



## Recovery of genetic diversity levels of a Neotropical tree in Atlantic Forest restoration plantations



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### ABSTRACT

To support the long-term ecological viability of restoration projects, it is necessary to reach adequate levels of genetic diversity in spontaneously recolonizing and reintroduced populations. The importance of genetic diversity in the long-term viability of populations is acknowledged, but still poorly monitored in restoration projects. This study aimed to estimate the genetic diversity and inbreeding levels of populations of a tree species widely used in restoration projects in the Atlantic Forest of Brazil, *Centrolobium tomentosum*, exploring the potential of active restoration in successfully reestablishing populations with higher chances of long-term perpetuation in agricultural landscapes. We used both nuclear and chloroplast microsatellite markers to assess genetic parameters in juveniles and adult individuals in two high-diversity restoration plantations (28 and 60 years old), one disturbed fragment, and one large and well conserved protected area. We observed similar levels of genetic diversity and inbreeding, for juveniles and adults, in both restored and natural populations. Surprisingly, haplotype diversity was higher in restoration sites. We also found private alleles in juveniles in both restoration areas, and this is evidence of gene flow between restored and neighboring natural populations. However, we observed negative effects of inbreeding on the effective population size of populations from the disturbed natural remnant and restoration areas. These results provide evidence of the capacity of restoration plantations for recovering high levels of genetic diversity and the importance of maintaining large and well-conserved forest remnants to be used as seed sources for restoration efforts.

### 1. Introduction

Many international restoration initiatives have been launched to mitigate negative consequences of deforestation, habitat fragmentation, and other anthropogenic impacts on biodiversity and human wellbeing (Chazdon et al., 2015). These programs aim to restore millions of hectares of forest ecosystems and landscapes over the next decades and reestablish new populations of native tree species where they were locally extinct (Holl, 2017). The massive financial investments and political commitments to support restoration programs highlight the need for reliable monitoring approaches to safeguard key ecological principles for sustaining restoration success (Suding et al., 2015).

Biodiversity monitoring in restoration projects has been mostly focused on plant taxonomic diversity (Ruiz-Jaen and Mitchell Aide, 2005; Wortley et al., 2013) and functional diversity (Brancalion and

Holl, 2016), with few studies on phylogenetic (Schweizer et al., 2015) or genetic diversity (Rodrigues, 2013; Neto et al., 2014). Consequently, little is known about the potential of restoration interventions to reestablish similar genetic diversity levels compared to reference ecosystems. Although some conceptual frameworks have been recently proposed to monitor genetic issues in restoration projects (Thomas et al., 2014; Mijangos et al., 2015), on-the-ground assessments are scarce (but see Salas-Leiva et al., 2009; Neto et al., 2014).

The inbreeding level is another important genetic parameter for monitoring reintroduced populations in restoration programs, since the mating of closely related individuals may lead to a reduction in fitness-related traits such as survival and fertility, a phenomenon called inbreeding depression (Charlesworth and Willis, 2009). Inbreeding depression in plants, which is more common in trees than in annual herbs (Angeloni et al., 2011), may lead to reduced tree population

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viability in forest restoration areas. This issue may play an even more relevant role in restoration plantations in the tropics because most tree species are pollinated by animals (Bawa, 1990), and their maximum flight distances are not considered when distributing seedlings in the field. Therefore, it would be grounds for concern if inbreeding coefficients in the tree populations of restoration areas are higher than their normal levels found in natural, conserved populations, as observed in populations of *Avicennia germinans* (Salas-Leiva et al., 2009), and *Inga vera* (Neto et al., 2014).

Another threat to natural populations is the loss of diversity by genetic drift, which is stronger in small and isolated populations (Ellstrand and Elam, 1993; Frankham et al., 2014), like those typically found in restoration projects. If restoration initiatives are implemented to increase gene flow among fragments, this threat may be reduced. For example, a study of populations in second-growth forests indicated reduced genetic diversity in founding tree populations, reflecting a strong founder effect, and a shift towards genetically rich populations in the mid and long term due to gene flow at the landscape level (Sezen et al., 2007). Complementary, a study with the Neotropical tree *Inga vera* found reduced genetic diversity in adult individuals in restoration sites, but higher diversity in seedlings, probably due to gene flow from natural remnants to the sites ongoing restoration (Neto et al., 2014).

The use of genetics as a source of information to support decision-making in restoration programs is particularly important in developing tropical countries, where most of the global biodiversity hotspots are located (Myers et al., 2000). The restoration programs envisaged for tropical regions include the ambitious goal of restoring 20 million hectares of forest ecosystem and landscapes in Latin America and the Caribbean by 2020 (WRI, 2016) and restoring 15 million hectares of Brazil's Atlantic Forest by 2050 (Melo et al., 2013). The Aichi target 15 of the Convention on Biological Diversity, in particular, would require genetics to monitor its achievements, since restoration programs linked to this target are expected to contribute to conserving biodiversity at all hierarchical levels, from ecosystem to genes (Janishevski et al., 2015).

Although genetic studies on tropical trees in restoration projects may provide a necessary knowledge platform to plan, implement, and monitor restoration programs, few restoration genetics studies have been carried in tropical regions. Also, genetic concerns started to be considered just a few decades ago (Thomas et al., 2014; Mijangos et al., 2015).

In this study, we estimated the genetic diversity and inbreeding levels of populations of *Centrolobium tomentosum*, a tree species widely used in restoration projects in the Atlantic Forest of Brazil. Our aim was to address the potential of active restoration in successfully reestablishing populations with higher chances of long-term perpetuation in agricultural landscapes. To achieve this goal, we tested the following hypotheses: (i) even restoration areas with high species diversity were implanted in the past with low genetic diversity; (ii) populations from restoration areas have lower levels of genetic diversity than observed in natural remnants; (iii) populations from restoration areas have higher levels of inbreeding than those from natural remnants; (iv) there is no gene flow between restoration areas and neighboring areas as a consequence of their isolation in highly fragmented landscapes.

## 2. Material and methods

### 2.1. Study species

We selected *Centrolobium tomentosum* Guill. ex Benth (Fabaceae) as the model for this study, because this is a species widely used in the Atlantic Forest's restoration, and it is self-compatible (Aidar, 1992), which may lead to high levels of inbreeding in the absence of a pollinator. Therefore, this is a suitable model for assessing the limitation and the potential of restoration to recover adequate levels of genetic diversity and gene flow to sustain population persistence in restoration sites. Given these natural limitations on the recovery of

genetic diversity and breeding rates in restoration projects, positive results with this species may indicate that sufficient genetic conservation may have been achieved in other tree species used in restoration.

*C. tomentosum* is a typical gap, intermediate succession species, with relatively fast growth and symbiotic associations with nitrogen-fixing microorganisms (Carvalho, 2005; Pagano, 2008). The main pollinators are large bees with long-distance flight capacity (genus *Xylocopa*, *Bombus*, *Centris*, and *Megachile*) (Aidar, 1992), which are one of the most common groups of pollinators of tropical canopy tree species (Bawa, 1990). Fruits are large samaras (approximately 9 g each) dispersed by wind, but most fruits fall under the canopy of the mother tree (Aidar and Joly, 2003). Although this species is self-compatible, most seeds that germinate are the result of outcrossing (Sujii et al., 2017).

### 2.2. Study sites and sampling

We selected four sample sites, all located within the seasonal semi-deciduous forest domain of the Brazilian Atlantic Forest of São Paulo state, southeastern Brazil, a global hotspot for biodiversity conservation (Myers et al., 2000). This is one of the most threatened vegetation types of the Atlantic Forest, with only 7.5% of its natural cover remaining (Ribeiro et al., 2009). All sites had a Cwa Köppen climate and were embedded in human-modified landscapes, dominated by sugarcane plantations, pastures, or urban areas.

We evaluated populations from two restoration sites (Rest). The first restoration area (Rest1) is a 15-ha plantation established from 1955 to 1960 along the riparian buffer of the Jaguari River, on a sugarcane farm in Cosmópolis municipality. The restoration model used was the random distribution of a high diversity of trees (71 species; 70% native), regardless of their successional performance, at a density of 833 individuals per hectare (Nogueira, 1977; Schweizer et al., 2015). The second restoration area (Rest2) is a 21-ha, high-diversity (141 species; 77% native) plantation established from 1988 to 1990 onto the borders of Iracemópolis municipality's water-supply reservoir (Brançalion et al., 2014). Restoration was based on the combination of tree species of different successional stages in planting modules (6 pioneers and 2 early secondary, 1 late secondary or climax). Seedlings of Rest1 were mostly produced with seeds harvested in a 1901 reforestation site in Piracicaba, approximately 100 km away from Rest1, while seedlings used to establish Rest2 were obtained from two commercial forest nurseries of the region, but seed origin is unknown (Rodrigues et al., 1992).

We selected two natural remnants to compare with the forest restoration sites. The first natural remnant (Ref) was the Caetetus Ecological Station, the largest (2170 ha) and best conserved forest patch in the region (Durigan et al., 2000), chosen as the reference ecosystem for this study. The second natural remnant (Frag) was the Municipal reserve of Santa Genebra Forest, the largest urban semi-deciduous seasonal forest fragment in São Paulo State (252 ha), which was historically submitted to human-mediated disturbances typical of the study region: selective logging, fires, and edge effects, which have collectively led to the proliferation of ruderal climbers (Farah et al., 2014).

We sampled a total of 343 individuals (140 adult and 187 juvenile). From each restoration area, we sampled all adult individuals found in the site (large-sized trees found in the planting lines) and at least 30 juveniles. From each natural remnant, we sampled at least 30 adults and 30 juveniles (Table 1). Up to two juvenile individuals were sampled close to each adult individual, to avoid sampling a large proportion of siblings. From each individual, we collected plant tissue (leaf or vascular cambium) for DNA extraction (Cavallari et al., 2014), and obtained the coordinates with a GPS (GPSMAP62, Garmin).

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