

PHENOLOGY AND FRUIT TRAITS OF *ARCHONTOPHOENIX CUNNINGHAMIANA*, AN INVASIVE PALM TREE IN THE ATLANTIC FOREST OF BRAZIL

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Abstract. The Australian palm *Archontophoenix cunninghamiana* was introduced into Brazil as an ornamental species, and became a dangerous invader of remnant Atlantic forest patches, demanding urgent management actions that require careful planning. Its fruits are greatly appreciated by generalist birds and its sudden eradication could be as harmful as its permanence in the native community. Our hypothesis was that *A. cunninghamiana* phenology and fruit traits would have facilitated the invasion process. Hence the aim of the study was to characterize the reproductive phenology of the palm by registering flowering and fruiting events, estimating fruit production, and evaluating fruit nutritional levels. Phenological observations were carried out over 12 months and analyzed statistically. Fruit traits and production were estimated. Pulp nutritional levels were determined by analyzing proteins, lipids, and carbohydrates. Results showed constant flowering and fruiting throughout the year with a weak reproductive seasonality. On average, 3651 fruits were produced per bunch mainly in the summer. Fruit analysis revealed low nutrient contents, especially of proteins and lipids compared with other Brazilian native palm species. We concluded that the abundant fruit production all year round, and fruit attractiveness mainly due to size and color, may act positively on the reproductive performance and effective dispersion of *A. cunninghamiana*. As a management procedure which would add quality to frugivore food resources we suggest the replacement of *A. cunninghamiana* by the native palm *Euterpe edulis*, especially in gardens and parks near to Atlantic forest fragments.

Key words: alien species, Arecaceae, bioinvasion, fruit nutritional level, reproductive phenology.

INTRODUCTION

Invasive species are defined as exotic to a given environment and able to establish, reproduce, and disperse quickly in this new habitat (Cronk & Fuller 1995, Pysek 1995, Richardson *et al.* 2000). These species may cause negative impacts at different levels in the invaded habitat: on the physical environment (changes in soil properties and the hydrological cycle), on native organisms (behavior, growth, death), on gene pools (gene flow, hybridization), on population dynamics (abundance, mortality, growth rates, extinction), on the community (species composition and diversity, trophic structure), and on ecosystem processes (nutrient cycles, productivity, decomposition, disturbance regimes) (Cronk & Fuller 1995, Williamson 1996, Parker *et al.* 1999, Byers 2002, D'Antonio & Kark 2002, Traveset & Richardson 2006). Therefore they can modify ecosystem structure, composition, and function.

Human actions are certainly the main causes of biological invasions. In the case of plants, introductions of alien species may be purposeful, brought as ornamental species or food crops, or accidental. Combined with disturbances in the physical environment or in the community that creates niche opportunities – (e.g.) soil fertilization, microclimatic modifications, or the elimination of undesirable species – exotic species may spread and become dominant in the native community (Williamson 1996, McNeely *et al.* 2001, Mooney *et al.* 2005).

Episodes of biological invasion are expected to intensify in the next decades as a consequence of common modern practices, such as the frequent movement of people and goods around the world, or the fragmentation of natural habitats as a result of anthropogenic land use (Williamson 1996, Mooney *et al.* 2005, Maynard & Nowell 2009). Habitat fragmentation typically produces an edge effect in the remaining habitat patches, such as microclimate changes and soil disturbances, creating conditions favoring these opportunistic species to establish, and

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in many cases to dominate the community. Habitat fragmentation also promotes patch isolation, making inter-patch biological flow difficult and contributing to species composition changes in the native community (Murcia 1995, Turner 1996, Oosterhoorn & Kappelle 2000, Schnitzer & Bongers 2002, Fahrig 2003).

Small and isolated remnant patches of the Atlantic forest in southern Brazil are currently subjected to bioinvasion processes, especially by the Australian palm tree *Archontophoenix cunninghamiana* H. Wendl. & Drude (Dislich *et al.* 2002, Zenni & Ziller 2011). Introduced to urban gardens and squares for ornamental purposes, it spread to some remnant patches of the native forest, where it has become dominant (Dislich *et al.* 2002). More recently, *A. cunninghamiana* was cultivated commercially for its meristem – the palm heart, a food delicacy – as an alternative to the endangered native *Euterpe edulis* Martius (Vallilo *et al.* 2004). This practice can spread the alien palm even further to uncontrollable levels.

Those invaded forest fragments require immediate restoration management actions. However, actions addressing biological invasions require careful planning and must examine all possible scenarios involving the biological communities in the invaded area and surroundings. There are situations when the invasive species becomes an important source of food or shelter for the native fauna. In these cases, its sudden eradication may be as harmful as its permanence in the native community. It is relatively common to find invasive plants offering more nectar and fruit resources than native species, attracting a large number of mainly generalist pollinators and dispersers, with whom they establish mutualistic relationships (Gosper *et al.* 2005, Traveset & Richardson 2006, Bull & Courchamp 2009). These mutualistic relationships facilitate even further the spread of the invader. The flowers of *A. cunninghamiana* are visited by several species of social bees in search for pollen or nectar (Pirani & Cortopassi-Laurino 1994), and its very attractive red fruits are consumed and effectively dispersed by a relatively large number of generalistic urban birds (Hasui & Hofling 1998, Christianini 2006).

Besides visual appeal, fruit accessibility, quantity (fruit crop size), temporal availability, palatability and nutritional quality are features that affect its selection by birds (Morellato *et al.* 1990, Williams & Karl 1996, Hasui & Hofling 1998, Gosper *et al.* 2005). As the fruit choice by birds also depends on nutri-

tional gain, their preferences are also influenced by nutritional components (Stiles 1993). Thus the development of management strategies against fleshy-fruited invasive species requires information on the quantity and quality of food resources that they offer to the fauna, as well as on their seasonal dynamics.

Based on this scenario, our study was aimed at characterizing *Archontophoenix cunninghamiana* phenological patterns, and determining the nutritional quality of its ripe fruits in comparison with other native palm species. Our main hypothesis was that one of the mechanisms for the spread of *A. cunninghamiana* was its high reproductive and dispersal capability in southeastern Atlantic forest fragments. Therefore we focused on the following specific objectives: (1) to describe the reproductive phenology of *A. cunninghamiana* at the individual and population level; (2) to determine the average fruit size and the quantity of fruits produced per individual, and (3) to evaluate the nutritional quality of ripe fruits by quantifying their level of lipids, carbohydrates, and proteins. Together, these objectives were used to estimate the reproductive ability of *A. cunninghamiana* and its potential influence on the feeding behavior of frugivorous birds in the invaded community. We also suggest management practices to control this invasive species in small patches of Atlantic forest.

MATERIALS AND METHODS

Study area. This study was conducted in the surroundings and borders of a forest reserve inside the University of São Paulo (USP) (São Paulo, SP, Brazil: 23°33'44" – 23°34'02"S, 46°43'38" – 46°43'49"W). São Paulo city lies on the Tropic of Capricorn and its climate is a transition between tropical humid with dry season and subtropical permanently humid climates. The mean temperature in the coldest month, June, is 14°C, and in February, the hottest month, is 23°C; the mean annual rainfall is 1207 mm (230 mm in January, the wettest month, and 40 mm in August, the driest; Dislich & Pivello 2002). The relief is characterized by hills with altitudes of approximately 700 m. In the study site, soils are clayey, acidic, nutrient-poor and aluminum-rich (Varanda 1977). Like the climate, the vegetation is also transitional, between dense ombrophilous forest and seasonal semi-deciduous forest (*sensu* Veloso *et al.* 1991).

The USP campus comprises approximately 443.4 ha (Hofling & Camargo 1996), including the forest reserve of 10.2 ha (Dislich & Pivello 2002). This reserve is a mosaic of Atlantic forest patches in vari-

ous stages of degradation and regeneration where a late secondary successional stage prevails (Rossi 1994, Dislich & Pivello 2002). It represents one of the few fragments of regional native vegetation in São Paulo State, with more than 120 native woody species (Rossi 1994). Several buildings of the university are surrounded by large gardens where *A. cunninghamiana* was planted during the period 1950-1960.

Study species. *Archontophoenix cunninghamiana* H. Wendl. & Drude (Arecaceae) is a solitary and endemic palm tree, native to rainforests of the central eastern Australian coast (Waterhouse & Quinn 1978, Global Invasive Species Database 2005, PACSOA 2011). In its native range it fruits and flowers all year round, producing a large quantity of seeds that are dispersed by birds (Zona & Henderson 1989, Global Invasive Species Database 2005). This palm tree is shade tolerant, but it grows faster in full sun and maintains its reproductive potential for several years, adapting well to the subtropical conditions of southeastern Brazil (since the climatic and topographic conditions are similar to those of its native habitat) (Lorenzi *et al.* 2004, Global Invasive Species Database 2005, PACSOA 2011).

The Australian palm has pinnate leaves and pendulous inflorescences that mature into infructescences (hereafter generically called bunches). Fruits are small, spherical drupes that turn red when ripe; the endocarp consists of one hard and fibrous stone which comprises most of the fruit volume, and a thin mesocarp and an epicarp that comprise the pulp.

Six decades ago *A. cunninghamiana* was brought to São Paulo State, where it has been commonly used as an ornamental plant in gardens and urban squares (Pirani & Cortopassi-Laurino 1994). However the species spread into Atlantic forest fragments and started a biological invasion process. Nowadays invasion by this palm has been described from different Atlantic forest types, and even from other countries such as New Zealand (Global Invasive Species Database 2005, Zenni & Ziller 2011). Studies conducted in a patch invaded by the Australian palm showed its growth rate to be considerably higher than that found for the native arboreal species of tropical forests (Silva Matos & Pivello 2009). Periodic surveys conducted in a 2.1 ha plot inside the USP forest reserve revealed an alarming trend: the number of individuals with diameter at breast height (DBH) \geq 9.5 cm showed growth rates of 6.31% per year from 1999 to 2002 and 8.63% per year from 2002 to 2005. The diameter distribution curve indicates that

A. cunninghamiana trees are still growing while the native community shows negative annual growth rates. Compared with other tree species in the reserve, *A. cunninghamiana* represented almost a third of the total number of individuals (Dislich *et al.* 2002, Pivello *et al.* 2003, Zupo & Pivello 2007).

Phenological patterns. Phenological observations were carried out every 14-15 days during 12 months, from September 2006 to August 2007. We followed 30 mature, reproductive and healthy individuals with DBH \geq 19 cm in two open areas where palm tree density was very high. We chose such open areas based on the assumption that those individuals were the producers of propagules that strongly contributed to the invasion process inside the forest fragment, and continuously provided seeds which were carried by birds to the forest fragment.

In the phenological observations we counted the number of mature green leaves and bunches, and quantified flowering and fruiting events. The flowering phases were defined as "flower bud" and "open flower", and fruiting phases were characterized according to fruit ripeness: unripe (green fruits), semi-ripe (yellow fruits), and ripe (red fruits). Dry bunches were also included because they can provide information on the species dynamics; since each bunch produces flowers and fruits only once, a dry bunch represents the interruption of the phenological phase or the end of a reproductive cycle.

We characterized the reproductive phenology at population and individual levels based on the percentage of individuals showing the phenological phase at each observation, in addition to counts of inflorescences and infructescences per plant. We obtained information on the number of bunches per individual and per phenological phase throughout the year. The percentage of individuals showing each phase was calculated to determine the timing and extent of the phenological phase, as well as intraspecific synchrony (Martin-Gajardo & Morellato 2003).

To examine the seasonal patterns of the six defined phenological phases we performed a circular statistical analysis and the Rayleigh test (Zar 1999). The Rayleigh test (z) determines the significance of the average angle found by circular analyses. Months were then converted into angles, from 0° (January first fortnight) to 345° (December second fortnight). To calculate phase intensity, we estimated the following parameters: average angle (a , in our case represented by the average date), angular dispersion (represented by the circular standard deviation, s),

and vector (r , which measures the concentration around the average angle). The r vector is a measure of the degree of seasonality and does not have a unit, ranging from 0 (phenological activity uniformly distributed) to 1 (strong seasonality) (Zar 1999, Morellato *et al.* 2000).

Fruit traits. During both wet and dry months (December and July respectively), we collected bunches of ten randomly chosen individuals with ripe fruits to estimate fruit production and for morphometric measurements. Ten fruits per bunch (total of 100 fruits) were used for morphometric measurements (length and largest diameter) soon after collection to prevent desiccation and deformities. From the same bunches we also collected 100 fruits to determine fruit mass. All selected fruits had similar color and consistency, indicating the same ripening stage. Pulp and stone were manually separated and individually weighed (fresh weight). The dry weight was determined by heating the material in a laboratory oven at 105°C until constant weight. Ripe fruits were also separated for nutritional analysis, performed in triplicates with dry ground pulp. Lipids were quantified using the Soxhlet extraction with *n*-hexane, and this solvent was evaporated to constant weight (Ahmad *et al.* 1981). Total soluble sugars were determined by the phenol-sulphuric acid method (Dubois *et al.* 1956) with 5 cycles of extraction and glucose as standard. Proteins were quantified by the Bradford method (Bradford 1976).

RESULTS

Phenology. We found on average 12.32 ± 0.32 mature green leaves per *A. cunninghamiana* tree. The number of leaves was stable throughout the year, thus a leaf fall period was lacking. A monthly mean of 4.35 bunches per individual was counted (Table 1), most of them bearing unripe fruits (1.27 ± 0.43 bunches per individual).

Statistical analyses revealed seasonal patterns for the phenological phases: dry bunches, open flowers, semi-ripe, and ripe fruits (Table 2). The seasonal intensity of flowering was higher than that of fruiting when considering their final stages, open flowers and ripe fruits respectively (Table 2).

At the population level, fruiting was continuous over the year, comprising all stages of fruit ripeness (Figure 1). Despite that, the absence of seasonality was statistically confirmed only by the phenological phase “unripe fruits”. A tendency towards a three-month period of fruit ripeness was found during the summer (Figure 1; December to February, with high rainfall and temperatures); ripe reddish fruits peaked in December and January, comprising around 91% of individuals. More than 90% of individuals had unripe fruits in September and October (Figure 1), resulting in 2.5 infructescences per individual in these months. Semi-ripe yellowish fruits peaked in November and December. There was a gradual decline in the number of infructescences towards fruit ripening, since on average 29.7% of palm individuals

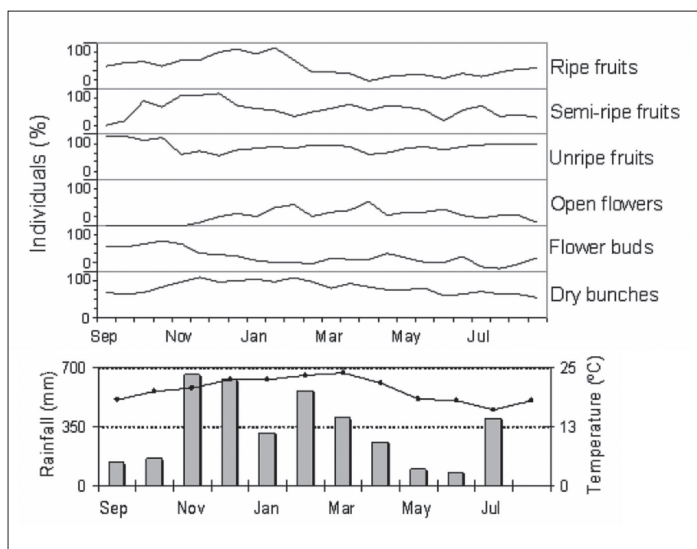


FIG. 1. Phenogram (percentage of individuals) showing ripe fruits, semi-ripe fruits, unripe fruits, open flowers, flower buds, and dry bunches produced by *A. cunninghamiana* in the study site (September 2006 to August 2007). The climate diagram (bottom graph) shows values of monthly rainfall (bars) and average temperature (dots) recorded at the Universidade de São Paulo (USP) during the sampling period (data from Experimental Meteorology Station, Laboratório de Climatologia e Biogeografia, USP).

TABLE 1. Means and standard deviations of monthly counts on bunches (inflorescences and infructescences) showing different phenological phases during the sampling period September 2006 to August 2007.

Phenological phase	Bunches (absolut values)	Bunches per individual	Percentage
Dry bunches	36.58 (± 9.00)	1.22 (± 0.30)	28.18 (± 5.92)
Flower buds	10.46 (± 5.64)	0.35 (± 0.19)	7.83 (± 3.60)
Open flowers	6.38 (± 4.60)	0.21 (± 0.15)	5.15 (± 3.80)
Immature fruits	38.13 (± 12.84)	1.27 (± 0.43)	29.70 (± 10.04)
Semi-ripe fruits	22.25 (± 9.86)	0.74 (± 0.33)	16.85 (± 6.18)
Ripe fruits	16.67 (± 8.90)	0.56 (± 0.30)	12.29 (± 5.24)
Total	130.46 (± 18.63)	4.35 (± 0.62)	100

carried unripe fruits, 16.85% semi-ripe fruits, and only 12.29% carried ripe fruits (Table 1).

From mid-November to February more than 80% of individuals had dry bunches, while the lowest values were found from August to October (Figure 1). Flower buds were produced throughout the year, peaking in October, without a clear seasonal pattern (Figure 1). Flowers began to open in November, when rainfall indices and temperature started to increase, and peaked in April.

Fruit traits. The number of fruits produced per bunch varied from 3860 ± 1392 in the summer (December to March) to 3442 ± 1669 in the winter (June to September). The small spherical fruits showed an average length of 9.08 ± 0.39 mm, and a largest diameter of 8.45 ± 0.60 mm. The pulp represented about 19.8 ± 6.92% of the fruit dry mass, and about

63.3 ± 2.62% of the pulp was water. Therefore we could estimate that only about 7% of the fruit mass represented a food resource for frugivorous birds, who only eat the pulp.

Pulp nutritional analysis revealed low levels of protein (7.83 ± 1.13 mg/g of dry mass) in comparison with the concentrations of lipids and soluble sugars: 45.14 ± 15.08 mg/g and 63.28 ± 9.80 mg/g of dry mass respectively.

DISCUSSION

Each individual of *A. cunninghamiana* produced on average 4.35 bunches at a time, compared with one or two produced by most palm species (De Steven *et al.* 1987). In addition, *A. cunninghamiana* is very prolific and produces more than 3000 fruits per

TABLE 2. Quantification of phenological variables and the results of circular statistical analyses and Rayleigh's test (ns = non-significant).

	Phenological variables					
	Dry bunches	Flower buds	Open flowers	Unripe fruits	Semi-ripe fruits	Ripe fruits
Observations (<i>N</i>)	465	232	153	531	399	348
Mean angle (°)	58.41	277.95	177.65	104.79	64.58	331.64
Circular standard deviation (<i>S</i>)	115.44	127.79	75.33	131.06	125.59	93.83
Mean vector length (<i>r</i>)	0.13	0.08	0.42	0.07	0.09	0.26
Rayleigh test (<i>p</i>)	0.0003	0.2012	<0.0001	0.0586	0.0380	<0,0001
<i>z</i>	8.02	1.60	27.17	2.84	3.27	23.81
Seasonality	yes	ns	yes	ns	yes	yes

bunch. Christianini (2006) also quantified the fruit production of this species inside the USP forest reserve, and found a much lower value, a mean of 1373 fruits per bunch. We attribute this discrepancy to local shading, as the author surveyed individuals in forest gaps, while we selected ornamental individuals in full sun or half shade in the surroundings of the forest fragment. A similar finding was reported by Koike (2006), who observed the life history of *Trachycarpus fortunei*, an invasive palm tree in Japan, and found lower flowering rates when it was growing inside a forest patch compared with open areas. Christianini (2006) estimated that each individual palm tree inside the forest can potentially produce around 4000 seeds per year, while our results indicate figures three times higher for trees growing in sunny areas.

The ability to produce large amounts of seeds in the colonized environment is one of the features that distinguishes invasive species, since it confers high reproductive potential (Bleher & Böhning-Gaese 2001). Moreover, the phenological pattern of *A. cunninghamiana* also potentializes its invasive ability, given that fruit production is continuous throughout the year. Its reproductive phenology also aids efficient dispersal, since ripe fruits are more abundant in the hottest and rainiest months of summer, when the activity of dispersers (especially birds) is higher (Rathcke & Lacey 1985).

The fruits produced by *A. cunninghamiana*, although abundant, do not represent a valuable and nourishing food resource for frugivorous birds, both because they contain little nutritive mass (only about 7% of the fruit dry weight provides any nourishment

for pulp consumers) and because they are of poor nutritional value. According to Stiles (1993), lipids constitute an important trait in fruit selection by birds. High lipid-content fruits provide more energy for the pulp mass ingested, and are therefore preferred by birds when the choice is available (Stiles 1993). Comparing the levels of lipids, carbohydrates (soluble sugars), and proteins contained in the fruits of other Brazilian Arecaceae, the pulp of *A. cunninghamiana* fruits contains the lowest values of lipids and proteins (Table 3). *Eliaes guineensis*, for example, is very rich in lipids and soluble sugars while *Euterpe oleraceae* and *E. edulis* are rich in proteins.

Despite their poor nutrient supply, the fruits of the invasive palm are very attractive to frugivorous birds. The species shows a generalized dispersal system (according to Howe 1993), offering superabundant fruits of lower nutritional reward (high carbohydrate content but less energy-rich), relying on opportunistic frugivores that disperse seeds effectively. Hasui and Hofling (1998) observed that the fruits of *A. cunninghamiana* were among the preferred fruits by birds in the USP forest reserve. Some visual characteristics of its fruits – such as bright red color, small size (< 10 mm) and round shape – make them very attractive to generalist birds (Hasui & Hofling 1998, Gosper *et al.* 2005). We observed four bird species removing *A. cunninghamiana* fruits during the period of the present study: *Aratinga leucophthalmus*, *Brotogeris chiriri*, *Pitangus sulphuratus*, and *Turdus rufiventris*. These are indeed generalist bird species, and are frequently found in the study area (Hasui & Hofling 1998, Christianini 2006).

Fruits with characteristics attractive to birds are

TABLE 3. Mean percentage of lipids, carbohydrates (soluble sugars), and proteins in the fruit pulp of different Arecaceae species. (1) = native to eastern Australia; (2) = native to Brazilian Atlantic forest; (3) = native to northeastern Brazil; (4) = native to Brazilian Amazon.

Species	Lipids	Carbohydrates	Proteins	Author
<i>A. cunninghamiana</i> (1)	4.5	6.3	0.8	this study
<i>Attalea oleifera</i> (2)	33.1	-	2.1	Pimentel & Tabarelli (2004)
<i>Euterpe edulis</i> (2)	6.0	1.5	6.0	Galetti <i>et al.</i> (1999), Rufino <i>et al.</i> (2009)
<i>Syagrus romanzoffiana</i> (2)	7.5	-	5.4	Coimbra & Jorge (2011)
<i>Eliaes guineensis</i> (3)	73.2	13.3	3.4	Bora <i>et al.</i> (2003)
<i>Syagrus coronata</i> (3)	4.5	-	3.2	Crepaldi <i>et al.</i> (2001)
<i>Euterpe oleraceae</i> (4)	32.5	1.3	8.1	Schauss <i>et al.</i> (2006), Rufino <i>et al.</i> (2009)

more efficiently dispersed, and therefore alien plant species would have higher chances of becoming invasive (Gosper *et al.* 2005). Fruit traits also influence the activity patterns of dispersers as well as trophic relationships in the entire community. This has been verified concerning plant invader species (Williams & Karl 1996, Gosper *et al.* 2005) and, although not yet investigated specifically for *A. cunninghamiana*, is very likely to occur in the forest fragment inside the studied area, as the alien palm tree exhibits all the favorable characteristics like fruit accessibility, crop size, and temporal availability.

Given this scenario, we recognize an urgent need to implement management actions towards eliminating this invasive palm species in the surroundings of Atlantic forest fragments and also inside the fragments where it has already established. In our case, as the invasive palm tree is already integrated with the local fauna, its removal without replacing the food resource it offers could be detrimental to frugivores. Although there are other food options within the university campus, especially inside the forest reserve (see Hasui & Hofling 1998), the demand for food could be much higher than the supply. It would be necessary, therefore, to replace the individuals removed with native fruit trees, and preferably including *Arecaceae* species – considered keystone resource for frugivore communities of tropical forests (Terborgh 1986).

Previous surveys conducted inside the USP forest reserve revealed that the only palm tree species present other than the invasive one was *Syagrus romanzoffiana* (Dislich & Pivello 2002), native and very common in semi-deciduous Atlantic forests. It produces sugar-rich fruits all year round (more between May and August) (Fleurya & Galetti 2006, Giombini *et al.* 2009), usually having two bunches at a time each bearing around 600 fleshy fruits (Galetti *et al.* 1992, Brancalion *et al.* 2011). Moreover, *S. romanzoffiana* fruits contain higher amounts of lipids and proteins compared with *A. cunninghamiana* (Table 3), hence it is a good nutrient supply for frugivores. But unlike *A. cunninghamiana*, the main consumers and dispersers of *S. romanzoffiana* are mammals such as squirrels, monkeys, small rodents, tapirs, and peccaries (Galetti *et al.* 1992, Fleurya & Galetti 2006, Giombini *et al.* 2009), although its fruits can be consumed by birds (Hasui & Höfling 1998, Giombini *et al.* 2009). This is probably due to a difference in fruit size, since various bird species consume the fruits of both the invasive and this na-

tive palm where the two species co-exist (Hasui & Höfling 1998).

Another palm tree native to and very common in the southeastern Atlantic forest is *Euterpe edulis* (Galetti *et al.* 1999), whose fruits and consumers are much more similar to those of *A. cunninghamiana*. *E. edulis* occurred in the study area in the past but it is currently extinct inside the forest reserve and its surroundings (Dislich & Pivello 2002), as it is in most parts of the Atlantic forest due to deforestation and overexploitation (Galetti & Aleixo 1998). *E. edulis* is considered a keystone species, due to its large production of fruits when other fruit-bearers are not producing, and also because its fruits are consumed by a large assemblage of frugivores (Pizo *et al.* 1995, Galetti & Aleixo 1998). Like *A. cunninghamiana*, *E. edulis* also produces ripe fruits during the driest and coldest seasons, from May to August (Galetti & Aleixo 1998, Castro *et al.* 2007). Its fruits have high amounts of protein compared with other palm trees (Table 3), and higher amounts of lipid compared to *A. cunninghamiana* – the nutrient most strongly correlated with bird preference (Stiles 1993). In addition, a generalized frugivore bird assemblage disperses *E. edulis* fruits (Galetti *et al.* 1999), so the same generalist birds who visit *A. cunninghamiana* in the invaded areas could also use the native palm as a food resource.

Comparing the fruit production of both native and invasive palm trees, *E. edulis* is also very prolific, with one to ten infructescences per individual over the year. Each infructescence bears approximately 850 fruits, and can produce more than 1500 fruits per season (Silva Matos & Watkinson 1998, Galetti *et al.* 1999). Because *E. edulis* has not been observed in the USP forest reserve since at least 1950 (July 1950, Dislich & Pivello 2002), despite being one of the commonest species in this type of forest (Queiroz 2000, Reis *et al.* 2000), it is possible that the invasive palm tree occupied parts of the same functional niche of the native species, benefiting from the latter's local extinction. Consequently, *E. edulis* has been suggested as the most adequate species to replace *A. cunninghamiana* in gardens – especially if near Atlantic forest fragments – as it is also very ornamental.

We then concluded that the Australian palm tree *A. cunninghamiana* has phenological and reproductive traits that possibly enhance its ability to disperse into new habitats and to become an invader species. Along with the continuous production of flowers and fruits throughout the year, the copious fruit produc-

tion by this species indicates a massive investment in reproduction. This reproductive performance probably confers a competitive advantage over native species, although not specifically tested in this study. Its fruits are visually very attractive to generalist birds, but represent a poor food resource in comparison with other *Arecaceae* native species. This implies a rapid consumption of a high number of fruits and many discarded seeds, contributing to the process of biological invasion even further. Examining the seed rain in the forest fragment inside the study area we found that the majority of zoochoric diaspores belong to *A. cunninghamiana*, confirming a high propagule pressure on the native community (A.L.T Mengardo, C.L. Figueiredo, L.R. Tambosi, and V.R Pivello, unpublished data).

The substitution of this alien species by the native palm tree *Euterpe edulis* in gardens would help prevent the continuous spread of *A. cunninghamiana* in remnant forest patches and improve the quality of the food resources for the local fauna. Moreover, forest enrichment with *E. edulis* is recognized as a positive factor in the enhancement of secondary Atlantic forest biodiversity (Nodari *et al.* 2000).

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