Local extinction of an important seed disperser does not modify the spatial distribution of the endemic palm *Astrocaryum aculeatissimum* (Schott) Burret (Arecaceae)

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ABSTRACT

Spatial pattern of the palm *Astrocaryum aculeatissimum* was investigated in an urban Atlantic Forest fragment (Tijuca National Park, Brazil) where its main seed disperser, the red-rumped agouti *Dasyprocta leporina*, is locally extinct. A 120 × 130 m plot (1.56 ha) was established in which all *A. aculeatissimum* individuals were quantified, georeferenced, and classified by ontogenetic stages, namely, seedling, infant, juvenile, immature individual, and adult. Analyses were performed using Ripley's *K* function. We recorded 376 individuals, most of which were in the juvenile stage (n = 228). The spatial pattern was aggregated as observed for other palm species. Seedlings and infants were not associated with adults, whereas juveniles and immature individuals were observed closer to adults than expected. The distance between each seedling and the nearest adult ranged from 3 to 30 m (mean ± sd = 11.8 ± 7.8), which is similar to the agouti dispersal distances reported in other studies. Despite the importance of agoutis for the seedling recruitment of *A. aculeatissimum*, their short-term absence does not affect the spatial distribution of this palm in the studied area.

Keywords: Atlantic Forest, palm, recruitment distances, Ripley's *K* function, spatial patterns

Introduction

Description of spatial patterns is a central focus in ecology, providing important information regarding the processes that structure plant populations (Barot *et al.* 1999; Costa & Santos 2011). Many factors, either biotic or abiotic, influence distribution patterns of individuals in a population (Barot *et al.* 1999; Condit *et al.* 2000; Capretz *et al.* 2012). Among biotic factors, the processes related to seed dispersal and predation have been recognized as important determinants of tree spatial arrangement in the tropics (Janzen 1970; Connell 1971; Augspurger 1984; Forget *et al.* 1994; Seidler & Plotkin 2006).

In tropical forests, most trees produce fruits dispersed by vertebrates (Howe & Smallwood 1982; Howe 1984). Thus, the lack or low density of seed dispersers causes an accumulation of seeds beneath parent plants (Galetti *et al.* 2006; Wang *et al.* 2007; Kurten 2013). Such accumulation can reinforce density-dependent effects (Janzen 1970; Connell 1971), resulting in reduced seedling recruitment (Chapman & Chapman 1995; Cordeiro & Howe 2001; Wright 2003; Terborgh *et al.* 2008). In contrast, in fragmented sites, where seed predators are also absent or less abundant, recruitment increases near parent plants (Wright & Duber

2001; Dracxler 2012). In both cases, there is a reduction in seedling recruitment distances, suggesting that the foraging behavior of seed dispersers may have a strong effect on plant spatial distributions (Jordano 2000). Several studies have reported that as a consequence of anthropogenic disturbance defaunation can affect the long-term spatial distribution of plant species (e.g., Wright *et al.* 2000; Silva & Tabarelli 2001; Webber *et al.* 2010). However, even in areas where this process has more recently occurred (e.g., <40 years), changes in plant species spatial distributions may also follow (e.g., Almeida & Galetti 2007; Cramer *et al.* 2007).

Among the plants that rely on animals for seed dispersal, palm trees (Arecaceae) are dominant in tropical forests (Henderson *et al.* 1995). For large-seeded species (≥1.5 cm, Tabarelli & Peres 2002), such as those from the genus *Astrocaryum*, seed dispersal is dependent on medium and large-sized mammals (Zona & Henderson 1989; Zona 2006; Andreazzi *et al.* 2009). Among these animals, agoutis (*Dasyprocta* spp.) have been recognized as the most important dispersers (Smythe 1989; Pires & Galetti 2012). Recent studies have demonstrated that in fragmented or defaunated forests, where agoutis are rare or have been absent for at least 40 years, *Astrocaryum* seedling recruitment was greatly reduced (Galetti *et al.* 2006; Donatti *et*

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al. 2009; Jorge & Howe 2009) and more aggregated around parent trees (Dracxler 2012). However, the consequences of the absence of these animals for palm spatial patterns remains poorly understood.

Herein, we investigated the spatial distribution of *Astrocaryum aculeatissimum* in a large urban Atlantic Forest fragment, where its main seed disperser, the red-rumped agouti *Dasyprocta leporina*, is locally extinct. More specifically, we investigated the spatial pattern of the population, the spatial relationship between individuals of different ages, and the distance between seedlings and adults. The following hypotheses were tested: (i) the population distribution is aggregated, (ii) seedlings and infants are spatially associated with reproductive adults, and (iii) distances between seedlings and adults should be lower than the dispersal distances commonly performed by agoutis.

Material and methods

Studied species

Astrocaryum aculeatissimum (Schott) Burret (brejaúva palm) is endemic to the Brazilian Atlantic Forest, occurring from Bahia to Santa Catarina (Henderson *et al.* 1995). Stems are solitary or aggregated and can reach 8 m in height. The fruits are spiny, ovoid, or pyriform, with a thin and fibrous mesocarp, and a hard endocarp (Lorenzi *et al.* 2004). Fruit length and diameter are 3.5–4.5 and 3.0–3.5 cm, respectively (Henderson *et al.* 1995). Fruiting is annual with a peak between December and March (Lorenzi *et al.* 2004). Fruit productivity is high, with 100–500 fruits per stem (Pires 2006; Dracxler *et al.* 2011). Seed germination is slow, taking from 3 to 18 months (Lorenzi *et al.* 2004; Zucaratto 2013), with a high seedling establishment rate (ca. 87%; Portela *et al.* 2010). Besides their large size, the absence of pulp further reduces the range of frugivorous vertebrates that consume *A. aculeatissimum* fruits. Small rodents (*Trinomys* spp.), squirrels (*Guerlinguetus ingrami* Thomas), and collared peccaries (*Pecari tajacu* L.) are reported consumers of these fruits (Andreazzi *et al.* 2009; Donatti *et al.* 2009; Pires & Galetti 2012). Among invertebrates, bruchine and scolytine beetles are the most important seed predators (Dracxler *et al.* 2011). Agoutis (*Dasyprocta* spp.) have been identified as the main seed dispersers of this palm species (Donatti *et al.* 2009; Pires & Galetti 2012).

Study area

The study was conducted in the Tijuca National Park (TNP), Rio de Janeiro, Brazil (22º55'–23º00' S and 43º11'–43º19' W). With a total area of 3,593 ha, the Park is divided into four sectors: Floresta da Tijuca, Serra da Carioca, Pedra Bonita/Pedra da Gávea, and Pretos Forros/Covanca. This study was conducted only in the Floresta da Tijuca sector. The region has a tropical climate, with wet (September–April)

and dry (May–August) seasons. Annual precipitation exceeds 2,000 mm, and mean monthly temperatures vary between 18°C and 22°C. Altitude varies between 80 and 1,020 m. The vegetation is in an advanced stage of regeneration, resulting from human interventions that occurred between the 17th and 19th centuries (Drumond 1988; ICMBio 2008). Due to anthropogenic impacts, many animal and plant species have become locally extinct (ICMBio 2008). *Dasyprocta leporina* L. was considered rare in the area in the late 70s when some individuals were released to reinforce population sizes (Coimbra-Filho & Aldrighi 1971). However, these releases were made only in the Carioca sector and in different locations (Coimbra-Filho & Aldrighi 1971; Coimbra-Filho *et al.* 1973). Despite this repopulation attempt, the low number of released individuals (n = 25; Coimbra-Filho *et al.* 1973) and the absence of monitoring suggests that restocking was unsuccessful. As reported by Cid *et al.* (2014) and indicated by interviews with former TNP employees, agoutis have not been sighted in the last 20 years, although these animals are easily sighted (Jorge & Peres 2005). At the end of 2009, an agouti reintroduction program was initiated in the area (Cid *et al.* 2014) to restore ecological processes. However, as animal releases were only performed in a small area of the Floresta da Tijuca sector, most of the Park is still uninhabited by them, as shown by continuous camera-trapping and radio-tracking monitoring (Zucaratto 2013; Cid *et al.* 2014).

Sampling

Astrocaryum aculeatissimum individuals were sampled in a plot of 120×130 m (1.56 ha) from June to August 2012. The plot was demarcated in an area where agoutis had not yet established (Zucaratto 2013), the terrain slope was not exceptionally steep, and no trails crossed (22º57'39.0" S–43º17'50.2" W). All *A. aculeatissimum* individuals in the plot were sampled, and their geographic coordinates were recorded with the aid of a GPS device (Garmin eTrex® H). Additionally, each individual was classified into one of the following ontogenetic stages (Portela & Santos 2011): (1) seedling, individuals with bifid leaves; (2) infant, individuals with transitional leaves (between bifid and pinnate); (3) juvenile, individuals with pinnate leaves but no aerial stems; (4) immature, individuals with apparent stems but no sign of reproductive structures; and (5) adult, individuals with signs of previous reproductive events (presence of inflorescences or infructescences). When a palm clump was sampled, only the individual in the highest ontogenetic stage was recorded and considered in the analyses. This procedure was adopted to avoid an overestimation of aggregation degree, resulting from clonal growth (Portela 2008).

Data analyses

The analysis of spatial distribution was performed using Ripley's *K* function (Ripley 1977). Ripley's *K* function is a

density probability function that permits a second-order analysis. It is based on second-order measures, *i.e.*, the variance of all point-to-point distances (Ripley 1977; Haase 1995). Ripley's *K* function is considered the most appropriate statistical tool for the analysis of spatial patterns (Haase 1995; Dixon 2002). The procedure comprises delimitating a circle of radius *s* centered on each point and counting the number of neighbors within this circle (Haase 1995; Anjos *et al.* 1998). By varying the radius *s*, it is possible to determine the pattern at different distance scales. To facilitate the visualization of the results, the *K(s)* function was transformed into an *L(s)* function (Ripley 1979).

To analyze the spatial distribution of the species, we used the univariate *K* function. Deviations were tested for complete spatial randomness (CSR) through 500 Monte Carlo simulations that generates maximum and minimum confidence intervals. Positive values of *L(s)* indicate aggregation, and negative values indicate regularity. If the spatial pattern is completely random, the *L(s)* function will appear as a line within confidence intervals. The relationship of dependence or independence between adults and other ontogenetic stages was analyzed using the bivariate *K* function. In this case, deviations were tested for complete spatial independence (CSI). Maximum and minimum confidence intervals were also generated, and their interpretation was analogous to that of the univariate *K* function. Positive values of *L(s)* indicate association, and negative values indicate repulsion. To avoid inaccurate estimates, the radius used to calculate the *K* function ranged from 1 to 60 m with a constant increment (1 m) up to the maximum scale of analysis, which corresponds to half of the smallest side of the plot (Ripley 1977). All analyses and their confidence intervals were generated using the SpPack software (Perry 2004).

The distances between each seedling and the nearest adult were considered the minimum dispersal distance and obtained using the geographic coordinates of each individual. The comparison with individual recruitment in the area where agoutis were reintroduced was not possible because the agouti population was not completely established when this study was conducted as well as the long germination time of *Astrocaryum* spp. (>13 months; Potvin *et al.* 2003). As an alternative analysis, we compared our results with the dispersal distances attributed to agoutis when dispersing *A. aculeatissimum* and other *Astrocaryum* seeds. All studies considered used comparable methods.

Results

We found 376 individuals of *A. aculeatissimum* in the sampled area. Individuals of all ontogenetic stages were found. Most sampled individuals belonged to the juvenile stage (c. 60%, n = 228), followed by the immature stage (c. 18%, n = 67). Adults corresponded to 8% (n = 31) of all individuals registered, whereas infants and seedlings corresponded to 7% each (n = 25).

The overall population demonstrated an aggregated pattern, and CSR was rejected across all distance classes (Fig. 1). Given the spatial relationship between individuals of different ontogenetic stages and adults, an association was found only at advanced stages. Seedlings and infants revealed CSI from adults, although a trend to repulsion was observed at short distances (<2 m; Fig. 2A-B). Juveniles and immature individuals were associated with adults, particularly in the greater distances analyzed (Fig. 2C-D).

The distance between each *A. aculeatissimum* seedling and the nearest adult ranged from 3 to 30 m (mean ± sd = 11.8 ± 7.8), and 72% of them were recruited in the immediate vicinity of parent palms (<15 m; Fig. 1A).

Discussion

At the analyzed scale, *A. aculeatissimum* individuals have an aggregated distribution, as observed of other palms (e.g., Silva & Tabarelli 2001; Silvius & Fragoso 2003; Almeida & Galetti 2007). One explanation for the aggregated pattern usually observed among plants in the Arecaceae is seed dispersal limitation because the typical large size of their seeds limits the number of animal species that can carry them over long distances (Silvius & Fragoso 2003).

Considering the spatial relationship between individuals of different ages, we did not find an association among individuals at earlier stages and adults as expected. The repulsion observed among seedlings and infants very close to adults (<2 m) can be explained by the high mortality of seeds accumulated immediately around parent trees. In these areas, predation by invertebrates is usually very intense (e.g., Galetti *et al.* 2006), limiting seedling recruitment. However, we did not observe predation of *A. aculeatissimum* seeds by bruchines in the park, and few endocarps (five of 41) had signs of damage by scolytines (Zucaratto 2013). In this case, the predation intensity could not have been distance-dependent or may also have been substantially away from parent trees (Dracxler *et al.* 2011). Ultimately, invertebrate seed predation did not appear to be a factor that affected the association between individuals at earlier stages and adults.

The physical damage caused by the falling of vegetative structures is one factor that may explain the repulsion found among seedlings and infants very close to adults (<2 m); it has been considered a major cause of seedling mortality in the vicinity of arboreal palms (e.g., Peters *et al.* 2004). This was demonstrated by Silva and Tabarelli (2001) in a study performed on the palm *Bactris acanthocarpa* in a remnant of Atlantic Forest in northeast Brazil. They found that approximately 80% of seedling mortality occurred under the adult palm crowns (<4 m).

The survival of individuals farthest from parent trees may be one of the factors responsible for the spatial association between the more advanced ontogenetic stages and adults, especially at the higher distances analyzed. Additionally, soil characteristics and topography, which have been
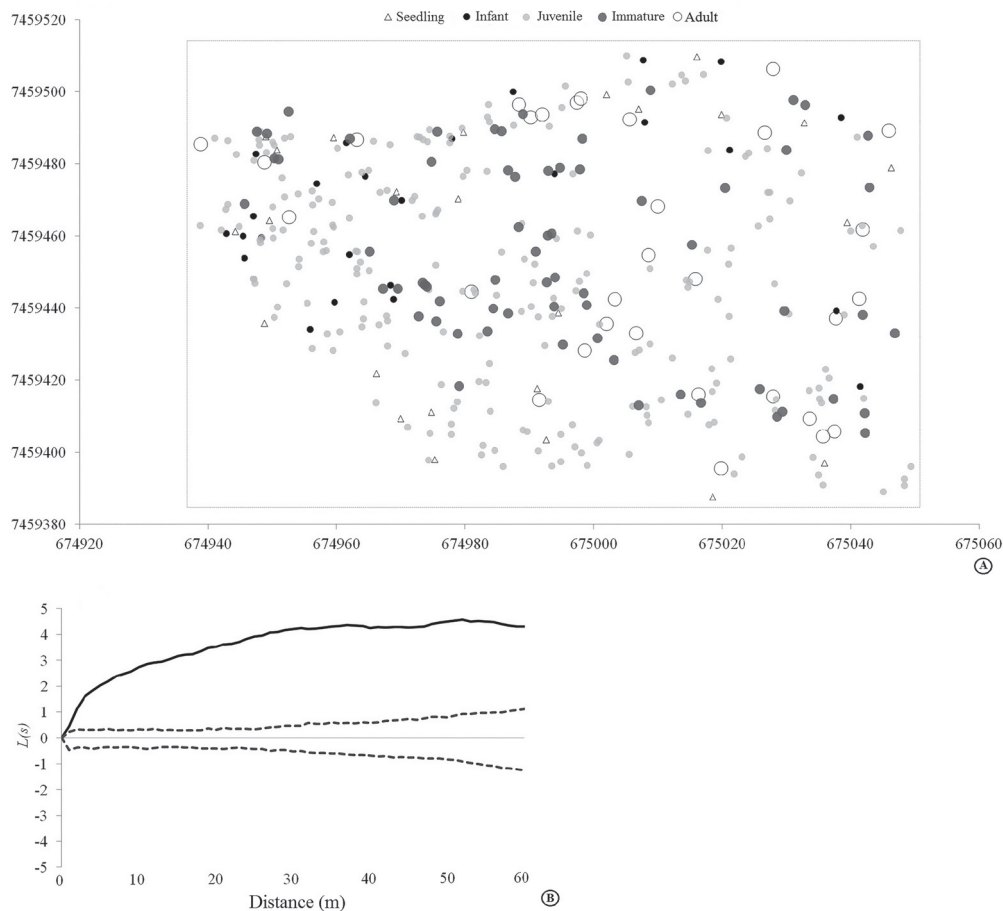
Figure 1. (A) Distribution map of the palm *Astrocaryum aculeatissimum* in Tijuca National Park, Rio de Janeiro, Brazil. The map is in UTM coordinates, and the dashed rectangle represents the sampled plot. (B) The adjustment for Ripley's *K* function *L(s)* univariate case. The dashed lines indicate the confidence envelops (99%), within which the hypothesis of complete spatial randomness (CSR) is accepted.
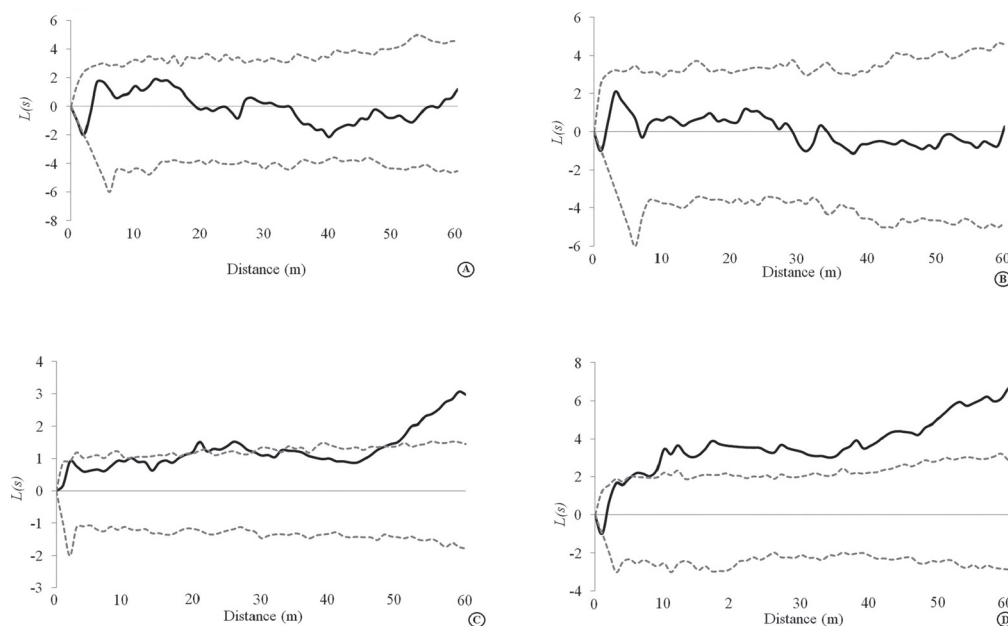

Figure 2. The adjustment for Ripley's K function *L(s)* bivariate case calculated for (A) seedlings, (B) infants, (C) juveniles, and (D) immature individuals, all with adults. The dashed lines indicate the confidence envelops (99%), within which the hypothesis of complete spatial independence (CSI) is accepted.

identified as determinants of the spatial distribution of the palms (Clark *et al.* 1995; Vormisto *et al.* 2004; Svenning *et al.* 2009), may also contribute to our result. This pattern occurs because surviving individuals are generally concentrated on resource-rich patches with suitable soil and topography. Thus, individuals in the advanced ontogenetic stages tend to remain in areas near other adults, which would be the areas with the best resource conditions. However, because of the high intraspecific competition in these patches, only a few individuals survive until the final stage (Barot *et al.* 1999), which may explain the more marked pattern of association between immature individuals and adults. Considering the importance of dispersers in this process, this may also have been influenced by the dispersal distances promoted by rodents (Svenning 2001).

As a previous study revealed that agoutis disperse *A. aculeatissimum* seeds over longer distances than spiny rats or squirrels (Donatti 2004), a shortening in distances between seedlings and adults in the absence of agoutis was expected. However, most of the seedlings were recruited at mean distances commonly reported in other studies involving *Astrocaryum* spp. and agoutis (Jorge & Howe 2009, 6.4 m; Pires & Galetti 2012, 6.8 m, Hirsch *et al.* 2012, 16.8 m; Kuprewicz 2013, 6.6 m). Given that these recruitment distances do not differ from those in places where agoutis are present, these dispersal distances may have been facilitated by other small rodents present in the area. Furthermore, in a study comparing *A. aculeatissimum* seed dispersal in areas with and without agoutis in TNP, dispersal distances via small rodents and agoutis were not observed to differ (Zucaratto 2013). Although small rodents are primarily seed predators, some of them act as effective dispersers by scatter hoarding seeds on favorable germination sites; thus, protecting them from other predators (e.g., Forget 1991; Hoch & Alder 1997; Brewer & Rejmáneck 1999).

As large-seeded palms (≥1.5 cm) usually have an aggregated spatial distribution and the seedling recruitment distances observed were similar to those performed by agoutis in other areas, the absence of these animals does not appear to have affected the spatial patterns of *A. aculeatissimum*. However, agoutis also have great influence on seedling recruitment rates for this palm (e.g., Galetti *et al.* 2006, Donatti *et al.* 2009). In the studied area, the *A. aculeatissimum* seedling-to-adult ratio was lower than that reported in large (>3,000 ha) Atlantic Forest remnants, and the population structure demonstrated a different pattern from a J-reverse curve (Zucaratto 2013). The observed pattern is characteristic of a population imbalance and can lead to a population decline if it persists (Hall & Bawa 1993). Therefore, with the reintroduction of agoutis in the studied area, an increase in the abundance and density of seedlings is expected, with corresponding changes in the population structure. However, specific changes in the spatial patterns are not expected; because of the high complexity of animal–plant interactions, this cannot be predicted with certainty. Future increases in the abundance of agoutis could

alter palm distributions through their caching behavior, including high seed pilferage and high rates of re-caching. In such cases, seeds can be carried into areas of low-adult density, and thus maintain a low background seed density, in which seeds have a lower probability of being stolen by competing rodents (Hirsch *et al.* 2012). If this occurs, palm spatial structure can be affected; future studies are necessary to determine the effects of agouti reintroduction on palm spatial structure.

Acknowledgments

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