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Effects of neighborhood on pollination and seed dispersal of a threatened palm

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ABSTRACT

Changes in the spatial density and availability of resources offered by plants due to habitat fragmentation and overexploitation of the natural environment are likely to affect mutualistic interactions. We tested whether changes in the density of neighborhood conspecific and heterospecific plants and in the availability of resources influence the frequency and composition of floral and frugivorous visitors of eleven individuals of the same population of the threatened palm *Euterpe edulis* in Brazil. The frequency of floral visitors was positively associated with conspecific density and availability of resources. Species composition was affected by the availability of resources since some bee species were associated with palms that offered more flowers, whereas others were associated with palms that offered less. Two bee species may be able to mediate long-distance pollen-flow for *E. edulis*: an undetermined species of Euglossini and *Apis mellifera*. Frugivorous birds were not influenced by any of the factors investigated. Birds of the genus *Turdus* predominated in the assemblage and were responsible for most of the interactions. This is probably due to the fact that, unlike larger birds, species of *Turdus* are considered resilient to environmental disturbances. Due to the continuous defaunation and fragmentation of the Atlantic Forest, the number of large birds that can promote long-distance seed dispersal is declining, with implications for the genetic diversity of *E. edulis*. Measures to restore the population density of *E. edulis* will likely favor the recovery of its genetic diversity due to its high capacity for distant pollen dispersal. Recovering and protecting large frugivorous birds may also contribute to the maintenance of the population density and genetic diversity of *E. edulis*.

1. Introduction

Habitat fragmentation and overexploitation of the natural environment affect the reproductive capacity of plants (Ellstrand and Elam, 1993; Frankham, 1995; Tamaki et al., 2009; González-Varo et al., 2010). Such disturbances can impact mutualisms involved in plant reproduction, specifically pollination and seed dispersal. For example, habitat fragmentation and overexploitation may reduce pollinator richness and abundance (Steffan-Dewenter and Westphal, 2008) and change pollinator composition (Steffan-Dewenter and Westphal, 2008; Ferreira et al., 2015), with direct effects on plant reproduction (Campbell et al., 2018). These factors may also reduce seed dispersal services, decreasing seedling recruitment in fragmented areas (Cordeiro and Howe, 2003). Furthermore, habitat fragmentation and overexploitation may increase isolation and alter the density, size, and shape of plant populations (Gibbs, 2001).

Disturbances to plant population structure alter the density of conspecific and heterospecific plants, as well as the availability of resources provided by trees, with effects on pollinators and seed dispersers (Ghazoul, 2005). Both the composition (Lázaro et al., 2009) and frequency of floral visitors (Jennersten and Nilsson, 1993; Hegland and Totland, 2005) are influenced by variation in the density of neighborhood plants and the availability of floral resources (e.g. pollen, nectar; Lázaro et al., 2009; Lázaro and Totland, 2010; Nielsen et al., 2012; Janovský et al., 2013). Pollinator-mediated interactions with conspecific plants can either increase visitation rates, because neighboring

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plants can attract pollinators, or decrease visitation rates, because of competition among plants for shared pollinators (Ghazoul, 2005; Nottebrock et al., 2017). In the case of heterospecific plants, competitive and facilitative interactions in the neighborhood can be mediated by generalist pollinators (Moeller, 2004; Sargent and Ackerly, 2008; Mitchell et al., 2009; Nottebrock et al., 2017). Thus, changes in conspecific and heterospecific density and resource availability may affect plant reproductive success (Field et al., 2005; Bosch and Waser, 2001) due to their effects on pollen-mediated gene flow by pollinators (Castilla et al., 2017). Likewise, the frequency and composition of frugivorous birds can be influenced by variation in conspecific and heterospecific plant densities and fruit availability in the neighborhood (Beck and Terborgh, 2002; Carlos and Morales, 2008; García et al., 2011; Morales et al., 2012), and thus are relevant to structuring the seed dispersal process (Carlos and Morales, 2008).

The palm *Euterpe edulis* Mart. (Arecaceae), also popularly known as palmeira juçara, is pollinated by several groups of insects (Reis et al., 2000) and its seeds are dispersed by vertebrates, but mainly frugivorous birds (Reis and Kageyama, 2000; Galetti et al., 2013). This palm is considered a key species for floral visitors and frugivores in the Atlantic Forest because it offers floral resources (pollen and nectar) and fruit in abundance, even in times of scarcity (Galetti and Aleixo, 1998). Nevertheless, populations of *E. edulis* have been extremely reduced in several remnants of the Atlantic Forest (Galetti et al., 2013). The apical meristem of this plant, known in Brazil as palmito, is sought as a culinary delicacy (Marcos and Silva Matos, 2003; Raupp et al., 2009; Silva et al., 2009; Sessegolo et al., 2011; Melito et al., 2014). Its exploitation has brought the species to near extinction in the country, and to extinction in many areas of its original distribution (Reitz, 1974; Nodari and Guerra, 1986; Fantini et al., 2000).

Considering the influence of plant density and resource availability on small-scale mutualistic interactions, our objective was to determine if changes in neighborhood conspecific and heterospecific plant densities and the availability of flowers and fruits affect mutualistic interactions between *E. edulis* and pollinators and seed dispersers. We expected that individuals of *E. edulis* in neighborhoods with low conspecific and heterospecific plant densities and which produce less flowers or fruits would experience reduced frequencies of floral and frugivorous visitors and changes in the composition of their assemblages.

2. Materials and methods

2.1. Study area and focal species

The study was carried out in the Reserva Natural Salto Morato (RNSM), located in the southern portion of the Atlantic Forest (S25°10′56, W48°17′55 ″). The RNSM encompasses distinct stages of ecological succession and is adjacent to areas of old-growth forests (Guapyassú et al., 2011). The studied palms were located in an area of forest that has been under restoration for the last 20 years.

Euterpe edulis is monoic (Mantovani and Morellato, 2000). Its inflorescence is arranged in rachillae, united in triads, with one female and two male flowers (Henderson et al., 1995; Henderson, 2000; Mantovani and Morellato, 2000). Male flowers offer nectar and pollen, while female flowers offer only nectar (Reis et al., 2000; Dorneles et al., 2013). Male and female flowers remain open for about seven days. The anthesis of male flowers occurs two to four days before that of female flowers. *Euterpe edulis* is considered an allogamous plant, as the dichlinous inflorescence shows marked protandry (Cardoso et al., 2000; Mantovani and Morellato, 2000). The fruits are drupaceous, and purple when ripe (Mantovani and Morellato, 2000). They have a thin fleshy mesocarp that is unisseminated, with a lateral embryo and abundant and homogeneous albumen (Reitz, 1974).

2.2. Data survey

Eleven focal *E. edulis* palms (FIP - Focal Individual sampled for Pollination data) were selected inside the area of RNSM and observed for a combined total of 120 h. Nine FIPs were observed for two nonconsecutive days and two for one day, with the focal observations lasting six hours (07:00 a.m. to 1:00 p.m.) each day for all FIPs (survey data in Santos et al., 2018a). This time span was selected based on pilot fieldwork to determine the time of activity of floral visitors. Individual palms were selected based on their phenological stage (i.e., having female flowers in anthesis), and to encompass the range of densities of *E. edulis* identified by the RNSM management plan (Guapyassú et al., 2011). Visitors to female flowers, the frequency of their visits, and their contact with reproductive structures were recorded through direct observation (Dafni, 1992) during the flowering period (between October and December 2013). The number of hours of observation for each FIP was used to calculate visitation frequency ("3. frequency" spreadsheet in survey data in Santos et al., 2018a). To identify potential pollinators of *E. edulis* palms, visitors were collected when visiting inflorescences of a FIP (female flowers in anthesis) and on palms that had male flowers in anthesis and were the closest palm to a FIP. The insects were considered pollinators if they i) visited both male and female floral inflorescences; and ii) contacted both reproductive structures (Gómez et al., 2014; plantingscience, 2016). The visitors were collected with entomological nets, and one specimen of each floral visitor species was deposited in the Entomological Collection Fr. Jesus Santiago Moure, Federal University of Paraná.

In order to test the effects of conspecific and heterospecific plant density and the availability of floral resources on the observed frequency and composition of floral visitors of each FIP, the following predictor variables were established: (i) average distance of the three nearest neighbors as a measure of conspecific aggregation (CAp; range: 0–18.3 m), representing conspecific plant density; (ii) total basal area (BAp; range: 0–0.23 m^2) of all woody plants with DBH ≥ 5 cm within a radius of five meters from the FIP as a measure of heterospecific plant density; (iii) number of rachillae (NR; range: 45 to 119) per observed inflorescence; and (iv) presence/absence of inflorescences with flowers in anthesis (FA) for the three nearest *E. edulis* palms of the FIP. The variables NR and FA were used as measures of resource availability for floral visitors (see survey data in Santos et al., 2018a for data details).

Another eleven focal *E. edulis* palms (FID - Focal Individual sampled for Seed Dispersal data) were selected inside the area of RNSM and observed for a combined total of 75 h. Nine FIDs were observed for two nonconsecutive days — two of them with varying times of observation on the second day — and two FIDs for one day. Focal observations lasted four hours (06:30 a.m. and 10:30 a.m.; survey data in Santos et al., 2018a). This time span was chosen based on pilot fieldwork to determine the time of activity of frugivorous visitors. Individual palms were selected based their phenological stage (having ripe fruits), and to encompass the range of densities of *E. edulis* identified by the RNSM management plan (Guapyassú et al., 2011). Foraging frugivores of *E. edulis* infructescences, and their foraging behavior and frequency, were recorded by direct observation using the focal-tree method (Galetti et al., 2003) during the fruiting period (May–June 2014). Foraging frugivores were recorded from the time they started foraging on the infructescence until they left. The number of hours of observation for each FID was used to calculate visitation frequency ("3. frequency" spreadsheet in survey data in Santos et al., 2018a). As for floral visitors, the effects of conspecific and heterospecific plant density and the availability of fruits on the observed frequency and composition of the frugivore assemblage was tested. The following predictor variables were established for each FID: (i) average distance of the three closest conspecific neighbors as a measure of conspecific aggregation (CAd; range: 2–24 m); (ii) total basal area (BAd; range: 0–15.2 m^2) of all woody plants with DBH ≥ 5 cm, within a radius of five meters from the FID; (iii) number of fruits per infructescence (NF; range: 378 to 1765);