to be influenced by habitat (Augspurger, 1983) and the successional stages of the forest; Opler et al. (1980) noted that flowering of early successional species have more extended periods than those in mature communities and Bawa and Ng (1990) suggested that perturbed areas may present different phenological patterns than well preserved areas because characteristics such as microhabitat and distribution of conspecific trees may be altered, influencing the number of individuals in fruit. Moreover, Tabarelli et al., (1999) mentioned a change in the species composition of fragmented areas, where ruderal species substitute the main vertebrate seed dispersed plants.

Fruit fall on Anchieta Island differed between palms and trees and was extremely low when compared with other sites, with trees showing a lower fruit fall biomass than palms (see Table 4). However, these values could be biased since they are not a direct measure of the real standing crop. They constitute fruits that were eaten by neither arboreal nor terrestrial frugivores and, in the present study, they are certainly affected by the high density of frugivores on the island (Chapman and Chapman, 1994).

Table 4. Estimates of fruit fall biomass (kg/ha/yr) of fruiting species and methods in the neotropics

Country	Field Station	Fruit fall (kg/ha/year)	Methods	Reference
Peru	Cocha Cashu	1990	Fruit traps	Terborgh, 1983
Panama	Barro Colorado	2180	Fruit traps	Smythe, 1970
Brazil	Saibadela	370	Fruit traps	Galetti, 1996
Brazil	Cardoso Island	127	Trail census	Castro, unpublished data
Brazil	Serra do Mar	228	Trail census	Marques, 2004
Brazil	Anchieta Island	119	Trail census	Genini, 2006

Among the causes that can influence fruit fall are forest composition, soil characteristics and the level of disturbance of the forest (Ganzhorn 1995, Marques 2004, Khan et al., 2005). In Serra do Mar State Park fruit fall biomass of a mid successional secondary forest was higher than in well preserved or high-disturbed forests (Marques 2004). In disturbed areas of Madagascar Ganzhorn (1995) found that fruit fall was higher along logging trails than in the forest interior. Khan et al. (2005) reported that fruit production was higher in moderately disturbed areas and lowest in undisturbed areas but the mean weight of fruits decreased with increasing disturbance, which might be related to failure of pollination, resource limitation and physiological stress in fragmented areas. The overall low fruit fall biomass on Anchieta may be related to the absence of large-seeded plant species, such as Myristicaceae and Lauraceae due to the island flora impoverishment, and to the fact that most of the trees produce small seeded fruits, which is supported by the best represented fruits in the plots (Sapindaceae, Melastomataceae, Myrsinaceae and Nyctaginaceae). The low fruit fall on Anchieta

Island may have critical consequences for the elevated densities of mammal species present in the study area, especially considering that they cannot move to other sites to exploit alternative food resources.

In respect to palms, several studies have shown that reproductive phenological behavior is extremely variable (see Table 5) (Henderson, 2002), flowering can be restricted to a particular season presenting staggered patterns throughout the flowering period and frequently fruiting is non seasonal.

Table 5. Phenological studies on palm species showing flowering and fruiting period in several neotropical sites. (\*\*\*) not evaluated)

Country	Field Station	Season		Rainfall (mm)
		Flowering	Fruiting	
México *	Los Tuxtlas	Dry season (April-May)	All year	4725
Panama †	Barro Colorado	Rainy season (May to mid-December)	All year	2400
Brazil ‡	Manaus	Dry season (July- September)	***	2186
French Guiana §	Cayenne	Dry season (Aug- Sept)	Wet season (Dec-Jan)	3108
Brazil <i>f</i>	Urucu	***	All year	3256

\* Ibarra-Manríquez, 1992

† De Steven et al., 1987

‡ Henderson, 2000

§ Sist, 1989

*f* Peres, 1994b

Fruit syndromes suggest that different groups of animals exploit distinct resources, and as a result, distinct seed dispersed groups would exhibit reduced diet overlap (Gautier-Hion et al., 1985; van der Pijl, 1972). It was found that fruiting patterns of different seed dispersed groups of palms were different. Fruiting showed a low overlap, with mixed seed dispersed palms presenting ripe fruits after rodent and before bird seed dispersed palm species. The patterns observed

in this study suggest that fruits of palms are available all year for different kind of vertebrate frugivores.

Palms offered food resources for scatter hoarding rodents such as agoutis for extended periods, mainly when tree species fruits were not available. *Syagrus pseudococos* presented the major relative contribution and the more extended fruiting periods along with *Astrocaryum aculeatissimum*, while *Attalea humilis* showed an irregular fruiting pattern. Nonetheless, from April to August rodent seed dispersed palms presented a period of near fruit unavailability. This period can be critical to these animal and they may switch their diet to other fruit sources or rely on hoarded seeds (Forget, 2001). In fact, Smythe (1978) noted that during periods of food abundance, agoutis hoard more seeds than they eat and in periods of food scarcity they lived almost entirely off the scatter hoarded seeds. Donatti (2004) found elevated removal rates for *A.aculeatissimum* seeds in Anchieta. Agoutis and pacas could also employ mixed dispersed palm fruits, mainly *Syagrus romanzoffiana*, or rely on seedlings or other seeds in periods of low fruit availability (Henry, 1999). Fadini (2005) noted that agoutis on Anchieta Island might be preying upon *Euterpe edulis* saplings.

*Euterpe edulis* and *Livistona chinensis* presented very similar fruiting patterns, offering fruits from February to June. Fadini (2005) recorded three bird species consuming *E. edulis* fruits on Anchieta. *L. chinensis* is an exotic palm and presents a wide distribution on Anchieta, and several birds and also agoutis were seen preying upon its fruits (R. Fonseca pers comm.). The fruiting period for tree species begins in November, but from August to October there is no fruit resource for birds on the Island. Insect availability may be more important in this period than fruit availability (Levey, 1988a; Louiselle and Blake, 1991; Poulin et al., 1992)

Palms are also important if it is considered that their fruit fall biomass constituted more than 80 percent of the overall fruit fall. In other sites of the Atlantic rain forest it was reported that 80 percent (Galetti, 1996) and 61 percent (Marques, 2004) of the fruit fall biomass corresponded to *E.edulis* fruits. At Anchieta, *Syagrus pseudococos* is the dominant palm and its fruit fall biomass corresponded to 42 percent of the overall fruit production while *E. edulis* fruit fall corresponded to 12 percent of the total. Both species constitute an important food resource for different vertebrate frugivores, *S. pseudococos* is the main resource for agoutis and pacas while *E. edulis* is eaten by at least 30 species of frugivores (Galetti and Pedroni, 1992). From June to August fruit fall was nil for palms and trees, although 30 percent of palms individuals were bearing ripe fruits, possibly suggesting high removal rates of fruits in that period of less fruit availability, and hence the importance of palms as a food resource in times of low fruit availability on Anchieta Island for vertebrate frugivores.

Kinnaird (1992) suggested that groups of species that present fruiting times slightly shifted from one other or from the community peak may provide food resources during months of low production. This is partly true on Anchieta, where the differences in the times of occurrence of the phenophases between palms and trees may provide food resources for longer periods. Although palms may constitute an alternative food resource in periods of low fruit availability, they do not provide resources for all the assemblage of vertebrate frugivores on the Island all year.

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Appendix 1: List of palms and tree species observed on Anchieta Island, N=number of individuals, seed dispersal syndrome (Animal, Wind, Auto=Autochory and Und=undetermined syndrome), seed dispersal sub-syndrome and phenology (---irregular \*\*\*\* without event).

Family/specie	N	Syndrome	Sub-syndrome	Phenology	
				Flowering	Fruiting
ANNONACEAE					
<i>Annona cacans</i> Warm.	1	Animals	mammals	Dec	Dec-Jan
ARECACEAE					
<i>Astrocaryum aculeatissimum</i> (Schott) Burret	10	Animals	Rodents	Jan- June	March-Dec
<i>Attalea humilis</i> Mart. ex Sprengel	15	Animals	Rodents	-----	-----
<i>Bactris setosa</i> Mart.	12	Animals	Carnivores, birds	Nov	Nov-Fev
<i>Euterpe edulis</i> Mart.	11	Animals	Birds,bats, primates	Sept-Jan	Nov-June
<i>Livistona chinensis</i> (Jacq.) R. Br.	12	Animals	Birds	Sept-April	Sept-July
<i>Syagrus pseudococos</i> (Raddi) Glassman	36	Animals	Rodents	All year	All year
<i>Syagrus romanzoffiana</i> (Cham.) Glassman	20	Animals	Rodent, peccaries, birds, ungulates and primates	Sept-Dec	Out-June
APOCYNACEAE					
<i>Tabernaemontana laevis</i> Vell. cf	1	Animals	Birds	Set-Nov	Dec-April
AQUIFOLIACEAE					
<i>Ilex theazans</i> Mart. cf	8	Animals	Birds	Nov	Dec-May
ARALIACEAE					
<i>Schefflera morototoni</i> (Aubl.)	4	Animals	Birds	Set-Nov	Nov-May
ASTERACEAE					
<i>Gochnatia polymorpha</i> (Less.) Cabrera	2	Wind		May-Nov	*****

**Apendix 1-**

Family/Specie	N	Syndrome	Sub-syndrome	Phenology	
				Flowering	Fruiting
<b>BIGNONIACEAE</b>					
<i>Cybistax antisiphilitica</i> (Mart.) Mart.	11	Wind		Jul-Aug, Oct-Nov,	Ago-Set Dec-Fev
<b>CLETHRACEAE</b>					
<i>Clethra scabra</i> Pers.cf	1	Wind		Dec	Jan
<b>CECROPIACEAE</b>					
<i>Cecropia glaziovii</i> Snethl.	6	Animals	Birds	Nov-May	Dec -May
<b>CLUSIACEAE</b>					
<i>Clusia criuva</i> Cambess.	3	Animals	Birds	Sept-Nov	Nov-Jan
<b>ERYTHROXYLLACEAE</b>					
<i>Erythroxylum pulchrum</i> A. St.-Hill	16	Animals	Birds	June-Jan	Nov-Fev
<b>EUPHORBIACEAE</b>					
<i>Croton floribundus</i> Sprengel	10	Auto	ants	Nov-Dec	Dec-Jan
<i>Croton</i> sp.1	12	Auto		-----	Dec-April
<i>Pera glabrata</i> (Schott.) Poepp. ex Baill. cf	12	Animals	Birds	Sept-April	Dec-May
<i>Sapium glandulosum</i> (L.) Morong	1	Animals	Birds	Dec	*****
<b>FABACEAE</b>					
Faboideae					
<i>Machaerium nyctitans</i> (Vell.) Benth.	2	Wind		Fev	Fev-March
Fabaceae sp.1	1	und		Fev	****
Mimosoideae					
<i>Inga luschnathiana</i> cf Benth.	17	Animal	mammals	-----	Sept-May

<i>Inga</i> sp. 1	4	Animal	mammals	Nov-Dec	Nov-Fev
<b>Appendix 1-</b>					
Family/Specie	N	Syndrome	Sub-syndrome	Phenology	
				Flowering	Fruiting
<b>FLACOURTIACEAE</b>					
<i>Casearia decandra</i> Jacquin	3	Animal	Birds	June-Sept	Aug-Nov
<b>LAURACEAE</b>					
<i>Lauraceae</i> sp.1	1	Animal		Dec	Dec-April
<b>MELASTOMATACEAE</b>					
<i>Miconia cinnamomifolia</i> (DC.) Naudin	13	Animal	Birds	Sept-Nov	Nov-April
<i>Tibouchina mutabilis</i> (Vell)Cogn.	4	Wind		Nov-Fev	Nov-May
<b>MELIACEAE</b>					
<i>Guarea macrophylla</i> Vahl.	1	Animal	Birds	Jan	*****
<b>MORACEAE</b>					
<i>Ficus</i> sp.1	1	Animal		*****	Fev-April
<i>Moraceae</i> sp 1	1	und			
<i>Moraceae</i> sp 2	1	und		April September	April Sept-Oct
<b>MYRSINACEAE</b>					
<i>Rapanea umbellata</i> (Mart.) Mez	12	Animal		April-July	-----
<i>Rapanea ferruginea</i> (Ruiz&Pav.) Mez	2	Animal		May-July	April-Oct
<b>MYRTACEAE</b>					
<i>Eugenia</i> sp. cf	1	Animal		July	*****
<b>NICTAGINACEAE</b>					
<i>Guapira opposita</i> (Vell.) Reitz	54	Animal	Birds	Aug-Dec	Oct-Fev

<i>Guapira</i> sp.	7	Animal	Birds	Nov-Dec	Nov-Dec
<b>Appendix 1-</b>					
<b>Family/Species</b>	<b>N</b>	<b>Syndrome</b>	<b>Sub-syndrome</b>	<b>Phenology</b>	
				<b>Flowering</b>	<b>Fruiting</b>
RUBIACEAE					
<i>Rubiaceae</i> sp.1	1	und		May, Sept-Nov	June, Jan-May
RUTACEAE					
<i>Dictyoloma vandellianum</i> A. Juss.	2	Wind		July-Nov	Nov
SAPINDACEAE					
<i>Matayba guianensis</i> Aublet	3	Animal	Birds	June-Nov	July-Nov
SOLANACEAE					
<i>Aureliana fasciculata</i> (Vell.) Sendtn.	2	Animal		Nov	Dec-May
<i>Solanum</i> sp.	1	Animal		May-June	July
VERBENACEAE					
<i>Citharexylum myrianthum</i> Cham.	4	Animal	Mixed	Nov	Dec-Fev
<i>Aegiphila sellowiana</i> Cham.	1	Animal	Birds	Nov	Nov-Jan
Undetermined					
Undetermined 1	1	und		Dec	Jan -March
Undetermined 2	1	und		Dec	Dec-Jan
Undetermined 3	1	und		May-July	July- Aug
Undetermined 4	1	und		Sept-Oct	*****
Undetermined 5	1	und		Sept	*****
Undetermined 6	2	und		Dec	Dec-Jan
Undetermined 9	1	und		Dec	Dec-Jan

Undetermined 10	1	und	July	Oct-Dec
Undetermined 11	1	und	Jan	Jan
Undetermined 12	1	und	Dec	Dec-Jan
Undetermined 12	1	Wind	Dec	Jan-April



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