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Reproductive phenology, seed removal and early regeneration in relation to distance from parental plants of a native palm in small Atlantic forest fragments

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ABSTRACT

The Brazilian Atlantic Forest is a global biodiversity hotspot, but most of what remains are small fragments. Small fragments are often harsh environments for forest plant recruitment due to edge effects and the loss of frugivorous animals that provide seed dispersal. We recorded the one-year reproductive phenology of the keystone palm *Syagrus romanzoffiana* in small (<2.5ha) Atlantic Forest fragments in southeastern Brazil. We tested the Janzen-Connell hypothesis with seed-removal experiments and followed the five-year survival of recruits in relation to the distance from parental plants. Palms produced many fruits throughout the year (mean 2,600/plant). More seedlings were found away from parental plants than near them, thereby supporting the Janzen-Connell hypothesis. Almost 45% of seedlings alive in 2010 were dead five years later, but recruitment of new seedlings compensated for this mortality. Distance-dependent factors influenced the density of early ontogenetic stages, but had limited effects on juveniles or on seed removal. High seed production, seed dispersal provided by disturbance-tolerant frugivores and the relatively long-term survival of adults, seedlings and juveniles seem to allow the persistence of *S. romanzoffiana* in the forest fragments, but possibly at the cost of an increased clumped distribution and reduced gene flow at the landscape scale.

Keywords: Brazilian Atlantic Forest, crop size, habitat fragmentation, Janzen-Connell hypothesis, large seeds, palms, seed dispersal, seed predation, seedling survival, *Syagrus romanzoffiana*

Introduction

The Brazilian Atlantic Forest is considered a hotspot of biodiversity with high levels of endemism (Myers *et al.* 2000). This biome originally covered an area of 1.5 million km^2 along eastern Brazil, but an extensive habitat loss and fragmentation reduced forest cover to about 11%-16%, with 80% of the remnants smaller than 50 ha (Ribeiro *et al.* 2009). Small fragments are under an increasing influence of edge effects that change microclimate conditions and affect the plant community, especially the early stages of regeneration (Tabarelli *et al.* 2010 and references therein). Habitat fragmentation also increases the accessibility of hunters to the remnants. Habitat loss, fragmentation and hunting interact synergistically contributing to decrease the abundance of many vertebrate frugivores and seed dispersers, with large animals being more susceptible to local extinctions (Peres & Palacios 2007). Plants with large seeds (>15 mm) are more susceptible to the loss of dispersers because their regeneration is strongly seed-limited (Moles &

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Westoby 2002) and these plants rely heavily on large-bodied animals as seed dispersers (Silva & Tabarelli 2000; Wright & Duber 2001; Cordeiro & Howe 2003; Galetti *et al.* 2006; 2013; Terborgh *et al.* 2008). For instance, defaunation of large-gaped frugivorous birds has been pointed out as the main source of rapid evolutionary change in seed size of the palm *Euterpe edulis* in remnants of the Brazilian Atlantic forest (Galetti *et al*. 2013). Therefore, large-seeded plants should be more susceptible to reductions in seed dispersal in fragmented and defaunated sites than small-seeded plants.

Seed dispersal is a key process to plant community structure and diversity (Schupp & Fuentes 1995) and provides the template for plant recruitment and spatial distribution of seedlings, juveniles and saplings (Wang & Smith 2002; Swamy & Terborgh 2010). From 70 to 90 percent of tree and shrub species in tropical forests rely on animals to disperse their seeds (Jordano 2000). Therefore, an assessment of how frugivorous animals influence seed dispersal is key to understand plant recruitment and population dynamics (Jordano 2000). Frugivorous animals are often profoundly affected by fruit production and adjust their reproduction and movements in the landscape according to the abundance and seasonality of fruit production (Terborgh 1986; Genini *et al*. 2009; Morellato *et al*. 2016). Changes in microclimate conditions and abundance of pollinators driven by habitat fragmentation and edge-effects may alter reproductive plant phenology, with possible consequences on frugivores (e.g., Morellato *et al.* 2016).

Seed dispersal and predation are in the core of the Janzen-Connell hypothesis that explains the high diversity of tree species in tropical forests (Janzen 1970; Connell 1971). This hypothesis considers that the likelihood of seed and seedling survival is negatively correlated with seed density and the distance from parental plants. Many plant pests are host-specific and congregate near dense aggregations of hosts. Most seeds produced usually fall beneath the parental plants or are dispersed at short distances from it (e.g., Swamy *et al*. 2011). The high density of seeds near parental plants enhances the risk of spread of pathogens and the attraction of specialized seed predators, such as weevil beetles (Wright & Duber 2001). Even if some seeds survive and germinate they will face high sibling competition and herbivory, all of which increase the mortality of seedlings found in high densities near parental plants (Harms *et al.* 2000). All those effects generate a low per capita likelihood of recruitment for seeds that fall near the parental plants (Janzen 1970; Connell 1971). On the other hand, seeds carried beyond the parent plant crown by dispersal agents are deposited on the ground at lower densities, and exhibit a decreased risk of mortality. Thus dispersal enhances the per capita likelihood of recruitment (Harms *et al.* 2000; Hyatt *et al.* 2003; Swamy *et al.* 2011; Terborgh 2013). Distance- and density-dependent mechanisms, as those predicted by Janzen-Connell hypothesis, seem to be pervasive in tropical tree communities (Harms *et al.* 2000; Swamy *et al.* 2011). However, the role of those processes that influences plant recruitment in small forest fragments is not clear. Some sources of mortality of early stages near parental plants may be relaxed or be compensated by other species. For instance, a higher number of undispersed seeds may accumulate beneath parental plants in fragmented sites in response to a decrease in vertebrate seed dispersers. However, invertebrate seed predators may not be able to compensate the mortality of higher numbers of seeds in fragments, allowing unexpected increases in recruitment near parental plants (Wright & Duber 2001; Wright 2003; Terborgh 2013). Although the effects of habitat loss and fragmentation on species composition and community structure of plants are reasonably well know (Tabarelli *et al*. 2010; Laurance *et al*. 2011), the effects upon interactions with seed predators and dispersers (e.g., Mendes *et al*. 2015) and the way they could cascade and influence plant recruitment is much less understood (e.g., Galetti *et al*. 2006; Uriarte *et al*. 2010).

Palms are typical components of the Brazilian Atlantic Forest, where there are about 45 species, many of them endemic (Henderson *et al*. 1995). Palms are key species to the maintenance of frugivores because of high fruit production in periods of scarcity of other resources and the consumption by a wide variety of animals (Terborgh 1986; Genini *et al.* 2009). Several palms from Brazilian Atlantic Forest have suffered the effects of forest fragmentation, selective harvest and loss of seed dispersers (reviewed in Montúfar *et al.* 2011). However, little is known about recruitment and long-term persistence of these palms in small Atlantic Forest fragments (e.g. Souza & Martins 2004; Galetti *et al.* 2006; Portela *et al.* 2010). Most studies investigating interactions between palms and seed predators or dispersers in fragments make inferences about the delayed consequences of these interactions for plant recruitment but do not include data on latter stages such as seedlings and juveniles (e.g., Fleury & Galetti 2006; Andreazzi *et al*. 2012; Meiga & Christianini 2015; Mendes *et al*. 2015). Studies that simultaneously include data on latter stages of recruitment, such as seedlings, juveniles and adults are rare (Galetti *et al.* 2006) but are demographically much more relevant (Wang & Smith 2002; Bruna *et al.* 2009).

Here we describe the reproductive phenology of *Syagrus romanzoffiana*, a large-seeded Atlantic forest palm, and test the Janzen-Connell hypothesis for the regeneration of this species in small (<2.5 ha) Atlantic forest fragments. We evaluate the spatial dynamics of long-term (five year) survival of seedlings and juveniles in relation to distance from parental plants.

Materials and Methods

Study site

This study was carried out from July 2010 to October 2015 in Universidade Federal de São Carlos, southeast Brazil

(47º31'28"E; 23º34'53"S). The average annual temperature and rainfall are 22ºC and 1490 mm, respectively (CBA 2006). The vegetation in our landscape is comprised by a transitional ecotone between evergreen and seasonally dry forests, and savanna-like (Cerrado) vegetation (Corrêa *et al.* 2014; Kortz *et al.* 2014). The region has a long history of habitat disturbance and is heavily fragmented with 83% of the remnants in the watershed smaller than 20 ha (Kronka *et al.* 2005). The study site has five small patches (up to 2.4 ha) of secondary semideciduous Atlantic Forest fragments isolated from each other by a matrix of pastureland and dirty roads. Although we do not have data on abiotic variables at different distances from the border of fragments it is likely that edge effects are pervasive due to the small size of patches and their irregular shape. Most area of the fragments are secondary forests at least 60 years old, based on aerial photographs from 1962 (Corrêa *et al.* 2014). Myrtaceae and Fabaceae are the most common families in those fragments and lianas are also abundant. Some plant species from Cerrado are found in the pasturelands (Kortz *et al.* 2014). Details about the floristics of the study site can be found in Kortz *et al.* (2014). The study site is deprived of most species of large-body seed-dispersing frugivorous animals. Tegu lizards *Salvator merianae* (Duméryl & Bibron, 1839) are ocasionaly seem, as well as the Crab-eating Fox *Cerdocyon thous* Linnaeus, 1766. and the Rusty-margined Guan *Penelope superciliaris* Temminck, 1815, the largest mammal and bird dispersers of *Syagrus romanzoffiana* that can still be found in the area (A.V. Christianini unpubl. res.).

Plant species

Syagrus romanzoffiana (Cham.) Glassman (Arecaceae) is a large-seeded palm that reaches 10 to 15 meters height (Lorenzi 2002; Bernacci *et al.* 2008) and has a wide distribution in South America from northeastern Brazil to Argentina (Henderson *et al.* 1995). Mature fruits have a fibrous and fleshy orange mesocarp and only one seed (Lorenzi 2002). The seeds have on average 20.3 mm long, 11.6 mm wide and 1.1 g in weight based on N=50 seeds measured. Fruits of *S. romanzoffiana* are consumed by many frugivores including at least 60 species of insects and vertebrates including small rodents, squirrels, agoutis, pacas, marsupials, coatis, peccaries, tapirs, monkeys, as well as Tegu lizards and birds such as guans (Galetti *et al.* 1992; Genini *et al.* 2009; Silva *et al.* 2011; Sica *et al.* 2014; Mendes *et al.* 2015). In contrast to frugivores few species are able to prey on the seed, which is protected by a thick endocarp. Seed predators include beetle larvae (especially *Revena rubiginosa* (Boheman, 1836), Curculionidae) and squirrels (*Guerlinguetus ingrami* (Thomas, 1901), Sciuridae) (Galetti *et al.* 1992; Fleury & Galetti 2006; Freire *et al.* 2013; Mendes *et al.* 2015).

Plant phenology

To evaluate plant phenology we marked a total of 16 adult *S. romanzoffiana* individuals distributed in the five forest fragments. Only reproductive plants that allow good visibility of the crown at distance were chosen for sampling. Every month, from September 2010 to September 2011, we recorded the number of bunches with inflorescences, unripe or ripe fruits in the marked individuals. Fruit production per plant was estimated based on the mean number of fruits produced per bunch (800 fruits) reported in Galetti *et al.* (1992) times the number of reproductive bunches with unripe fruits produced per plant in a year.

Distribution and survival of seedlings and juveniles

To assess the spatial dynamics of seedlings and juveniles we marked all *S. romanzoffiana* at these stages found in five transects (0.5 x 20 m), each one departing from the base of five adult palms in a random direction. Palms were at least 60 m away from another reproductive palm. The closer adult was considered the parental plant. Transects were located in three fragments with 0.1, 1.9 and 2.4 ha, which were distant 75 to 270 m from each other. Seedling and juvenile stages were classified according Bernacci *et al.* (2008). Briefly, seedlings were individuals with narrow entire leafs, while juveniles were those with leaves ≥ 2cm width or with segmented leaves. Each individual was labeled with a numbered plastic tag. To assess the long term survival, three censuses were conducted in each transect with an interval of one and five years from the first sampling (July 2010, July 2011 and October 2015), representing cohorts 1, 2 and 3, respectively. To evaluate the influence of the distance from the parental plants on seedling and juvenile distribution and survival, we divided the records into two broad categories: near to the parent plants - up to 3 meters away from palm trunk and under the influence of the adult canopy, or far from the parental plant - between 3.1 and 20 m from palm trunk.

Seed removal experiments

To evaluate if the survival of dispersed seeds varies with distance from parental plants and test the Janzen-Connell hypothesis, we carried out seed removal experiments during the *S. romanzoffiana* fruiting period. Seeds were obtained from ripe fruits fallen to the ground. We selected seeds with no signs of predation or infection by weevils and the fruit pulp was manually removed. Seeds were marked with a small dot of enamel paint (Testors, Rockford, USA), allowing us to distinguish seeds used in the experiment from naturally fallen ones. We placed a group of five seeds on the ground under five parent plant canopies and another five seeds 20 m away. Seeds were monitored during 6 months at regular intervals of 15 days (September 2010 to March 2011). We recorded the number of seeds germinated, preyed on or removed (which were not found in a 30 cm radius). To evaluate the fate of removed seeds we carried out another removal experiment (May 2012) beneath five adults. We placed five seeds without fruit pulp beneath the canopy of five reproductive palms. Seeds were individually attached to polyamide threads with a red ribbon at the other end to facilitate their recovery in the field. After seven days we did a search for marked seeds in a 10 m radius.

Data analysis

To test the Janzen-Connell hypothesis and evaluate the relationships between densities of seedlings and juveniles in cohorts 1 and 3 and the categories of distances from parental plants we used a repeated-measures ANOVA. Plant stage (seedling or juvenile), distance from parental plant (near or far) were treated as fixed factors, and cohort 1 and 3 as the repeated-measure dependent variable. Residuals were checked for normality and homocedasticity. To assess the relation between seedling and juvenile mortality and the proportion of recruits that changed its ontogenetic stage we performed one-way ANOVAs. To evaluate the relation between distance from parental plants and number of seeds preyed on or removed we performed one-way ANOVA.

Results

Plant phenology

Plants bear reproductive bunches during the whole year, with peaks of flowering from September to March and unripe fruits from September to April (Fig. 1). A few bunches with ripe fruits were found every month, with the exception of November, December and February (Fig. 1). Each palm bear up to five bunches at a time. An adult plant produced annually 2.8 ± 1.2 inflorescences (mean ± SD), 3.2 ± 1.9 unripe infructescenses and 1.0 ± 0.8 ripe infructescenses. A palm was able to produce a mean of nearly 2,600 seeds/year (considering the mean number of bunches with unripe fruits produced by each plant annually). No adult palm died in five years.

Distribution and survival of seedlings and juveniles

The cohort 1 (July 2010) consisted of 32 seedlings and 38 juveniles of *S. romanzoffiana*, representing a density of 1.40 early plants/m². Cohort 2 (July 2011) consisted of 30 seedlings and 38 juveniles, with a density of 1.36 plants/m². Two seedlings died and there was no recruitment of new seedlings between cohort 1 and 2. The cohort 3 (September 2015) had 31 seedlings and 35 juveniles, in a total of 1.32 plants/m². A recruitment of 21 new seedlings occurred in the five-year period between cohort 1 and 3. In general, there were more seedlings far from parents than near, but juveniles were relatively well distributed at both distances (Tab. 1; Fig. 2). These effects were consistent between cohorts 1 and 3 (Tab. 1). There was no interaction between cohort and stage or cohort and distance from parental plants (Tab. 1). There was a mortality of 17 seedlings and 14 juveniles from cohort 1 to 3 (44.3% of total; Fig. 3). During this five-year period 15 recruits changed its ontogenetic stage. This represented 33.3% ± 27% and 14.3% ± 3.8% (mean ± SD) of the total number of survivors recruiting near and far from parental plants, respectively. There was no effect of distance from parental plants on seedling ($F_{1,7}$= 0.05; p= 0.83; Fig. 3) or juvenile mortality ($F_{1,18}$= 3.7; p= 0.09; Fig. 3). Distance from parental plants had no effect on number of recruits that changed its ontogenetic stage after five years ($F_{1,8}$= 3.70; p= 0.09).

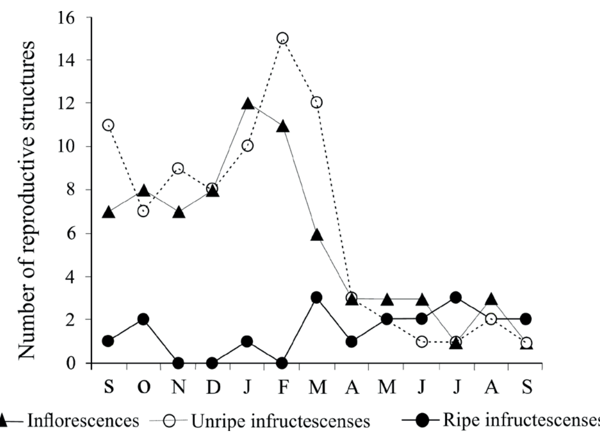

Figure 1. Reproductive phenology of *Syagrus romanzoffiana* in small Atlantic forest fragments in southeastern Brazil. Total number of inflorescences (solid lines and triangles), unripe (dashed line and white circle) and ripe infructescenses (solid line and black circle) produced by 16 adult palms from September 2010 to September 2011.

Table 1. Repeated-measures analysis of variance for the effects of plant stage (seedling or juvenile) and distance from parent tree (near or far) on the density of plants of *Syagrus romanzoffiana* in small Atlantic forest fragments over a five year period (cohort 1 and 3 measured in 2010 and 2015 respectively). See text for details.

Source	df	MS	F	p
Stage	1	2.741	5.807	0.028
Distance	1	0.518	1.097	0.311
Stage*Distance	1	6.521	13.816	0.002
Error	16	0.471		
Cohort	1	0.003	0.0035	0.954
Cohort*Stage	1	0.0223	0.023	0.881
Cohort*Distance	1	0.618	0.631	0.439
Cohort*Stage*Distance	1	0.481	0.492	0.493
Error	16	0.979		

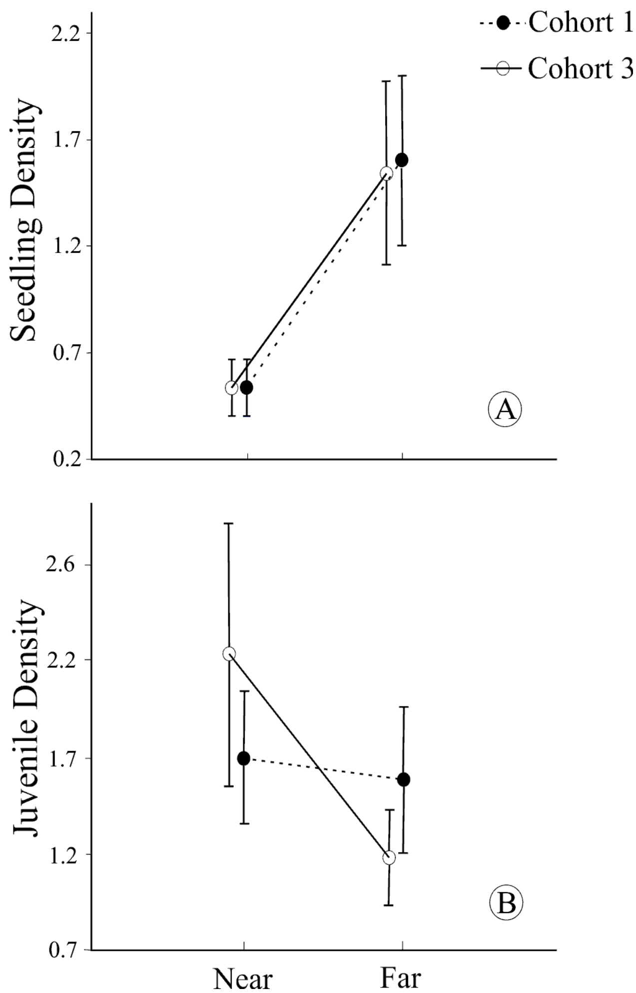

Figure 2. Seedling and juvenile spatial distribution according to the distance from parental plants of *Syagrus romanzoffiana* in small Atlantic forest fragments. Densities of seedlings (A) and juveniles (B) found near (up to 3 m away) and far (between 3 and 20 m away) from parental plants. Data are means ± SE of the number of individuals/m^2. Densities are presented for cohort 1 (sampled in 2010, black circles) and 3 (sampled in 2015, white circles).

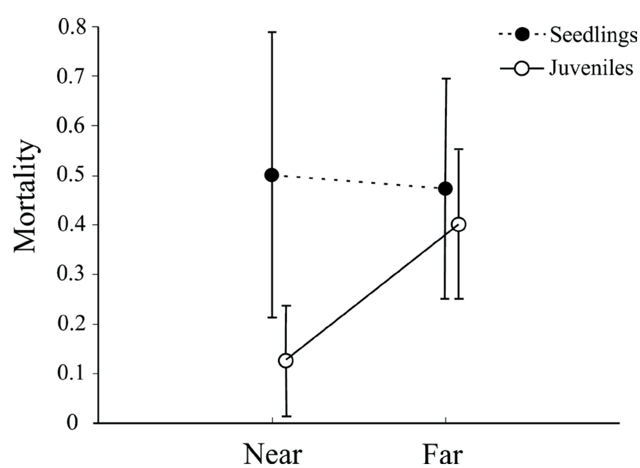

Figure 3. Five-year mortality of seedlings and juveniles of *Syagrus romanzoffiana* according to the distance from parental plants in small Atlantic forest fragments. Mean (± SE) proportion of seedlings (black circles) and juveniles (white circles) that died in the period between cohorts 1 (sampled in July 2010) and 3 (sampled in October 2015).

Seed removal experiments

After six months, 24 seeds (48%) were preyed on or removed from experiments representing 1.64 ± 1.9 seeds (mean ± SD) near and 1.18 ± 1.29 far from parental plants. Therefore, there was no effect of distance from parental plants on seed removal ($F_{1,8}$= 0.4; p= 0.55). No seed germinated during this period. Considering the removal experiment with seeds attached to threads, 20% of them were found away partially buried or on the surface with the thread still attached after a week, and thus could be considered dispersed away (1 ± 0.9 seeds; mean ± SD; N=5)

Discussion

Syagrus romanzoffiana produces fruits and seeds during the whole year (see also Genini *et al*. 2009; Liebsch & Mikich 2009; Freire *et al*. 2013) offering fruits during the winter, which is the usual period of scarcity of fleshy fruits (see Morellato *et al*. 2000; Genini *et al*. 2009). This highlights the potential role of this palm as a keystone resource for frugivores in small Atlantic forest fragments (Silva *et al*. 2011). Each palm produces a high number of fruits/seeds per year (2,600 seeds). There is evidence that forest palms, such as *Attalea speciosa* and *A. humilis*, invest more resources to reproduction whenever exposed to the high light conditions found in disturbed tracts of forests near edges (Barot *et al*. 2005; Andreazzi *et al*. 2012). High seed production may satiate seed predators enhancing the chances of per capita seed survival (Wright & Duber 2001; Andreazzi *et al*. 2012; Meiga & Christianini 2015). Predator satiation and high adult survival (no death in five years) may allow the long-term persistence of palm populations in disturbed Atlantic forest fragments, as suggested by detailed long-term studies working with other Atlantic forest palms (Souza & Martins 2004; Portela *et al*. 2010).

Although it is common to find many seeds of *S. romanzoffiana* accumulated beneath parental palms (V. Mariano unpubl. res.), seedling densities increase with distance from parental plants, indicating that distance- and density-dependent processes may affect recruitment in this early stage like expected from the Janzen-Connell model. This supports the importance of seed dispersal for recruitment at this early stage (Hyatt *et al*. 2003; Swamy *et al*. 2011). However, the density of later stages is not affected by distance from parental plants up to 20 m, suggesting that mortality related to distance from parents affect especially early stages at this spatial scale. Smaller plants, such as seedlings, are usually more susceptible to environmental stressors (shade, herbivory) than larger plants, such as juveniles (Moles & Westoby 2004). Seedlings and juveniles may also have different requirements of light and humidity, which vary at small scales. A good spot for a seedling may be a bad spot for a juvenile creating stage-related spatial mismatch in recruitment (Schupp 1995). After five years the mortality of early stages was virtually compensated by recruitment of new seedlings and transitions to the next ontogenetic stage. More than 60% of the plants that survived did not change its ontogenetic stage, suggesting a slow development (Bernacci *et al*. 2008) and a long-term persistence of seedlings and juveniles in the small fragments. A demographic approach with data on juvenile to sapling and adult transitions is needed to confirm if the repeated recruitment of seedlings and long-term persistence of juveniles is enough to allow adult recruitment in the fragments (Bruna *et al*. 2009; Portela *et al*. 2010).

It is known that medium and small-sized forest fragments presented biotic and abiotic conditions that affect *S. romanzoffiana* seed predation in idiosyncratic ways (Fleury & Galetti 2006; Mendes *et al*. 2015). Defaunation and habitat disturbances can synergistically affect seed predation, dispersal and/or recruitment of large-seeded palms such as *Astrocaryum aculeatissium* (Galetti *et al*. 2006) and *Attalea dubia* (Meiga & Christianini 2015) in Atlantic forests. However, some seed predators, such as squirrels, may occasionally act as seed dispersers allowing a certain degree of seed distribution (Terborgh 2013). The squirrel *Guerlinguetus ingrami* is an important seed predator and possibly disperser of *S. romanzoffiana* (Paschoal & Galetti 1995; Bordignon *et al*. 1996; Fleury & Galetti 2006; Freire *et al*. 2013; Mendes *et al*. 2015). In spite seed predation by squirrels is not reported in other Atlantic forest fragments smaller than 10 ha (Fleury & Galetti 2006; Freire *et al*. 2013) our small fragments are not very distant apart from each other which allow movements of squirrels among some of them (V. Mariano & A.V. Christianini unpubl. res.). Large-bodied frugivores such as tapirs behave as main seed dispersers of *S. romanzoffiana* in more pristine habitats (Sica *et al*. 2014) but are extinct in our site. However, other animals that still persist in the region like squirrels, Crab-eating fox *Cerdocyon thous*, Guans *Penelope superciliaris*, and Tegu lizards *Salvator teguixin* may provide some seed dispersal (Mendes *et al*. 2015; A.V. Christianini unpubl. res.). Our results suggest that even this vestigial dispersal can be important to allow early palm regeneration in small fragments, distributing seeds some distances away in the absence of major dispersers.

The Janzen-Connell hypothesis is supported by several studies (see reviews in Hyatt *et al*. 2003; Terborgh 2013) but it is still poorly investigated in Atlantic forests (e.g., Pizo 1997; Pinto *et al*. 2009). In small forest fragments, distance-dependent factors seem to influence the density of early ontogenetic stages of *S. romanzoffiana*, but with a limited effect on juveniles. The high seed production, some seed dispersal provided by disturbance-tolerant species and the relatively long-term survival of seedlings, juveniles and adults are probably allowing the persistence of the large-seeded *S. romanzoffiana* in our fragments. This does not mean that *S. romanzoffiana* is free from negative effects produced by habitat fragmentation. We have no information about the genetic structure of *S. romanzoffiana*, but data on one of the most common local trees, the bird-dispersed legume *Copaifera langsdorffii*, is available (Martins *et al*. 2016). In the study sites *C. langsdorffii* has abundant seedlings and saplings and its regeneration is not influenced by the proximity to edges or distance- and density-dependent effects (Martins *et al*. 2016). However, genetic analyses at landscape scale have revealed a decrease in genetic diversity of seedlings compared to adults (Martins *et al*. 2016) in line with theoretical expectations of habitat fragmentation (Young *et al*. 1996). The loss of genetic diversity is compatible with restricted seed dispersal and increased recruitment near parental plants (Martins *et al*. 2016). Restricted dispersal is also expected to produce increasing levels of clumped spatial distribution (Souza & Martins 2004; Sica *et al*. 2014) potentially enhancing distance- and density-dependent effects that decrease seedling density and survival, as demonstrated here.

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