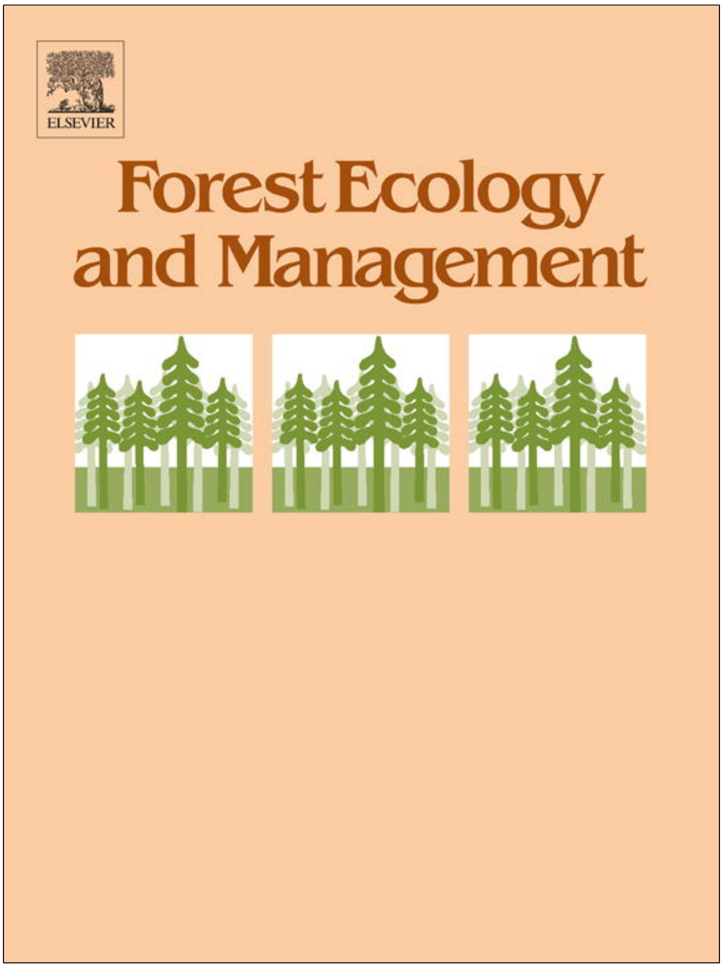
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Soil-mediated effects on potential *Euterpe edulis* (Arecaceae) fruit and palm heart sustainable management in the Brazilian Atlantic Forest

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ABSTRACT

Euterpe edulis is an endangered species due to palm heart overharvesting, the most important non-timber forest product of the Brazilian Atlantic Forest, and fruit exploitation has been introduced as a low impacting alternative. However, *E. edulis* is a keystone species for frugivores birds, and even the impact of fruit exploitation needs to be better investigated. Since this species occurs over contrasting habitats, the establishment of site-specific standards and limits for exploitation may also be essential to achieve truly sustainable management. In this context, we sought to investigate how soil chemical composition would potentially affect *E. edulis* (Arecaceae) palm heart and fruit exploitation considering current standards of management. We studied natural populations found in Restinga Forest and Atlantic Rainforest remnants established within Natural Reserves of São Paulo State, SE Brazil, where 10.24 ha permanent plots, composed of a grid of 256 subplots (20 m × 20 m), were located. In each of these subplots, we evaluated soil chemical composition and diameter at breast height of *E. edulis* individuals. Additionally, we evaluated fruit yield in 2008 and 2009 in 20 individuals per year. The Atlantic Rainforest population had a much higher proportion of larger diameter individuals than the population from the Restinga Forest, as a result of habitat-mediated effects, especially those related to soil. Sodium and potassium concentration in Restinga Forest soils, which have strong negative and positive effect on palm growth, respectively, played a key role in determining those differences. Overall, the number of fruits that could be exploited in the Atlantic Rainforest was four times higher than in Restinga Forest. If current rules for palm heart and fruit harvesting were followed without any restriction to different habitats, Restinga Forest populations are under severe threat, as this study shows that they are not suitable for sustainable management of both fruits and palm heart. Hence, a habitat-specific approach of sustainable management is needed for this species in order to respect the demographic and ecological dynamics of each population to be managed. These findings suggest that any effort to create general management standards of low impacting harvesting may be unsuccessful if the species of interest occur over a wide range of ecosystems.

1. Introduction

Soil is a major determinant of the composition and functioning of terrestrial ecosystems (Lambers et al., 2008). Variations in the precipitation regime, relief position, and parent material may result in a highly heterogeneous mosaic of soil types in the landscape (Brady and Weil, 1996). In particular, tropical forests are recognized for their habitat heterogeneity, including small-scale variation in soil attributes, resulting in soil-related habitat specialization in plant species (Fine et al., 2004; Palmiotto et al., 2004; Baltzer et al., 2005; John et al., 2007). As a result, if a given commercial tropical forest species occur over contrasting soil types, some of its important life-history traits can be affected. Consequently, site-specific standards and limits for exploitation may be essential to achieve truly sustainable management. Indeed, the proposal of any strategy of sustainable management of forest products has to be supported by empirical and/or scientific data on the ecology and demography of the population to be managed within a given geographical distribution (Ticktin and Shackleton, 2011). As highlighted by Ticktin (2004), "environmental variation presents a challenge to our current understanding of ecological impacts of non-timber forest products extraction". However, this question has not been broadly investigated to date (Ticktin, 2004).

The exploitation of the neotropical palm *Euterpe edulis* – locally know as "palmiteiro" – provides a valuable template for studying the possible need for site-specific standards of management as a

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result of soil-mediated effects on plant growth and reproduction. This understory palm (5–20 m tall) endemic to the Atlantic Forest biome occurs in different forest types from 30°S to 15°S (Henderson et al., 1997; Silva Matos et al., 1999). Palmiteiro provides the edible palm heart, the apical meristem and developing undifferentiated leaves of palms' stem, which is the most important non-timber forest product exploited from the Brazilian Atlantic Forest. Additionally, palmiteiro fruit pulp has also been introduced as a southeastern equivalent of the Amazonian "açaí" (*Euterpe oleraceae*) – a concentrated lipid- and sugar-rich pulp of palm fruits used for several edible purposes (Fagnani, 2007) – and now standards for sustainable fruit exploitation are needed to supply this new production chain.

However, historical overharvesting for palm heart production has drastically reduced its population to the level of risk of extinction (Dransfield et al., 1988), and several local extinctions have been observed (Galetti and Fernandez, 1998). As differentiated from *E. oleraceae*, an indigenous palm of Amazonian basin which is also used for fruit and palm heart exploitation (Muñiz-Miret et al., 1996; Pollak et al., 1995), palmiteiro is a single-stemmed palm and does not re-sprout after harvesting, which leads to the death of the palm after the stem is cut for palm heart extraction (Reis et al., 2000). In order to compensate for the collapse of palm heart supply in privately owned forest fragments, illegal extraction has reached alarming levels inside protected areas and has ultimately endangered the last pristine and old-growth remnants (Galetti and Chivers, 1995; Orlande et al., 1996; Galetti and Fernandez, 1998; Reis et al., 2000). To aggravate the problems derived from overharvesting, palmiteiro is consumed in periods of food scarcity by at least 30 bird and 13 mammal species, some of which are endangered (Galetti and Fernandez, 1998; Fadini et al., 2009). As in other cases of overharvesting, several ecological, economic, and social problems have been observed as a result of uncontrolled exploitation of this species (Peres, 2010).

Three important lessons have emerged from this critical situation: (1) simple top-down prohibition of palmiteiro extraction is not effective (Orlande et al., 1996); (2) non-controlled, business-as-usual extraction of this keystone species results in overharvesting, (3) sustainable management of palm heart, and especially fruits, may be the solution for reconciling palmiteiro exploitation with its long-term conservation in managed forests. Fortunately, methods of palm heart sustainable management have been investigated in the last years (Reis et al., 2000; Freckleton et al., 2003). However, none of these studies considered variations of potential palm heart exploitation in the different habitats occupied by the species. Consequently, the application of current management standards in populations growing in sites with different soil characteristics and population dynamics may produce different results, including overharvesting. Fruit exploitation has not being explored so far by research. Hence, there is growing demand for implementing and improving palmiteiro exploitation in natural populations, and habitat heterogeneity is one of the key factors to be incorporated into future programs of sustainable management. As with palmiteiro, other commercial tropical species exploited for non-timber forest products grow under different, and sometimes contrasting, habitat conditions (Ticktin and Shackleton, 2011), therefore this case study may provide relevant insights into the need for site-specific standards of low-impact forest management.

We sought to investigate in this work how habitat-mediated effects, and specifically soil chemical composition, would potentially affect palmiteiro palm heart and fruit exploitation, considering current standards of management, in different forest types of the Brazilian Ombrophilous Dense Atlantic Forest. Additionally, we discussed the need for site-specific standards for improving current proposals of low-impact harvest regimes for this species.

2. Materials and methods

2.1. Study sites

We studied palmiteiro populations of Restinga Forest and Atlantic Rainforest within Natural Reserves of São Paulo State, SE Brazil, where 10.24 ha (320 × 320 m) permanent plots were located (Fig. 1). The study areas of Restinga Forest and Atlantic Rainforest in which these plots are located are 22,500 ha and 37,793 ha in size, respectively. Palmiteiro is the most abundant species in the areas of Restinga Forest and Atlantic Rainforest included in this study, corresponding respectively to 19.8% (300 individuals/ha) and 21.5% (240 individuals/ha) of the trees with diameter at breast height (DBH) > 4.8 cm (Projeto Parcelas Permanentes, 2006). Restinga Forest and Atlantic Rainforest are vegetation types included in the Ombrophilous Dense Atlantic Forest, which is part of the Atlantic Forest domain. Thereby, they are contiguous vegetation types included in the same ecosystem. We chose to study soil-mediated effects on potential palmiteiro exploitation in Restinga and Atlantic Rainforest because palm heart has been harvested predominantly in these forest types and the emerging exploitation of fruits can follow the same trend. The Atlantic Rainforest occurs throughout the Atlantic mountain range, predominantly in steeper slopes from 50 to over 1500 m above sea level, as well as in lowlands from 0 to 50 m, while Restinga forests occur over geologically young sandy and nutrient-poor lowlands created and destroyed by cyclical changes in the sea level (Gomes et al., 2007) (Fig. 1). The mosaic of vegetation types of Restinga constitutes marginal habitats predominantly formed by the colonization of other flora present in neighboring areas at the Atlantic mountain range (Scarano, 2002). Despite the high floristic richness of the permanent plots of Atlantic Rainforest (205 species with DBH > 4.8 cm) and Restinga Forest (114 species with DBH > 4.8 cm), these study areas had less than 14% species similarity (Projeto Parcelas Permanentes, 2006), which reflects their different habitat conditions. Since Restinga Forest and Atlantic Rainforest share large areas of contact (no dispersal limitation) and are submitted to the same Equatorial Climate (Af according to Köepen classification), divergences in vegetation composition are probably driven by their remarkable soil differences (Table 1).

2.2. Palm size and soil chemical content

Each permanent plot was composed by a grid of 256 subplots (20 m × 20 m), which were individually used for evaluating DBH of palmiteiro individuals and soil chemical content. Only individuals with DBH > 4.8 cm were considered. Soil samples obtained at 5–25 cm depth were used in the analysis. We chose to evaluate the effect of soil chemical content in palm size by using only 5–25 cm depth samples because most nutrient-absorbing palm roots are included in this soil layer. In addition, we were more interested in evaluating the direct effects of soil, so that we preferred to not evaluate the samples obtained at 0–5 cm depth, which are basically constituted by litterfall; deeper soil samples (80–100 cm) were not used because they poorly contribute to nutrient supply as a result of the low concentration of fine roots in this soil layer and reduced cation content. Soil pH was determined by potentiometry in $CaCl_2$ solution, Al was extracted in KCl and determined by acid–base titulation, and H + Al was extracted in SMP buffer and determined by potentiometry (van Raij et al., 2001). P, K, Ca, Na, and Mg were extracted in ion exchange resin (EMBRAPA, 1997). Soil cations were determined by spectrophotometry and P by colorimetry (van Raij et al., 2001). The dataset of the Permanent Plots Project-BIOTA/FAPESP were used to access these data.

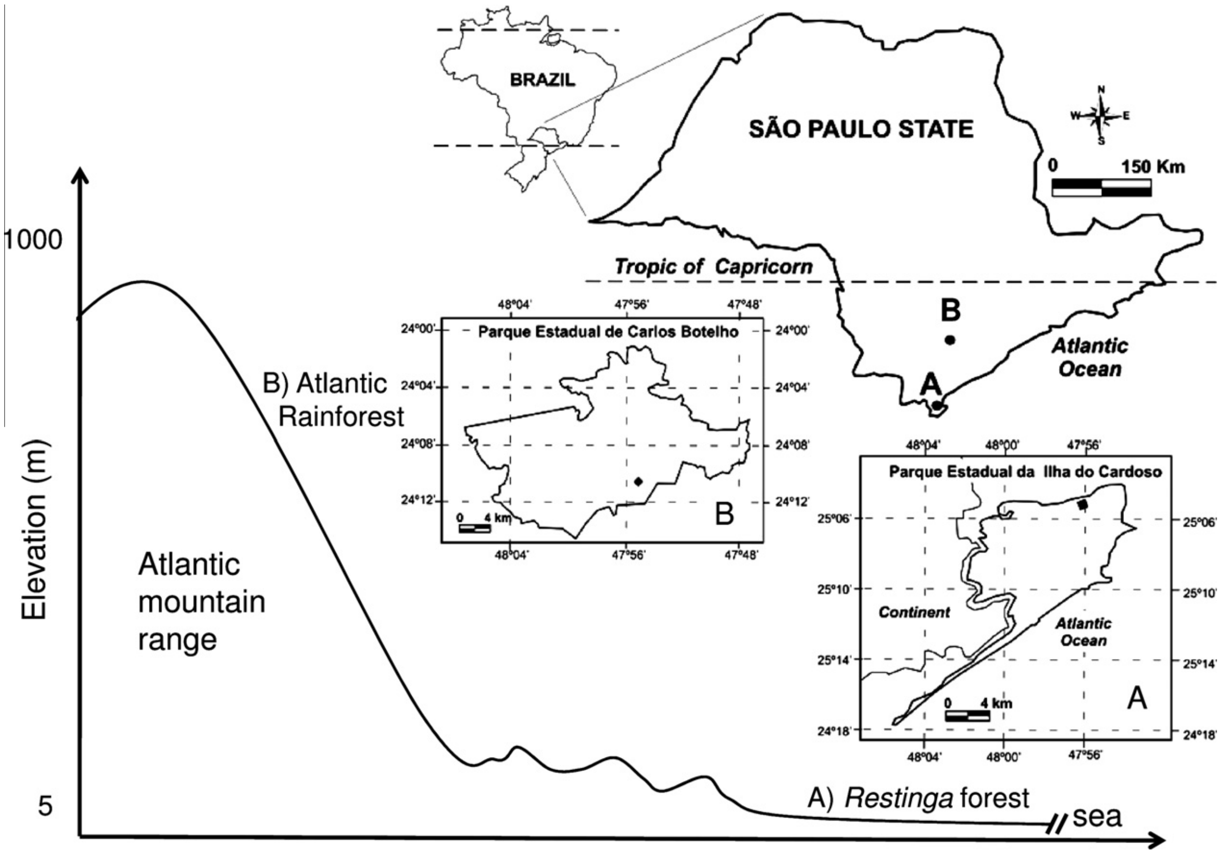

Fig. 1. Study sites where *Euterpe edulis* (Arecaceae) populations were studied in the Ombrophilous Dense Atlantic Forest of southeastern Brazil: Parque Estadual da Ilha do Cardoso (A – Restinga Forest) and Parque Estadual de Carlos Botelho (B – Atlantic Rainforest), and a schematic representation of the topographic range where these sites where located. The black squares inside each area represent 10.24 ha permanent parcels whose interior and surroundings were used in the study.

Table 1
Major soil characteristics of the forest types included in the Ombrophilous Dense Atlantic Forest of southeastern Brazil where *Euterpe edulis* populations were studied (data obtained 256 plots with 20 × 20 m from 10.24 ha permanent plots located in each forest type).

Soil information Soil classification (Brazilian soil classification system)	Restinga Forest Orthic and hydromorphic carbic spodosol			Atlantic Rainforest Dystrophic Tb haplic cambisol (Inceptisol)		
Sample depth	0–5 cm	5–25 cm	80–100 cm	0–5 cm	5–25 cm	80–100 cm
Soil texture						
Sand (%)	92 ± 3	92 ± 3	92 ± 3	50 ± 10	51 ± 9	44 ± 10
Silt (%)	3 ± 2	3 ± 1	3 ± 2	15 ± 5	13 ± 4	14 ± 4
Clay (%)	5 ± 2	5 ± 2	5 ± 2	35 ± 8	36 ± 9	42 ± 11
Density (g/cm^3)	1.4 ± 0.1	1.4 ± 0.1	1.4 ± 0.1	1.0 ± 0.1	1.3 ± 0.1	1.3 ± 0.1
pH $CaCl_2$	1.0 ± 1.5	0.9 ± 1.5	0.9 ± 1.5	3.6 ± 0.3	3.8 ± 0.2	4.0 ± 0.1
Organic matter (g/dm^3)	84.4 ± 54.2	40.4 ± 36.2	27.3 ± 23.7	46.2 ± 14.1	36.0 ± 12.2	17.0 ± 6.3
Chemical content						
P (mg/kg)	25.7 ± 27.4	4.6 ± 8.5	2.5 ± 7.0	15.6 ± 7.4	3.5 ± 2.3	1.4 ± 1.6
Na (mmol/kg)	2.7 ± 1.4	1.3 ± 1.8	0.6 ± 0.7	1.1 ± 0.5	0.6 ± 0.3	0.4 ± 0.2
K (mmol/kg)	3.3 ± 2.8	0.8 ± 1.1	0.4 ± 0.9	4.2 ± 1.9	1.9 ± 1.1	1.1 ± 0.6
Ca (mmol/kg)	19.2 ± 28.8	2.1 ± 4.7	1.8 ± 4.0	18.6 ± 20.0	3.8 ± 5.8	1.4 ± 1.1
Mg (mmol/kg)	19.3 ± 23.5	3.0 ± 6.7	2.0 ± 5.0	9.5 ± 5.2	3.2 ± 1.7	1.6 ± 0.8
Al (mmol/kg)	12.3 ± 6.8	9.4 ± 8.7	28.8 ± 23.7	18.8 ± 7.9	18.5 ± 6.2	13.5 ± 4.4
H + Al (mmol/kg)	121.9 ± 60.4	62.0 ± 53.2	85.3 ± 54.4	101.4 ± 23.7	72.9 ± 18.5	46.8 ± 10.2
Sum of bases (mmol/kg)	44.6 ± 49.5	7.2 ± 12.0	4.9 ± 9.4	33.5 ± 25.3	9.5 ± 7.6	4.5 ± 2.0
T (mmol/kg)	166.6 ± 95.7	69.2 ± 60.1	90.2 ± 57.6	134.9 ± 33.1	82.4 ± 20.9	51.3 ± 10.4
V%	23.1 ± 15.6	11.3 ± 6.9	6.8 ± 8.8	23.6 ± 11.9	11.4 ± 6.9	9.1 ± 4.8
m%	33.3 ± 19.9	58.9 ± 14.7	81.5 ± 17.8	40.2 ± 19.1	67.3 ± 15.6	74.1 ± 10.5

2.3. Fruit crop

Production of ripe fruits was monitored on a monthly basis from October 2007 to October 2008 for 15 palm trees per forest type. Seeds were harvested in May 2008 and in May 2009 from 20 palmiteiros in each forest type, considering a minimum distance of 50 m from each other. Different individuals were harvested each year. Before each harvesting event, the number of palm bunches bearing ripe and unripe fruits per plant were recorded. To evaluate ripe fruit production, we placed a plastic tarpaulin under each

Table 2
Akaike Information Criterion (AIC) for distribution models for palmiteiro (*Euterpe edulis* – Arecaceae) diameter at breast height in two forest types included in the Ombrophilous Dense Atlantic Forest of southeastern Brazil (data obtained in plots with 20 × 20 m from 10.24 ha permanent plots located in each forest type).

Distribution model	df	Akaike Information Criterion (AIC)		
		General	Atlantic Rainforest	Restinga Forest
Gaussian	2	27717.57	12942.52	10900.21
Gamma	2	26233.26	12694.71	10546.95
Weibull	2	27515.11	12810.77	11735.98
Lognormal	2	25724.53	12683.71	10460.19

reproductive palm and cut the ripe bunch, collecting and counting all falling fruits. Unripe bunches were not harvested. See details on fruit harvesting in Brancalion et al. (2011).

2.4. Questions addressed and data analysis

Based on the dataset obtained with the evaluations described above, we addressed the following questions:

2.4.1. Are there differences in population structure and potential for heart palm harvesting between the Atlantic Rainforest and Restinga Forest populations?

We compared the DBH distribution of Atlantic Rainforest and Restinga Forest palmiteiro individuals by three approaches: (i) comparing location statistics of DBH: minimum value, first quartile, median, mean, third quartile and maximum value; (ii) comparing the graphics of the empirical cumulative distribution of DBH of the two forest types. We chose as a reference value the minimum DBH of 9 cm for harvest, defined by a specific legislation of the state of São Paulo for sustainable management of palmiteiro palm heart (São Paulo, 1994); (iii) fitting probability distribution models for the DBH data. First, we compared the Gaussian (normal), Gamma, Weibull and Lognormal distribution models (Burnham and Anderson, 2002). Second, we compared the best distribution model (Lognormal model – Table 2) as a general (overall) model for the whole dataset, and models for each type of forest. The models were compared with the Akaike Information Criterion (AIC) (Akaike, 1985).

2.4.2. Do soil chemical content differ between Atlantic Rainforest and Restinga Forest sites? How does soil chemical content influence palmiteiro DBH?

We applied the multivariate normal distribution as an overall model to compare P, Na, Ca, K, Mg, and Al concentration between Atlantic Rainforest and Restinga Forest soils, separately. In order to test which soil element better explains the variation of palmiteiro DBH, we used classical linear models in which the DBH was the response variable and soil elements were the prediction variables. Forest type was also tested as a predictor variable. Since soil nutrients are frequently correlated, we tested their influence in two groups separately, in which one of them was composed by P, Ca, Mg, and Al, and the other group by Na and K. Sodium and K were tested independently from the other elements because of their well-documented negative (Schachtman and Liu, 1999) and positive (Broschat, 2008) effect on palm growth, respectively. We have not included organic matter in the analysis because in tropical soils as such as those under study in this work there is a strong overlapping and complementarity of organic matter and nutrient availability. Thereby we preferred to evaluate the effect of cations and, in particular, of those more indicated in the literature as having a major importance for palm growth.

2.4.3. Which differences can be found in palmiteiro fruit production between the Atlantic Rainforest and Restinga Forest populations? How would eventual habitat-mediated differences in fruit production affect harvesting standards?

First, we fit generalized linear models of the "Poisson" family to the number of fruits per bunch and to the potential fruit yield (fruit number per bunch *x* bunch number per plant), including the year and the forest type as prediction variables. Secondly, we simulated palmiteiro fruit management considering the current recommendation of harvesting regime adopted in the state of São Paulo (2008), in which: (i) if the individual has a single bunch, it can be exploited; (ii) if the individual has two bunches, one of them can be exploited; (iii) if the individual has three bunches, two of them can be exploited; (iv) if the individual has four bunches, two of them can be exploited.

3. Results

The DBH distribution of the palmiteiro population from the Atlantic Rainforest included a much higher proportion of larger diameter individuals than the population from the Restinga Forest (Table 3). The DBH distribution of such populations was also explained by different models, reinforcing the differences between Atlantic Rainforest and Restinga Forest palmiteiro population structures (Table 4). Such results suggest remarkable differences in the potential for sustainable harvesting according to recommended DBH for cutting, since 90% of the Restinga Forest individuals would not be thick enough for palm heart exploitation, while 45% of Atlantic Rainforest palmiteiros would be (Fig. 2).

The multivariate normal distribution model indicated that Atlantic Rainforest and Restinga Forest had different soil chemical composition in terms of K, Ca, Mg, Al, P, and Na (Table 5). Mean vectors indicated that Atlantic Rainforest has higher content of K, Ca, Mg, and Al, while Restinga forest soil had higher concentration of P and Na (Table 1). When evaluating the effect of soil chemical content in palmiteiro DBH, models indicated that the two groups of soil elements (P, Ca, Mg, and Al; and Na and K) were important in defining palmiteiro DBH, even when Na and K were tested after the other group of nutrients (Table 6). However, the influence of soil nutrients on DBH was directed related to differences in forest types. When forest type was included in the model, soil nutrients were no longer relevant in the prediction of DBH (Table 6). In fact, the inclusion of soil nutrient as predictor after forest type made the model worse, i.e., soil effects were more related to forest type than to soil variability within each forest type.

The number of fruits per bunch was affected by both year and forest type (Table 7). In 2008, the number of fruits per bunch of

Table 3
Statistics of diameter at breast height distribution for palmiteiro (*Euterpe edulis* – Arecaceae) in two forest types included in the Ombrophilous Dense Atlantic Forest of southeastern Brazil (data obtained in 256 plots with 20 × 20 m from 10.24 ha permanent plots located in each forest type).

Forest type	Diameter at breast height (cm) statistics						
	n	Minimum	1st. Quartile	Median	Mean	3rd. Quartile	Max.
Atlantic Rainforest	2308	4.8	6.7	9.5	10.0	14.0	32.0
Restinga Forest	3076	4.8	6.4	7.3	7.4	8.2	22.0

Table 4
Parameter estimates and Akaike Information Criterion (AIC) for Lognormal distribution models of diameter at breast height for palmiteiro (*Euterpe edulis* – Arecaceae) populations growing in two forest types included in the Ombrophilous Dense Atlantic Forest of southeastern Brazil (data obtained in 256 plots with 20 × 20 m from 10.24 ha permanent plots located in each forest type). The values within parenthesis are the standard error of estimates.

Distribution models	*n*	Mean	Standard deviation	AIC
General	5384	2.1009 (0.0044)	0.3226 (0.0031)	25724.53
Atlantic Rainforest	2308	2.2570 (0.0082)	0.3949 (0.0058)	12683.71
Restinga forest	3076	1.9838 (0.0033)	0.1821 (0.0023)	10460.19

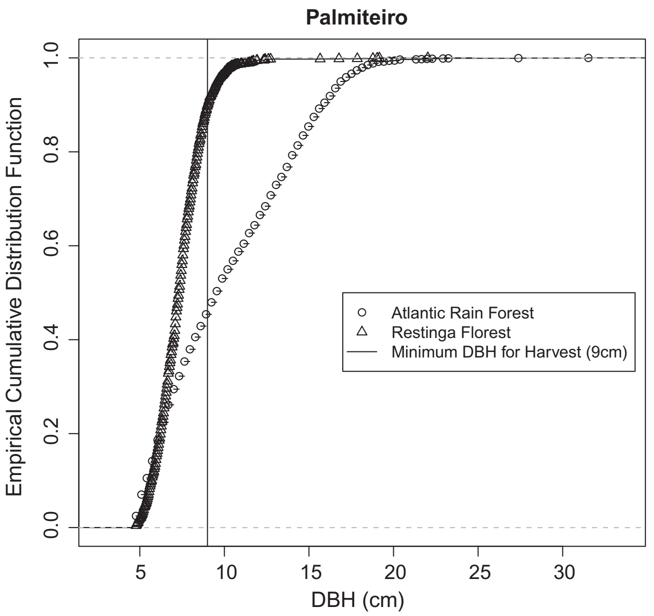

Fig. 2. Empirical cumulative distribution of diameter at breast height (DBH) of palmiteiro (*Euterpe edulis* – Arecaceae) populations from the Atlantic Rainforest and Restinga Forest, both included in the Ombrophilous Dense Atlantic Forest of southeastern Brazil. We chose as a reference value the minimum DBH of 9 cm for harvest, defined by a specific legislation of the state of São Paulo for sustainable management of palmiteiro palm heart.

Atlantic Rainforest individuals (969 ± 526, mean ± 1SD) was almost four times higher than that produced by Restinga Forest individuals (252 ± 162). In 2009, a remarkable increase in fruit yield was observed (Atlantic Rainforest = 1610 ± 685; Restinga Forest = 476 ± 189), but a similar proportional difference between forest types was kept. The coefficient of variation of fruit crop was about 50% in both years and forest types. There was also an interaction effect between year and forest type, i.e., the influence of year was not the same in both forest types. Additionally, the number of bunches per palm was affected by forest type, but not year (Table 7). As a result, the potential number of fruits (fruit number per bunch *x* bunch number per plant) was affected by both year and forest type. Overall, there was also a marked effect of the interaction between year and forest type, i.e., the influence of the year varied from the Atlantic Rainforest to the Restinga Forest (Table 7). These differences would have strong implications in the volume of fruit crop allowed for exploitation, considering the current recommended harvesting regime adopted in the state of São Paulo

Table 6
Influence of different groups of soil elements (a), as well as forest types (b), in the determination of palmiteiro (*Euterpe edulis* – Arecaceae) diameter at breast height (DBH) within two forest types included in the Ombrophilous Dense Atlantic Forest of southeastern Brazil (data obtained in 256 plots with 20 × 20 m from 10.24 ha permanent plots located in each forest type). Diameter (DBH) was modeled as a linear model of soil element groups, and forest types and their influence was measured by change in Akaike Information Criterion (AIC).

Model	df	AIC	Δ AIC
(a) Without considering forest types			
DBH ~ μ	2	11,184	–
DBH ~ μ + (P, Ca, Mg, Al)	6	11,051	−132.8
DBH ~ μ + (P, Ca, Mg, Al) + (Na, K)	8	10,884	167.5
(b) Considering forest types			
DBH ~ μ	2	11,184	–
DBH ~ μ + forest type	3	1063	553.5
DBH ~ μ + forest type + (P, Ca, Mg, Al)	7	10,633	−2.46
DBH ~ μ + forest type + (P, Ca, Mg, Al) + (Na, K)	9	10,632	0.39

Table 7
Effect of year (2008 and 2009) and forest type (Atlantic Rainforest and Restinga Forest) in the number of fruits per bunch (a), the number of bunches per individual (b), and in the potential fruit yield (number of fruits per bunch x number of bunches per individual) of palmiteiro (*Euterpe edulis* – Arecaceae) (data obtained in 256 plots with 20 × 20 m from 10.24 ha permanent plots located in each forest type). The number of fruits per bunch, number of bunches per individual, and potential fruit yield were modeled as a Poisson generalized linear model of year and forest types and their influence were measure by change in Akaike Information Criterion (AIC).

Model	df	AIC	Δ AIC
(a) Fruit number per bunch			
n ~ μ	1	41,001	–
n ~ μ + year	2	36,425	4,575.6
n ~ μ + year + forest type	3	14,458	31,849.9
n ~ μ + (year *x* forest type)	4	14,419	39.8
(b) Bunch number per individual			
n ~ μ	1	227.5	–
n ~ μ + year	2	228.6	−1.1
n ~ μ + year + forest type	3	216.0	12.6
n ~ μ + (year x forest type)	4	217.9	−1.8
(c) Potential fruit yield per individual			
n ~ μ	1	147,019	–
n ~ μ + year	2	132,297	14,721
n ~ μ + year + forest type	3	46,567	85,719
n ~ μ + (year *x* forest type)	4	46,314	253

Table 5
Akaike Information Criterion (AIC) for distribution models for soil chemical content in two forest types included in the Ombrophilous Dense Atlantic Forest of southeastern Brazil (data obtained from 0 to 20 cm depth in 256 plots with 20 × 20 m from 10.24 ha permanent plots located in each forest type).

Model	Number of variables	*n*	df	AIC
General	6	501	42	15,292
Atlantic Rainforest + Restinga Forest	6	501	84	13,398
Atlantic Rainforest	6	245	42	5674
Restinga Forest	6	245	42	7723

Table 8
Number of bunches of palmiteiro (*Euterpe edulis* – Arecaceae) allowed for harvesting considering the total crop of 20 individuals per year in different forest types included in the Ombrophilous Dense Atlantic Forest of southeastern Brazil.

Parameters of fruit crop	Atlantic Rainforest		Restinga Forest	
	2008	2009	2008	2009
% of individuals with 1 bunch	20	15	95	70
% of individuals with 2 bunch	45	35	5	25
% of individuals with 3 bunch	30	40	0	5
% of individuals with 4 bunch	5	10	0	0
Total number of bunches[a]	44	49	21	27
% of bunches allowed for exploitation[b]	61	61	95	78

[a] Considering twenty individuals per forest type in each year.
[b] Considering the following common recommendation of forest managers in the state of São Paulo, where the research was carried out: if the individual has a single bunch, it can be exploited; if the individual has two bunches, one of them can be exploited; if the individual has three bunches, two of them can be exploited; if the individual has four bunches, two of them can be exploited.

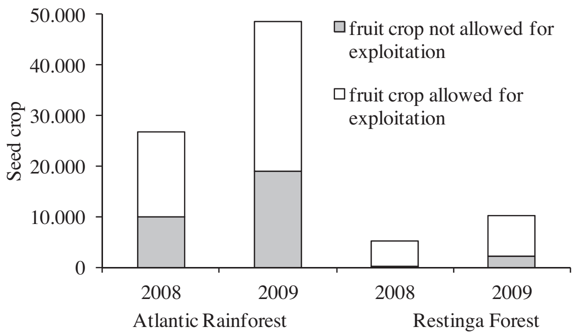

Fig. 3. Simulation of sustainable management of palmiteiro (*Euterpe edulis* – Arecaceae) fruits considering the total crop of 20 individuals per year in different forest types included in the Ombrophilous Dense Atlantic Forest of southeastern Brazil, and the common recommendations of forest managers in the state of São Paulo, where the research was carried out.

(Table 8). Overall, the percentage of fruit crop allowed for exploitation in the Atlantic Rainforest was 63% and 61%, respectively, in 2008 and 2009. In the Restinga Forest, 97% and 78% of fruit yield could be exploited considering the management standards recommended (Fig. 3). Additionally, we found palmiteiro individuals bearing ripe fruits at the Atlantic Rainforest from March to August 2008, while in the Restinga Forest the fructification season was limited to half of this period, from March to May 2008.

4. Discussion

Habitat-mediated effects, especially those related to soil, were shown to have remarkable effects on palmiteiro DBH, with immediate consequences for palm heart potential exploitation. In addition, fruit crop differed remarkably between the studied populations, suggesting that each of them needs specific harvesting standards as means of avoiding overexploitation. Therefore, a habitat-specific approach of sustainable management is needed for this species in order to respect the demographic and ecological dynamics of each population to be managed. These findings suggest that any effort to create general models of low impacting harvesting may be unsuccessful if the species of interest occur over a wide range of ecosystems. This proposal is in accordance with the recommendations provided by Ticktin (2004) in a review about the ecological implications of harvesting non-timber forest products. Although habitat-mediated effects on non-timber forest products exploitation has not been broadly investigated to date, we believe that such population differences may be more common than previously imagined.

In this case study of palmiteiro in the Brazilian Atlantic Forest, nutrient-poor and sodium-rich soils of Restinga Forest, as well as other habitat-mediated differences not investigated in this work, limited the potential of palm heart sustainable harvesting based on current minimum values of DBH for cutting. As a result of the lower thickness attained by this palm tree in the Restinga Forest, most of the individuals would not be allowed for cutting. In a review about palmiteiro management, Reis et al. (2000) suggested that, in the best harvesting regimes, only palms >8 cm DBH are exploited. However, this reduction of 1 cm in the minimum DBH for cut would not be enough to support palmiteiro management in the studied Restinga Forest. Since palm heart yield is positively associated to palm stem DBH (Reis et al., 2000), a reduction of the minimum DBH for cut in Restinga Forests would not be enough to obtain a relevant palm heart yield. Additionally, low potassium availability and high sodium content in the soil may limit palmiteiro growth rates in Restinga Forest, which may delay the recruitment of the species after harvesting and, consequently, the potential to keep satisfactory levels of palm heart yield over time.

Potassium is one of the most important nutrients for palm species growth, and its deficiency is very common in palms growing in highly leached sandy soils (Broschat, 2008), such as the soils found in the sedimentary coastal plains of the Restinga Forest (Gomes et al., 2007). As highlighted by Broschat (2008), "potassium deficiency is perhaps the most widespread of all palm nutrient deficiencies, occurring in most palm-growing regions of the world". Potassium deficiency in Restinga Forest palmiteiros may occur not only as a result of the lower concentration of potassium in the soil than found in Atlantic Rainforest, but also due to its higher concentration of sodium. In saline soils, such as that found near the sea level along the Brazilian eastern coast, sodium may compete with potassium for uptake across the cells plasma membrane, and consequently increase problems of potassium deficiency (Schachtman and Liu, 1999). On the other hand, the higher cellular concentration of potassium is important to keep a high cytosolic potassium/sodium ratio, which is an important factor determining plant salt tolerance (Maathuis and Amtmann, 1999). Hence, low potassium and high sodium concentration in Restinga Forest soil can be considered a key factor determining palmiteiro stem diameter and, consequently, palm heart yield. Potassium and sodium may have indeed a strong influence in palm growth because although the Atlantic Rainforest population was constituted by larger individuals, its soil showed lower sum of bases and, in particular, reduced concentration of phosphorous and magnesium compared to Restinga Forest soil. Surprisingly, phosphorous, which is a nutrient of major importance in tropical leached soils (Vitousek and Sanford, 1986), was shown to have a lower influence in this palm species growth than potassium.

Similarly, fruit yield would also differ between studied sites. Castro et al. (2007) had already argued that low soil fertility would be the cause of lower palmiteiro fruit crop in Restinga Forest, but this hypothesis had not been tested to date. As a result of the differences in the potential seed crop, as well as in the length of the fruiting season, the current regime indicated for sustainable fruit management would result in different levels of harvesting impact among populations. Although the Restinga Forest population would be the most negatively affected, both populations studied would have a large portion of the produced fruits and seeds exploited if the current rule was followed (Fig. 3), which implies in different levels of impact in the community of frugivores that feed on palmiteiro fruits. It is important to mention that a trade-off exists between the level of impact of fruit exploitation and the potential profitability of the activity. In the short-term, management standards have to balance these opposite elements in order to support the economic and ecological viability of fruit production. In the medium and long term, the seeds resulted from pulp extraction could be used to increase palmiteiro population density through direct seeding, especially in overharvested forest remnants, so that compensating fruit removal and keeping an adequate food supply to frugivores. The keystone role of palmiteiro for avian frugivores has not been fully understood (Galetti and Fernandez, 1998), but the importance of this species for conservation of frugivorous birds and mammals of the Atlantic Forest is undeniable (Galetti and Fernandez, 1998; Reis et al., 2000; Fadini et al., 2009), and have to be taken into account when designing management regimes. Palmiteiro seeds, a co-product obtained with fruit pulp extraction, are another valuable non-timber forest product currently exploited from this species. However, the studied Restinga Forest population also has the limitation of producing seeds with lower physiological potential (Brancalion et al., 2011).

Heavy regimes of fruit harvesting could result in the demographic collapse of palmiteiro populations, as already observed for the Brazilian tree nut *Bertholletia excelsa* in the Brazilian Amazon (Peres et al., 2003). Similar to other tropical species, population distribution of palmiteiro follows the "reverse J-shaped curve" pattern, resulted from high mortality rates at the first life stages caused by seed predation by rodents (Fleury and Galetti, 2004) and scolytid beetles (Pizo et al., 2006), density-dependence and distance-related factors (Silva Matos et al., 1999), heterozygote advantage (Gaiotto et al., 2003), and competition (Fantini and Guries, 2007). Additionally, palm heart harvesting increases palmiteiro seed predation by rodents and consequently increases the amount of seeds needed to support regeneration (Pizo and Vieira, 2004). Hence, large volumes of seeds are necessary to keep an adequate recruitment of palmiteiro to sustain species perpetuation and economic exploitation. A recommended action in palmiteiro sustainable management for fruit production would be the use of seeds obtained from fruit pulp extraction for broadcasting and direct sowing in the managed forest understory.

5. Conclusion

If current rules for palm heart and fruit harvesting were followed without any restriction to different habitats, Restinga Forest populations are under severe threat, as this study shows that they are not suitable for sustainable management of both fruits and palm heart. Hence, a habitat-specific approach of sustainable management is needed for this species in order to respect the demographic and ecological dynamics of each population to be managed.

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