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Pollination partial recovery across monospecific plantations of a native tree (*Inga vera*, Leguminosae) in the Atlantic forest: Lessons for restoration

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ABSTRACT

In the last decades several approaches have been adopted for tropical assisted forest restoration from monospecific plantations to the establishment of highly-diverse tree stands. However, the long-term viability of restored forest and their capacity to provide the required services demand continuous evaluation to guide future initiatives. We aimed to evaluate the existence of pollination recovery in monospecific tree plantations in a hyper fragmented landscape of the Atlantic forest in northeast Brazil. By using *Inga vera* as a model species, we compared several relevant aspects relative to tree reproduction such as reproductive phenology, floral structures, nectar consumption, fruit- and seed-set, between monospecific plantations and native conspecific populations. Populations of *I. vera* from both native forest stands and planted areas flowered in overlapping periods in the dry season, while fruiting occurred at the beginning of the rainy season. Flowers of planted populations were significantly larger (11% in the size of the calyx, corolla and androecium – staminal tube and filaments) relative to natural populations. Flowers of both planted and natural populations secrete ca. 46 µl of nectar with concentration of 20.2% and 45.8 mg of sugars throughout the anthesis. However, the average volume of nectar consumed by visitors per flower in planted populations was 30% lower than in natural populations. The frequency of pistils with pollen tubes and the average number of seeds per fruit were similar between natural and planted populations. Nevertheless, surprisingly, the natural fruit set was 49% lower in planted relative to natural populations. Lower consumption of nectar and natural fruit set in planted populations of *I. vera*, in relation to the natural populations, indicate a partial recovery of the pollination process through the practice of planting single species of a tree in clusters of individuals. Our results add some doubts about the long-term viability and the ability of monospecific plantations in delivering services such as increased pollination capacity in human-modified landscapes.

1. Introduction

The accelerated proliferation and dispersion of human activities in tropical regions directly convert large tracts of old-growth natural forests into many old-growth, regenerating and secondary forests patches (e.g. Hansen et al., 2013; Keenan et al., 2015). During the creation of these human-modified landscapes (hereafter as HMLs), natural forest remnants are gradually embedded in a matrix of human managed habitats (Tabarelli et al., 2004; Ribeiro et al., 2009). Expansion of HMLs are thought to affect ecosystem services by changing nutrient cycling and compromising the microclimate, water and air quality (e.g. Pugh et al., 2012; Haddad et al., 2015; Hardwick et al., 2015; Lamy et al., 2017), to reduce the diversity of plants at species, functional and phylogenetic levels (Girão et al., 2007; Lopes et al., 2009; Santos et al., 2014; Rocha-Santos et al., 2017) and to disrupt key ecological interactions (e.g. Aguilar and Galetto, 2004; Aguilar et al., 2006). Thus, the stability of many communities, the maintenance of biodiversity, the providing of ecosystem services (Thompson et al., 2017) and the human well-being as a whole (Raudsepp-Hearne et al., 2010) may be distinctly affected by the expansion of HMLs.

The widespread deforestation, which has increased in the tropics over the past half century, has already resulted in the loss of more than a third of all forest cover worldwide (Hansen et al., 2013). As a consequence of this intense deforestation in many tropical forests, a subset of edge associated species tend to increase in abundance in forest remnant patches, promoting reductions and local extinction of many forest dependent species (Tabarelli et al., 2010). Specifically, forest edges and small forest remnants in tropical regions move toward an

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early successional systems (Tabarelli et al., 2008) and are not expected to naturally recover patches of old growth forests (Chazdon, 2008). In order to recover biodiversity and reestablish the ecosystem services and functions in these highly fragmented landscapes, active forest restoration initiatives are needed (Haddad et al., 2015; Ghazoul and Chazdon, 2016).

Many forest restoration initiatives, which applied distinct techniques, have already been implemented in tropical regions (e.g. Zahawi, 2008; Omeja et al., 2011; Corbin and Holl., 2012; Lindell et al., 2013; Stanturf et al., 2014). Although forest restoration provides opportunities for the reestablishment of reference habitats, these new forests emerged in HMLs, does not match the composition of species and vegetation structure of original old-growth forests (*sensu* Crouzeilles et al., 2016). The resilience and maintenance of plant and animal communities in these tropical forests are closely related to the recovery of animal-mediated interactions (e.g. Menz et al., 2011; Kaiser-Bunbury et al., 2017). Functionally effective reforested stands should maintain ecological interactions, such as pollination, in order to create biologically viable patches (Forup et al., 2008), to promote gene flow among reforested, old growth and secondary forests (e.g. Cruz-Neto et al., 2014) and contribute to long-term persistance of many forest restoration initiatives in HMLs.

Pollination represents one of the most important ecological functions in forest ecosystems since it is associated with the maintenance and stability of many groups of plants and pollinators (e.g. Ollerton et al., 2011). The current expansion of HMLs is directly associated with the disruption of pollination as an ecological function (Aguilar and Galetto, 2004; Aguilar et al., 2006) and service (Ricketts et al., 2008; Garibaldi et al., 2016). Populations of pollinators and flowering plants, mainly those with specialized reproductive traits, are frequently reduced or locally extinct in HMLs (Girão et al., 2007; Lopes et al., 2009). In addition, geographic isolation of populations in forest remnants of HMLs limits the pollen flow among populations, further reducing reproductive success of plant species (e.g. Ricketts et al., 2008; Llorens et al., 2012). Indeed, pollination as an ecological function and service seems to be in decline on a global scale (Potts et al., 2010). This degradation of pollination interactions may be at least partially reversible by forest restoration initiatives (Kaiser-Bunbury et al., 2017), which may support the pollination of agricultural crops and of native plant populations (e.g. Kremen et al., 2007; Frick et al., 2014; Martins et al., 2015).

In the perspective of pollination recovery, complementary reproductive phenology (Garcia et al., 2014) and similar floral dimensions (e.g. Ishii and Harder, 2006) among planted and natural populations inhabiting surrounding forest remnants should be ensured in forest restoration initiatives. Both flowering and fruiting mismatches are expected to compromise the stability of distinct relationships among plants and their animal mutualists (Morellato et al., 2016), while changes in inflorescences and floral traits may negatively affect the effectiveness of pollen deposition on stigmatic surface by shifting the way pollinators interact with flowers (e.g. Ishii et al., 2008; Karron et al., 2012). Additionally, planted stands would be strategic located close to forest remnants since the efficiency of pollen grains transference by pollinators and the female reproductive success are positively influenced by the amount of floral resources, such as nectar (e.g. Fisogni et al., 2011), and reduced distance between natural patches (e.g. Ricketts et al., 2008), In synthesis, disruption of plant-pollinator interactions can reduced both plant fruit and seed set (e.g. Aguilar and Galetto, 2004; Xiao et al., 2016) and jeopardize the sustainability of planted populations in reforested areas.

Excellent opportunities to evaluate how forest restoration initiatives affect ecological functions and services, such as pollination, may be found in hyper fragmented tropical forest. The Atlantic forest originally extended along approximately 1.5 million km^2, stretching across the Brazilian Atlantic coast with an extension toward the west into Paraguay and Argentina (Silva and Casteleti, 2003). In the case of the Brazilian Atlantic forest, expansion of agricultural frontiers, followed by industrialization and urban development, has confined the biota to only ~11.7% (163,377 km^2) of its original extent, which is mainly distributed in forest remnants up to 50 ha (Ribeiro et al., 2009). Reductions in species and functional diversity, associated with the disruption of ecological interactions in these forest remnants, strongly threats the maintenance of the biodiversity in the Brazilian Atlantic forest (e.g. Girão et al., 2007; Lopes et al., 2009; Tabarelli et al., 2010), indicating an urgent need for effective restoration initiatives in this fragmented phytogeographical domain.

In the last decades many restoration initiatives, have been implemented in the Atlantic forest (Rodrigues et al., 2009). While many of these initiatives have generated a diverse set of guidelines that have permitted forest restoration and creation of forests patches, other initiatives, such as the planting of small number of fast-growing species in high density, creates habitat with low biological and functional diversity (Rodrigues et al., 2009). This is the case of restoration initiatives in the Pernambuco Endemism Centre, which is also, the third most threatened region of Atlantic forest (Ribeiro et al., 2009). Plantations of the native trees *Inga edulis* and *I. vera* (Leguminosae), in high density are common restoration initiatives in this region of Atlantic forest. Although plantations with low biological and functional diversity fail in self-perpetuation (Barbosa et al., 2003), little is known about the role of these patches regarding the recovery and maintenance of ecological interactions in Atlantic forest. We aimed to understand the role of these plantations of *Inga* species regarding the creation of functional patches in a hyper-fragmented landscape. We analysed the reproductive phenology, availability of floral nectar, reproductive success and floral traits of *I. vera* in natural and restored populations. In addition, we tested the hypothesis that effectiveness of *I. vera* pollination, measured by fruit- and seed-set and proportion of pistils with pollen tubes, is reduced in planted stands relative to natural populations.

2. Material and methods

2.1. Study site and species

This study was carried out at the Usina Serra Grande (USGA), a private property located in the state of Alagoas, northeastern Brazil (8°58′50″S, 36°04′30″W). The total area is 24,000 ha, of which ca. 9000 ha represents Atlantic forest remnants. Coimbra forest (ca. 3500 ha), located in the study site, is one of the largest remnants of Atlantic forest in the Pernambuco endemism center. The forest remnants are scattered in an agricultural matrix, dominated by sugar cane plantations and pastures (sensu Girão et al., 2007; Lopes et al., 2009).

The Serra Grande landscape is located on a low-altitude plateau (300–400 m above sea level) containing two similar classes of dystrophic soils with high clay fractions: yellow–red latosols and yellow–red podzols, according to the Brazilian soil classification system (IBGE, 1985). The vegetation in the area is classified as moist tropical forest under the Holdridge system, with a dry season (< 60 mm/month) from October to February and a rainy season (> 60 mm/month) from April to September. The richest plant families in the study site is the Leguminosae (30 spp., 14 of which belong to Mimosoideae and eight to *Inga*), followed by Sapotaceae (13 spp.) and Lauraceae (11 spp.) (Girão et al., 2007; Lopes et al., 2009).

The sugar cane cultivation in the region began about 300 years and resulted in the loss of large areas of climax forest (Coimbra-Filho and Câmara, 1996). In the early 1980's, the landowners reforested areas along river courses as a measure to improve water and soil quality. The reforested patches contain *Inga vera* and/or *Inga edulis*, trees of which are planted in single species clumps at a density ranging from 20 to 240 (159 ± 90) trees ha^{-1}. These single species patches are physically isolated from natural areas (Fig. 1).

Inga vera Wild. is a tree broadly distributed in South and Central America from Mexico to Uruguay. It is a common tree in tropical