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Reproductive phenology of *Euterpe edulis* (Arecaceae) along a gradient in the Atlantic rainforest of Brazil

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Abstract. The palm *Euterpe edulis* Mart. is one of the dominant tree species in the Atlantic rainforest and considered a key resource for many frugivorous birds. We compared the reproductive phenology of *E. edulis* in three types of Atlantic rainforest (two lowland forests, restinga and coastal-plain, and a premontane forest) on Cardoso Island (Cananéia, São Paulo, Brazil), aiming to answer the following questions: (i) whether the reproduction of *E. edulis* is annual and seasonal across the years in the three forest types studied; (ii) what are the environmental factors influencing the reproductive phenology of *E. edulis*; and (iii) how does the timing of fruiting and fruit production of *E. edulis* vary among the three forest types? We evaluated the presence of flowers and fruits (immature, unripe and ripe) from August 2001 to July 2004 in 150 individuals (50 per forest), and estimated the number of infructescences with ripe fruits and the production of fruits and seeds by collecting them on the forest floor in the three forest types. Flowering and fruiting of *E. edulis* were annual and significantly seasonal in the three forest types, with a high synchrony of flowering and medium to low synchrony of fruiting. Flowering peaked in November and December, and immature and unripe fruits peaked in January and March, all during the rainy season. Immature and unripe fruit phases were correlated with the daylength, precipitation and temperature, important factors for fruits development. Ripe fruits peaked in April and May, in the less rainy season, with significant differences in the mean dates among forests. The number of infructescences with ripe fruits and the biomass of fruits and seeds collected on the ground also differed significantly among the forest types, being greater in the restinga and coastal-plain forests, respectively. Differences in productivity were related to palm density in each area and the soil fertility. The complementary fruiting pattern of *E. edulis* in the forests studied may affect the distribution and abundance of certain frugivorous bird species that feed on their fruits.

Introduction

Palms are an important food resource for many species of animals (Terborgh 1986; Peres 1994; Galetti *et al*. 1999), with highly seasonal availability of flowers and fruits in some species (De Steven *et al*. 1987; Galetti and Aleixo 1998; Rosa *et al*. 1998; Mantovani and Morellato 2000). In the tropics, various species of frugivores, mainly birds, depend on this seasonal supply of fruits for their survival (Levey *et al*. 1994), and some species must move seasonally among different environments in search of temporally abundant fruits (Loiselle and Blake 1991; Malizia 2001).

Despite the wide distribution of palms in tropical regions, with ~60 genera and 550 species (Henderson *et al*. 1995), and the great ecological importance of this group, whose seeds are dispersed primarily by animals (Henderson 2000), studies focusing on their phenology are still scarce. Little is known about the patterns of reproduction and resource supply of the family (De Steven *et al*. 1987; Lugo and Frangi 1993; Martén and Quesada 2001; Otero-Arnaiz and Oyama 2001; Calderón 2002; Berry and Gorchov 2004), which hampers understanding, management and conservation of the species. In tropical forests, phenological studies of palms are recent (Callazos and Mejía 1988; Scariot and Lleras 1991, 1995; Peres 1994; Henderson *et al*. 2000; Martén and Quesada 2001; Miller 2002; Ruiz and Alencar 2004), with most palms showing seasonal patterns of flowering and fruiting.

Approximately 45 species of palms occur in the Atlantic rainforest region (Henderson *et al.* 1995), and most are threatened by the destruction of habitat, the loss of seed dispersers because of forest fragmentation and extraction for harvesting palm heart (Souza and Martins 2004; Tabarelli *et al*. 2004; Galetti *et al*. 2006). One example is the *Euterpe edulis*, a dominant tree species in preserved areas of the Atlantic rainforest, but extinct in many places as a result of predatory exploitation (Galetti and Fernandez 1998; Guilherme *et al*. 2004). Flowering occurs annually and these monoecious palms are pollinated by bees, beetles and by wind (Mantovani and Morellato 2000), as reported for other species in the same genera (Küchmeister *et al*. 1997). Fruiting of this palm is seasonal in different areas of the Atlantic rainforest (Galetti *et al*. 1999; Fisch *et al*. 2000; Mantovani and Morellato 2000; Bencke and Morellato 2002), and the fruits are consumed by various

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species of frugivorous vertebrates, such as thrushes (*Turdus* spp. and *Turdus flavipes*), guans (*Penelope* spp.), toucans (*Ramphastos* spp.), solitary tinamou (*Tinamus solitarius*), bats (*Artibeus* spp.), tapirs (*Tapirus terrestris*), peccarie (*Tayassu pecari*) and agoutis (*Dasyprocta* spp.), most of which disperse the seeds (Rodriguez *et al.* 1993; Galetti *et al.* 1999, Galetti *et al.* 2001). Because of its importance in the diet of frugivorous animals, some authors have proposed that this palm could be considered a 'key resource' for frugivorous birds in the Atlantic rainforest (Sick 1997; Galetti *et al.* 1999).

Analysis of some studies (Laps 1996; Galetti *et al.* 1999) suggests that the fruiting phenology of the *E. edulis* may vary with altitude, beginning to produce fruits first in lower areas (lowland forests), followed later by higher-altitude areas (slopes and mountain forests). Frugivorous bird species such as the yellow-legged thrush (*T. flavipes* (Turdidae)) and the piping-guan (*Aburria jacutinga* (Cracidae)) may migrate in altitude, following the fluctuation of this resource (Laps 1996; Sick 1997; E. R. Castro, M. C. Côrtes, L Navarro, L. P. C. Morellato and M. Galetti, unpubl. data).

The objective of the present study was to compare the reproductive phenology of *E. edulis* in three different types of Atlantic rainforest (two lowland forests, restinga and coastal-plain, and a premontane forest) durng a period of 3 years, to answer the following questions:

(1) Does *E. edulis* present annual and seasonal reproduction across the years in the three types of vegetation studied? We expected the phenological pattern of *E. edulis* to be annual and seasonal in the three types of vegetation, as has been observed for palms in tropical forests (De Steven *et al.* 1987; Mantovani and Morellato 2000).
(2) What environmental factors influence the reproductive phenological patterns of *E. edulis*? We expected the flowering and fruiting phases to be related to the temperature and daylength, as suggested by Morellato *et al.* (2000) for trees in the Atlantic rainforest.
(3) How does the timing of fruiting and the fruit production of *E. edulis* vary among the three types of forest? Because of the importance of the *E. edulis* fruits for the frugivorous fauna (Galetti *et al.* 1999), we expected the production of ripe fruits to be annual and seasonal, with no difference in the time among years in each forest type, and that the supply of fruits in the three forest types would be complementary so as to maintain the supply of resources for the fauna of frugivorous dispersers.

Materials and methods

Study area

This study was conducted on Cardoso Island, off the southern coast of the state of São Paulo, Brazil, near the border with the state of Paraná, comprising a protected area of ~151 km^2 referred to as the Parque Estadual da Ilha do Cardoso (25°03′05″S, 48°53′48″W) (Bernardi *et al.* 2005). The vegetation on Cardoso Island is composed exclusively of Atlantic rainforest, and the flora has been studied in detail (Barros *et al.* 1991; Melo and Mantovani 1994; Sugyama 1998). We found five forest types on the island (Barros *et al.* 1991), and the present study was developed in three of them: two lowland forests, restinga forest (at sea level) and coastal-plain forest (0.5–3.0 m above sea level), and a premontane forest (250–300 m above sea level).

Vegetation

The restinga forest is distributed across the quaternary coastal plain on sandy soil of marine origin. It constitutes a very diverse ecosystem (Lima and Capobianco 1997) and is characterised by a low-canopy forest vegetation composed of 8-m-high trees with branched trunks. The plant families with the largest number of species are Myrtaceae (18 species), Arecaceae (5 species), Melastomataceae (4 species) and Aquifoliaceae (4 species) (Sugyama 1998). The soil is sandy, poor in nutrients and very permeable, receives intense sunlight, and has an herbaceous stratum of bromeliads, pteridophytes, bryophytes and lichens (Conselho Estadual do Meio Ambiente 2001). The coastal-plain forest is contiguous to the restinga forest, typically medium to high, ombrophyla, composed of trees with straight trunks and few branches, presenting the following two strata: canopy (20 m) and sub-canopy (8–10 m) (Barros *et al.* 1991). The families with the largest number of species are Myrtaceae (16 species), Euphorbiaceae (7 species), Fabaceae (6 species) and Lauraceae (5 species) (Pinto 1998). The soil is less sandy, rich in organic matter and receives little sunlight, with an herbaceous–shrubby stratum composed mainly of *Heliconia velloziana* (Heliconiaceae) and *Calathea* cf. *longibracteata* (Marantaceae) (Barros *et al.* 1991). The premontane forest covers the slopes of the central mountains, with a clay soil, and occupies almost 70% of Cardoso Island. It is characterised by medium to high trees and the folloiwng three more-or-less continuous arboreal strata: lower (5–10 m); medium (15–21 m) and high (24–28 m) (Barros *et al.* 1991). The families with the greatest number of species are Myrtaceae (24 species), Rubiaceae (10 species), Fabaceae (9 species), Euphorbiaceae (7 species), Moraceae (6 species), Meliaceae (6 species) and Lauraceae (5 species) (Melo and Mantovani 1994). A large number of species is found in the premontane forest compared with the restinga and coastal-plain forests (Barros *et al.* 1991).

Climate

The climate on Cardoso Island is influenced by local factors such as proximity to the ocean, irregular topography and high rainfall reaching an annual total of 3000 mm (Conselho Estadual do Meio Ambiente 2001). Meteorological data were obtained from the Oceanographic Institute of the University of São Paulo (USP) in the municipality of Cananéia, and from the Experimental station of the Núcleo Perequê, on Cardoso Island. The average climate, obtained from data collected over 30 years (1956–1985), is characterised by average annual rainfall of 2248 mm, with one very rainy season, from October to May, when monthly rainfall is >100 mm, and a less-rainy season from June to September, when rainfall is less frequent and may fall under 100 mm per month. The mean annual temperature is 23.8°C. During the study period (August 2001 to July 2004), the rainfall in Cananéia was below the 30-year average, with the total annual rainfall ranging from 1476 to 2007 mm (Fig. 1*a*). The data on daylength are for the latitude of 25° and follow Pereira *et al.* (2001).

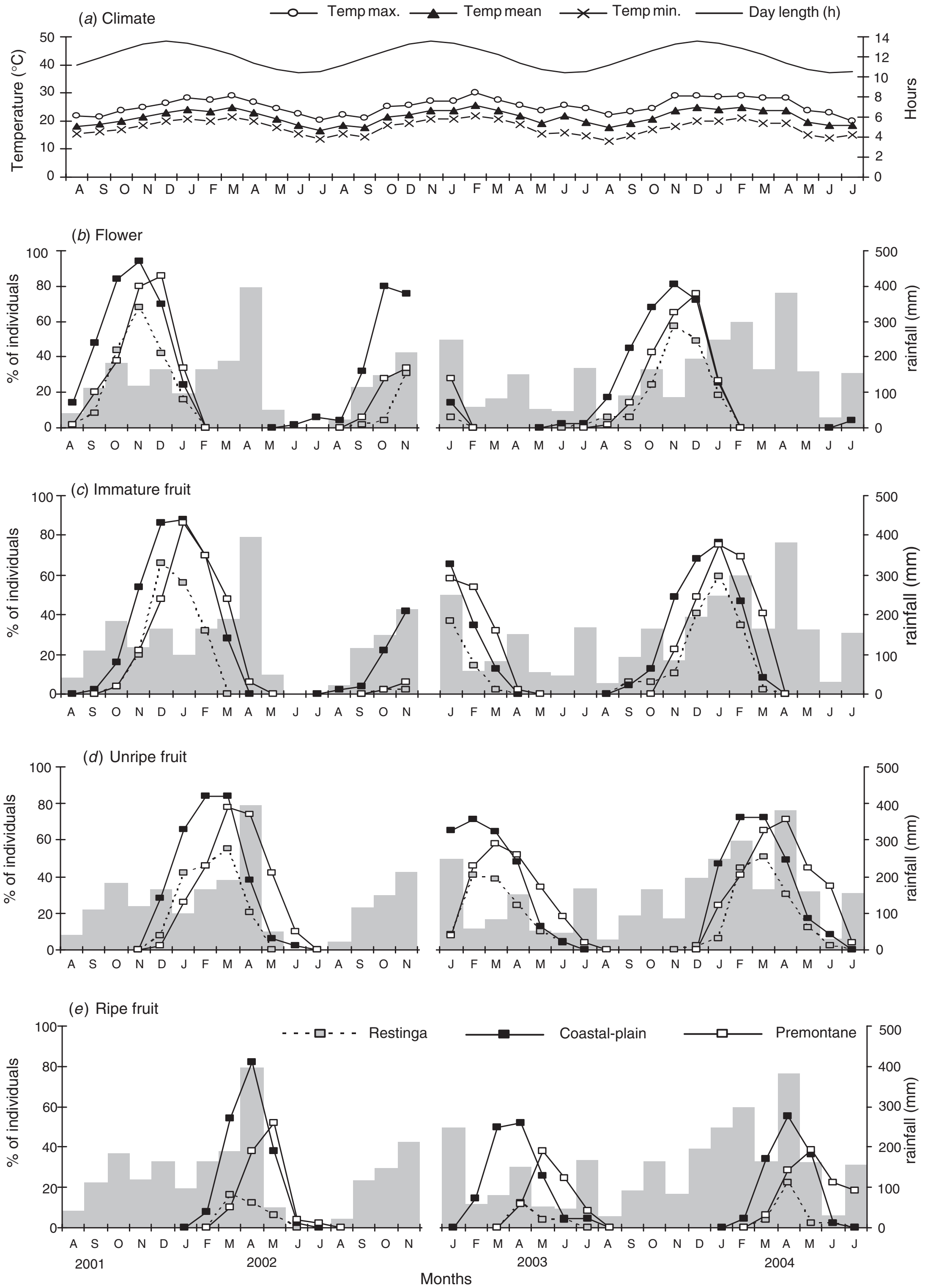

Fig. 1. (*a*) Temperature values and day length during the study period (2001–2004) at the latitude 25° for the municipality of Cananéia, São Paulo State, Brazil (source: Pereira *et al.* 2001). Percentage of *Euterpe edulis* individuals (*b*) flowering, and with (*c*) immature, (*d*) unripe and (*e*) ripe fruits in three types of Atlantic forest at Cardoso Island, Brazil. Grey bars are rainfall.

Phenology and fruit production

In the restinga forest, we selected three trails totalling ~1.15 km, beginning in the low restinga, near the base of Cardoso Island. In the coastal-plain forest, we marked three trails totalling 1.0 km. In the premontane forest, we selected just one existing trail of ~1.5 km. The *E. edulis* were marked with aluminium tags according to their order of appearance on both sides of the trails, by using the following criteria: maximum of 10 m from either side of the trail; visibility of the canopy sufficient for phenological observation; minimum distance of 20 m from one palm to the next; and only mature, reproductive individuals. *E. edulis* were considered mature or reproductive if they presented inflorescence, infructescence and/or scars indicating previous occurrence of a reproductive event (Reis and Kageyama 2000). A total of 150 *E. edulis* was sampled, 50 in each forest type.

The phenological observations were conducted monthly, from August 2001 to July 2004, except in December 2002, always in the second half of the month, with binoculars, recording the presence or absence of flowering, and immature, unripe and ripe fruits. The four reproductive phases of the *E. edulis* were characterised as follows: *flowering* – when the inflorescences presented flowers; *immature fruit* – when the fruit was green-yellow, with a soft endocarp, easily opened with a fingernail; *unripe fruit* – when the fruit approximated the size of the ripe fruit but the colour was green and the endocarp was harder; *ripe fruit* – when the fruit had a red to dark red colour and the endocarp and endosperm were very hard (Mantovani and Morellato 2000). When a doubt arose in the field regarding differentiation between immature and green fruits, the consistency of the fallen fruits beneath the observed *E. edulis* was manually tested.

During the same period, for all the 150 individuals sampled, the infructescences with ripe fruits were counted and the biomass of *E. edulis* fruits and seeds produced per forest was estimated. Fruit biomass data provide insight into resource levels for frugivores; the biomass ground survey is an easy method to assess fruit production in the forest and reflect well the seasonal variations (Zhang and Wang 1995). To estimate the biomass, 10 points along the trails in each forest were randomly selected each month, and all the *E. edulis* fruits and seeds were collected, dried in oven at 50°C for 1 week and then weighed (Charles-Dominique *et al.* 1981), and the values transformed into $\mathrm{kg\,ha^{-1}\,month^{-1}}$ for each forest type. The area sampled at each point measured 1 m to either side of the trail, beginning at the centre, and was 50 m long, covering a total area of $100\,\mathrm{m}^2$ (2.0×50.0 m). The total area sampled to quantify monthly fruit production was 0.3 ha (0.1 for each forest type). The collection of the *E. edulis* fruits and seeds was carried out according to the following criteria: only fruits and seeds within the randomly selected patch were collected; very old fruits which were likely to be from another reproductive season were excluded; and seeds beginning to germinate were not collected as this would affect their weight.

Data analysis

The activity index or percentage of individuals was used to estimate the intra-specific synchrony in each forest, indicating the proportion of individuals sampled in each area manifesting a given phenological phase (Bencke and Morellato 2002). A phenological event was considered to present high synchrony when >60% of individuals were in the phase; low synchrony when 20–60% were in the phase; and not synchronous or asynchronous when <20% were in the phase (Bencke and Morellato 2002). The number of infructescences with ripe fruits and the biomass of dry *E. edulis* fruits and seeds were compared among years, in the same type of forest, and among forests, during the 3 years of the study, by the Kruskal–Wallis test.

Circular statistical analyses were conducted with the phenological variables flowering and fruiting (immature, unripe, and ripe fruit) to define the occurrence of seasonal pattern and to compare the phenological patterns among years, in each forest, and among forest types (Morellato *et al.* 2000). To calculate the parameters for the circular statistic, the months were converted into angles, with 0° = January, successively up to 330° = December, at intervals of 30°.

The hypotheses tests were carried out as described by Morellato *et al.* (2000). To test for the occurrence of seasonality in each year and forest type, the Rayleigh (z) test was applied to determine the significance of the mean angle or mean data (Zar 1996). The null hypothesis (H_0) states that when the angles or dates are distributed uniformly throughout the year, there is no mean direction, i.e. there is no seasonality. If the H_0 is rejected, the mean angle is significant and the pattern is seasonal. The intensity of the concentration around the mean angle, represented by r, can be considered a measure of the degree of seasonality. The vector r has no units and may vary from 0 (when reproductive activity is distributed uniformly throughout the year) to 1 (when reproductive activity is concentrated around one single date or time of the year) (Morellato *et al.* 2000). The significant mean dates (seasonal pattern) were compared among years and forest types by the Watson–Williams test (F). The circular statistics analysis was performed by the ORIANA program (Kovach 1994).

The Spearman (r_s) correlation test was applied to verify the relation between the climatic factors during the study period (mean temperature, maximum temperature, minimum temperature, total monthly rainfall and daylength) and the *E. edulis* phenology (number of individuals flowering, with immature, unripe and ripe fruits per month). These correlations were tested for the 3 years of the study: 2001 (August 2001–July 2002), 2002 (August 2002–July 2003) and 2003 (August 2003–July 2004) for the three types of forest.

Results

During the 3 years of the study, only 2.6% of the total individuals of *E. edulis* observed in the three types of forest failed to flower, whereas 26% of the individuals did not form ripe infructescences. Flowering began in August, at the end of the less rainy season (June–September) for the three forest types, with the largest percentage of individuals flowering in November, at the beginning of the rainy season (Fig. 1*b*). Fruiting began in October, in the first month of the rainy season, with the largest percentage of individuals bearing immature fruit in December and January, unripe fruit in March and April, and ripe fruit in April and May (Fig. 1*c*, *e*).

Flowering

Flowering was highly synchronous in the three forest types, with the largest percentage of *E. edulis* individuals flowering in November and December (Fig. 1*b*). The greatest activity peaks were recorded in November 2001 for the restinga forest (68%

of individuals flowering) and the coastal-plain forest (94% of individuals), and in December 2001 for the premontane forest (86% of individuals), during the rainy season (Fig. 1*b*). The duration of the flowering ranged from 5 to 6 months. The mean dates of flowering were significant for every year of the study, showing a highly seasonal pattern with r between 0.6 and 0.7 (Table 1). Comparisons of the mean flowering dates among years in the same forest type showed no significant differences for the restinga and premontane forests. For the coastal-plain forest, however, the mean flowering dates were significantly different between 2001 and 2002 [$F\ (1, 273) = 4.67$; $P < 0.05$], and between 2002 and 2003 [$F\ (1, 250) = 6.07$; $P < 0.05$]. When the different types of forests were compared, the mean flowering dates were significantly different between the restinga and coastal-plain forests and the coastal-plain and premontane forests for the 3 years of the study (Table 2). Flowering showed a significant positive correlation with rainfall for 2002 and also with day length for 2001 and 2003 in the restinga forest (Table 3). For the coastal-plain forest, flowering showed a significant positive correlation with day length for 2003 only, and for the premontane forest only, a significant positive correlation with day length for all 3 years (Table 3).

Immature fruit

Production of immature fruits was highly synchronous in the three forest types, with the largest percentage of *E. edulis* individuals bearing immature fruits in December and January (Fig. 1*c*). The greatest activity peak was in December 2001 for the restinga forest (66% of individuals), and in January 2002 for the coastal-plain (88% of individuals) and premontane forests (86% of individuals). This was always in the rainy season (Fig. 1*c*). The duration of the immature-fruit phase varied from 5 to 7 months in the three forest types. The mean dates for the immature-fruit phase were significant for every year, showing a highly seasonal pattern with r above 0.68 (Table 1). Comparisons among years in the same forest type showed significant differences in the mean dates for the immature-fruit phase for restinga forest between 2001 and 2002 [$F\ (1, 116) = 10.67$; $P < 0.05$], and between 2002 and 2003 [$F\ (1, 104) = 4.25$; $P < 0.05$], and for premontane forest between 2001 and 2002 [$F\ (1, 214) = 8.40$; $P < 0.05$], and between 2002 and 2003 [$F\ (1, 201) = 9.06$; $P < 0.05$]. In the coastal-plain forest, no significant differences in the mean dates for the immature-fruit phase were found among years. Among forest types, the mean dates for the immature-fruit phase differed significantly between restinga and premontane forest, and between coastal-plain and premontane forest for all 3 years (Table 2). Significant differences were found between the restinga forest and the coastal-plain forest for 2002 only (Table 2). The immature-fruit phase showed a significant positive correlation with rainfall for 2002, and with day length and temperature for most of the 3 years in the three forest types (Table 3).

Unripe fruit

Unripe-fruit phase showed medium to high synchrony in the three forest types, with the largest percentage of *E. edulis* individuals bearing unripe fruits in February, March and April for

Table 1. Circular statistical analysis for the occurrence of seasonality of *Euterpe edulis* phenology in the three types of Atlantic forest at Cardoso Island, Brazil

Variable	2001				2002				2003			
	Flower	Immature fruit	Unripe fruit	Ripe fruit	Flower	Immature fruit	Unripe fruit	Ripe fruit	Flower	Immature fruit	Unripe fruit	Ripe fruit
Restinga forest												
Observations (N)	90	90	85	17	22	28	62	10	79	78	73	15
Mean angle (a)	301.46	345.23	36.53	80.85	299.57	5.69	58.73	107.37	307.16	350.41	59.16	91.48
Mean date	2 Nov.	16 Dec.	8 Feb.	22 Mar.	1 Nov.	7 Jan.	28 Feb.	18 Apr.	8 Nov.	21 Dec.	28 Feb.	2 Apr.
Circular deviation	31.65	29.92	32.96	22.61	34.03	24.90	34.32	22.54	33.70	35.81	32.32	18.15
Length of mean vector (r)	0.86	0.87	0.85	0.93	0.83	0.91	0.83	0.92	0.84	0.82	0.85	0.95
Rayleigh test (P)	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Coastal-plain forest												
Observations (N)	170	172	154	91	105	90	129	72	147	125	125	62
Mean angle (a)	289.64	349.61	35.90	84.85	279.37	343.10	45.18	82.18	291.50	342.96	52.11	89.62
Mean date	20 Oct.	21 Dec.	7 Feb.	26 Mar.	10 Oct.	14 Dec.	16 Feb.	23 Mar.	22 Oct.	14 Dec.	23 Feb.	1 Apr.
Circular deviation	41.62	40.64	37.99	24.30	32.42	49.79	36.87	31.41	41.43	37.60	37.89	24.16
Length of mean vector (r)	0.77	0.78	0.80	0.91	0.85	0.68	0.81	0.86	0.77	0.80	0.80	0.91
Rayleigh test (P)	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Premontane forest												
Observations (N)	130	139	138	53	48	77	110	41	111	126	140	56
Mean angle (a)	309.04	7.53	69.24	105.77	303.84	21.80	76.18	130.01	307.53	7.09	80.04	124.53
Mean date	10 Nov.	9 Jan.	10 Mar.	17 Apr.	5 Nov.	23 Jan.	17 Mar.	11 May	8 Nov.	8 Jan.	21 Mar.	6 May
Circular deviation	34.41	37.21	39.73	23.63	38.84	29.53	40.91	23.90	32.97	34.85	44.91	33.22
Length of mean vector (r)	0.83	0.81	0.79	0.92	0.79	0.87	0.77	0.91	0.84	0.83	0.73	0.84
Rayleigh test (P)	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00

Table 2. Results of Watson–Willians test (*F*) for the comparisons of mean angles between the types of Atlantic forest at Cardoso Island, Brazil
Correlations shaded in grey are significant ($P < 0.05$)

Phenophase	2001 (Aug. 2001–July 2002)	2002 (Aug. 2002–July 2003)	2003 (Aug. 2003–July 2004)
Flower	Restinga × coastal-plain F (1, 258) $= 5.77$; $P < 0.05$	Restinga × coastal-plain F (1, 125) $= 6.37$; $P < 0.05$	Restinga × coastal-plain F (1, 224) $= 8.13$; $P < 0.05$
	Restinga × premontane F (1, 218) $= 2.78$; $P > 0.05$	Restinga × premontane F (1, 68) $= 0.18$; $P > 0.50$	Restinga × premontane F (1, 188) $= 0.00$; $P > 0.50$
	Coastal-plain × premontane F (1, 298) $= 16.60$; $P < 0.00$	Coastal-plain × premontane F (1, 151) $= 15.06$; $P < 0.00$	Coastal-plain × premontane F (1, 256) $= 10.85$; $P < 0.05$
Immature fruit	restinga × coastal-plain F (1, 260) $= 0.85$; $P > 0.05$	Restinga × coastal-plain F (1, 116) $= 5.87$; $P < 0.05$	Restinga × coastal-plain F (1, 201) $= 1.86$; $P > 0.05$
	Restinga × premontane F (1, 227) $= 23.26$; $P < 0.00$	Restinga × premontane F (1, 103) $= 6.13$; $P < 0.05$	Restinga × premontane F (1, 202) $= 10.16$; $P < 0.05$
	Coastal-plain × premontane F (1, 309) $= 16.19$; $P < 0.00$	Coastal-plain × premontane F (1, 165) $= 34.71$; $P < 0.00$	Coastal-plain × premontane F (1, 249) $= 26.29$; $P < 0.00$
Unripe fruit	Restinga × coastal-plain F (1, 237) $= 0.01$; $P > 0.50$	Restinga × coastal-plain F (1, 189) $= 5.63$; $P < 0.05$	Restinga × coastal-plain F (1, 196) $= 1.70$; $P > 0.05$
	Restinga × premontane F (1, 221) $= 41.02$; $P < 0.00$	Restinga × premontane F (1, 170) $= 7.81$; $P < 0.00$	Restinga × premontane F (1, 211) $= 12.40$; $P < 0.00$
	Coastal-plain × premontane F (1, 290) $= 53.35$; $P < 0.00$	Coastal-plain × premontane F (1, 237) $= 35.75$; $P < 0.00$	Coastal-plain × premontane F (1, 263) $= 28.22$; $P < 0.00$
Ripe fruit	Restinga × coastal-plain F (1, 106) $= 0.37$; $P > 0.50$	Restinga × coastal-plain F (1, 80) $= 5.75$; $P < 0.05$	Restinga × coastal-plain F (1, 75) $= 0.07$; $P > 0.05$
	Restinga × premontane F (1, 68) $= 14.34$; $P < 0.00$	Restinga × premontane F (1, 49) $= 6.33$; $P < 0.05$	Restinga × premontane F (1, 69) $= 13.34$; $P < 0.00$
	Coastal-plain × premontane F (1, 142) $= 25.29$; $P < 0.00$	Coastal-plain × premontane F (1, 111) $= 65.60$; $P > 0.05$	Coastal-plain × premontane F (1, 116) $= 39.23$; $P < 0.00$

the restinga, coastal-plain and premontane forests, respectively (Fig. 1*d*). The greatest activity peak was recorded in March 2002 for restinga (55% of individuals) and premontane forest (78% of individuals), and in February and March 2002 for the coastal-plain forest (84% of individuals), at the end of the rainy season (Fig. 1*d*). The duration of the unripe-fruit phase ranged from 5 to 7 months in the three forests. The mean dates for the unripe-fruit phase were significant for all 3 years, showing a highly seasonal pattern with r between 0.73 and 0.85 (Table 1). Comparisons among years in the same forest type showed significant differences in the mean dates for unripe-fruit phase in the restinga forest between 2001 and 2002 [F (1, 145) $= 15.17$; $P < 0.00$], and between 2001 and 2003 [F (1, 156) $= 18.22$; $P < 0.00$]; in the coastal-plain forest between 2001 and 2002 [F (1, 281) $= 4.21$; $P < 0.05$], and between 2001 and 2003 [F (1, 277) $= 12.30$; $P < 0.00$]; and in the premontane forest between 2001 and 2003 [F (1, 276) $= 4.39$; $P < 0.05$]. Among forest types, mean dates differed significantly between the restinga and premontane forests, and between the coastal-plain and premontane forests for all 3 years. Mean dates between the restinga and the coastal-plain forest differed significantly for 2002 only (Table 2). Unripe-fruit phase showed a significant positive correlation with rainfall for 2001 and 2003 in the restinga forest, and for 2003 in the coastal-plain forest (Table 3). With respect to temperatures, unripe-fruit phase showed significant positive correlations for most years in the three forest types; however, there was no significant correlation between unripe-fruit phase and day length (Table 3).

Ripe fruit

Ripe-fruit phase was generally highly synchronous in the coastal-plain forest, presented medium synchrony in the premontane forest and low synchrony in the restinga forest, with the highest percentage of individuals bearing ripe fruits in April and May (Fig. 1*e*). The greatest activity peak was recorded in April 2002 in the coastal-plain forest (82% of individuals) and in May 2002 in the premontane forest (52% of individuals). This was always in the less rainy season. No activity peak for ripe-fruit phase was observed in the restinga forest (Fig. 1*e*). The duration of ripe-fruit phase varied from 3 to 6 months in the three forests studied. The mean dates for the ripe-fruit phase were significant for all 3 years, showing a highly seasonal pattern with $r > 0.84$ (Table 1). Comparisons of the mean dates for ripe-fruit phase among years in the same forest showed significant differences in the restinga forest between 2001 and 2002 [F (1, 25) $= 7.66$; $P < 0.05$], and in the premontane forest between 2001 and 2002 [F (1, 92) $= 22.49$; $P < 0.00$] and 2001 and 2003 [F (1, 107) $= 10.96$; $P < 0.05$]. Mean dates for the ripe-fruit phase were not significantly different among years for the coastal-plain forest. Among the three forest types, the mean dates for the ripe-fruit phase were significantly different between the restinga and coastal-plain forests for all 3 years, and between the coastal-plain and premontane forests for 2001 and 2003. The mean dates for the ripe-fruit phase differed significantly between restinga and coastal-plain forests for 2002 only (Table 2). Ripe-fruit phase was not significantly correlated with rainfall nor temperature during the 3 years of the study in the three forest types. However, a significant negative correlation with day

Table 3. Spearman correlation tests between *Euterpe edulis* phenology and the climatic variables during the study period in the three types of Atlantic forest at Cardoso Island, Brazil

Correlations in grey are significant ($P < 0.05$)

Climatic variable		Restinga forest								Coastal-plain forest								Premontane forest							
		Flower		Immature fruit		Unripe fruit		Ripe fruit		Flower		Immature fruit		Unripe fruit		Ripe fruit		Flower		Immature fruit		Unripe fruit		Ripe fruit	
	Year	rs	*P*	rs	*P*	rs	*P*	rs	*P*	rs	*P*	rs	*P*	rs	*P*	rs	*P*	rs	*P*	rs	*P*	rs	*P*	rs	*P*
Rainfall	2001	0.18	0.58	0.27	0.39	0.58	0.05	0.48	0.12	0.00	0.99	0.40	0.20	0.43	0.16	0.53	0.08	0.19	0.56	0.57	0.05	0.42	0.17	0.00	0.99
	2002	0.71	0.01	0.71	0.01	−0.25	0.44	−0.31	0.33	0.28	0.37	0.33	0.30	−0.10	0.76	−0.29	0.36	0.56	0.06	0.38	0.22	−0.22	0.50	−0.26	0.41
	2003	−0.15	0.63	0.42	0.18	0.69	0.01	0.22	0.50	−0.23	0.47	0.40	0.20	0.64	0.03	0.42	0.17	−0.19	0.56	0.53	0.08	0.52	0.08	0.05	0.89
Temperature Max.	2001	−0.04	0.91	0.48	0.12	0.89	0.00	0.47	0.12	−0.32	0.32	0.64	0.03	0.88	0.00	0.56	0.06	−0.01	0.98	0.89	0.00	0.78	0.00	0.09	0.77
	2002	−0.07	0.84	−0.07	0.84	0.56	0.06	−0.18	0.57	−0.35	0.26	0.44	0.16	0.64	0.03	0.22	0.50	−0.01	0.97	0.75	0.00	0.46	0.14	−0.31	0.33
	2003	0.34	0.27	0.79	0.00	0.49	0.10	−0.10	0.77	0.20	0.54	0.81	0.00	0.40	0.19	0.12	0.70	0.25	0.44	0.83	0.00	0.11	0.74	−0.40	0.20
Mean	2001	0.00	0.99	0.48	0.12	0.89	0.00	0.47	0.12	−0.27	0.39	0.68	0.01	0.86	0.00	0.56	0.06	0.03	0.92	0.89	0.00	0.75	0.00	0.05	0.87
	2002	−0.39	0.71	−0.12	0.71	0.53	0.08	−0.17	0.60	−0.42	0.17	0.35	0.26	0.57	0.05	0.22	0.49	−0.06	0.85	0.69	0.01	0.42	0.18	−0.32	0.32
	2003	0.19	0.55	0.75	0.00	0.62	0.03	−0.05	0.87	0.07	0.83	0.76	0.00	0.51	0.09	0.20	0.53	0.10	0.77	0.84	0.00	0.25	0.42	−0.28	0.38
Min.	2001	0.00	0.99	0.48	0.12	0.89	0.00	0.47	0.12	−0.27	0.39	0.68	0.01	0.86	0.00	0.56	0.06	0.03	0.92	0.89	0.00	0.75	0.00	0.05	0.87
	2002	−0.04	0.91	−0.04	0.91	0.52	0.08	−0.17	0.60	−0.31	0.33	0.49	0.10	0.62	0.03	0.10	0.76	0.09	0.79	0.78	0.00	0.34	0.28	−0.38	0.22
	2003	0.12	0.71	0.72	0.01	0.63	0.03	−0.02	0.95	0.01	0.98	0.74	0.01	0.57	0.05	0.20	0.53	0.05	0.87	0.86	0.00	0.32	0.31	−0.24	0.45
Day length	2001	0.68	0.02	0.89	0.00	0.49	0.10	−0.21	0.51	0.47	0.12	0.94	0.00	0.33	0.30	−0.13	0.68	0.72	0.01	0.84	0.00	0.04	0.89	−0.63	0.03
	2002	0.36	0.25	0.36	0.25	−0.02	0.94	−0.55	0.06	0.13	0.69	0.64	0.03	0.11	0.73	−0.43	0.16	0.50	0.10	0.59	0.04	−0.25	0.44	−0.75	0.00
	2003	0.70	0.01	0.94	0.00	0.11	0.73	−0.44	0.15	0.59	0.04	0.96	0.00	0.03	0.93	−0.34	0.29	0.62	0.03	0.80	0.00	−0.30	0.34	−0.72	0.01

length was observed for the 3 years in the premontane forest (Table 3).

Fruit production

The number of infructescences with ripe fruits did not differ significantly from one year to the next in the restinga, coastal-plain and premontane forests (Fig. 2*a*). However, a highly significant difference was observed among the three forest types (Kruskal–Wallis, $H = 0.91$, $P = 0.01$) in all 3 years of the study (Fig. 2*a*). The coastal-plain forest produced the largest number of infructescences with ripe fruits during the 3 years (241), followed by the premontane forest (148) and the restinga forest (41).

With respect to biomass, production of *E. edulis* fruits and seeds was seasonal (Fig. 2*b*) and did not differ significantly among years for the restinga, coastal-plain and premontane forests. Considering all 3 years of the study, a highly significant difference in monthly fruit production was observed among the three types of forest (Kruskal–Wallis, $H = 10.71$, $P = 0.00$). This difference was highly significant between the restinga and coastal-plain forests (Kruskal–Wallis, $H = 5.69$, $P = 0.01$) and the restinga and premontane forests (Kruskal–Wallis, $H = 10.70$, $P = 0.00$). However, no significant difference in monthly fruit production was observed between the coastal-plain and the premontane forests.

Discussion

Euterpe edulis presented a seasonal flowering pattern in the three forest types studied on the Cardoso Island, with flowering beginning in August (end of the less rainy season) and peaking between October and December (rainy season), as expected. Similar flowering pattern during the period of heavier rainfall has been described in other phenological studies of palms in tropical regions (De Steven *et al*. 1987; Scariot and Lleras 1991; Ratsirarson and Silander 1996; Martén and Quesada 2001) and in the Atlantic rainforest (Rosa *et al*. 1998; Mantovani and Morellato 2000; Mikich and Silva 2001; Voeks 2002). Some studies, however, have reported flowering in the dry or less rainy season for some species of palms (Callazos and Mejía 1988; Sist 1989; Henderson *et al*. 2000; Ruiz and Alencar 2004).

Flowering of *E. edulis*, although seasonal, was not correlated with temperature. Flowering showed a significant positive correlation with day length in some years, as observed for tree species in the Atlantic rainforest (Morellato *et al*. 2000; Talora and Morellato 2000). In forests where the seasons are not very marked, studies of tree communities point to day length and temperature as the most important abiotic factors triggering and synchronising flowering (Wright and van Schaik 1994; Morellato *et al*. 2000; Talora and Morellato 2000; Stevenson 2004). However, synchrony of flowering may also be related to biotic factors such as pollination, predation and competition, rather than climatic variables alone (Rathcke and Lacey 1985; Van Schaik *et al*. 1993; Alencar 1994; Sakai *et al*. 1999).

Differences in the mean date of flowering among the three forest types could be related to the temporal variation of certain environmental conditions specific to each forest type, especially edaphic factors related to the seasonal flooding of the soil. Bencke and Morellato (2002) related differences in flowering of some tree species such as *Guatteria australis* A.St.-Hil and *Schefflera calva* (Cham.) Frodin & Faschi, found in restinga and premontane Atlantic rainforest in Ubatuba, São

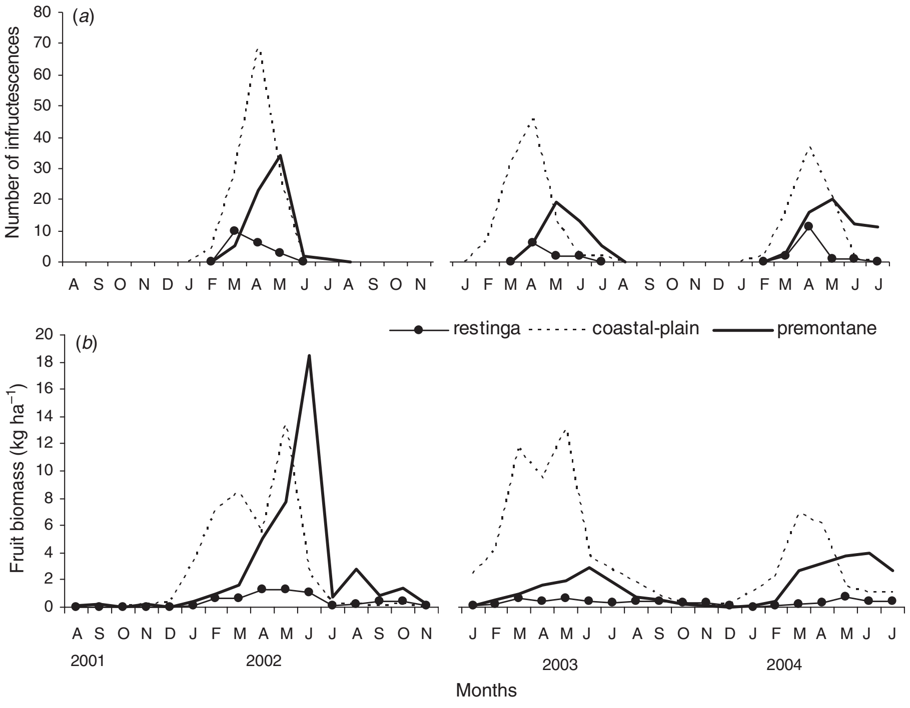

Fig. 2. Seasonal production of *Euterpe edulis* (*a*) ripe infructescences and (*b*) fruit biomass on the forest floor, in three types of Atlantic forest at Cardoso Island, Brazil.

Paulo, Brazil, to the seasonal flooding of the restinga soils, which occurs only occasionally in the coastal-plain forest. Rathcke and Lacey (1985) suggested that abiotic factors may limit the flowering season by affecting the plant's ability to produce flowers.

Immature- and unripe-fruit phases were also seasonal, as expected, and occurred in greater proportion during the rainy season from October to May, showing a significant positive correlation with rainfall and temperature in the three forest types. The hot and humid season probably favoured the development of *E. edulis* fruits in the three forests studied. Other studies have reported fruit production precisely in the periods of higher temperatures and rainfall (Rathcke and Lacey 1985; Peres 1994; Rosa *et al*. 1998; Galetti *et al*. 1999; Chapman *et al*. 2005). On the other hand, Talora and Morellato (2000), when studying the tree phenology in the restinga Atlantic rainforest, observed peak production of immature fruits during the colder, less rainy season of the year, with significant negative correlations with temperature and day length.

Ripe-fruit phase showed a seasonal pattern in the three forest types, as expected, beginning in February and extending across 5 months, and peaking between April and May in the less rainy season. The long ripe-fruit phase has been observed also in other studies on palm phenology in tropical forests (De Steven *et al*. 1987; Peres 1994; Galetti *et al*. 1999). The presence of ripe fruits mainly during the coldest, less rainy season has been reported for other palm trees (Sist 1989; Peres 1994; Miller 2002) and can be related to the reduction in the activity of pathogens and insects/invertebrates that prey on the seeds.

Production of ripe fruits was highly synchronous in the coastal-plain forest but showed medium to low synchrony in the restinga and premontane forests. The high synchrony of fruiting may facilitate seed dispersal, as it increases the number of frugivorous animals or their movement among the plant species (Wheelwright and Orians 1982). In addition, the intense and concentrated availability of fruits could satisfy the predators and thus allow some seeds to escape (Janzen 1974; Van Schaik *et al*. 1993; Curran and Leighton 2000). Seed predation has great ecological and evolutionary importance as it affects the diversity of plants, as well as their demography and phenology (Crawley 1983; Curran and Leighton 2000). Seed predation of *E. edulis* in the Atlantic rainforest is carried out largely by a species of Scolytidae beetle (*Coccotrypes palmarum* Eggers 1933) (Pizo and Simão 2001; Von Allmen *et al*. 2004; Pizo *et al*. 2006), which could influence the pattern of high synchrony observed for *E. edulis* in the coastal-plain forest. On the other hand, the low synchrony of *E. edulis* in the restinga forest, which has also been observed in other studies of the same species by Galetti *et al*. (1999), Mantovani and Morellato (2000) and Bencke and Morellato (2002), could confer upon the palm an important role as a food source for many frugivorous vertebrates over a longer period. However, a large quantity of fruiting tree species was observed fruiting throughout the year in the forests studied (E. R. Castro, pers. obs.), overlapping the fruiting period of the *E. edulis* in all three forests studied. Despite the quantity of fruits produced (see below) at this study site, *E. edulis* could not be characterised as a key species since the supply of fruits did not occur in the period of food scarcity in the forest community (Peres 2000).

Time of fruiting and ripe-fruit production of *E. edulis* differed among the types of forest studied but not from year to year in each forest, as predicted. The mean date for the occurrence ripe fruit differed significantly between the restinga and premontane forests, and between the coastal-plain and premontane forests. Differences in the timing of fruit supply may be related to the temporal variation of certain environmental conditions in each forest, as discussed in the sections about flowering and immature and unripe fruits (Sakai *et al*. 1999; Morellato *et al*. 2000; Bencke and Morellato 2002), or to the action of seed dispersers (Wheelwright and Orians 1982).

As expected, the production of ripe fruits by *E. edulis* on Cardoso Island began in the lower areas (restinga and coastal-plain forests), followed by the higher areas (premontane forest), confirming the occurrence of altitudinal variation in the supply of *E. edulis* fruits as suggested in other studies of the Atlantic rainforest (Laps 1996; Galetti *et al*. 1999). The quantity of ripe infructescences differed significantly among the three types of forest, with higher production in the coastal-plain forest and lower production in the restinga forest. The biomass of *E. edulis* fruits collected on the ground also differed among the forest types. Again, higher production occurred in the coastal-plain and premontane forests, and lower production in the restinga forest. Differences in the number of infructescences and fruit production may be related to environmental factors such as soil fertilityl, providing nutrients for development of the fruits, but may also be the result of differences in the density of *E. edulis* in each area. Studies in the forests of Cardoso Island by Pinto (1998) showed that the soils of the coastal-plain and premontane forests have a higher clay content, higher fertility and better cycling of nutrients than the soils in the restinga forest, which may explain the differences in productivity of the *E. edulis* observed in these forests. Regarding tree density, Melo and Mantovani (1994) showed that in the premontane forest, *E. edulis* is the tree species with the highest density. In the coastal-plain forest, Kojima (2004) found a similar result. In the restinga forest, Sugyama (1998) alleged that the density of *E. edulis* is very low, with this species not being among the 10 most abundant species. The higher density of plants may attract more pollinators and result in greater fruit producition (Ghazoul *et al*. 1998; Somanathan and Borges 2000). Reis and Kageyama (2000) conjectured that the sizeable increase in *E. edulis* fruit production from one year to the next may be related to the variation in the composition of inflorescences, i.e. the percentage of masculine flowers produced, which would affect the number of infructescences formed and the number of fruits produced.

Differences in phenology and fruit production of *E. edulis* among the three forest types are important because the species maintains the fruit supply during long periods and affects the populations of vertebrate frugivores consuming the fruits (Laps 1996; Galetti *et al*. 1999). Many endangered species of birds in the Atlantic rainforest depend on *E. edulis* fruits. Some birds such as the yellow-legged thrush (*Turdus flavipes*), the piping-guan (*Aburria jacutinga*) and the bare-throated bellbird (*Procnias nudicollis*) make seasonal altitudinal movements, apparently seeking *E. edulis* fruits (Collar *et al*. 1992; Sick 1997;

E. R. Castro, M. C. Côrtes, L. Navarro, L. P. C. Morellato and M. Galetti, unpubl. data). Thus, phenological studies involving species of palms in endangered biomes are fundamental for understanding the ecological interactions with frugivorous species and the management and conservation of the palms and associated fauna.

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