UNIVERSIDADE ESTADUAL PAULISTA
"JÚLIO DE MESQUITA FILHO"
INSTITUTO DE BIOCIÊNCIAS - RIO CLARO

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PROGRAMA DE PÓS-GRADUAÇÃO EM ECOLOGIA E BIODIVERSIDADE

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EFETIVIDADE DE DISPERSÃO DE SEMENTES POR AVES DA PALMEIRA INVASORA *Archontophoenix* spp. NA MATA ATLÂNTICA

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Dissertação apresentada ao Instituto de Biociências da Universidade Estadual Paulista "Júlio de Mesquita Filho" - Câmpus de Rio Claro, como requisito para obtenção do título de Mestre em Ecologia e Biodiversidade.

Rio Claro
2016

UNIVERSIDADE ESTADUAL PAULISTA

Câmpus de Rio Claro

CERTIFICADO DE APROVAÇÃO

TÍTULO DA DISSERTAÇÃO: EFETIVIDADE DE DISPERSÃO DE SEMENTES POR AVES DA PALMEIRA INVASORA ARCHONTOPHOENIX SPP. NA MATA ATLÂNTICA
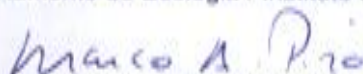
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Rio Claro, 08 de abril de 2016

"Existe uma teoria que diz que, se um dia alguém descobrir para que serve o Universo e porque ele está aqui, ele desaparecerá instantaneamente e será substituído por algo ainda mais estranho e inexplicável.

Existe uma segunda teoria que diz que isso já aconteceu."

Douglas Adams *em "O Restaurante no Fim do Universo"*, 1980.

AGRADECIMENTOS

RESUMO

O sucesso de estabelecimento de plantas invasoras depende, além de outros fatores, das relações mutualísticas estabelecidas no novo habitat. No presente estudo, nós caracterizamos as relações mutualísticas entre aves frugívoras nativa e uma palmeira invasora (*Archontophoenix* spp.) e investigamos o potencial de competição por dispersores de sementes com uma palmeira nativa, o palmito juçara (*Euterpe edulis*), na Mata Atlântica brasileira. As duas palmeiras tem sua dispersão mediada por aves, e ocorrem em florestas tropicais úmidas. Nós registramos 40 espécies de aves consumindo frutos de *Archontophoenix* spp. e 60 espécies consumindo frutos de *E. edulis*, com uma sobreposição de 62%. Assim como esperávamos, o palmito juçara apresentou o menor valor do componente quantitativo da efetividade de dispersão de sementes quando em simpatria com a palmeira invasora e sobreposição da frutificação. Nossos resultados indicaram um alto potencial de competição por dispersores entre *Archontophoenix* spp. e o palmito juçara, mas essa competição variou entre as área devido às diferenças na fenologia das espécies. No entanto, a dispersão de sementes do palmito juçara pode ser negativamente afetada nas áreas onde ela frutifica concomitantemente com *Archontophoenix* spp. e a população de frugívoros tem sua abundância limitada. No cenário atual, em que a exploração ilegal do palmito juçara vem ameaçando a espécie, diminuindo a abundância natural de suas populações na maioria das áreas da Mata Atlântica, a ausência ou a extinção funcional desta palmeira nativa pode acelerar o processo de invasão de *Archontophoenix* spp., porque as aves podem utilizar os frutos desta palmeira invasora como um recurso alternativo aos frutos do palmito juçara.

Palavras-chave: *fenologia da frutificação, competição,* Turdus*, interações animal-planta*

ÍNDICE

Bird-mediated seed dispersal effectiveness of an invasive palm and potential competition with a native palm

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Abstract

For long ecologists try to understand how competition affects species fitness, but few attention has been given to the potential competition between native and invasive species for mutualistic partners. Here evaluated the mutualistic interactions between native frugivorous birds and an invasive palm (*Archontophoenix* spp.) and investigate the potential competition for dispersers with a native species (*Euterpe edulis*), in Brazilian Atlantic Rainforest. Both palms are bird-mediated dispersed and occur in humid tropical forests. We recorded 40 bird species feeding on fruits of *Archontophoenix* spp. and 60 feeding on fruits of the native *E. edulis*, with an overlap of 62%. As we expected, the native palm presented the lowest value of the quantitative component of seed dispersal effectiveness when the invasive palm was also present and its fruiting overlapped with the native species. Our results indicated a high potential of competition for dispersal services between *Archontophoenix* spp. and the native palm, but this competition varied in space due to phenological mismatches between species. However, seed dispersal of the native palm may be negatively affected in areas where it fruits at the same period of *Archontophoenix* spp. and frugivore activity or abundance is limited. In the current scenario in which illegal exploitation of the native palm is threatening the species by reducing its natural abundance in most areas in the Atlantic forest, the absence or the functional extinction of this native species may speed up the invasion process of *Archontophoenix* spp., because birds may use fruit of this invasive palm as an alternative resource to juçara fruits.

Keywords: *fruiting phenology, competition,* Turdus, *plant-animal interactions.*

1. Introduction

For long ecologists try to understand the role of competition in determining *fitness* of invasive and native species (Vilà and Weiner 2004), but most of the well-known competitive interactions among plants focus on abiotic factors, such as soil nutrients, light, space or water (Melgoza et al. 1990; D'Antonio and Mahall 1991; Eliason and Allen 1997; Tilman et al. 1999). In contrast, competition in mutualistic relationships remains a little-explored facet of biological invasions (Traveset and Richardson 2014).

Competition with invasive species can disrupt mutualistic interactions of the native species, such as when non-native species monopolizes pollination services, diminishing native plant reproduction (Brown et al. 2002, Chittka and Schurkens 2008). Several authors have suggested that such competition also have potential to disrupt seed dispersal mutualisms (Vilà and D'Antonio 1998; Richardson et al. 2000; Traveset and Richardson 2006; Greenberg and Walter 2010). However, dispersal competition has been rarely directly measured. It is unknown whether such competition is a widespread or significant impact of biological invasions.

Snow (1965) was the first to propose competition for dispersers as a possible factor determining fruiting phenology of plant species in tropical forests. He observed a staggered phenology pattern in *Miconia* species and discussed that this pattern may be favors the more efficient dispersal of their seeds. This is because staggering of fruiting seasons results in a constant fruit supply throughout the year, which helps to maintain populations of fruit-eating birds and other animals and reduce the competition for dispersers.

Seed dispersal by animals is a key mutualism in determining the success of a plant to establish in a new habitat (Mitchell et al. 2006; Richardson et al. 2000; Schupp et al. 2010). Animal-dispersed alien plants can quickly infiltrate into native dispersal networks by attracting dispersers, contributing to the rapid spread of introduced species (Padrón et al. 2011; Spotswood et al. 2012; Heleno et al. 2013). Despite the importance of mutualisms to the spread of invasive species, quantitative data on the effectiveness of these novel interactions are still scarce (Gosper et al. 2005; Traveset and Richardson 2014).

Invasive fleshy-fruited plants have potential to alter foraging patterns of native frugivore, which, in turn, may impact seed dispersal of native flora (Mokotjomela et al. 2013). A negative impact on seed dispersal of native plants can be expected in habitats

where plants compete for seed dispersers: wide fruit availability and limited supply of dispersal agents. Since frugivores can select fruits based on specific traits, such as fruit availability, color, size and energy content (Wheelright 1993; Jordano 2000; Levey et al. 2002; Gosper et al. 2005; Cazetta et al. 2009), invasive fruits may be more consumed than native if they are preferred (Sallabanks 1993; Greenberg and Walter 2010). For instance, European Starling (*Sturnus vulgaris*) and American Robin (*Turdus migratorius*) demonstrated significant preferences for invasive fruits over similar native fruits in captive experiments, and these preferences were related to the percentage of soluble carbohydrates and proteins in fruit pulp (Lafleur et al. 2007).

On the other hand, seed dispersal of native plants can be favored in habitats supporting a more diverse or abundant frugivore assemblage that may consume larger amounts of native fruits in addition to the consumption of fruits from invasive plants (Date et al. 1991; Gleditsch and Carlo 2010). In periods of fruit scarcity, invasive fruits can be an important resource maintaining frugivore populations, which otherwise would be less abundant (Carlo et al. 2003). Therefore, native plants with complementary fruiting phenology to invasive ones could be favored. Finally, seed dispersal of native plants would not be affected if native and invasive fruits were consumed by different disperser assemblages, if dispersal agents are not limiting, or if fruiting phenology do not overlap (Gosper et al. 2006).

Here we characterize mutualistic interactions between native frugivorous birds and an invasive palm (*Archontophoenix* spp.) to test the potential for competition with a native species (*Euterpe edulis*). *Archontophoenix* spp. and *E. edulis* are ecologically similar palm species - both have broad native range occurrence, are climax species, shade tolerant, grow in a range of soil conditions - and share some characteristics such as infructescence structure, fruit and seed size (Figure 1) suggesting substantial overlap in frugivore assemblages (Reis et al. 2000; Chistianini 2006; Williams 2008).

Figure 1. Infructescences and seeds of (A) *Euterpe edulis* and (B) *Archontophoenix* spp.

The alien palm has better performance in pre and early post-dispersal stages than *E. edulis*: *Archontophoenix* spp. has longer fruiting period and produces about three times more fruits than *E. edulis*; time to germination is shorter, germination success and seedling survival are four and eight times higher for the alien palm, respectively (Mengardo et al. 2012). Despite the evidences of high performance in pre and post dispersal stages, the seed dispersal process of *Archontophoenix* spp. is poorly documented on the invaded areas. High ability to spread of *Archontophoenix* spp. is mainly related to propagation and dispersal characteristics, therefore, understanding these processes is crucial for predicting potential impacts of the alien species on native biota (Buckley et al. 2006; Traveset and Richardson 2014).

To assess the potential of *Archontophoenix* spp. to compete for frugivore with *Euterpe edulis* we first characterized the frugivore assemblage of *Archontophoenix* spp. in Brazilian Atlantic Forest and compared it with the native *Euterpe edulis* frugivore assemblage. We estimated frugivore assemblage overlap between two palms throughout the entire Brazilian Atlantic forest and in areas where they occur in sympatry. We expected that the frugivore assemblage of the alien palm overlaps significantly with the native palm, because both species have similar fruit and seed shape and size. Second, we evaluated the quantitative component of seed dispersal effectiveness (SDE) of the native and exotic palm species in areas presenting different situations of occurrence: 1) each palm species occurring alone; 2) palms in sympatry without fruiting phenology

overlap; 3) palms in sympatry with overlap in fruiting phenology. If the alien palm is able to divert the dispersal services previously allocated to the native species, we expect that the quantitative component of SDE of the native palm *E. edulis* is reduced in the area where both palms occur with fruiting phenology overlap, because they may experience direct competition for dispersers. Finally, we evaluated the quantitative component of SDE of each bird species registered consuming fruits of *Archontophoenix* spp. and *E. edulis*. We expected that there are more legitimate seed dispersers for the alien palm (SDE > 0) because fruit size of *Archontophoenix* spp. is slightly smaller than *E. edulis* fruits (fruit diameter of 9.8 ± 0.97 mm and 11.98 ± 1.15 mm, respectively), allowing bird species with shorter gape width, like tanagers and finches (Thraupidae and Fringilidae families), to act as effective disperser for *Archontophoenix* spp., but not for *E. edulis*.

If frugivorous assemblages of the alien and the native palm overlap significantly and if they share effective seed dispersers, we can presume there is high potential for competition between *Archontophoenix* spp. and *E. edulis*, which, in turn, can affect seed dispersal of the native palm in areas supporting a limited supply of dispersal agents and/or where fruiting phenology overlaps with the invasive species.

2. Material and Methods

2.1 Study species

Euterpe edulis

Euterpe edulis is an endemic palm tree native to the Brazilian Atlantic Forest, popularly known as juçara palm. Occurrence area of this palm extends from south of Bahia to north of Rio Grande do Sul state (Henderson et al. 1995; Reis et al. 2000). Juçara palm is well adapted to low light conditions, occurring within different plant associations that provide shade. Originally, it was widely and abundantly distributed in the various plant formations of the Atlantic Forest. Illegal exploitation of juçara for extraction of the palm heart has caused the decline of remaining populations in many regions, leading the species to risk of extinction (Galetti, Fernandez 1998).

Each palm individual of *E. edulis* can produce 1 to 5 infructescences, containing more than 1,300 fruits per bunch. Fruits are globose drupes (fruit diameter of 11.98 ± 1.15 mm), with a thin black epicarp and a carbohydrate-rich mesocarp (pulp) enclosing a single seed (See table 1). Fruits are consumed by more than 50 bird species, from

thrushes to toucans, besides more than 10 mammal species (Galetti et al. 2013; Galetti et al. 1999).

Archontophoenix spp.

Archontophoenix is a plant genus comprising six palm species that are native to New South Wales and Queensland in eastern Australia (Dowe 2009). *Archontophoenix* species are widely cultivated as ornamental in the tropics. In Brazil, the Australian palm trees were introduced as ornamental plant and has been cultivated for palm heart production since 1990s (Lorenzi et al. 1996). In this study we refer to *Archontophoenix spp.* as the two species *Archontophoenix cunninghamiana* and *Archontophoenix alexandrae* and their hybrids, popularly known as king palms. There are subtle differences between *A. cunninghamiana* and *A. alexandrae* regarding the trunk width and color of leaves, flowers and crown shaft (Sunshine Coast Regional Council, 2012). However, these differences can be easily confounded by plant age or maturation stage, with difficult identification in the field. Thus, in the present study we did not attempt to distinguish the king palm species and we refer to *A. cunninghamiana, A. alexandrae* and their hybrids as *Archontophoenix* spp.

Archontophoenix spp. has monopodial growth and is a shade tolerant palm tree, but it grows faster at full sun. It is well adapted to the subtropical conditions, since climatic and topographic conditions are similar to those of its native range (Lorenzi et al. 2004). Because it is a highly prolific seeder, and tolerant to different soil conditions, king palms have become invasive in some countries, including areas of Australia, New Zealand, Hawaii and Brazil (Global Invasive Species Database, 2010). The species has extended fruiting period - flowering and fruiting the entire year in some areas - and produces small red drupes (fruit diameter of 9.8 ± 0.97 mm - see table 1) that are very attractive to birds (Mengardo and Pivello 2012). The only published data of frugivory on *Archontophoenix spp.* in Brazil come from a small urban fragment where eight bird species were registered consuming fruits of this alien palm (Christianini 2006; Hasui and Hofling 1998). Studies have shown that *Archontophoenix* share some seed dispersers with *Euterpe edulis*, but the magnitude of this overlap is still unknown.

Table 1. Summary of ecological and phenological traits of the alien (*Archontophoenix* spp.) and juçara palm (*Euterpe edulis*).* Fruit energy content was calculated considering amounts of lipid, carbohydrates and proteins following standardized table of energy densities (Available in ftp://ftp.fao.org/docrep/fao/006/y5022e/y5022e00.pdf) .

Trait	*Archontophoenix* spp.	*Euterpe edulis*
Fruit diameter (mm)	9.8 ± 0.97	11.98 ± 1.15
Infructescences/individual/year	1 to 3	1 to 3
Fecundity (Fruits/bunch)	3600	1300
Number of months fruiting	5 to 12	4 to 7
Time to seed germination (days)	75	90
Seedling survival after 1 year (%)	30	3.5
Fruit nutritional content	Lipids: 4.5% Carbohydrates: 6.3% Proteins: 0.8%	Lipids: 20% Carbohydrates: 70% Proteins: 8%
Fruit energy content (kJ/g)*	2.78	20.66

2.2   Study sites

The study was conducted during the fruiting period of *Archontophoenix* spp. and *Euterpe edulis* in four different sites located in Atlantic Forest domain, in São Paulo state, Brazil (Figure 2).
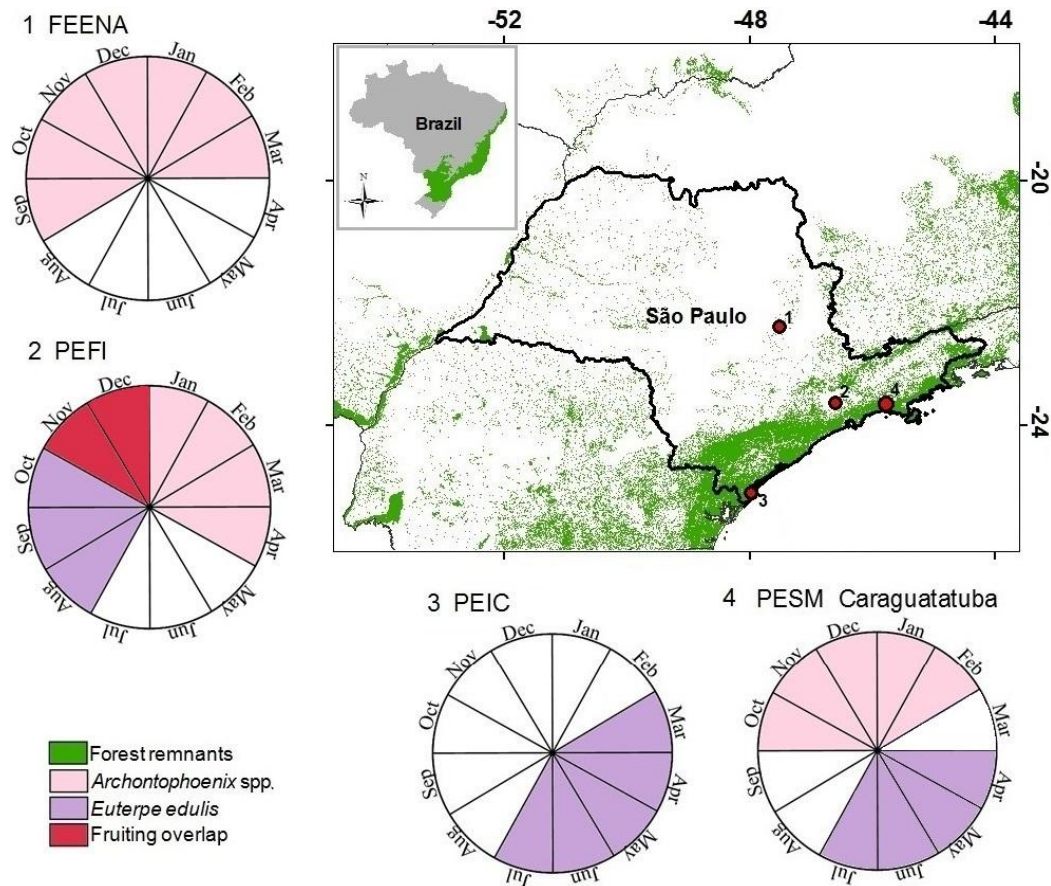
Figure 2. Location of study areas in state of São Paulo, Brazil. Ripe fruits availability of palm species in each study area. FEENA and PEIC are the areas where *Archontophoenix* spp. and *E. edulis* occur alone, respectively. PESM and PEFI are the areas where palm species occur in sympatry. Full colored slices indicate the months in which ripe fruits of *Archontophoenix* spp. (pink), *E. edulis* (purple) are available. Red slice indicates the month in which both palm species are bearing ripe fruits in the study area PEFI.

Edmundo Navarro de Andrade State Forest (FEENA)

Edmundo Navarro de Andrade State Forest (FEENA, hereafter - 22º25'S and 47º33'W) is located on Rio Claro city, in the south of São Paulo state, Brazil. The total area of FEENA is 2314 ha, divided into plots with predominance of exotic *Eucalyptus* species. Because it constitutes an unmanaged plantation area, the *Eucalyptus* forest has a growing understory of seasonal semi-deciduous flora. Remnants of riparian forests are also found in the area (Plattineti-Junior 1978). Avian community of FEENA is composed of about 290 species (Willis 2003; Gussoni 2007). *Turdus spp.* and *Thraupis sayaca* are among the most abundant frugivore, and the only large frugivorous in this area is *Ramphastos toco* (Gabriel 2009).

The surrounding area of FEENA consists primarily of the urban area of Rio Claro, sugarcane and pasture. The nearest native forest area is Mata São José, a

fragment of seasonal semi deciduous forest of 230 ha situated approximately 3 km. The climate at FEENA region is mesothermal, with dry winter and two distinct seasons: the rainy season, from October to March, and a dry season, from April to September (Köppen1948). During the rainy season, the average rainfall is 1200mm and in the dry season is approximately 200mm. Only *Archontophoenix* spp. was studied in this area because *Euterpe edulis* is absent.

Fontes do Ipiranga State Park (PEFI)

Fontes do Ipiranga State Park – PEFI (PEFI hereafter - 23°3'S and 46°36'W)is located southeast of São Paulo city, and has an area of 526,38 ha. The vegetation is characterized by areas of dense ombrophilous and seasonal semi deciduous forests. The regional climate is temperate with rainfall in the summer and dry winter. The annual rainfall is about 1540 mm, and monthly mean temperatures range from 15.7ºC in the coldest month and 22.4ºC in the hottest month (Santos and Funari 2002). The PEFI is considered one of the most significant urban Atlantic Forest remnants of Brazil (Barbosa et al. 2002). Disorders such as deforestation and pollution have increased the number of clearings and canopy discontinuity (Vinha 2008).

Both studied palm species are present in this area and their fruiting phenology overlaps in November and December (Figure 2). *Archontophoenix* spp. was introduced for ornamental purposes in built-up areas. The invasion of the exotic palm in the forest areas near to the Biological Reserve was reported in the literature, suggesting species management actions, but nothing was done up to now (Westphalen 2008).

Serra do Mar State Park - Caraguatatuba (PESM)

Serra do Mar State Park – Caraguatatuba (PESM hereafter - 23°32' to 23°42' S - 45°20' to 45°44' W,) is located in the northeast of São Paulo state, and has an area of 38,900 ha of dense ombrophilous forest. This area has high plant diversity and the avifauna is composed by more than 250 forest-dwelling species. The climate in the area is tropical superhumid with average annual temperatures ranging from 18 to 20°, and the average annual rainfall varying around 1200 to 2500 mm (Setzer 1996).

Archontophoenix spp. and *Euterpe edulis* are present in PESM but their fruiting phenology did not overlap in the year we carried out the study. *E. edulis* is present along the entire park, presenting a clustered distribution inside the forest (Fadini et al. 2009).

The exotic palm was planted in this area for ornamental purposes in the 80's, being present around the built-up areas of the park. The largest conglomerate of *Archontophoenix spp.* is located behind the headquarters, which is adjacent to the forest edge. The species is spreading along the edges of the park trails, but is practically absent inside the forest.

Ilha do Cardoso State Park (PEIC)

Ilha do Cardoso State Park (PEIC hereafter - 25°03'S and 48°53'W) is located in the south of São Paulo state. The PEIC covers an area of approximately 15,100 ha and is separated from the mainland by Tremendé channel (Bernardi 2001). The local climate is megathermal super humid, without defined dry season and with heavy rainfall in the summer with rainfall annual index of 3000 mm (Funari et al. 1987). The fauna is well preserved, with 80 recorded species of mammals and over 400 species of birds, among them, medium and large frugivorous like *Tinamus solitarius*, *Ramphastos vitellinus*, *Ramphastos dicolorus* and *Procnias nudicollis* (São Paulo 2011).

The vegetation of Ilha do Cardoso is formed by the following vegetation types: mangroves, pioneer vegetation of dunes, tree and shrub sandbank, tropical rainforest of coastal plains and premontane tropical rainforest (Noffs, Baptista-Noffs 1982). There are also shrub formations in the hill tops and secondary vegetation (Barros *et al.*, 1991). *Euterpe edulis* occurs in almost all forest formations, representing over 20% of individuals in the premontane forest (Melo and Mantovani 1994). *Archontophoenix* is absent in this area.

2.3   Frugivore assemblages of *Archontophoenix* spp. and *Euterpe edulis* in the Brazilian Atlantic forest

Characterization of the frugivore assemblages

In order to determine frugivore assemblage of *Archontophoenix* spp. and assess overlap of frugivore assemblages between the invasive and the native palm species throughout the entire Brazilian Atlantic Rainforest, we gathered information from four sources: frugivory data on focal observations of the present study (see section 2.4), scientific literature (*E. edulis*: Galetti et al. (2013) and Ribeiro (unp. data); *Archontophoenix* spp.: Christianini (2006), Hasui and Hofling (1998) and Constantini et

al.(unp. data); personal communication from other researchers and from WikiAves, a Brazilian online bird occurrence repository (WikiAves 2016). The resulting assemblages of this data survey are referred as *potential* frugivore assemblages hereafter. The set of assemblages registered only at focal observations is called *observed* frugivore assemblages.

Overlap between frugivore assemblages

We estimated the degree of overlap (or similarity) between frugivore assemblages registered of the two palm species using Sørensen and Bray-Curtis indexes, both calculated in the R software version 3.0.1 with *fossil* package (R Core Team 2013). Sørensen index (SI) is based on the presence/absence of species in paired assemblages. It is one of the most widely used similarity index for assessing compositional similarity of assemblages and hence, its complement, dissimilarity (Faith 1983; Magurran 1988). Sørensen index was used for *potential* and *observed* frugivore assemblages. The formula for calculating Sørensen index is $\text{SI} = 2A/(2A + B + C)$, where *A* is the number of shared species, *B* and *C* are the species present only in one of the assemblages.

Bray-Curtis similarity index was used only for analyzing the *observed* frugivore assemblages, because they provide quantitative variables (e.g. visit frequency, number of dispersed seeds), which can be incorporated in the similarity analysis as a measure of species abundance composing frugivore assemblages (Bray, Curtis 1957). The formula for calculating Bray-Curtis index is $\text{BC} = (2\Sigma \min Nab)/(\Sigma Sa + \Sigma Sb)$, where *Nab* is the smallest value of abundance of species in common between sites *a* and *b*, *Sa* and *Sb* are number of specimens registered in each site. Here we used the visit frequency as the abundance measure of species. The resulting value of Sørensen and Bray-Curtis indexes range from 0 to 1, in which 0 represents no similarity between assemblages, and 1 represents total similarity. Percentage similarity is given simply by multiplying the results by 100.

2.4   Quantitative component of seed dispersal effectiveness

We conducted focal observations on *Archontophoenix* spp. and *E. edulis* individuals in each study area at periods varying from 06:30 h to 11:00 h and from

14:30 h to 18:00 h (see table 3 in section 3.2). Data of frugivory on *E. edulis* at PEIC were obtained from Côrtes (2006).

In order to assess the quantitative component of seed dispersal effectiveness we recorded the bird species, number of visits, and number of fruits handled according to avian feeding behavior. Feeding behavior is an important aspect in determining the potential of bird species as a disperser. Birds that swallow or carry the fruits can be considered legitimate dispersers, because regurgitated seeds can be taken away from the mother plant and reach favorable micro-sites to germinate and establish a new individual (Howe et al. 1985). Birds that damage the seeds or eat the pulp and drop the fruit under mother plant do not contribute effectively to the dispersal process, because the damaged seeds lose their germination capacity, whereas dropped seeds will experience high mortality rates and intraspecific competition (Janzen 1970; Jordano and Schupp 2000).

We built rarefaction curves based on the number of palm individuals sampled and the number of bird species recorded in each study area to verify if sampling effort was sufficient in each area according to the curve shape, aiming to reach the asymptote (Gotelli and Cowell 2001). The number of recorded bird species was compared with the prediction of the first-order Jackknife estimator (Jackknife 1). Jackknife 1 estimates the expected species richness based on the amount of unique species contained in each observation considering the presence or absence of a species rather than the abundance of species (Smith and Pontius 2006). Rarefaction curves and the Jackknife estimator were generated in software R using *vegan* package (R Core Team 2013).

Quantitative component of palms

Values of the quantitative component of palms are useful to assess the overall effectiveness of dispersal service that each palm individual receives from its assemblage of dispersal agents (Schupp et al. 2010). The quantitative component (QC_{palm}) of each palm was calculated as the product of the frequency of visits of all birds in each palm individual (VF_{palm}, number of visits divided by the number of hours of observation) and the average fruit dispersal per visit in that palm (DFV, number of swallowed and carried fruits divided by the number of visits). Thus, $QC_{palm} = VF_{palm} \times DFV$.

We tested for differences of the values of QC_{palm} between the two palm species in each study area using non-parametric tests. We performed Mann-Whitney-Wilcoxon

test to compare values of QC calculated in PESM and PEFI study areas. Kruskal-Wallis test was used to compare values of QC of palm species calculated in the three areas where each one occurs. Both analyses were performed in the R software version 3.0.1 with *stats* package (R Core Team 2013).

Quantitative component of birds

The quantitative component (QC) of birds represents the contribution of each bird species to the overall seed dispersal service of the plant (Schupp et al. 2010). The QC of bird species (QC_{bird}) was calculated as the product of the frequency of visits of each bird species in all observed palms (VF_{bird}, total number of visits divided by the number of hours of observation), handling rate (HR, the ratio between the number of handled fruits and number of visits) and dispersal probability (DP, number of dispersed fruits in relation to total number of handled fruits). Thus, $QC_{bird} = VF_{bird}$ x HR x DP.

3. Results

3.1 Frugivore assemblage of *Archontophoenix* spp. and *Euterpe edulis* in the Brazilian Atlantic forest

Characterization of frugivore assemblages

Potential frugivore assemblages: We registered 40 bird species consuming fruits of *Archontophoenix* spp. and 60 bird species consuming *E. edulis* fruits, considering all surveyed data from the Brazilian Atlantic forest (Table 2). The invasive and the native palm shared 31 frugivores, from a total of 67 birds species registered. Only 9 species were recorded interacting exclusively with fruits of the invasive *Archontophoenix* spp. By contrast, 28 bird species were found to be frugivores exclusive of the native palm *E. edulis*.

Frugivore assemblage of *E. edulis* has been significantly described in the scientific literature and some studies have dedicated large sampling effort on it (Côrtes 2006, Galetti et al. 2013, T. Ribeiro unpublished data). By contrast, frugivory data of *Archontophoenix* spp. in Brazil are scarce. The observations conducted in this study increased 32 bird species to previously known 8 frugivores of *Archontophoenix* spp. in Atlantic Forest.

Table 2. Birds recorded consuming fruits of *Archontophoenix* spp. and *Euterpe edulis*. Columns presents, respectively, birds registered consuming only *E. edulis* fruits; birds registered consuming only *Archontophoenix* spp. fruits; and birds registered consuming fruits of both palms. Numbers beside the bird species names indicate data source (1-Galetti et alm. 2013; 2-Focal observations of this study; 3- Constantini et al.; 4-Hasui, Hofling 1998; 5-Christianini 2006); 6- Ribeiro unp. data; 7- Marco A. Pizo, personal communication, 8- Marina C. Côrtes, personal communication.

E.edulis exclusive frugivores	*Archontophoenix* spp. exclusive frugivores	Frugivores overlap
Aramides cajanea[1,6]	*Aratinga leucophtalmus*[2]	*Aburria jacutinga*[1,3,6]
Basileuterus culicivorus[1,6]	*Cyanocorax cristatellus*[7]	*Baryphthengus ruficapillus*[1,2,3,6]
Carpornis cucullata[1,6]	*Elaenia spp.*[2]	*Brotogeris chiriri*[1,2,5,6]
Celeus flavescens[1,6]	*Passer domesticus*[2]	*Euphonia violacea*[1,2]
Coereba flaveola[1,6]	*Piaya cayana*[2]	*Forpus xantopterygius*[2]
Crypturellus tataupa[1,6]	*Ramphocelus carbo*[2]	*Megarynchus pitangua*[2,6]
Cyanocorax caeruleus[1,2,6]	*Tyrannus melancholicus*[2]	*Mimus saturninus*[1,3]
Cyclarhis gujanensis[1,6]	*Tyrannus savana*[2]	*Myiodynastes maculatus*[1, 2,6]
Dacnis cayana[1,6]	*Zonotrichia capensis*[2,4]	*Penelope superciliaris*[3,6]
Euphonia pectoralis[1,2,6]		*Penelope obscura*[1,2,3,6]
Geotrygon montana[1,]		*Pionus maximiliani*[1,2,6]
Laniisoma elegans[1,6]		*Pitangus sulphuratus*[1,2,3,4,5]
Lipaugus lanioides[1,6]		*Pteroglossus aracari*[2,3]
Mionectes rufiventris[1,6]		*Pyroderus scutatus*[1,2,3]
Odontophorus capueira[1,6]		*Ramphastos dicolorus*[1,2,4,6]
Orthogonys chloricterus[1,6]		*Ramphastos toco*[8]
Procnias nudicollis[1,2,3,6]		*Ramphastos vitellinus*[1,2,3,6]
Pteroglossus bailloni[1,6]		*Saltator similis*[5,6]
Pteroglossus castanotis[1,6]		*Selenidera maculirostris*[1,2,3]
Pyrrhura frontalis[1,6]		*Tangara cyanocephala*[1,2]
Tachyphonus coronatus[1,6]		*Tangara cyanoptera*[6]
Tangara cayana[6]		*Tangara seledon*[1,2,6]
Tangara cyanocephala[1,6]		*Thraupis ornata*[1,2]
Tinamus solitarius[1,6]		*Thraupis palmarum*[1,2]
Trichotraupis melanops[1,6]		*Thraupis sayaca*[1,2]
Triclaria malachitacea[1,6]		*Tityra cayana*[1,3,6]
Trogon viridis[1,2,6]		*Turdus albicollis*[1,2]
Turdus subalaris[1,6]		*Turdus amaurochalinus*[1,2,3,6]
		Turdus flavipes[1,2,3,6]
		Turdus leucomelas[1,2,3,4,5,6]
		Turdus rufiventris[1,2,3,4,5,6]

Sørensen index of *potential* frugivore assemblages between both palms pointed out a similarity of 0.62. For the *observed* frugivore assemblages, the Sørensen index was 0.36. Bray-curtis index calculated for PESM and PEFI study areas were, 0.14 and 0.30, respectively.

3.2 Quantitative component of seed dispersal effectiveness

The total sampling effort in all study areas was 612.2 hours of focal observations. We sampled an average of 24 (SD±7.26) palm individuals of both species in each study area (Table 3). We recorded a total of 36 bird species interacting with palm fruits, of which 25 species were recorded on *Archontophoenix* spp. and 16 on *Euterpe edulis* (Table 2). The richest avian assemblage was registered in FEENA for *Archontophoenix spp.* with 19 species recorded consuming fruits, of which 15 acted as effective dispersers.

The rarefaction curve closest to the asymptote was from FEENA study area, where we sampled 27 palm individuals of *Archontophoenix* spp. and recorded 19 bird species (Supp. Mat., Figure S1). Although the rarefaction curves did not reach an asymptote, the sampling effort was sufficient in all areas, according to the first order jackknife estimator (Supp. Mat., Figure S1, Table S1)

Table 3. Number of palm individuals sampled, hours of observations and number of frugivores recorded consuming fruits of *Archontophoenix spp.* and *E. edulis* in each study area. Legitimate (or effective) dispersers are species registered swallowing or carrying fruits. Pulp consumers and seed predators are not considered effective dispersers. A= Presence of *Archontophoenix* spp.; E= Presence of *E. edulis*; AE= Presence of *Archontophoenix spp.* and *E. edulis*; AE*=Presence of *Archontophoenix* spp. and *E. edulis* with fruiting phenology overlap.

Study area	Palm species	Sampled individuals	Hours of observation	Number of frugivores	Legitimate dispersers
PESM[AE]	*Archontophoenix*	29	141.5	07	06
	Euterpe edulis	24	101	09	08
PEFI[AE*]	*Archontophoenix*	17	61.8	09	06
	Euterpe edulis	14	50.9	07	06
PEIC[E]	*Euterpe edulis*	33	165	08	07
FEENA[A]	*Archontophoenix*	27	92	19	15

Quantitative component of palms

As we expected, the values of QC_{palm} registered for *E. edulis* were lower in PEFI study area, where both palms occurs with fruiting overlap (Supp. Mat., Table S2; Figure 3). While in PEFI the average QC_{palm} of *E. edulis* was of 0.68 (±0.84), in PESM and PEIC the values registered were of 1.87 (SD±2.53) and 1.90 (SD±3.51), respectively. The highest value of the quantitative component of palms was registered for

Archontophoenix spp. in FEENA, the study area where the invasive palm occurs alone (Figure 3; Supp. Mat., Table S2). In FEENA the mean value of QC was of 13.30 (SD±13.19), in PESM and PEFI the values of QC of *Archontophoenix* spp. were 0.37 (SD±1.16) and 2.24 (SD±3.90), respectively.

Comparing the quantitative components of the native and the invasive palm in areas where they occur in sympatry, in PESM study area, where fruiting phenologies do not overlap, the value of QC of *E. edulis* was five times higher than of *Archontophoenix* spp. (Supp. Mat.,Table S2). In contrast, in PEFI study area, where fruiting phenologies overlap, the value of QC of *Archontophoenix* spp. was 3.5 times higher than *E. edulis* (Figure 3).

Mann-Whitney Wilcoxon tests revealed significant difference only between QC values of *Archontophoenix* spp. in PESM and PEFI (p=0.0003) and between *Archontophoenix* spp. and *E. edulis* in PESM (p=0.005). Kruskal-Wallis test revealed significant difference between QC values of *Archontophoenix* spp. in PESM, PEFI and FEENA (p<0.0001).
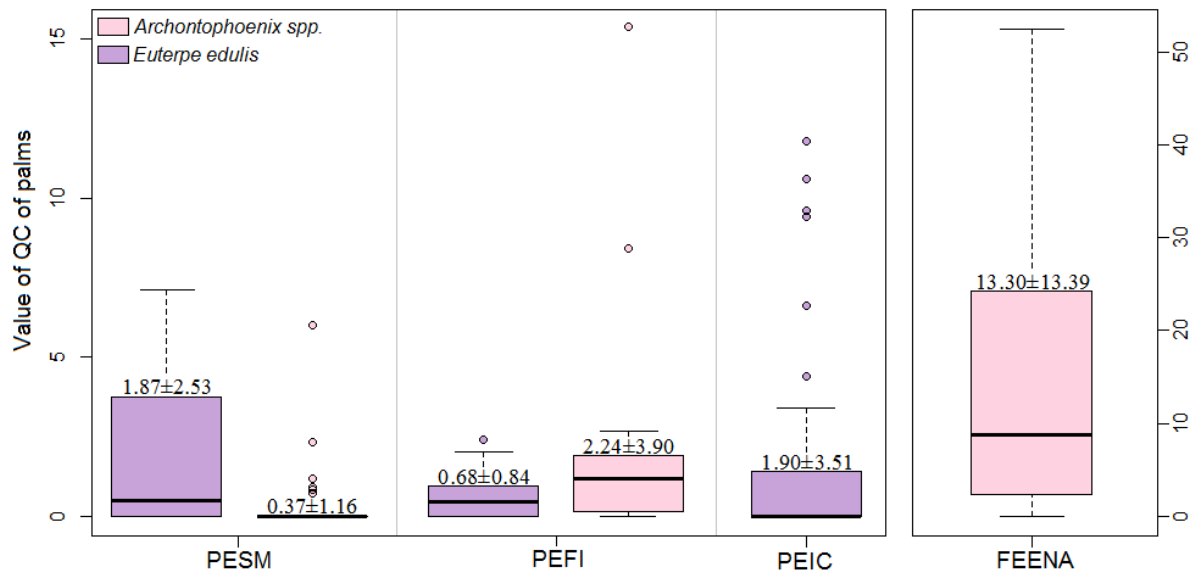

Figure 3. Quantitative component of SDE of palm species in each study area. Specified values in are the mean value of the quantitative component ± standard deviation. It is important to note that boxplot of *Archontophoenix* spp. in FEENA study area is on a different scale in *y* axis values (specified values on the right side of the graph) in relation to other boxplots.

Quantitative component of birds

Bird species of *Turdidae* and *Ramphastidae* families were the species with the highest values of the quantitative component, being among the three most effective

species in all study areas (Figure 4; Supp. Mat., Figures S2 to S7). *Turdus leucomelas* was the most commonly recorded species, present in five of the six sampled assemblages and being the most effective disperser of *Archontophoenix* spp. in two study areas. Bird species of *Thraupidae* family were also sampled in five of the six assemblages.

Ranked distribution curves of bird species based on the quantitative components of SDE show a similar pattern in all study areas except in FEENA (Figure 4). Frugivore assemblages of *E. edulis* presented a homogeneous variation in the quantitative components of birds in all areas, with little redundancy between species. For *Archontophoenix* spp. two bird species prevailed with highest and similar values of QC in each study area. In FEENA it has been registered several bird species with similar values of QC, resulting in an assembly with high redundancy between species (Figure 4).

As we expected, bird species with shorter gape width acted as legitimate dispersers for *Archontophoenix* spp., but not for *E. edulis*. We registered *T. ornata*, *T. palmarum*, *T. sayaca* and *E. violacea* dispersing seeds of *Archontophoenix* spp., although some of these species also acted as pulp consumers of the invasive palm. *T. seledon* and *E. pectoralis* were registered acting only as pulp consumers of *E. edulis* fruits.
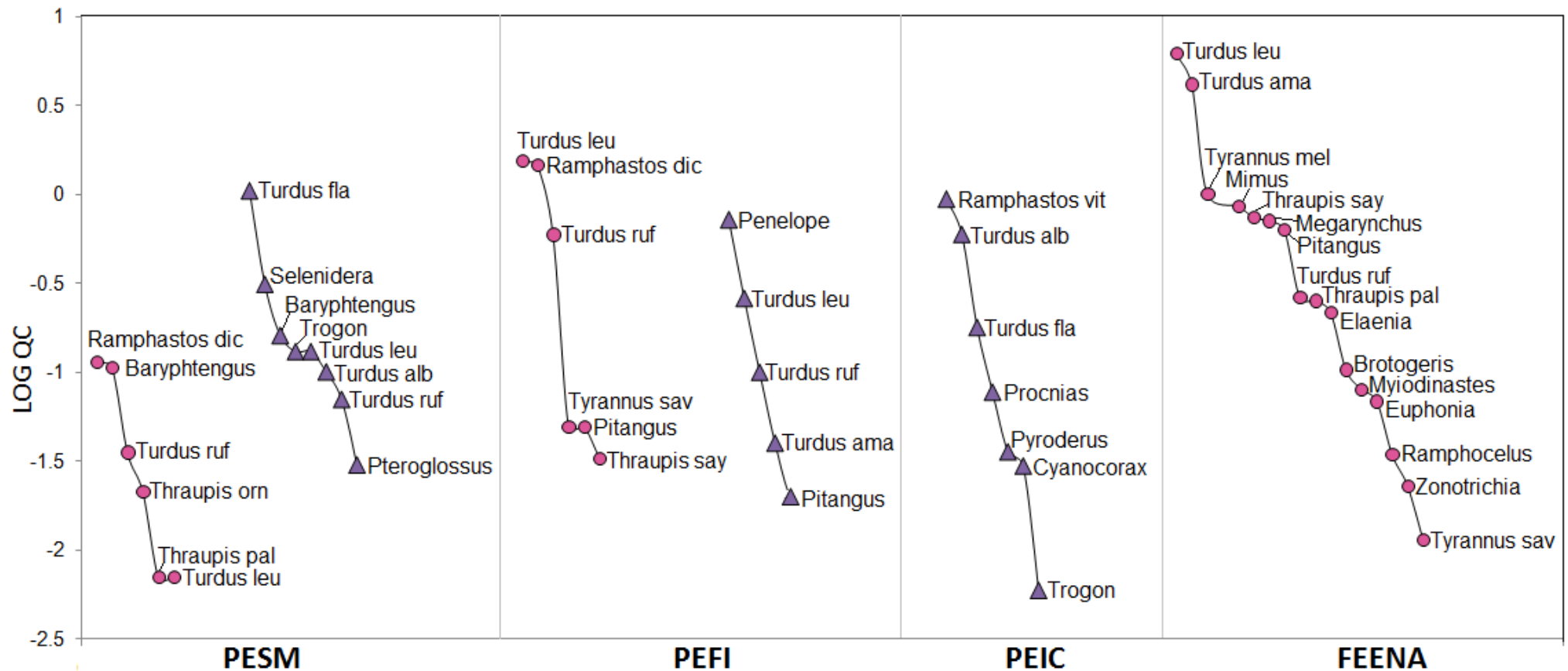
Figure 4. Ranked distribution curves of the quantitative components of bird species in each study area. Birds are ranked in decreasing order of the value of QC. Pink circles and purple triangles represent birds consuming *Archontophoenix* spp. and *Euterpe edulis*, respectively. Bird species are distributed in decreasing order of the quantitative component. Here we only represented bird species with the QC value > 0, because logarithmic transformation do not represent adequately the position of this species in relation to the rest of the assemblage.

4. Discussion

Our results indicated a high potential of competition for dispersal services between *Archontophoenix* spp. and the native juçara palm, but this competition varied in space due to phenological differences between palm species. Although studies of biological invasions have generated notable understanding of the mechanisms and consequences underlying the spread of introduced species, it has been proven difficult to identify particular traits explaining the tendency of plant species to invade certain environments (Simberloff 2013). Invasiveness depends not only on the non-native species traits, but also on the interaction between these traits with characteristics of the invaded habitats (Alpert et al. 2000).

The traits consistently explaining variation among species in invasiveness are broad native range and rapid dispersal (Pysek et al. 1995, Rejmánek 1996, Richardson 1998). In turn, rapid dispersal of invasive plants is related to several traits such as generation time, fruiting phenology, fecundity, fruit and seed size, seed viability and dispersal syndrome (Gosper 2009; Aslan and Rejmánek 2012). In this sense, the invasive *Archontophoenix* spp. has several traits that may enhance its invasion: the species produces fleshy fruits with small seeds, adapted to bird-mediated seed dispersal; it has extended fruiting phenology, producing conspicuous infructescences and fruiting almost throughout the year in some areas (Mengardo and Pivello 2012); and as shown in this study, it establishes highly generalized dispersal interactions (Malmborg and Willson 1988). In addition, traits related to dispersal ability, the invasive palm has high survival rates in post-dispersal stages when compared with the native juçara palm, showing longer seed viability, higher seed germination rate and seedling survival (Mengardo et al. 2012).

A dramatic increase in the richness of frugivore assembly can be seen when comparing FEENA with the remaining study areas. We also see that frugivore assemblage of *Archontophoenix* spp. in this area was the only characterized by redundancy between seed dispersers concerning the value of the quantitative component. This redundancy provides robustness for established mutualisms between the native birds and the invasive palm, which contributes to rapid spread of this plant to further areas (Jordano 1987).

In addition, we recorded several medium and large frugivore such *B. ruficapillus*, *Penelope* spp. and *Ramphastos* spp. acting as seed dispersers of

Archontophoenix spp. The consumption of invasive fruits by medium and large frugivore is worrisome when dealing with invasive species because these frugivore usually have a longer retention time of seeds in digestive tract and may act as long distance dispersers (Proctor 1968; Fukui 1996; Myers et al. 2004; von der Lippe and Kowarik 2007).

We found that the quantitative component of seed dispersal effectiveness is 3.3 times lower for *E. edulis* than for invasive palm where they occur in sympatry with fruiting overlap. Since seed dispersal is a critical stages in plants life-cycle (Wang and Smith 2002), we can predict that in areas where *Archontophoenix* spp. is already established, *E. edulis* could face a strong dispersal limitation.

We estimated *fitness* of *Archontophoenix* spp. and *E. edulis* in the area where they occur in sympatry with fruiting phenology overlap (PEFI) gathering our dispersal data and data from Mengardo et al. (2012). *Fitness* of both palms was calculated as the product of probabilities of dispersal, seed germination and seedling survival after 1 year. The resulting value of fitness indicates the probability of a seed to survival until became a seedling, what we have called *success of establishment*.

Surprisingly, we found that the success of establishment of *Archontophoenix* spp. is twenty-one times higher than the native juçara palm when they are in sympatry with fruiting overlap (see Supplementary Material - Note 1). This implies that the higher seed dispersal effectiveness of *E. edulis* in other areas occurring in sympatry with *Archontophoenix* spp., is not enough to overcome the success of the invasive palm on the early post-dispersal stages.

The magnitude of the change in seed dispersal effectiveness found here for the native palm in sympatry with *Archontophoenix* spp. could be greater in areas where frugivores are limited (Aslan and Rejmánek 2012). In these scenarios, frugivore preferences would play an important role in determining dispersal probabilities of palms. Accounting for fruit traits, Buckley et al. (2006) suggest that plants that have fruits more highly preferred by frugivores are expected to be more invasive.

Although in this study we have not tested if frugivore prefers fruits of the invasive or the native palm, we can use evidences shown in the literature to explore this point. For instance, nutritional contents and energy yield are known to be important in fruit choice by birds (Schaefer et al. 2003). *E. edulis* fruits provide more than 7 times the energy yield than the same quantity of *Archontophoenix* spp. fruits (Galetti et al. 2011, Mengardo and Pivello 2012), considering carbohydrate, lipid and protein

amounts. In addition, *E. edulis* fruits are a rich source of anthocyanins, a phenolic compound directly related to antioxidant activity (Brito et al. 2007). Antioxidant-rich fruits are important dietary sources for combating oxidative stress in animals, and birds are able to discriminate the presence of anthocyanins using fruit colour as a visual signal of the presence of this compound (Schaefer et al. 2008). These evidences lead us to expect that fruits of the native palm may be preferred in detriment of *Archontophoenix* spp. fruits.If we consider this scenario to be true, a possible management action in invaded areas where mechanical control of *Archontophoenix* spp. is unfeasible, planting juçara palm may help to slow dispersal rates of the invasive palm.

Sallabanks (1993) proposed that plant species with high-density of fruit display per plant can have greater removal success because fruits are conspicuous and more likely to be seen; and once the plant has been found, frugivores can quickly obtain nutritional rewards. *Archontophoenix* spp. has brightly-coloured fruits displayed on conspicuous infructescences, with bunches containing almost three times more fruits than the native *E. edulis*. So, we can also expect that visual attraction and high fruit abundance could lead birds to prefer the invasive fruits instead those from the native palm. However, a bird must eat eight *Archontophoenix* spp. fruits to get the similar energy reward provided by one *E. edulis* fruit. From the perspective of birds, this may not be advantageous regarding the lower feeding-efficiency provided by *Archontophoenix* spp. fruits, but this invasive palm would be benefited if birds energy requirements implicate in high fruit removal rates. Fruit choice experiments are needed to conclude if birds show preferences toward the invasive or the native palm fruits and which fruit characteristics account for this possible preference.

Our results are not sufficient to conclude that the presence of *Archontophoenix* spp. directly results in lower seed dispersal effectiveness of the native juçara palm because we were unable to replicate this work in multiple areas varying in situations of occurrence of both palms due to their rarity. Instead, our study demonstrates the high potential for competition for frugivore between the invasive and the native palm, given that they potentially share most frugivore birds which can effectively disperse seeds.

Particularly, seed dispersal of *Euterpe edulis* would be negatively affected in areas where it fruits at the same time as *Archontophoenix* spp. and frugivore are limited. In the current scenario in which illegal exploitation of juçara is threatening the species by reducing its natural abundance in most areas of Brazilian Atlantic forest, the absence or the functional extinction of this native species may speed up the invasion process of

Archontophoenix spp., because birds may use fruit of this invasive palm as an alternative resource to juçara fruits.

Acknowledgements

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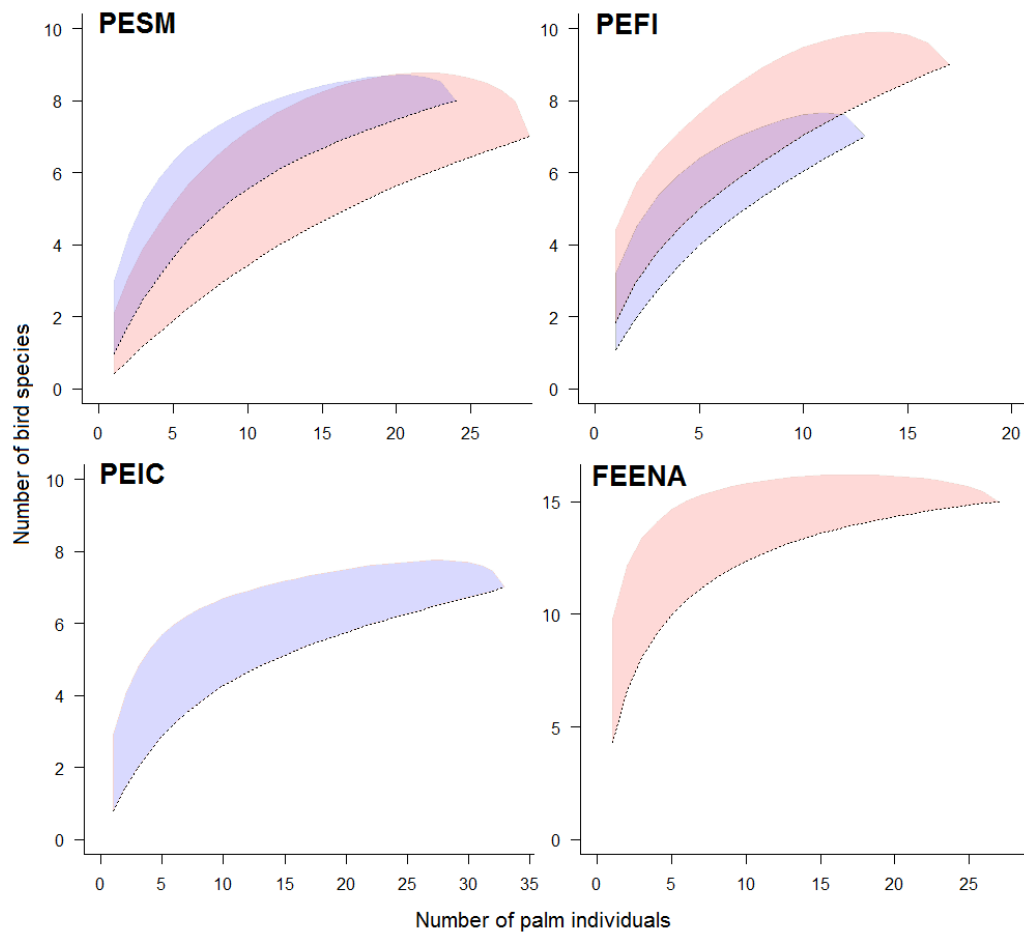
Supplementary Material

Figure S1. Rarefaction curves based on the number of palm individuals sampled and the number of bird species recorded in each area. Study areas are specified on the top left side of each graph. Pink represents *Archontophoenix* spp. and blue represents *Euterpe edulis*.

Table S1. Number of bird species recorded in focal observations, and bird richness estimated by first order Jackknife estimator for each palm specie in study areas. A= Presence of *Archontophoenix* spp.; E= Presence of *E. edulis*; AE= Presence of *Archontophoenix spp.* and *E. edulis*; AE*=Presence of *Archontophoenix* spp. and *E. edulis* with fruiting phenology overlap.

Study area	Palm species	Birds species recorded	First order jackknife CI ± 95%
PESM[AE]	*Euterpe edulis*	09	10.87±3.23
	Archontophoenix	07	10.68±6.03
PEFI [AE*]	*Euterpe edulis*	07	10.69±3.60
	Archontophoenix	09	12.76±3.68
PEIC[E]	*Euterpe edulis*	08	9.90±3.27
FEENA[A]	*Archontophoenix*	19	16.92±2.66

Table S2. Mean value and standard deviation (SD) of the quantitative component (QC) of SDE of palm species in each study area. Fruit dispersal rate is calculated by the reason between total number of dispersal fruits and the hours of observation. A= Presence of *Archontophoenix* spp.; E= Presence of *E. edulis*; AE= Presence of *Archontophoenix spp.* and *E. edulis*; AE*=Presence of *Archontophoenix* spp. and *E. edulis* with fruiting phenology overlap.

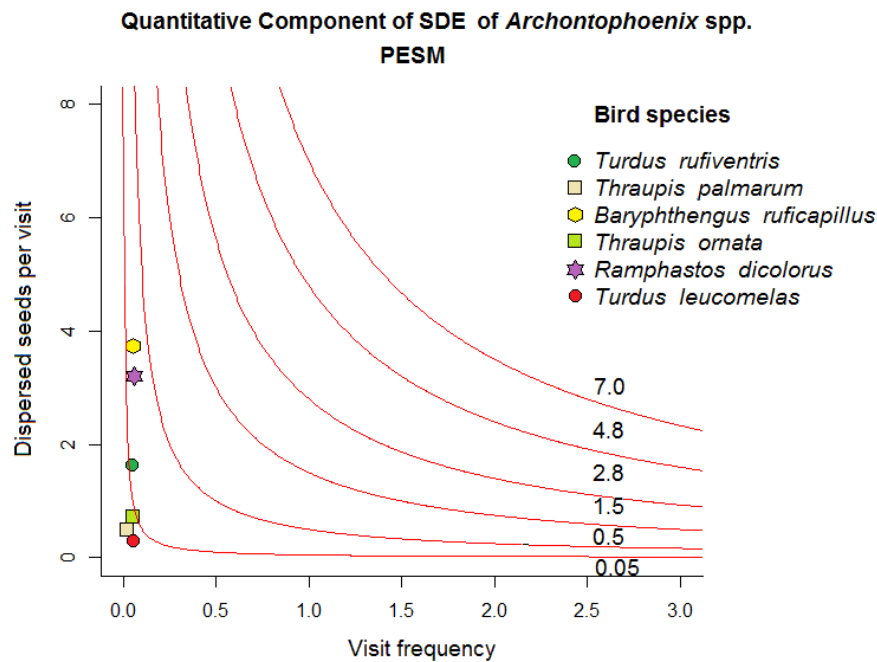| Study area	Palm species	Mean QC ± SD	Fruit dispersal rate (dispersed fruits per hour)
PESM[AE]	*Euterpe edulis*	1.87±2.53	1.95
	Archontophoenix	0.37±1.16	0.25
PEFI[AE*]	*Euterpe edulis*	0.68±0.84	1.17
	Archontophoenix	2.24±3.90	2.58
PEIC[E]	*Euterpe edulis*	1.90±3.51	1.90
FEENA[A]	*Archontophoenix*	13.30±13.39	14.51

Figure S2. Quantitative component of seed dispersal effectiveness of birds registered consuming fruits of *Archontophoenix* spp. in PESM study area, where palm species are in sympatry without fruiting phenology overlap. Isoclines represent all combinations of quantity and quality that yield the same SDE. Numbers between isoclines correspond to values of the quantitative component of birds within that range. Specified value of QC shows the highest value registered in the study area.
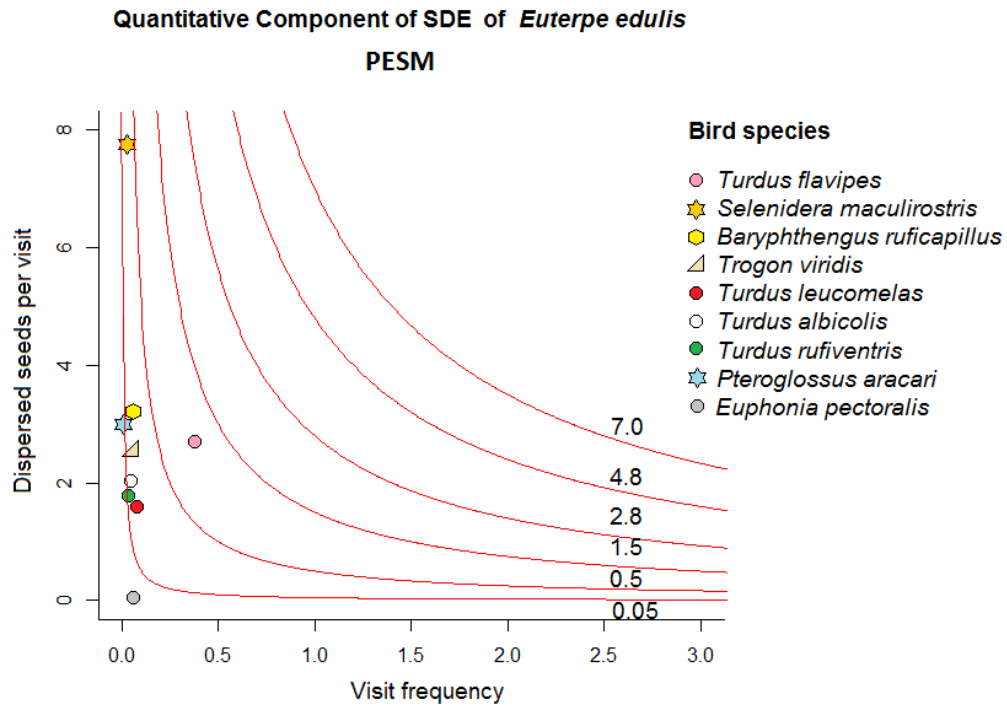
Quantitative Component of SDE of _Euterpe edulis_

PESM

Figure S3. Quantitative component of seed dispersal effectiveness of birds registered consuming fruits of _Euterpe edulis_ in PESM study area, where palm species are in sympatry with fruiting phenology overlap. Isoclines represent all combinations of subcomponents that yield the same SDE. Numbers between isoclines correspond to values of the quantitative component of birds within that range. Specified value of QC shows the highest value registered in the study area.
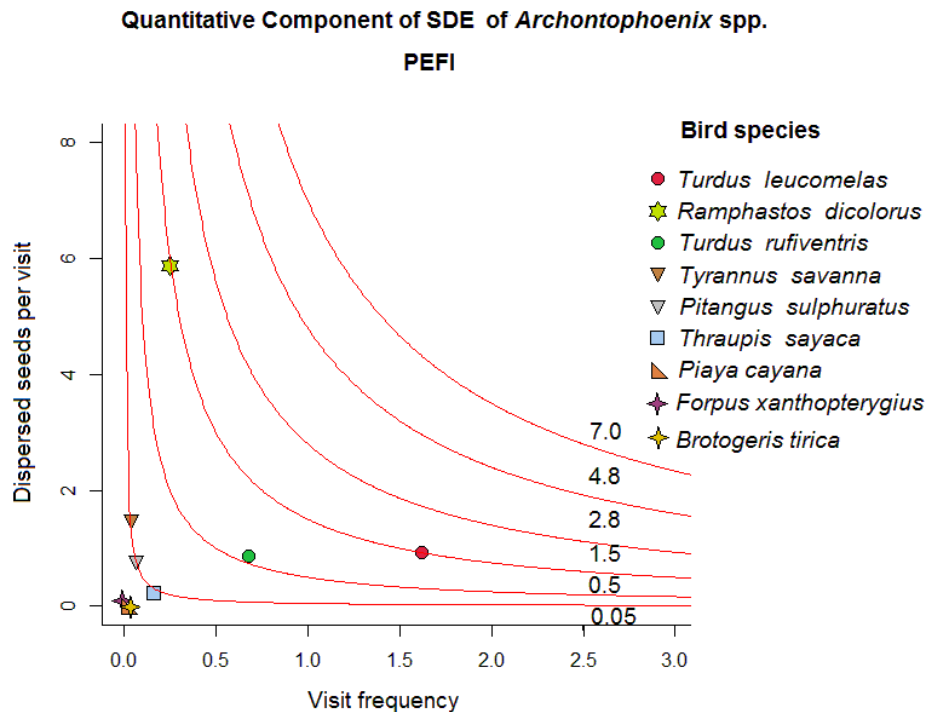
Quantitative Component of SDE of _Archontophoenix_ spp.

PEFI

Figure S4. Quantitative component of seed dispersal effectiveness of birds registered consuming fruits of _Archontophoenix_ spp. in PEFI study area, where palm species are in sympatry with fruiting phenology overlap. Isoclines represent all combinations of subcomponents that yield the same SDE. Numbers between isoclines correspond to values of

the quantitative component of birds within that range. Specified value of QC shows the highest value registered in the study area.
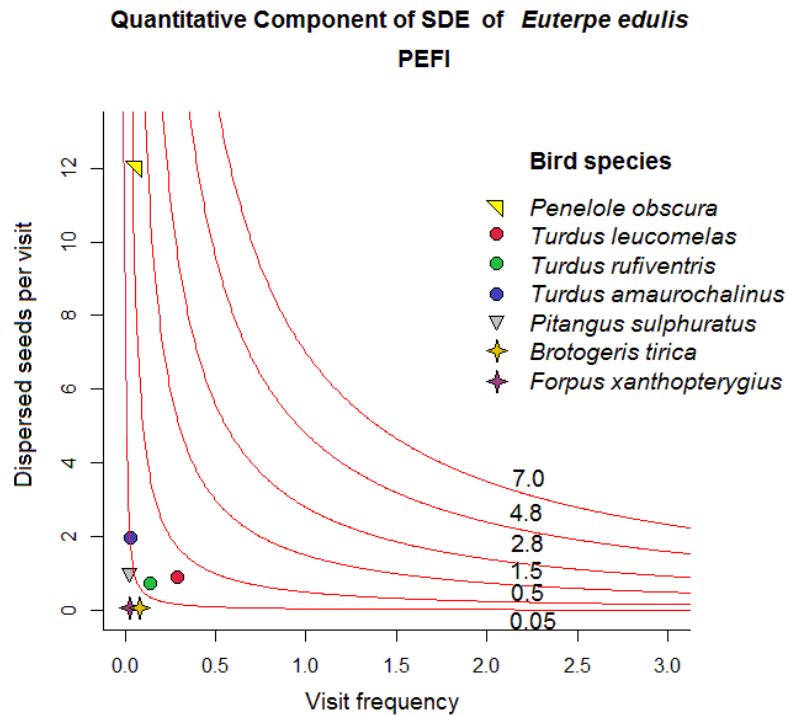

Figure S5. Quantitative component of seed dispersal effectiveness of birds registered consuming fruits of *Euterpe edulis* in PEFI study area, where palm species are in sympatry with fruiting phenology overlap. Isoclines represent all combinations of subcomponents that yield the same SDE. Numbers between isoclines correspond to values of the quantitative component of birds within that range. Specified value of QC shows the highest value registered in the study area.
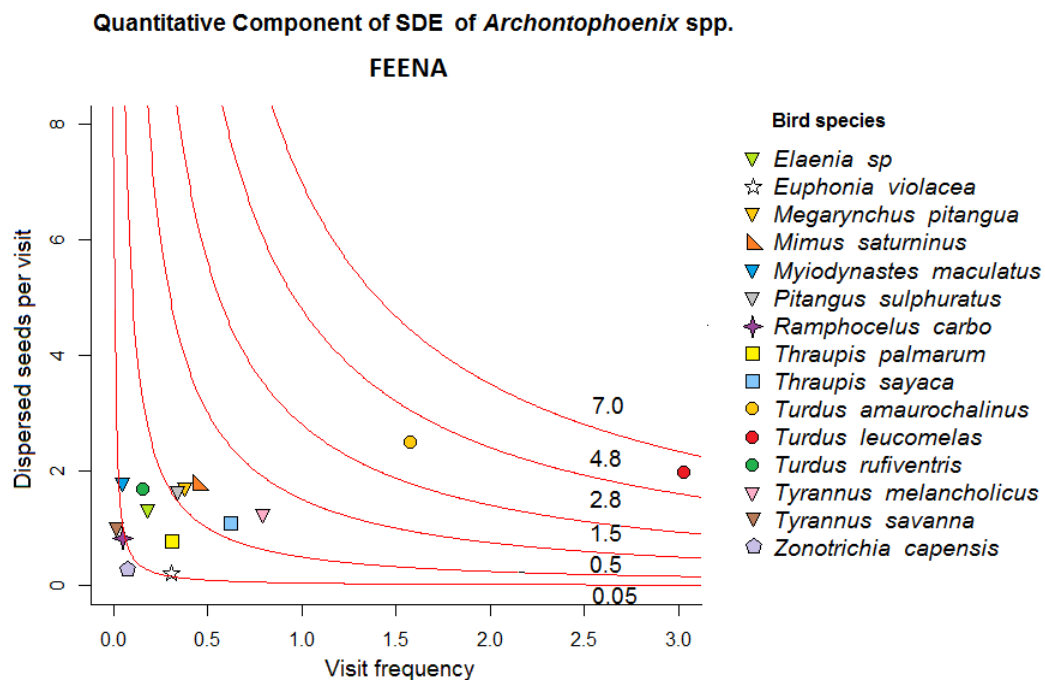

Figure S6. Quantitative component of seed dispersal effectiveness of birds registered consuming fruits of *Archontophoenix* spp. in FEENA study area, where only *Archontophoenix*

spp. occurs. Isoclines represent all combinations of subcomponents that yield the same SDE. Numbers between isoclines correspond to values of the quantitative component of birds within that range. Specified values of QC shows the highest values registered in the study area.
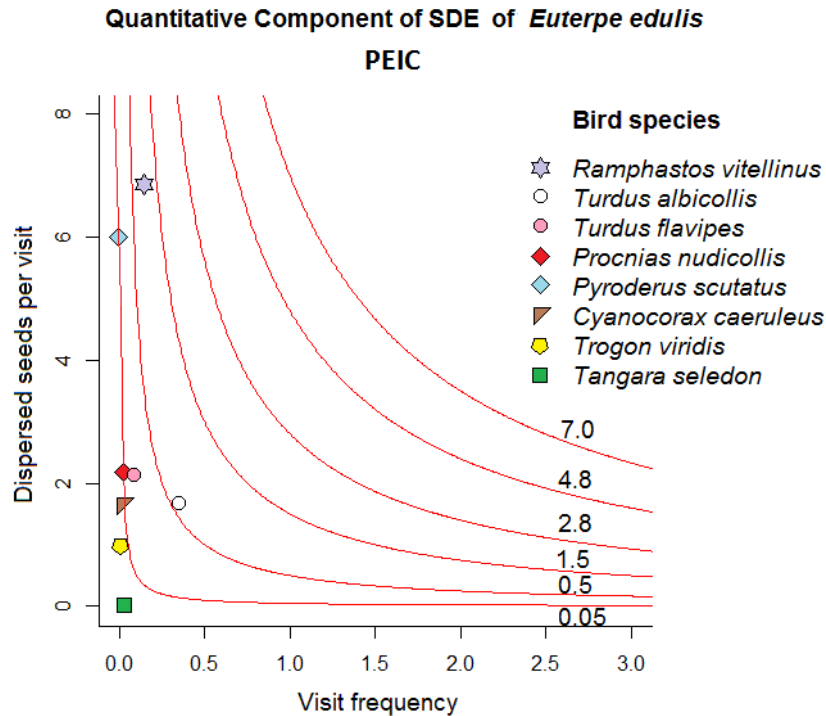

Figure S7. Quantitative component of seed dispersal effectiveness of birds registered consuming fruits of *E. edulis* in PEIC study area, where only *E. edulis* occurs. Isoclines represent all combinations of subcomponents that yield the same SDE. Numbers between isoclines correspond to values of the quantitative component of birds within that range. Specified values of QC shows the highest values registered in the study area.

Note 1 - Calculating the *fitness* of *Euterpe edulis* and *Archontophoenix* spp.

The formula used to calculate the *fitness*(*F*) was *F= Dp* x *Gp* x *Ssp* where:

Dp = dispersal probability, calculated from data of this study as the reason between the number of dispersed fruits (swallowed and carried) and the number of manipulated fruits (swallowed, carried, pulp-detached, preyed and dropped) for each palm species in PEFI study area.

Gp = germination probability, obtained from Mengardo *et al.* (2012) by a seed burial test in a forest fragment located in São Paulo - SP, calculated as the reason between the germinated seeds and the number of sowed seeds.

Ssp = Seedling survival probability after 1 year, also obtained from Mengardo *et al.* (2012) by a seed sowing experiment, calculated as the reason between the number of seedlings and the number of sowed seeds.

We know that are limitations of using transitions probabilities obtained in a different study area. But, having in mind that the forest fragment studied by Mengardo et al. (2012) is also located in São Paulo, only 20 km apart from PEFI, we consider that seeds and seedlings are under similar abiotic conditions.