

The risks of introduction of the Amazonian palm *Euterpe oleracea* in the Atlantic rainforest

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Received: July 7, 2014 – Accepted: November 27, 2014 – Distributed: February 29, 2015
(With 1 figure)

Abstract

The introduction of a species may alter ecological processes of native populations, such as pollination and dispersal patterns, leading to changes in population structure. When the introduced and the native species are congeners, interference in pollination can also lead to hybridization. We aimed to understand the ecological aspects of *Euterpe oleracea* introduction in the Atlantic forest and the possible consequences for the conservation of the native congener *Euterpe edulis*. We analysed the population structure of palm populations, including hybrids, and observed the interaction with frugivorous birds of both palm species after *E. oleracea* introduction. We observed that *E. edulis* had significantly lower density and a smaller number of seedlings when occurring with *E. oleracea*. Native and introduced *Euterpe* species shared nine frugivorous bird species. *E. oleracea* and hybrids had dispersed outside the original planting area. Consequently, the risks of introduction of *E. oleracea* may mostly be related to the disruption of interactions between *E. edulis* and frugivorous birds and the spontaneous production of hybrids. Finally, the cultivation of *E. oleracea* and hybrids in Atlantic rainforest could affect the conservation of the already endangered *E. edulis*.

Keywords: hybridization, frugivorous birds, exotic plants, population structure, *Euterpe edulis*.

Os riscos da introdução da palmeira amazônica *Euterpe oleracea* na Floresta Atlântica

Resumo

A introdução de uma espécie pode alterar processos ecológicos de populações nativas, tais como padrões de polinização e dispersão, levando a mudanças na estrutura populacional. Quando espécies introduzidas e nativas são congêneres, a interferência na polinização pode levar também à hibridização. Nossos objetivos foram entender os aspectos ecológicos da introdução de *Euterpe oleracea* na Floresta Atlântica e as possíveis consequências sobre a conservação da congênera nativa *Euterpe edulis*. Para isso, analisamos a estrutura populacional, incluindo híbridos, e observamos a interação de aves frugívoras com ambas as espécies de palmeira após a introdução de *E. oleracea*. Observamos que *E. edulis* apresentou densidade total e número de plântulas menores quando coocorrente com *E. oleracea*. As palmeiras congêneras compartilharam nove espécies de aves frugívoras. *E. oleracea* e híbridos foram dispersos além da área original de plantio. Consequentemente, os riscos da introdução de *E. oleracea* podem estar principalmente relacionados com o possível deslocamento de interações entre *E. edulis* e aves frugívoras e com a produção de híbridos. Desta forma, o cultivo de *E. oleracea* e híbridos podem afetar a conservação da já ameaçada *E. edulis*.

Palavras-chave: hibridização, aves frugívoras, plantas exóticas, estrutura populacional, *Euterpe edulis*.

1. Introduction

Palms play an important role in natural communities as many palm species are important resources for animals (Tomlinson, 2006; Henderson et al., 1995). Fruits, palm heart, leaves and stems are also commonly exploited by human populations (Henderson et al., 1995). Because of their economic importance palms are one of the groups

most dispersed by humans (Tomlinson, 2006). In fact, the introduction of many palm species is stimulated by their beauty and effortless cultivation – mostly in tropical regions. This may create challenges to manage these the exotic species and to conserve native communities (Van Wilgen and Richardson, 2014). Still, few studies

have assessed the ecological aspects of exotic palms and their effects on the local plant populations (Meyer et al., 2008; Christianini, 2006; Dislich et al., 2002).

Although palm species are rarely considered invasive, the general impact of exotic species on biodiversity and ecosystems has long been recognized (Richardson and Réjmanek, 2011; Simberloff, 2005; Elton, 2000). Exotic plants species may cause many impacts on the ecological patterns of the local community and when congeneric with local species, they may promote competition for pollinators or lead to interspecific interference with pollen in native flowers (Albrecht et al., 2012; Lopezaraiza-Mikel et al., 2007; Traveset and Richardson, 2006). This interference may result in hybridization, which has been considered a serious threat for conservation (Wolf et al., 2001).

Hybridization may lead to species extinction in two ways: when the hybrids exhibit lower fitness than parental taxa, the less abundant parental species may decline; alternatively, if the hybrids are fertile and have low fitness reduction, they may displace conspecifics of one or both parental taxa (Wolf et al., 2001). Also, exotic species may disrupt the relationship between seed dispersers and native plants (Spotswood et al., 2012). This could decrease the effective seed dispersal, leading to a reduction on the quality and quantity of native seeds, negatively affecting their germination or seedling establishment (Aslan and Rejmánek, 2010). Thus, a disturbance in reproductive mutualisms may affect the growth rate (Aslan and Rejmánek, 2010) and therefore modify the structure and spatial distribution of plant populations. Nevertheless, many exotic species may create conflicts of interest when they are both useful to humans and able to cause harm (Dickie et al., 2013; Simberloff et al., 2013).

In the Atlantic rainforest, an endangered palm species is confronting a new threat. After decades of indiscriminate exploitation for palm heart production, *Euterpe edulis* Mart. (Arecaceae) – a native species from the Atlantic Forest – has been legally protected (Silva Matos and Bovi, 2002; Galetti and Fernandez, 1998). However, the over-exploitation of *E. edulis*, has contributed significantly to changes in its populations structure leading this species to extinction in several forest fragments (Melito et al., 2014; Silva Matos and Bovi, 2002). To guarantee the continuous production of palm heart, several species have been introduced in this ecosystem. Nowadays, nearly 50% of palm heart production is given by exotic introduced palms in the Atlantic Forest area (São Paulo, 2008a). One of the commonest introduced species is *Euterpe oleracea* Mart. (Arecaceae), which is native from Amazon rainforest where it grows in similar conditions as *E. edulis* (Bovi et al., 1987). This species was once considered the solution for the vulnerability of *E. edulis* to harvesting. These congeneric palms are able to produce *E. edulis* x *E. oleracea* hybrids under experimental management (Tiberio et al., 2012; Campos et al., 1991; Bovi et al., 1987) and these hybrids are also used in palm heart crops. However, neither the ecology of *E. oleracea* in this new area nor *E. edulis* responses in sites where the exotic palm was introduced are known. Yet, *E. oleracea*

introduction in Atlantic rainforest has increased in the last few years not only because of the exploitation of palm hearts, but also for the production of “assai” pulp from its fruits.

Due to their great biological similarity, we expect that these *Euterpe* species have also the same ecological requirements and, therefore, *E. oleracea* might successfully establish in Atlantic rainforest. These similarities also lead us to expect the interaction with local fauna. The main objective of this study was to understand the ecological aspects of *E. oleracea* introduction in Atlantic rainforest and the possible consequences for the native *E. edulis*. To clarify these aspects, we separately accessed the following questions: 1. To investigate whether the introduced palm *E. oleracea* is able to establish populations and spread in the Atlantic rainforest, we evaluated the introduced population structure by analysing the frequencies of ontogenetic stages and its spatial distribution; 2. To verify if *E. oleracea* is able to interact with local bird community, we observed the visits of frugivorous birds to both *E. oleracea* and *E. edulis*; 3. To understand the possible effects of *E. oleracea* introduction on *E. edulis* population structure we compared the frequencies of ontogenetic stages and the spatial distribution of this palm populations in sites with and without *E. oleracea*; 4. To investigate if *E. oleracea* and *E. edulis* may generate spontaneous hybrids (i.e. generated in the wild and not produced by men), we separately identified and quantified these individuals.

2. Methods

2.1. Species description

Euterpe edulis occurs in the Atlantic rainforest from Southern Brazilian coast up to Paraguay and Argentina (Henderson et al., 1995). It has a single stem reaching 20 m height and produces globular purple-black fruits 1-1.4 cm diameter (Henderson et al., 1995) which are food resource for many animal species, typically birds (Galetti et al., 2013; Pizo and Vieira, 2004; Galetti and Aleixo, 1998). This species produces the most economically valuable palm heart but, as it produces a single stem and does not resprout, individuals are killed for the palm heart extraction. In the southeast region, the presence of *E. edulis* is commonly restricted to the remaining areas of Atlantic rainforest and particularly in some protected areas of Rio de Janeiro, São Paulo and Paraná states, in southeast of Brazil (Silva Matos and Bovi, 2002).

Euterpe oleracea (“assai palm”) is commonly found along the Amazon River basin in Northern Brazil. *E. oleracea* has multiple stems, reaching 12-20 meters high (Henderson et al., 1995). It bears purple-black globular fruits 1-2 cm diameter which are dispersed by several bird species (Moegenburg and Levey, 2003; Henderson et al., 1995). The palm heart from *E. oleracea* does not have the same economical value as the ones from *E. edulis* but, as a multiple stemmed plant, palm heart production may be higher and the plants are not necessarily killed

during exploitation. Also, its fruits are used for “assaí” cream production.

Although these palm species show naturally distinct distributions (Henderson et al., 1995), both Atlantic and Amazon rainforests present similar characteristics mostly defined by their wet and high temperature climates (above 25 °C), with even rainfall distribution along the year.

2.2. Study sites

In order to compare areas differentiated only by the presence of *E. oleracea*, we selected two areas 75 Km apart, but having the same vegetation type and environmental conditions. Thus, we conducted the research at two protected areas of Atlantic rainforest: Carlos Botelho State Park (24° 06' 55" W, 24° 14' 41" S and 47° 47' 18", 48° 07' 17" W) and Ilha do Cardoso State Park (48° 05' 42" W, 25° 03' 05" S and 48° 53' 48" W, 25° 18' 18" S). These parks belong to a continuous area of Atlantic rainforest in Southeast Brazil. *E. oleracea* was introduced at Carlos Botelho State Park in the 1970s. This population was once cut as an attempt to remove the species from the park, but most of individuals resprouted. Hereafter, we refer to Carlos Botelho State Park as site of introduction and to Ilha do Cardoso State Park as control site.

This region has tropical rainforest climate with annual rainfall ranging between 1700 and 2400 mm and average temperature between 19 °C and 27 °C (São Paulo, 2008b; Melo and Mantovani, 1994). Both study sites are located in floodplain areas and exhibit alluvial rainforest vegetation with the same plant species composition (São Paulo 2008b; Melo and Mantovani, 1994).

2.3. Data sampling and analysis

From July 2009 to March 2010 we sampled all individuals (except seedlings) of *E. edulis* and *E. oleracea* within 35 contiguous plots (10×10m) in a grid, in both introduction and control sites. The contiguous plot design was selected to keep focus on the area where *E. oleracea* population were first introduced, also including the immediate surrounding area. We sampled seedlings in randomly located sub-plots (2×2m) within each 100 m² plot. We identified the hybrids based on leaves shape and leaflets spacing (Tiberio et al., 2012). No individuals of *E. oleracea* were to be found at control site.

Individuals from each population were then divided into five ontogenetic life stages according to their morphology: seedling, juvenile I, juvenile II, immature, reproductive adult (Tiberio et al., 2012). Besides height and diameter, we also observed leaf and leaflet shape and signs of reproduction such as presence of inflorescences, infrutescences or its scars on the stems (previous reproduction). We evaluated differences between population structures comparing the distribution of relative stage frequencies, using chi-squared test in the program Past version 2.01 (Hammer et al., 2001). Although the multiple stems of *E. oleracea* are biologically recognized as only one individual, we considered each stem as a distinctive unit, in order to also account for resprouting.

Frugivory was recorded at the site of introduction, from March to September 2007-2009, when fruits of both species were ripe. We detected the abundance of birds visiting *E. edulis* and *E. oleracea*, by viewing or by vocalizations, walking along transects within areas where these species were present. The work was done from 30 min before sunrise until 30 min after dusk, at least two days per month. Amongst all birds, we observed and identified those feeding on fruits of both *Euterpe* species using 8×40 binoculars. The resulting sampling effort was of 214 hours. In order to assess each palm species effects on birds attraction, we evaluated the correlation of total number of visits with the number of observed consumers for each species using the Spearman coefficient (rs).

3. Results

At the control site, we recorded 2374 individuals of *E. edulis* (6782.8 ind. ha⁻¹), while at the site of introduction we found 400 individuals of *E. edulis* (1142.8 ind. ha⁻¹), 68 of *E. oleracea* (194.3 ind. ha⁻¹) and 72 hybrids (205.7 ind. ha⁻¹). Likewise overall density, *E. edulis* ontogenetic structure was significantly different between control site and site of introduction ($\chi^2=248.55$; $p=0.00001$, Figure 1). Total density and frequency of seedlings of *E. edulis* were higher in the control site. The ontogenetic structure of *E. edulis* and *E. oleracea* at the site of introduction also differed significantly ($\chi^2=36.62$; $p=7.11 \times 10^{-7}$). We did not find seedlings within *E. oleracea* population, however juveniles were the most frequent stage (Figure 1) and were mostly originated as sprouts (82%). We did not find any hybrids seedlings and reproductive adults, but intermediary stages were still present (Figure 1). Some individuals of *E. oleracea* and hybrids were located outside the original planting area.

We observed an overlap between fructification periods of native and introduced species: *E. edulis* produced ripe fruits from March to September and *E. oleracea* from June to September. In this period, we observed 19 bird species consuming fruits: 16 species consumed *E. edulis* and 12 consumed *E. oleracea* (Table 1). The native and exotic *Euterpe* species shared nine of the frugivorous bird species located at the site of introduction, while seven species were detected exclusively on *E. edulis* and three visited only *E. oleracea* (Table 1). The observations of fruit consumption for *E. edulis* was not correlated with the total bird species recorded (rs=0.36, p=0.12), while for *E. oleracea* we obtained a significant positive correlation between fruit consumption and bird visits (rs=0.62, p=0.004).

4. Discussion

Our results provided evidences that the Amazonian palm tree *E. oleracea*, introduced in the Atlantic Forest, is able to establish through sexual reproduction and vegetative growth, to produce non-mediated hybrids with the native palm species and to interact with local bird community, including dispersers of *E. edulis*.

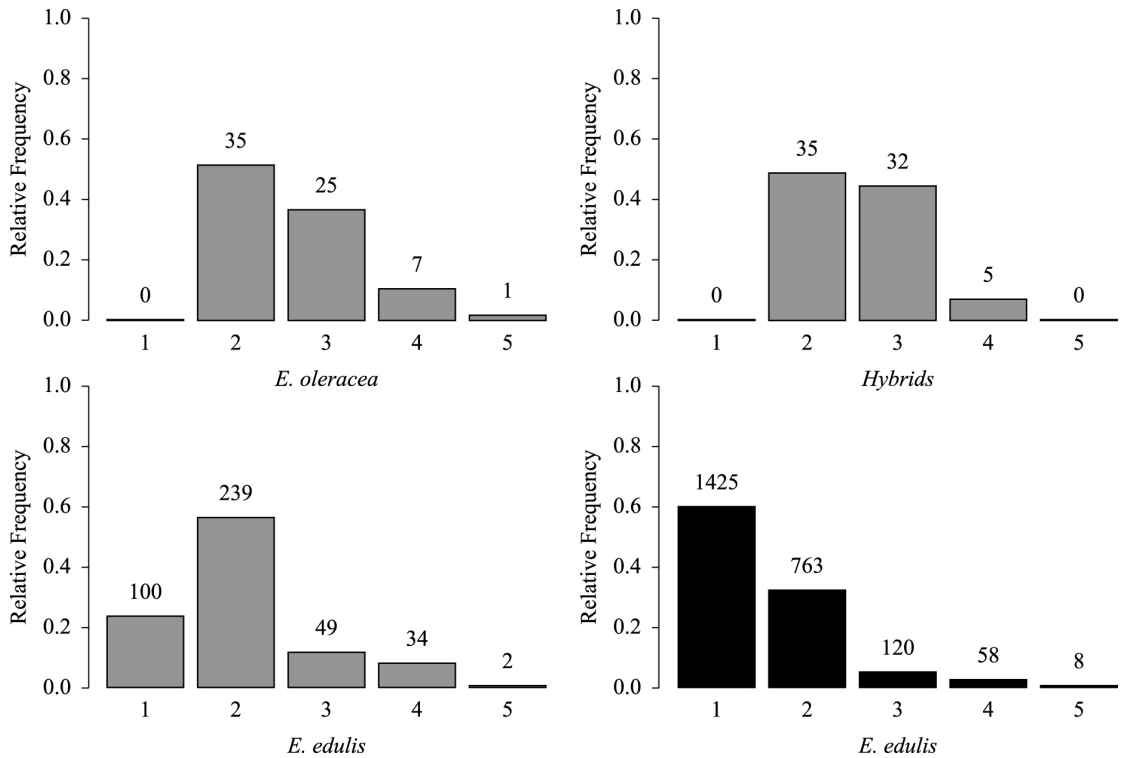


Figure 1. Ontogenetic structure of *E. oleracea* and hybrids at the site of introduction and of *E. edulis* at the introduction and control sites. Grey: populations at site of introduction; black: populations at control site. Ontogenetic stages: 1-seedling, 2-juvenile I, 3-juvenile II, 4-immature, 5-reproductive adult.

We observed that even though the original plantation of *E. oleracea* have already been cut down, most of the clumps have resprouted. In our case, *E. oleracea* resprouting ability may increase its resilience to disturbances when compared to the native palm species, since *E. edulis* is unable to resprout after being cut. We can conclude that *E. oleracea* is also able to establish populations and to resprout in the novel area even after its clumps have been completely cut. Nevertheless, variation between sexual reproduction or vegetative growth, may indicate that the absence of seedlings of this species do not automatically represent population instability in the new environment (Hallé et al., 1978).

In contrast, what we observed for *E. edulis* may suggest instability of the population that co-occurs with the exotic palm. The density of *E. edulis* population at the site of introduction was significantly lower than expected for this species along the Atlantic Forest (Fantini and Guries, 2007; Conte et al., 2003; Reis et al., 2000). This difference was mostly caused by the lower seedling density in the site where *E. oleracea* was introduced. At the same region of our site of introduction, *E. edulis* populations usually have higher densities and negative exponential distribution of stages (Silva Matos and Bovi, 2002). *E. edulis* also shows high fruit production patterns (von Allmen et al., 2004; Silva Matos and Watkinson, 1998) and germination rates (Leite et al., 2012; Tiberio et al., 2012), and also keeps

seedling banks instead of seed banks. So it is always expected to find high abundance of seedlings, specially after fruit production period. The same pattern of high frequency of seedlings has been also detected in other regions of the Atlantic Forest (Silva et al., 2009; Fantini and Guries, 2007; Conte et al., 2003; Silva Matos and Bovi 2002; Reis et al., 2000; Silva Matos and Watkinson, 1998). Therefore, the significant reduction of seedlings observed at the site of introduction, when compared to the control site and to many examples in the literature, can be considered a concern for the population stability.

The presence of spontaneous hybrids at the site of introduction indicates that the exchange of pollen between *E. oleracea* and *E. edulis* may occur when flowering periods of these palms overlap. Considering that these species can spontaneously produce viable hybrid seeds (Tiberio et al., 2012) and that hybrids may reach the reproductive stage (Bovi et al., 1987), the introduction of *E. oleracea* increases the vulnerability of the native species. The cross pollination between congener species may decrease the number of viable seeds of the native species consequently dropping the number of seedlings (Traveset and Richardson, 2006) and, finally, the total population density. As indicated by our results, this scenario can be observed for *E. edulis* population at the site of introduction. Moreover, these hybrids are expected to backcross to parental populations (Campos et al., 1991) resulting in a high gene pool mixtures

Table 1. Birds recorded feeding on fruits of *E. edulis* and *E. oleracea* and total number of visits obtained at the site of introduction - Carlos Botelho State Park, SP, Brazil.

Species	Total visits [§]	<i>E. edulis</i>	<i>E. oleracea</i>
Cracidae			
<i>Penelope obscura</i> (Temminck 1815)	13	3	1
<i>Aburria jacutinga</i> (Spix 1825)	9	3	
Columbidae			
<i>Patagioenas plumbea</i> (Vieillot 1818)	14	2	
Psittacidae			
<i>Pyrrhura frontalis</i> (Vieillot 1817)	389	68	26
<i>Brotogeris tirica</i> (Gmelin 1788)	313	10	4
Trogonidae			
<i>Trogon viridis</i> (Linnaeus 1766)	94	3	1
Momotidae			
<i>Baryphthengus ruficapillus</i> (Vieillot 1818)	62	1	
Ramphastidae			
<i>Ramphastos vitellinus</i> (Lichtenstein 1823)	61	12	3
<i>Ramphastos dicolorus</i> (Linnaeus 1766)	42	23	7
<i>Selenidera maculirostris</i> (Lichtenstein 1823)	28	4	
<i>Pteroglossus bailloni</i> (Vieillot 1819)	6	2	
Tyrannidae			
<i>Myiozetetes similis</i> (Spix 1825)	21		1
Cotingidae			
<i>Procnias nudicollis</i> (Vieillot 1817)	40	1	
<i>Pyroderus scutatus</i> (Shaw 1792)	5	2	
Turdidae			
<i>Turdus flavipes</i> (Vieillot 1818)	56	19	13
<i>Turdus rufiventris</i> (Vieillot, 1818)	10		2
<i>Turdus amaurochalinus</i> (Cabani, 1850)	3	1	1
<i>Turdus albicollis</i> (Vieillot 1818)	183	7	4
Thraupidae			
<i>Tangara seledon</i> (Statius Muller 1776)	638		12

[§]Total of visits are related to all individuals observed along transects. These individuals were not necessarily consuming fruits of *E. edulis* or *E. oleracea* every time they were registered.

between both palm species. This process may threaten mostly small populations, as it is the current status of *E. edulis* in many forest fragments, which could result in a “silent invasion” as already observed for other organisms (Miglietta and Lessios, 2009).

Individuals of *E. oleracea* were also found outside the original planting area, which demonstrates its capability of being efficiently dispersed. Both *E. oleracea* and *E. edulis* are zoophilic species and produce fruits very similar in size, weight and colour (Tiberio et al., 2012; Henderson et al., 1995). Thus, as expected, we observed that most frugivorous birds feed on the fruits of both species. Only two species, *Pyrrhura frontalis* and *Brotogeris tirica*, may not act as seed dispersers as they can also consume the endocarp of seeds (Galetti et al., 2013; Pizo et al., 2006). Still, five of the species observed in our study have wide distribution that include the region of natural occurrence of *E. oleracea* in the Amazon rainforest (Sick, 1997). *Patagioenas plumbea*, *Trogon viridis*, *Ramphastos vitellinus*, *Myiozetetes similis* and *Turdus albicollis* occur in the Atlantic rainforest as

well as in the Amazon rainforest. Therefore, these bird species are also able to disperse seeds of *E. oleracea* in the Atlantic Forest. At family level, the community assemblage of visitors of each *Euterpe* palm in their native habitats is also similar. For example, in the Indigenous Land Waiãpi do Amapari, at Amapá state in north of Brazil, fruits of *E. oleracea* are eaten by: Cracidae (*Penelope marail*), Psittacidae (*Ara macao* and *Deroptyus accipitrinus*), Ramphastidae (*Ramphastos tucanus*) and Cotingidae (*Querula purpurata*) (A. Antunes, personal observation).

Seed dispersal of fleshy-fruited exotic species is known to play an important role in the invasion process (Gosper et al., 2005). The impoverishment or even the displacement of dispersers of *E. edulis* could directly influence the density and distribution of the this palm tree (Fadini et al., 2009). We observed that, as its native congener *E. edulis*, *E. oleracea* also attracts a broad range of frugivorous birds and also that few species that used to feed on the native were found exclusively feeding on the exotic palm. The large number of interactions with local

bird species including species with great moving capacity as *Ramphastos spp.* and *Turdus spp.* may certainly contribute to the spread of this exotic palm in the Atlantic rainforest.

In this study we observed that the Amazonian palm *E. oleracea* is able to establish populations and spread in the Atlantic rainforest and also to spontaneously hybridize with the native *E. edulis*. As *E. oleracea* showed a significant interaction with local frugivorous birds, it is necessary to evaluate how its presence may interfere in the dispersion of the native *E. edulis*. The small number of seedlings of *E. edulis* found at the site of introduction may also have resulted from a negative impact caused by the interaction between *E. oleracea* and local fauna. As a long-term effect, we could expect the same impacts in other areas as *E. oleracea* fruits are being dispersed by several frugivorous birds.

Many palm heart and fruit producers along the Atlantic forest have been adopting *E. oleracea* and even *E. oleracea* × *E. edulis* hybrids sold in the seedlings market. As exemplified by our study, *E. oleracea* might be able to interact with birds, spread and successfully establish in wild areas. Nevertheless, the final consequences of its introduction still needs to be addressed by researchers and environmental policy. As *E. oleracea*, several palm species can easily establish into new areas allowing it to spread and becoming invasive. Our study reveals that besides the dangers of habitat destruction and illegal exploitation (Silva Matos and Bovi, 2002), the indiscriminate introduction of exotic palms represents another risk to the maintenance of the native palm *E. edulis* in Atlantic rainforest.

Acknowledgements

We thank the funding agencies “Fundação de Amparo a Pesquisa do Estado de São Paulo” (FAPESP) and “Coordenação de Aperfeiçoamento de Pessoal de Nível Superior” (CAPES) for the scholarships provided for the first and second authors, respectively. We also thank two anonymous reviewers for comments on the manuscript.

References

ALBRECHT, M., SCHMID, B., HAUTIER, Y. and MÜLLER, C.B., 2012. Diverse pollinator communities enhance plant reproductive success. *Proceedings of the Royal Society B*, vol. 279, no. 1748, pp. 4845-4852. <http://dx.doi.org/10.1098/rspb.2012.1621>. PMID:23034701.

ASLAN, C.E. and REJMÁNEK, M., 2010. Avian use of introduced plants: ornithologist records illuminate interspecific associations and research needs. *Ecological Applications*, vol. 20, no. 4, pp. 1005-1020. <http://dx.doi.org/10.1890/08-2128.1>. PMID:20597286.

BOVI, M.L.A., GODOY JUNIOR, G. and SAES, L.A., 1987. Híbridos interespecíficos de palmito (Euterpe oleracea × Euterpe edulis). *Bragantia*, vol. 46, no. 2, pp. 343-363. <http://dx.doi.org/10.1590/S0006-87051987000200015>.

CAMPOS, S.D.S., BOVI, M.L.A. and IADEROZA, M., 1991. Características do palmito obtido de algumas combinações híbridas entre açaí e juçara cultivadas sob diferentes condições. *Pesquisa Agropecuária Brasileira*, vol. 26, pp. 637-646.

CHRISTIANINI, A.V., 2006. Fecundity, dispersal and predation of seeds of *Archontophoenix cunninghamiana*. Wendl. and Drude, an invasive palm in the Atlantic forest. *Brazilian Journal of Botany*, vol. 29, pp. 587-594. <http://dx.doi.org/10.1590/S0100-84042006000400008>.

CONTE, R., NODARI, R.O., VENCOSKY, R. and REIS, M.S., 2003. Genetic diversity and recruitment of the tropical palm, *Euterpe edulis* Mart., in a natural population from the Brazilian Atlantic Forest. *Heredity*, vol. 91, no. 4, pp. 401-406. <http://dx.doi.org/10.1038/sj.hdy.6800347>. PMID:14512956.

DICKIE, I.A., BENNETT, B.M., BURROWS, L.E., NUÑEZ, M.A., PELTZER, D.A., PORTÉ, A., RICHARDSON, D.M., REJMÁNEK, M., RUNDEL, P.W. and VAN WILGEN, B.W., 2013. Conflicting values: ecosystem services and invasive tree management. *Biological Invasions*, vol. 16, no. 3, pp. 705-719. <http://dx.doi.org/10.1007/s10530-013-0609-6>.

DISLICH, R., KISSER, N. and PIVELLO, V.R., 2002. The invasion of a forest fragment in São Paulo (SP) by the Australian palm *Archontophoenix cunninghamiana* H. Wendl. and Drude. *Brazilian Journal of Botany*, vol. 25, pp. 55-64. <http://dx.doi.org/10.1590/S0100-84042002000100008>.

ELTON, C.S., 2000. *The ecology of invasions by animals and plants*. Chicago: University of Chicago. 196 p.

FADINI, R.F., FLEURY, M., DONATTI, C.I. and GALETTI, M., 2009. Effects of frugivore impoverishment and seed predators on the recruitment of a keystone palm. *Acta Oecologica*, vol. 35, no. 2, pp. 188-196. <http://dx.doi.org/10.1016/j.actao.2008.10.001>.

FANTINI, A.C. and GURIES, R.P., 2007. Forest structure and productivity of palmito (Euterpe edulis Martius) in the Brazilian Mata Atlântica. *Forest Ecology and Management*, vol. 242, no. 2-3, pp. 185-194. <http://dx.doi.org/10.1016/j.foreco.2007.01.005>.

GALETTI, M. and ALEIXO, A., 1998. Effects of palm heart harvesting on avian frugivores in the Atlantic rain forest of Brazil. *Journal of Applied Ecology*, vol. 35, no. 2, pp. 286-293. <http://dx.doi.org/10.1046/j.1365-2664.1998.00294.x>.

GALETTI, M. and FERNANDEZ, J.C., 1998. Palm heart harvesting in the Brazilian Atlantic forest: changes in industry structure and the illegal trade. *Journal of Applied Ecology*, vol. 35, no. 2, pp. 294-301. <http://dx.doi.org/10.1046/j.1365-2664.1998.00295.x>.

GALETTI, M., GUEVARA, R., CÔRTEZ, M.C., FADINI, R., VON MATTER, S., LEITE, A.B., LABECCA, F., RIBEIRO, T., CARVALHO, C.S., COLLEVATTI, R.G., PIRES, M.M., GUIMARÃES JUNIOR, P.R., BRANCALION, P.H., RIBEIRO, M.C. and JORDANO, P., 2013. Functional extinction of birds drives rapid evolutionary changes in seed size. *Science*, vol. 340, no. 6136, pp. 1086-1090. <http://dx.doi.org/10.1126/science.1233774>. PMID:23723235.

GOSPER, C.R., STANSBURY, C.D. and VIVIAN-SMITH, G., 2005. Seed dispersal of fleshy-fruited invasive plants by birds: contributing factors and management options. *Diversity & Distributions*, vol. 11, no. 6, pp. 549-558. <http://dx.doi.org/10.1111/j.1366-9516.2005.00195.x>.

HALLÉ, F.O., OLDEMAN, R.A.A. and TOMLINSON, P.B., 1978. *Tropical trees and forests: an architectural analysis*. New York: Springer. 441 p. <http://dx.doi.org/10.1007/978-3-642-81190-6>.

HAMMER, Ø., HARPER, D.A.T. and RYAN, P.D., 2001. PAST: paleontological statistics software package for education and data analysis. *Palaeontologia Electronica*, vol. 4, no. 1, pp. 1-9.

HENDERSON, A., GALEANO, G. and BERNAL, R., 1995. *Field guide to the Palms of the Americas*. Princeton: Princeton University. 376 p.

- LEITE, A.D.B., BRANCALION, P.H.S., GUEVARA, R. and GALETTI, M., 2012. Differential seed germination of a keystone palm (*Euterpe edulis*) dispersed by avian frugivores. *Journal of Tropical Ecology*, vol. 28, no. 6, pp. 615-618. <http://dx.doi.org/10.1017/S0266467412000594>.
- LOPEZARAIZA-MIKEL, M.E., HAYES, R.B., WHALLEY, M.R. and MEMMOTT, J., 2007. The impact of an alien plant on a native plant-pollinator network: an experimental approach. *Ecology Letters*, vol. 10, no. 7, pp. 539-550. <http://dx.doi.org/10.1111/j.1461-0248.2007.01055.x>. PMID:17542933.
- MELITO, M.O., FARIA, J.C., AMORIM, A.M. and CAZETTA, E., 2014. Demographic structure of a threatened palm (*Euterpe edulis* Mart.) in a fragmented landscape of Atlantic Forest in northeastern Brazil. *Acta Botanica Brasílica*, vol. 28, no. 2, pp. 249-258. <http://dx.doi.org/10.1590/S0102-33062014000200011>.
- MELO, M.M.R.F. and MANTOVANI, W., 1994. Composição florística e estrutura de trecho de Mata Atlântica de encosta, na Ilha do Cardoso (Cananéia, SP, Brasil). *Boletim do Instituto de Botânica*, vol. 9, pp. 7-157.
- MEYER, J.Y., LAVERGNE, C. and HODEL, D.R., 2008. Time bombs in gardens: invasive ornamental palms in tropical islands, with emphasis on French Polynesia (Pacific Ocean) and the Mascarenes. *Palms*, vol. 52, pp. 23-35.
- MIGLIETTA, M. and LESSIOS, H., 2009. A silent invasion. *Biological Invasions*, vol. 11, no. 4, pp. 825-834. <http://dx.doi.org/10.1007/s10530-008-9296-0>.
- MOEGENBURG, S.M. and LEVEY, D.J., 2003. Do frugivores respond to fruit harvest? An experimental study of short-term responses. *Ecology*, vol. 84, no. 10, pp. 2600-2612. <http://dx.doi.org/10.1890/02-0063>.
- PIZO, M., VONALLMEN, C. and MORELLATO, L., 2006. Seed size variation in the palm *Euterpe edulis* and the effects of seed predators on germination and seedling survival. *Acta Oecologica*, vol. 29, no. 3, pp. 311-315. <http://dx.doi.org/10.1016/j.actao.2005.11.011>.
- PIZO, M.A. and VIEIRA, E.M., 2004. Palm harvesting affects seed predation of *Euterpe edulis*, a threatened palm of the Brazilian Atlantic Forest. *Brazilian Journal of Biology = Revista Brasileira de Biologia*, vol. 64, no. 3, pp. 669-676. <http://dx.doi.org/10.1590/S1519-69842004000400015>. PMID:15620006.
- REIS, M.S., FANTINI, A.C., NODARI, R.O., REIS, A., GUERRA, M.P. and MANTOVANI, A., 2000. Management and conservation of natural populations in Atlantic Rain Forest: the case study of palm-heart (*Euterpe edulis* Martius). *Biotropica*, vol. 32, no. 4b, pp. 894-902. <http://dx.doi.org/10.1111/j.1744-7429.2000.tb00627.x>.
- RICHARDSON, D.M. and REJMÁNEK, M., 2011. Trees and shrubs as invasive alien species: a global review. *Diversity & Distributions*, vol. 17, no. 5, pp. 788-809. <http://dx.doi.org/10.1111/j.1472-4642.2011.00782.x>.
- SÃO PAULO. Secretaria da Agricultura e Desenvolvimento. Coordenadoria de Assistência Técnica Integral – CATI-EA. Projeto Lupa, 2008a [viewed 18 December 2013]. *Levantamento Censitário das Unidades de Produção Agropecuária do Estado de São Paulo: região de Registro, SP* [online]. São Paulo. Available from: <http://rainforest.cati.sp.gov.br/projetolupa/dadosregionais/pdf/tedr33.pdf>
- SÃO PAULO. Secretaria do Meio Ambiente. Instituto Florestal, 2008b [viewed 18 December 2013]. *Plano de Manejo do Parque Estadual Carlos Botelho* [online]. São Paulo. Available from: <http://rainforest.ambiente.sp.gov.br/fundacaoflorestal/planos-de-manejo/planos-de-manejo-planos-concluidos/>
- SICK, H., 1997. *Ornitologia brasileira*. Rio de Janeiro: Nova Fronteira. 912 p.
- SILVA MATOS, D.M. and BOVI, M.L.A., 2002. Understanding the threats to biological diversity in southeastern Brazil. *Biodiversity and Conservation*, vol. 11, no. 10, pp. 1747-1758. <http://dx.doi.org/10.1023/A:1020344213247>.
- SILVA MATOS, D.M. and WATKINSON, A.R., 1998. The fecundity, seed, and seedling ecology of the edible palm *Euterpe edulis* in southeastern Brazil. *Biotropica*, vol. 30, no. 4, pp. 595-603. <http://dx.doi.org/10.1111/j.1744-7429.1998.tb00099.x>.
- SILVA, M., MARTINI, A. and ARAÚJO, Q., 2009. Population structure of *Euterpe edulis* Mart. in the Southern Bahia, Brazil. *Brazilian Journal of Botany*, vol. 32, no. 2, pp. 393-403. <http://dx.doi.org/10.1590/S0100-84042009000200017>.
- SIMBERLOFF, D., 2005. Non-native Species DO Threaten the Natural Environment! *Journal of Agricultural & Environmental Ethics*, vol. 18, no. 6, pp. 595-607. <http://dx.doi.org/10.1007/s10806-005-2851-0>.
- SIMBERLOFF, D., MARTIN, J.L., GENOVESI, P., MARIS, V., WARDLE, D.A., ARONSON, J., COURCHAMP, F., GALIL, B., GARCÍA-BERTHO, E., PASCAL, M., PYŠEK, P., SOUSA, R., TABACCHI, E. and VILÀ, M., 2013. Impacts of biological invasions: what's what and the way forward. *Trends in Ecology & Evolution*, vol. 28, no. 1, pp. 58-66. <http://dx.doi.org/10.1016/j.tree.2012.07.013>. PMID:22889499.
- SPOTSWOOD, E.N., MEYER, J.Y. and BARTOLOME, J.W., 2012. An invasive tree alters the structure of seed dispersal networks between birds and plants on islands. *Journal of Biogeography*, vol. 39, no. 11, pp. 2007-2020. <http://dx.doi.org/10.1111/j.1365-2699.2012.02688.x>.
- TIBERIO, F.C.S., SAMPAIO-E-SILVA, T.A., DODONOV, P., GARCIA, V.A. and SILVA MATOS, D.M., 2012. Germination and allometry of the native palm trees *Euterpe edulis* compared to the introduced *E. oleracea* and their hybrids in Atlantic rainforest. *Brazilian Journal of Biology = Revista Brasileira de Biologia*, vol. 72, no. 4, pp. 955-962. <http://dx.doi.org/10.1590/S1519-69842012000500025>. PMID:23295528.
- TOMLINSON, P.B., 2006. The uniqueness of palms. *Botanical Journal of the Linnean Society*, vol. 151, no. 1, pp. 5-14. <http://dx.doi.org/10.1111/j.1095-8339.2006.00520.x>.
- TRAVESET, A. and RICHARDSON, D.M., 2006. Biological invasions as disruptors of plant reproductive mutualisms. *Trends in Ecology & Evolution*, vol. 21, no. 4, pp. 208-216. <http://dx.doi.org/10.1016/j.tree.2006.01.006>. PMID:16701087.
- VAN WILGEN, B.W. and RICHARDSON, D., 2014. Challenges and trade-offs in the management of invasive alien trees. *Biological Invasions*, vol. 16, no. 3, pp. 721-734. <http://dx.doi.org/10.1007/s10530-013-0615-8>.
- VON ALLMEN, C., MORELLATO, L.C. and PIZO, M.A., 2004. Seed predation under high seed density condition: the palm *Euterpe edulis* in the Brazilian Atlantic Forest. *Journal of Tropical Ecology*, vol. 20, no. 4, pp. 471-474. <http://dx.doi.org/10.1017/S0266467404001348>.
- WOLF, D.E., TAKEBAYASHI, N. and RIESEBERG, L.H., 2001. Predicting the risk of extinction through hybridization. *Conservation Biology*, vol. 15, no. 4, pp. 1039-1053. <http://dx.doi.org/10.1046/j.1523-1739.2001.0150041039.x>.