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FRANCINE BEATRIZ DE SOUZA

Historic pollen and seed dispersal in fragmented populations of
Cariniana estrellensis **(Raddi) Kuntze and *Cariniana legalis* (Mart.)**
Kuntze

Ilha Solteira
2018

FRANCINE BEATRIZ DE SOUZA

**Historic pollen and seed dispersal in fragmented populations of
Cariniana estrellensis (Raddi) Kuntze and *Cariniana legalis* (Mart.)
Kuntze**

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Prof. Dr. Alexandre Magno Sebbenn
Orientador

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TÍTULO DA TESE: Dispersão histórica de pólen e sementes em populações fragmentadas de *Cariniana estrellensis* (Raddi) Kuntze e *Cariniana legalis* (Martl) Kuntze

AUTORA: FRANCINE BEATRIZ DE SOUZA

ORIENTADOR: ALEXANDRE MAGNO SEBBENN

Aprovada como parte das exigências para obtenção do Título de Doutora em AGRONOMIA, especialidade: SISTEMAS DE PRODUÇÃO pela Comissão Examinadora:



Prof. Dr. ALEXANDRE MAGNO SEBBENN
Secretaria do Meio Ambiente do Estado de São Paulo / Instituto Florestal de São Paulo - IFSP



Prof. Dr. MÁRIO LUIZ TEIXEIRA DE MORAES
Departamento de Fitotecnia, Tecnologia de Alimentos e Sócio Economia / Faculdade de Engenharia de Ilha Solteira - SP



Prof. Dr. MARCO EUSTAQUÍO DE SÁ
Departamento de Fitotecnia, Tecnologia de Alimentos e Sócio Economia / Faculdade de Engenharia de Ilha Solteira



Prof. Dr. CELSO LUIS MARINO
Departamento de Genética / Instituto de Biociências de Botucatu - UNESP



Prof. Dr. EDJAÍR AUGUSTO DAL BEM
Engenharia Florestal / Faculdade de Ciências Sociais e Agrárias de Itapeva

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“Que os vossos esforços desafiem as impossibilidades, lembrai-vos de que as grandes coisas do homem foram conquistadas do que parecia impossível.”

Charles Chaplin

RESUMO

Cariniana estrellensis e *Cariniana legalis* são uma das maiores árvores dos biomas florestais da Amazônia e Mata Atlântica, sendo atualmente vulneráveis à extinção devido ao intenso desmatamento desses biomas. Estratégias para conservação *in situ* e *ex situ* são urgentes e estudos de diversidade genética e fluxo de genes são chaves e para esses propósitos. Assim, investigamos a diversidade genética, a estrutura genética espacial (SGS) e o fluxo histórico de genes em populações fragmentadas de ambas as espécies, utilizando marcadores de microssatélites. Todas as árvores encontradas nas populações foram mapeadas, medidas para o diâmetro na altura do peito (DAP) e amostrado o cambio de casca. O índice de fixação (F), em alguns casos, foi significativamente maior em árvores com menor DAP, indicando que as árvores menores apresentam um maior parentesco do que as maiores. Foi detectada SGS significativa para populações de ambas as espécies (60-350 m), indicando um padrão de dispersão de genes de isolamento pela distância (IBD). Para ambas as espécies, foi observada alta imigração de semente (38,5-61,5%) e pólen (80,1-100%), mostrando que as populações não são isoladas geneticamente. Não foi detectada autofecundação, mas o cruzamento entre árvores relacionadas foi detectado nas espécies (8,9-12,5%), sugerindo uma seleção mais forte contra árvores de autofecundação do que se originou do cruzamento entre árvores relacionadas. A distância de dispersão de pólen e sementes em *C. estrellensis* atingiu longa distância (> 3 km) do que em *C. legalis* (máximo de 385 m). No entanto, o pólen e as sementes em *C. estrellensis* e o pólen em *C. legalis* foram dispersos em um padrão de IBD. Os resultados sugerem que as populações estudadas são adequadas para conservação *in situ* e *ex situ*.

Palavras-chave: Conservação genética *in situ*. Espécies arbóreas tropicais. Fluxo gênico histórico. Marcadores microssatélites. Análise de parentesco. Tamanho efetivo populacional.

ABSTRACT

Cariniana estrellensis and *Cariniana legalis*, two of the largest trees in the Amazon and Atlantic Forest biomes, are currently vulnerable to extinction due to the intense deforestation of these biomes. Strategies for *in* and *ex situ* conservation are urgent, and studies of genetic diversity and gene flow are key aspects needed to develop these strategies. Thus, we investigate the genetic diversity, spatial genetic structure (SGS), and historical gene flow in fragmented populations of both species, using microsatellite markers. All trees found in the study populations were mapped, measured for diameter at breast height (DBH), and sampled for bark cambium. Our results show that in some cases, fixation index (F) was significantly higher in trees with lower DBH, indicating that smaller trees have higher levels of inbreeding than larger ones. Significant SGS was detected in populations of both species (60-350 m), indicating a gene dispersal pattern of isolation by distance (IBD). For both species, we found high seed (38.5-61.5%) and pollen (80.1-100%) immigration demonstrating that populations are not genetically isolated. No self-fertilization was detected, but we did find evidence of mating among related trees (8.9-12.5%), suggesting stronger selection against selfed individuals than those originated from mating among relatives. Pollen and seed dispersal distance for *C. estrellensis* reached longer distances (> 3 km) than for *C. legalis* (maximum of 385 m). However, pollen and seeds of *C. estrellensis* and pollen of *C. legalis* were dispersed in an IBD pattern. The results suggest that the studied populations are suitable for *in* and *ex situ* conservation.

Keywords: Effective population size. Historical gene flow. *In situ* genetic conservation. Microsatellite loci. Parentage analysis. Tropical tree species.

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1 INTRODUCTION

Over the last several centuries, human intervention in forests has caused fragmentation which has led to the degradation of a variety of forest functions, such as productivity and plant pollination, while also reducing plant species richness (HADDAD et al., 2015). The intense exploitation of natural ecosystems for the extraction of forest resources, along with land conversion for agricultural and livestock production and urbanization, causes environmental imbalances that result in irreversible consequences, such as changes in the environment and the extinction of animal and plant species (KASHIMSHETTY; PELIKAN; ROGSTAD, 2015). The isolation of tree species populations in small fragments reduces the number of reproductive individuals and population density, affecting genetic processes such as genetic drift, gene flow, selection, and mating systems (YOUNG; BOYLE 2000), while also isolating reproductive populations and increasing spatial genetic structure within populations (CARVALHO et al., 2010).

Deforestation and a lack of forest conservation strategies leads to fragmentation, and without adequate intervention, can result in the disappearance of forests over time (KASHIMSHETTY; PELIKAN; ROGSTAD, 2015). Loss of alleles is inevitable in exploited forests, leading to changes in allele frequencies that can be detected in the mating systems of species due to the spatial distance between trees, affecting the outcrossing rate and paternity correlation. There is also an expected increase in the rate of self-fertilization and crosses between relatives resulting in changes to the effective size of populations.

Cariniana estrellensis (Raddi) Kuntze (Lecythidaceae), also known as jequitibá-branco, is one of the tallest tree species in Brazil (LISBOA et al., 2016). The species can reach between 35 to 45 m in height and 120 cm in diameter at breast height or DBH (LORENZI, 2002; CARVALHO, 2003). The species is considered a rare or low population density species within its region of occurrence (GUIDUGLI et al., 2011), and its wood can be used for a variety of purposes. Jequitibá Rosa, *Cariniana legalis* (Mart.) Kuntze (Lecythidaceae), in turn, can reach 60 m in height and 4 m in DBH (TAMBARUSSI et al., 2015). Because it has been widely exploited for use in the furniture industry (CARVALHO, 1994, TAMBARUSSI, et al., 2013), it is currently on the list of endangered species.

Information about gene flow through pollen and seeds is a key factor in understanding the evolutionary potential of tree species, providing support for conservation and management practices. Estimates of historical gene flow is an indirect method in which levels of gene flow

are estimated based on the distribution of genetic diversity among populations (HAMRICK; NASON, 1996). Pollen flow is considered to be one of the main aspects influencing the genetic structure of tree species. Broad gene flow through pollen generates high rates of genetic variation within populations and limited differentiation between populations, as it is the main mechanism that maintains the genetic cohesion of a species (DICK; ETCHELECU; AUSTERLITZ, 2003). Similarly, because seed flow accounts for more than half the size of the genetic neighborhood, understanding the extent of seed flow is of paramount importance in establishing the reproductive dimensions of tropical tree species populations (HAMILTON, 1999).

Genetic conservation combined with sustainable management of forests allows for the preservation of biodiversity, thus maintaining the genetic diversity of species and ensuring their suitability for reproduction. To achieve this ideal, it is essential to study the behavior of individuals in natural populations using methodologies based on parentage analysis through molecular markers, such as genetic diversity, pollination distance, spatial genetic structure, and other factors that may contribute to development (TAMBARUSSI et al., 2015). This information is crucial for the development of effective management and conservation programs.

1.1 OBJECTIVES

The aim of this study was to use microsatellite loci to investigate the genetic diversity, inbreeding, effective population size, intrapopulation spatial genetic structure (SGS), and historic pollen and seed dispersal distance in small, fragmented populations of *C. estrellensis* and *C. legalis*. We specifically addressed the following questions:

- 1) Is genetic diversity and inbreeding lower in trees with smaller diameter at breast height (DBH) than with larger DBH?
- 2) Is the effective population size sufficient for *in situ* conservation over the short and long term?
- 3) What is the rate of historic pollen and seed immigration and the distance and patterns within populations?
- 4) What is the historic effective neighborhood size within the populations?

2 LITERATURE REVIEW

2.1 FOREST FRAGMENTATION

The consequences of anthropogenic activities on forest areas are of concern to the scientific community, as well as to society in general. Forest fragmentation and the selective harvesting of trees alters the demography and size of reproductive tropical tree species populations and, consequently, their mating system and pollen and seed dispersal patterns (SEBBENN, 2006; DEGEN, SEBBENN, 2014). This may increase the rate of self-fertilization, correlated matings (YOUNG; BOYLE, 2000; DEGEN; SEBBENN, 2014), intrapopulation spatial genetic structure (SGS), and kinship within populations (CARVALHO et al., 2010). In addition, it leads to reproductive isolation of the remaining populations after fragmentation (FUCHS; LOBO; QUESADA, 2003; SEBBENN et al., 2011), resulting in mosaics of small fragments and isolated individuals across the landscape. This process reduces the efficiency of pollinators and dispersers especially for tropical forest tree species (RAMOS; LEMOS-FILHO; LOVATO, 2009). Several studies on tropical arboreal species in populations located in fragmented areas report a reduction in the rate of pollen migration (e.g., FUCHS; LOBO; QUESADA, 2003; BITTENCOURT; SEBBENN, 2007; COLLEVATTI et al., 2010; LLORENS et al., 2012; ROSAS et al., 2011; SEBBENN et al., 2011; MANOEL et al. 2012a; DEGEN; SEBBENN, 2014; TAMBARUSSI et al., 2015; SPOLADORE et al., 2017) and seed migration (eg, BITTENCOURT; SEBBENN, 2007; GAINO et al., 2010; SEBBENN et al., 2011). This can result in genetic drift, which increases relatedness and inbreeding within populations (COLLEVATTI et al., 2010; SEBBENN et al., 2011) and reduces the amount of fruit produced in comparison with non-fragmented environments (AIZEN; FEINSIGER, 1994). In the presence of appropriate pollinators, isolated plants tend to show an increase in pollen dispersal distance, but this increase is associated with the dominance of a few effective pollen donors, generating correlated mating and leading to an increase in kinship among the produced seeds (HANSON et al., 2008). A reduction in population size may also lead to random loss of rare alleles, and if isolation persists alleles may remain fixed within each fragment due to genetic drift (FUCHS; HAMRICK, 2011).

With forest fragmentation, there is an increase in the fixed genetic load within populations (WILLI; VAN BUSKIRK; FISHER, 2005) and small and isolated populations often show reduced fitness (SPIELMAN; BROOK; FRANKHAM, 2004; REED, 2005).

Genetic problems, coupled with a disruption of plant–pollinator interactions and demographic and environmental stochasticity, increase the risk of extinction for small, isolated populations (NEWMAN; PILSON, 1997; SACCHERI et al., 1998). For a given population, genetic issues can be severe as there is a tendency towards continuous accumulation of genetic load and inbreeding, leading to mutational fusion over time (LYNCH; GABRIEL, 1990). Plant populations in fragmented environments tend to exhibit an increase in rates of self-fertilization and correlated mating, which causes an increase in inbreeding and genetic divergence (HANSON et al., 2008). Inbreeding also reduces species heterozygosity and adaptability, thus increasing the likelihood of extinction (MATTHIES et al., 2004).

One strategy used to connect and increase the size of small populations has been the introduction of individuals from neighboring populations, which can neutralize genetic deterioration and make populations viable (ANDREWARTHA; BIRCH, 1954; HANSKI, 1999). Therefore, many populations may be viable as metapopulations, which consist of populations structured as interconnected demes, considering extinction and recolonization events (HANSKI, 1999). Studying the species *Silene latifolia* Poir, Richards, Emery, and McCauley (2003) considered several parameters, such as population size, within population genetic diversity (number of alleles and expected heterozygosity), and genetic differentiation among populations measured by F_{st} -statistics. They observed that some populations overcame inbreeding depression through gene flow across a group of small populations. In a study of the tree *Magnolia stellata*, which is threatened with extinction, Setsuko et al. (2007) used cpSSR and nSSR (nuclear DNA microsatellite markers) and found that gene flow via pollen and seeds was accompanied by a reduction in the differentiation between populations. They concluded that the maintenance of the entire population, preserving the metapopulation structure and gene flow among subpopulations, is important for the conservation of the species. Considering the current state of forest fragmentation in Brazil, this theme is highly relevant for several tree species, particularly large trees that occupy the upper canopy and are responsible for the formation of the forest structure. It is also relevant for species with low population density that produce economically valuable seeds consumed by animals and humans, such as *Araucaria angustifolia* Bert. O. Ktze, *Cariniana estrellensis* (Raddi) Kuntze, and *Cariniana legalis* Mart. O. Ktze, among many others.

2.2 GENE FLOW

Gene flow can be defined as the movement of genes within a population and from one population to another (SLATKIN, 1987). Gene flow is responsible for the spatial homogenization of genetic diversity within and between populations which counteracts the effects of natural selection, mutation, and genetic drift that lead to differentiation within and among populations (HAMRICK; MURAWSKI; NASON, 1993).

Estimates of pollen and seed flow are necessary to predict the effects of forest fragmentation on the genetic structure of arboreal species (AGUILAR et al., 2008). These estimates are also used to define the number of seed trees required for seed collection for *ex situ* conservation and reforestation for environmental restoration, as well as define the minimum distance required between fragmented populations (SEBBENN, 2006).

In general, studies of gene flow based on genetic markers can be classified as historical or realized (occurring either in the past or present), or effective, which occurs in the present (BURCZYK et al., 2004). The estimates of gene flow for trees can be obtained directly or indirectly. Historical gene flow can be investigated using: i) an indirect method based on the distribution of genetic diversity among populations (HAMRICK; NASSON, 1996); ii) an indirect method based on the model of equilibrium between gene immigration and genetic drift (VEKEMANS; HARDY, 2004); or iii) a direct method based on parentage analysis of established individuals (regenerants) in populations assessed through the sampling of seedlings or juveniles (MEAGUER; THOMPSON, 1987). Effective gene flow can be investigated using: i) an indirect method based on pollen dispersal models (AUSTERLITZ et al., 2001); and ii) a direct method based on parentage analysis of open-pollinated seeds (MEAGUER, 1986). Indirect methods use spatial genetic autocorrelation analysis and refer to the historical or realized gene flow (VEKEMANS; HARDY, 2004). Direct estimates of gene flow based on parentage analysis requires samples of regenerants (realized) and/or open-pollinated seeds from known mothers (effective) and all reproductive plants in the population, i.e., all possible parents of the regenerants and seeds. Parentage analysis is not based on the assumptions of dispersion models; thus, the observed patterns may represent the true patterns if the polymorphism of the loci used is sufficient to discriminate among parental candidates (paternity exclusion). Based on the dispersion of pollen obtained through paternity analysis, it is possible to determine the effective number of pollen donors that fertilize seeds from parent trees (SMOUSE; SORK, 2004; WANG et al., 2010; FUCHS; HAMRICK, 2011), which

enables estimates of the effective size of progeny arrays (GAINO et al., 2010; MORARES; SEBBENN, 2011). However, the difference between historical vs. realized pollen dispersal (i.e., fertilization vs. the establishment of seedlings and growth into juveniles) is substantial and many stochastic and deterministic processes may occur during this period (BURCZYK; DIFAZIO; ADAMS, 2004), including random mortality, predation, dispersal of seeds at a distance, and selection. The realized pollen and seed dispersal distances can be measured by sampling established seedlings and juvenile individuals (BURCZYK; LEWANDOWSKI; CHALUPKA, 2004).

Pollen dispersal distances vary according to the dispersal vector and is influenced by population density, reproductive neighborhood, mechanisms that impede self-fertilization, and abiotic factors (i.e., humidity, wind direction, etc.). For insect pollinated tree species, pollen dispersal has been detected at distances ranging from 5 to 10,800 m, with a mean of 489.4 m (Table 1). For bat pollinated trees, distances have been detected from 48 to 5,229 m, with a mean of 801.1 m (Table 2). For bee pollinated trees, distances range from 61 to 1,509 m, with a mean of 431.2 m (Table 3), while for bird pollinated trees, distances range from 8 to 963 m, with a mean of 173.2 m (Table 4). Finally, for wind pollinated trees the pollen dispersal distance ranges from 3 to 9,460 m, with a mean of 974 m (Table 5).

Similarly, for seed dispersal, the distance depends on several factors. Species for which seeds are dispersed by animals, the distance ranges from 3 to 6000 m with a mean of 917 m; for wind dispersion, the distance ranges from 8 to 140 m with a mean of 50.6 m. In some species, seed dispersal can occur by gravity, ranging from 9 to 175 m, with an average of 84 m (Table 6).

Table 1- Mean pollen dispersal distance for insect pollinated tree species.

Species	Mean (m)	Reference
<i>Acacia saligna</i>	381–997	Millar et al. (2012)
<i>Acacia saligna</i> subsp. <i>saligna</i>	37	Millar et al. (2008)
<i>Acacia lindleyi</i>	288–1,202	Millar et al. (2012)
<i>Acrocomia aculeata</i>	105	Araújo et al. (2017)
<i>Aesculus turbinata</i>	189–289	Isagi et al. (2007)
<i>Astrocaryum aculeatum</i>	81	Ramos et al. (2016)
<i>Aucoumea klaineana</i>	128	Born et al. (2008b)
<i>Baillonella toxisperma</i>	9,800 – 10,800	Ndiade-Bourobou et al. (2010)
<i>Baillonella toxisperma</i>	690	Duminil et al. (2016a)
<i>Cabrlea canjerana</i>	65–206	Melo; Franceschinelli (2016)
<i>Carapa guianensis</i>	175–195	Martins et al. (2012)
<i>Carapa guianensis</i>	75–268	Cloutier et al. (2007)
<i>Castanea crenata</i>	3–243	Hasegawa; Suyama; Seiwa (2009)
<i>Castanopsis sieboldii</i>	35	Nakanishi et al. (2012)
<i>Castanopsis sieboldii</i>	44	Nakanishi et al. (2015)
<i>Centaurea corymbosa</i>	21	Hardy et al. (2004)
<i>Dysoxylum malabaricum</i>	600–6,525	Ismail et al. (2012)
<i>Entandrophragma cylindrum</i>	266–385	Lourmas et al. (2007)
<i>Erythrophleum suaveolens</i>	195–1,001	Duminil et al. (2016b)
<i>E. aggregata</i> and <i>E. rubida</i>	22–64	Field et al. (2011)
<i>Eucalyptus caesia</i>	39	Bezemer et al. (2016)
<i>Eucalyptus camaldulensis</i>	94	Gonzaga et al. (2016)
<i>Eucalyptus globulus</i>	69–149	Mimura et al. (2009)
<i>Eucalyptus grandis</i>	58	Jones et al. (2008)
<i>Eucalyptus incrassata</i>	870–1,134	Breed et al. (2015)
<i>Eucalyptus wandoo</i>	30–49	Byrne et al. (2008)
<i>Eugenia dysenterica</i>	80	Rodrigues et al. (2016)
<i>Ficus cyrtophylla</i>	1,095–1,115	Zhou; Chen (2010)
<i>Ficus insipida</i>	3,000	Heer et al. (2015)
<i>Ficus pumila</i>	989–1,712	Wang et al. (2009)
<i>Gomortega keule</i>	709	Lander; Boshier; Harris (2010)
<i>Himatanthus drasticus</i>	65	Baldauf et al. (2014)
<i>Kandelia candel</i>	15	Geng et al. (2008)
<i>Magnolia obovata</i>	131	Isagi et al. (2000)
<i>Magnolia stellata</i>	19–25	Setsuko et al. (2007)
<i>Magnolia stellata</i>	602	Setsuko; Nagamitsu; Tomaru (2013)
<i>Malus sylvestris</i>	60	Larsen; Kjær (2009)
<i>Manilkara huberi</i>	47	Azevedo et al. (2007)
<i>Oenocarpus bataua</i>	303	Ottewell et al. (2012)
<i>Parashorea tomentella</i>	177–416	Kettle et al. (2011b)

Table 1- Mean pollen dispersal distance for insect pollinated tree species. (continued)

Species	Mean (m)	Reference
<i>Pithecellobium elegans</i>	142	Chase et al. (1996)
<i>Prosopis alba</i>	5–24	Bessegga et al. (2012)
<i>Prosopis flexuosa</i>	5–20	Bessegga et al. (2017)
<i>Prunus africana</i>	18–2,350	Yineger et al. (2015)
<i>Prunus avium</i>	45–162	Konnert et al. (2011)
<i>Prunus avium</i>	42–134	Jolivet et al. (2012)
<i>Prunus mahaleb</i>	100	Garcia et al. (2005)
<i>Prunus lannesiana</i> var. <i>speciosa</i>	12–15	Shuri et al. (2012)
<i>Sinojackia rehderiana</i>	24	Yao et al. (2011)
<i>Sinojackia xylocarpa</i> and <i>S. rehderiana</i>	185	Zhang et al. (2010)
<i>Shorea curtisii</i>	65–81	Tani et al. (2012)
<i>Shorea lumutensis</i>	122–220	Lee et al. (2006)
<i>Shorea maxwelliana</i>	662–817	Masuda et al. (2013)
<i>Shorea xanthophylla</i>	56–119	Kettle et al. (2011b)
<i>Sorbus domestica</i>	1,200	Kamm et al. (2009)
<i>Sorbus torminalis</i>	59–148	Hoebee et al. (2007)
<i>Sorbus torminalis</i>	267–1,077	Oddou-Muratorio; Klein; Austerlitz (2005)
<i>Sorbus torminalis</i>	248	Oddou-Muratorio; Klein, (2008)
<i>Sorbus torminalis</i>	738	Klein; Desassis; Oddou-Muratorio (2008)
<i>Swartzia glazioviana</i>	60–516	Spoladore et al. (2017)
<i>Theobroma cacao</i>	28	Silva et al. (2011a)
<i>Theobroma cacao</i>	826–922	Schawe et al. (2013)
<i>Vateria indica</i>	139–158	Ismail et al. (2014)
Mean	489.4	

Table 2- Mean pollen dispersal distance for bat pollinated tree species.

Species	Mean (m)	Reference
<i>Caryoca brasiliensis</i>	132	Collevattii et al. (2010)
<i>Ceiba aesculifolia</i>	166-316	Quesada et al. (2013)
<i>Hymenaea courbaril</i>	952	Carneiro et al. (2011)
<i>Hymenaea courbaril</i>	827	Lacerda; Kanashiro; Sebbenn (2008b)
<i>Hymenaea stigonocarpa</i>	860-5,229	Moraes; Sebbenn (2011)
<i>Pachira quinata</i>	48-438	Rymer et al. (2015)
Mean	801.1	

Table 3- Mean pollen dispersal distance for bee pollinated tree species.

Species	Mean (m)	Reference
<i>Cariniana legalis</i>	63–352	Tambarussi et al. (2015)
<i>Copaifera langsdorffi</i>	94	Sebbenn et al. (2011)
<i>Copaifera langsdorffi</i>	74	Tarazi et al. (2013a)
<i>Copaifera langsdorffi</i>	118	Carvalho et al. (2010)
<i>Copaifera langsdorffi</i>	63	Manoel et al. (2012a)
<i>Dicorynia guianensis</i>	142	Latouche-Hallé et al. (2004)
<i>Dinizia excelsa</i>	417–1,288	Dick (2001)
<i>Dinizia excelsa</i>	212–1,509	Dick; Etchelecu; Austerlitz (2003)
<i>Dipterocarpus tempehes</i>	192–222	Kenta et al. (2004)
<i>Dipterys odorata</i>	688–1,092	Vinson et al. (2015b)
<i>Dipteryx panamensis</i>	240–557	Hanson et al. (2008)
<i>Eurycorymbus cavaleriei</i>	85–164	Wang et al. (2010)
<i>Eurycorymbus cavaleriei</i>	1,118–1,308	Wang; Kang; Huang (2014)
<i>Eurycorymbus cavaleriei</i>	293	Wang et al. (2008)
<i>Guaiacum santum</i>	1,276	Fuchs; Hamrick (2011)
<i>Guibourtia chodatiana</i>	61–91	Ojeda-Camacho; Kjær; Philipp (2013)
<i>Jacaranda copaia</i>	401–538	Vinson et al. (2015b)
<i>Miconia affinis</i>	101–804	Jha; Dick (2010)
<i>Myracrodruon urundeuva</i>	138–252	Gaino et al. (2010)
<i>Neabalanocarpus heimii</i>	188–195	Konuma et al. (2000)
<i>Simarouba amara</i>	334	Hardesty; Hubbell; Bermingham (2006)
<i>Swietenia humilis</i>	347–841	Rosas et al. (2011)
<i>Swietenia macrophylla</i>	75–255	Sebbenn et al. (2012)
<i>Tabebuia aurea</i>	308–396	Braga; Collevatti (2011)
Mean	431.2	

Table 4- Mean pollen dispersal distance for bird pollinated tree species.

Species	Mean (m)	Reference
<i>Banksia hookeriana</i>	30	Krauss et al. (2009)
<i>Banksia menziesii</i>	84	Frick; Ritchie; Krauss (2014)
<i>Banksia sphaerocarpa</i> var. <i>caesia</i>	8–84	Llorens et al. (2012)
<i>Symphonia globulifera</i>	154–963	Carneiro et al. (2009)
<i>Symphonia globulifera</i>	27–53	Degen; Bandou; Caron (2004)
Mean	173.2	

Table 5- Mean pollen dispersal distance for wind pollinated tree species.

Species	Mean (m)	Reference
<i>Abies pinsapo</i>	1487–1857	Sánchez-Robles et al. (2014)
<i>Allocauarina verticillata</i>	70–200	Broadhurst (2015)
<i>Araucaria angustifolia</i>	344–2069	Bittencourt; Sebbenn (2007)
<i>Araucaria angustifolia</i>	105–298	Medina-Macedo et al. (2015a)
<i>Araucaria angustifolia</i>	343	Sant’Anna et al. (2013)
<i>Austrocedrus chilensis</i>	1032	Colabella et al. (2014)
<i>Bagassa guianensis</i>	308–844	Silva et al. (2008)
<i>Bagassa guianensis</i>	2501–2637	Arruda et al. (2015)
<i>Betula</i> spp.	1000	Siljamo et al. (2008)
<i>Cercidiphyllum japonicum</i>	666	Sato et al. (2006)
<i>Fagus crenata</i>	37	Hanaoka et al. (2007)
<i>Fagus crenata</i>	42–79	Oddou-Muratorio et al. (2010)
<i>Fagus sylvatica</i>	28–438	Wang (2004)
<i>Fagus sylvatica</i>	35–63	Gauzere; Klein; Oddou-Muratorio (2013)
<i>Fagus sylvatica</i>	62–162	Millerón et al. (2012)
<i>Fagus sylvatica</i>	133	Konnert et al. (2011)
<i>Fagus sylvatica</i>	24–184	Piotti et al. (2012)
<i>Fraxinus excelsior</i>	168	Beatty et al. (2015)
<i>Fraxinus excelsior</i>	206–285	Thomasset et al. (2014)
<i>Fraxinus excelsior</i>	2900	Bacles; Ennos (2008)
<i>Juglans ailantifolia</i>	233–392	Kimura et al. (2012)
<i>Juglans cinérea</i>	88	Hoban et al. (2012)
<i>Juglans mandshurica</i>	140	Bai et al. (2007)
<i>Larix decidua</i>	18	Pluess (2011)
<i>Larix olgensis</i>	95	Wei et al. (2015)
<i>Nothofagus nervosa</i>	11–312	Marchelli; Smouse; Gallo (2012)
<i>Olea europaea</i>	256,8	Beghe et al. (2017)
<i>Phoenix canariensis</i>	377,2	Saro et al. (2014)
<i>Picea abies</i>	9	Shimono et al. (2011)
<i>Picea glauca</i>	654–619	O’Connell; Mosseler; Rajora (2007)
<i>Pinus attenuata</i>	5	Burczyk; Adams; Shimizu (1996)
<i>Pinus cembra</i>	69–1266	Chybicki; Dzialuk (2014)
<i>Pinus densiflora</i>	10	Iwaizumi et al. (2010)
<i>Pinus densiflora</i>	325	Lian; Miwa; Hogetsu (2001)
<i>Pinus fexilis</i>	141–189	Schuster; Mitton (2000)
<i>Pinus parviflora</i> var. <i>parviflora</i>	371–1886	Iwasaki et al. (2013)
<i>Pinus pinaster</i>	78–174	de-Lucas et al. (2008)
<i>Pinus sylvestris</i>	17–29	Robledo-Arnuncio; Alía; Gil (2004)
<i>Pinus sylvestris</i>	37	Torimaru et al. (2012)
<i>Pinus sylvestris</i>	629	Robledo-Arnuncio; Gil (2005)
<i>Pistacia lentiscus</i>	229–412	Albaladejo et al. (2012)
<i>Populus nigra</i>	8198	Rathmacher et al. (2010)
<i>Populus nigra</i>	7652–9460	Niggemann et al. (2012)
<i>Populus nigra</i> x <i>P. canadensis</i>	10–230	Pospísková; Sálková (2006)
<i>Populus trichocarpa</i>	1249–7600	Slavov et al. (2009)

Table 5- Mean pollen dispersal distance for wind pollinated tree species. (continued)

Species	Mean (m)	Reference
<i>Quercus castanea</i>	5730–9160	Oyama et al. (2017)
<i>Quercus frainetto</i>	33–53	Curtu; Gailing; Finkeldey (2009)
<i>Quercus lobata</i>	65	Sork et al. (2002)
<i>Quercus lobata</i>	114	Pluess et al. (2009)
<i>Quercus lobata</i>	235–644	Sork et al. (2015)
<i>Quercus macrocarpa</i>	42	Craft; Ashley (2010)
<i>Quercus macrocarpa</i>	70–77	Dow; Ashley (1996)
<i>Quercus macrocarpa</i>	76	Dow; Ahley (1998)
<i>Quercus oleoides</i>	8	Deacon; Cavender-Bares (2015)
<i>Quercus petraea</i>	21–61	Curtu; Gailing; Finkeldey (2009)
<i>Quercus petraea</i>	24–49	Streiff et al. (1999)
<i>Quercus petraea</i>	69	Lagache et al. (2012)
<i>Quercus petraea</i>	92	Valbuena-Carabaña et al. (2005)
<i>Quercus pubescens</i>	37	Curtu et al. (2009)
<i>Quercus pyrenaica</i>	270	Valbuena-Carabaña et al. (2005)
<i>Quercus robur</i>	21–38	Streiff et al. (1999)
<i>Quercus robur</i>	13–48	Vranckx et al. (2014a)
<i>Quercus robur</i>	92	Curtu; Gailing; Finkeldey (2009)
<i>Quercus robur</i>	151	Lagache et al. (2012)
<i>Quercus robur</i>	8500	Moracho et al. (2016)
<i>Quercus robur</i> + <i>Q.petraea</i>	297–463	Chybicki; Burczyk (2010)
<i>Quercus rubra</i> , <i>Q. velutina</i> , <i>Q. falcata</i>	178.2	Moran; Clark (2011)
<i>Quercus salicina</i>	67	Nakanishi et al. (2004)
<i>Quercus salicina</i>	69	Nakanishi et al. (2009)
<i>Quercus semiserrata</i>	47–570	Pakkad; Ueno; Yoshimaru (2008)
<i>Quercus sp</i>	16–5371	Gerber et al. (2014)
<i>Quercus velutina</i>	24	Fernández-Manjarrés; Idol; Sork (2006)
<i>Ulmus glabra</i>	17–104	Nielsen; Kjær (2010)
<i>Ulmus minor</i> and <i>U. pumila</i>	2860–2930	Bertolasi et al. (2015)
Mean	794	

Table 6- Mean dispersal distance for animal, wind, and gravity seed dispersal vectors for tree species.

Species	Mean (m)	Reference
Animal		
<i>Attalea phalerata</i>	3	Choo; Juenger; Simpson (2012)
<i>Baillonella toxisperma</i>	4,000–6,000	Ndiade-Bourobou et al. (2010)
<i>Fagus crenata</i>	12	Oddou-Muratorio et al. (2010)
<i>Fagus sylvatica</i>	10	Oddou-Muratorio et al. (2010)
<i>Ficus cyrtophylla</i>	510–647	Zhou; Chen (2010)
<i>Ficus pumila</i>	< 989	Wang et al. (2009)
<i>Prunus africana</i>	80–2,159	Yineger et al. (2015)
<i>Prunus avium</i>	27–73	Konnert et al. (2011)
<i>Prunus mahaleb</i>	145	Garcia et al. (2007)
<i>Sorbus torminalis</i>	135	Oddou-Muratorio; Klein (2008)
Mean	917	
Wind		
<i>Abies alba</i>	34–42	Leonarduzzi et al. (2016)
<i>Aucoumea klaineana</i>	118	Born et al. (2008)
<i>Banksia hookeriana</i>	8	Krauss et al. (2009)
<i>Cariniana estrellensis</i>	120	Guidugli et al. (2016)
<i>Fraxinus excelsior</i>	14	Beatty et al. (2015)
<i>Jacaranda copaia</i>	40–59	Jones; Hubbell (2006)
<i>Juglans cinerea</i>	26	Hoban et al. (2012)
<i>Myracrodruon urundeuva</i>	124	Gaino et al. (2010)
<i>Pinus taeda</i>	50–140	Williams et al. (2006)
<i>Quercus petraea</i>	42	Valbuena-Carabaña et al. (2005)
<i>Quercus pyrenaica</i>	14	Valbuena-Carabaña et al. (2005)
<i>Quercus robur</i>	5–15	Vranckx et al. (2014a)
<i>Quercus robur</i> + <i>Q.petraea</i> (mixed)	9–16	Chybicki et al. (2010)
<i>Quercus rubra</i> , <i>Q. velutina</i> , <i>Q. falcata</i>	128	Moran; Clark (2011)
<i>Quercus salicina</i>	17	Nakanishi et al. (2009)
Mean	50.6	
Gravity		
<i>Aesculus turbinata</i>	25	Isagi et al. (2007)
<i>Araucaria angustifolia</i>	92	Bittencourt; Sebbenn (2007)
<i>Araucaria angustifolia</i>	131	Sant'Anna et al. (2013)
<i>Carapa guianensis</i>	114–175	Martins et al. (2012)
<i>Castanopsis sieboldii</i>	18	Nakanishi et al. (2015)
<i>Copaifera langsdorffii</i>	61	Sebbenn et al. (2011)
<i>Copaifera langsdorffii</i>	135	Tarazi et al. (2013b)
<i>Sinojackia rehderiana</i>	9	Yao et al. (2011)
Mean	84	

2.3 SPATIAL GENETIC STRUCTURE

Several evolutionary and ecological processes, such as seed dispersal, inter- and intraspecific competition, and environmental heterogeneity may affect the spatial distribution patterns of individuals within a population (LOVELESS; HAMRICK, 1984). Spatial aggregation of alleles in continuous populations is defined as spatial genetic structure or SGS (DERING; CHYBICKI; RACZKA, 2015). Restricted gene flow often results in intrapopulation SGS, which is as the non-random spatial distribution of genotypes within a population (VEKEMANS; HARDY, 2004). In addition, SGS may be the result of limited pollen and seed dispersal distance, local genetic drift, inbreeding, and selection, which may favor one or more genotypes (EPPERSON, 1992). As trees present long reproductive cycles, variations in intraspecific life histories of plants may arise due to phenotypic plasticity and shaped by environmental variation (KITTELSON; MARON, 2001), creating genetically different subpopulations as a result of spatial heterogeneity (JONES et al., 2005).

The identification of SGS within natural populations is important because it offers an understanding of the extent of gene dispersal within populations (ROUSSET, 2000; VEKEMANS; HARDY, 2004); therefore, it indirectly quantifies the dispersal distance of the species (ODDOU-MURATORIO et al., 2010) and provides insights into local reproduction and evolution (SMOUSE; PEAKALL, 1999). The knowledge and understanding of genetic diversity and micro-scale SGS are also important for the management of forest genetic resources, to evaluate the impacts of exploitation and fragmentation, and to establish sampling strategies in natural populations (SEBBENN, 2006). Forest fragmentation may increase SGS by disrupting gene flow and increasing local drift due to reduced population densities (YOUNG; MERRIAM, 1994). In contrast, changes in the landscape that improve the dispersal capacity of the species may reduce stochastic variables (YOUNG; MERRIAM, 1994). In the context of biological conservation, habitat fragmentation and disturbance may alter the SGS due to disruptions in the ecological processes that affect recruitment, such as competition with invasive plant species (EWERS; DIDHAM, 2006) and plant breeding (AGUILAR et al., 2006).

Since seeds and pollen are the two main agents of gene flow, the assessment of seed and pollen dispersal distances are essential to understanding SGS (HEUERTZ et al., 2003). Meanwhile, family structure is dependent on the dispersal of seeds and pollen. If the pollen is dispersed further than seeds, the SGS will be more influenced by maternal alleles and seed

dispersal than by pollen dispersal. However, if seeds are dispersed more widely than pollen, SGS will be more influenced by paternal alleles and pollen dispersal distances. If neither seeds nor pollen are widely dispersed, SGS will be influenced by both maternal and paternal alleles and determined by both seed and pollen dispersal distance (SEBBENN et al., 2011). For many temperate tree species that are wind pollinated, seed dispersal may have a much greater impact than pollen flow on SGS as seeds are not expected to travel as far as pollen (HEUERTZ et al., 2003; SATO et al., 2006). In the tropics, more than 90% of tree species depend on frugivorous animals to disperse their seeds (HOWE; SMALLWOOD, 1982).

Results obtained from analyses of SGS and contemporary gene flow have been used to identify gene flow patterns and support strategies for *in situ* and *ex situ* tree species conservation (RATHMACHER et al., 2010; GAINO et al., 2010; SANT'ANNA et al., 2013).

2.4 MICROSATELLITE MOLECULAR MARKERS (SSR)

The *in situ* and *ex situ* conservation of tree species depends directly on the knowledge obtained through ecological and genetic studies of populations, which are currently based on analyses of nuclear microsatellite markers. Microsatellite markers, also known as Simple Sequence Repeats (SSR), are an effective tool widely used in genetic studies of plant populations for a number of reasons: they are abundant and uniformly distributed throughout the genome; they have high polymorphism in terms of number of alleles within loci; they are reproducible and require small amounts of DNA; they have codominant inheritance, which allows the distinction between homozygous and heterozygous genotypes; and they present multi-allelism (BRONDANI et al., 2005).

Microsatellite markers are also useful for genetic mapping (GUPTA; VARSHNEY, 2000; BRONDANI et al., 2005), quantifying the genetic diversity and structure, inbreeding, kinship, intrapopulational spatial genetic structure, mating system, pollen and seed dispersal patterns (BRONDANI et al., 2005; ASHLEY, 2010; COLLEVATTI et al., 2010; MORAES; SEBBENN, 2011; MANOEL et al., 2012b; ELLSTRAND, 2014; TAMBARUSSI et al., 2015), assessing the origins of commercialized timber (DEGEN et al., 2007), and determining effective population size (SEBBENN, 2006; MORAES; SEBBENN, 2011). These markers are also valuable for phylogenetic studies between species (DEMASURE; COMPS; PETIT, 1996; COLLEVATTI et al., 2009, 2012) to determine the genetic proximity of individuals of different species, subspecies, and varieties of the same genus. This type of analysis is possible

because the DNA sequences flanking the microsatellite loci are generally conserved within the same species or between species of related genera (OLIVEIRA et al., 2006).

2.5 STUDIED SPECIES

2.5.1 *Cariniana estrellensis*

Cariniana estrellensis (Raddi) Kuntze (Lecythidaceae), or jequitibá-branco is an emerging Neotropical tree that prefers moist and deep soils (CARVALHO, 2003). The species occurs in Brazil from southern Bahia to Rio Grande do Sul and Acre, in the riparian forests of Central Brazil (CASTRO, 2011), Bolivia, Paraguay, and Peru (LEITE, 2007). In Brazil, *C. estrellensis* is one of the longest-living species and one of the few remaining large trees of this genus, reaching up to 45 m in height and 120 cm in diameter at breast height (DBH) (LORENZI, 2002; CARVALHO, 2003). The species is threatened with extinction due to intense exploitation of the biomes in which they occur (LISBOA et al., 2016). Populations may present low density, depending on the region of occurrence (LORENZI, 2002; CARVALHO, 2003). The species is hermaphroditic and pollination is carried out by small insects, mainly bees of the genus *Melipona* and *Trigona*. Fruits can contain up to 17 seeds, and the seeds are unilaterally winged, pyriform shaped, and dispersed by anemochory (LEITE, 2007), but this dispersion can be facilitated by monkeys (*Alouatta caraya*) that consume the seeds during the dry seasons (MORI, 1999; CARVALHO, 2003). The wood is considered to be hard and resistant, from light to moderately heavy, and offers good dimensional stability after manufacture (RECORD; HESS, 1972; CHUDNOFF, 1984). The species is also used in landscaping and has medicinal properties.

2.5.2 *Cariniana legalis*

Cariniana legalis (Mart.) Kuntze, commonly known as jequitibá-rosa is a Neotropical, late successional tree of the Lecythidaceae family that is one of the largest trees found in the Atlantic Forest (REITZ, 1981; CARVALHO, 2003; LORENZI, 2002). Trees of this species can reach 60 m in height and 4 m in DBH. The species is native to Brazil and found naturally in the south (Paraná State), southeast (Espírito Santo, Rio de Janeiro, São Paulo and Minas Gerais), northeast (Alagoas, Bahia, Paraíba and Pernambuco), and in Mato Grosso State (REITZ, 1981; CARVALHO, 2003). Endemic to the Atlantic Forest, *C. legalis* occurs at a

low population density (CARVALHO, 2003), generally less than one tree per hectare (SEBBENN et al., 2000; LEAL et al., 2014; TAMBARUSSI et al., 2015). The species is monoecious with hermaphrodite flowers and pollinated by bees of the genus *Melipona* and *Trigona* (PRANCE; MORI, 1979). Reproduction occurs mainly by outcrossing (SEBBENN et al., 2000; LEAL et al., 2014; TAMBARUSSI et al., 2015, 2016). Fruiting begins in trees at approximately 20 years of age and each fruit can contain more than ten seeds that are dispersed by gravity and anemochory (CARVALHO, 2003). Its wood is light and used in construction, as well as in the manufacture of furniture and shoes (CARVALHO, 2003). It is also used in the pulp industry to produce good quality paper (LORENZI, 2002).

The natural habitat of *C. legalis* has been degraded extensively in the last few decades, and the species has been heavily exploited for its wood. There are few remaining natural populations, which has led to the species being classified as endangered. Thus, it is necessary to develop *in situ* and *ex situ* conservation strategies of the remaining populations (SEBBENN et al., 2000), which requires an understanding of the species' genetic diversity, inbreeding, spatial genetic structure, mating system, and gene flow (SEBBENN et al., 2000; TAMBARUSSI et al., 2015).

3 MATERIAL AND METHODS

3.1 STUDY SITES AND SAMPLING

Samples were collected from two *Cariniana estrellensis* populations located in Ibicatu, São Paulo State, and Bataguassu, Mato Grosso do Sul State, and two populations of *C. legalis* in Ibicatu and Mogi-Guaçu, São Paulo State, Brazil.

3.1.1 Ibicatu

The Ibicatu State Forest (22°46' S, 47°43' W, altitude 448 to 576 m asl) is a 72 ha, spatially isolated forest fragment located near Piracicaba, São Paulo State, Brazil. The forest fragment is a remnant of a semi-deciduous forest that is currently bounded by agriculture, including sugarcane, eucalyptus, and pasture for livestock (Figure 1). In the past, the stand was subjected to several episodes of selective logging (about 30 years ago). Ibicatu is isolated from other populations or individuals of the species by at least 4 km. The climate is characterized as humid and mesothermal (Cwa, Köppen 1948) with the mean monthly temperature varying between 14.3° C and 24.7° C., a mean annual temperature of 23.9° C, mean minimum of 16.1° C, and a mean maximum of 25° C. Mean annual precipitation is approximately 1,320 mm, with a dry season from May to August, and 86% of the precipitation occurring during the rainy season (September to April). The soils are yellow regosol and red podzolic "intergrades".

All *C. estrellensis* and *C. legalis* trees in the site were sampled (bark cambium), mapped (GPS III-Garmin, USA), measured for diameter at breast height (DBH), estimated for age based on the annual mean DBH increment, and genotyped. From this study area, we sampled all 26 *C. estrellensis* adult trees (0.36 trees/ha) and 65 *C. legalis* adult trees (0.93 trees/ha). The DBH of *C. estrellensis* ranged from 13 to 248 cm (mean 68.5 cm) and the estimated age ranged from 21 to 400 years, with a mean 110 years. The DBH of *C. legalis* ranged from 25 to 325 cm (mean 121 cm) and the estimated age ranged from 24 to 570 years, with a mean 160 years (Table 7, Figures 2 and 3).

Table 7- Sample size (n), population density (trees/ha), mean, standard deviation (SD), minimum and maximum (Min/Max) DBH, and estimated age of trees that were assigned parents, assigned as putative parents by parentage analysis, and total sample of *C. estrellensis* and *C. legalis* in the Ibicatu (IB) (72 ha), Bataguassu (BA) (448.2 ha), and Mogi-Guaçu (MG) (7.2 ha) forest fragments. The mean annual DBH increment for *C. estrellensis* is 0.61 cm/year and for *C. legalis* is 0.79 cm/year (CARVALHO, 2003).

Sample		n	Trees/ha	Mean (SD) DBH (cm)	Min/Max (cm)	Mean age (years) (SD)	Min/Max (years)
<i>Cariniana estrellensis</i>							
Ibicatu	Assigned trees	16	-	45.1 (17.3)	13/76	73 (28)	21/121
Ibicatu	Assigned parents	11	-	96.6 (58.1)	41/248	156 (94)	66/400
Ibicatu	Total	26	0.36	68.5 (47.1)	13/248	110.3 (76)	21/400
Bataguassu	Assigned trees	123	-	56.8 (10.9)	37.6/95.5	91 (19)	36/157
Bataguassu	Assigned parents	93	-	76.9 (17.6)	48.7/147.1	126 (34)	80/241
Bataguassu ¹	Total	284	0.63	65.6 (17.9)	21/147	108 (29)	36/241
<i>Cariniana legalis</i>							
Ibicatu	Assigned trees	24	-	86.6 (37.6)	19/146	110 (48)	24/185
Ibicatu	Assigned parents	20	-	153.8 (52.8)	97/306	195 (67)	123/387
Ibicatu ²	Total	65	0.93	121 (68.9)	25/325	160 (88)	24/570
Mogi-Guaçu	Assigned trees	10	-	46.6 (16.0)	21/68	59 (20.1)	27/86
Mogi-Guaçu	Assigned parents	6	-	96 (19.9)	65/110	122 (25)	82/141
Mogi-Guaçu ²	Total	26	3.6	68 (26.3)	21/144	83 (33)	27/144

¹Kubota (2017); ²Tambarussi et al. (2015); $P < 0.05$.

Source: Prepared by author.

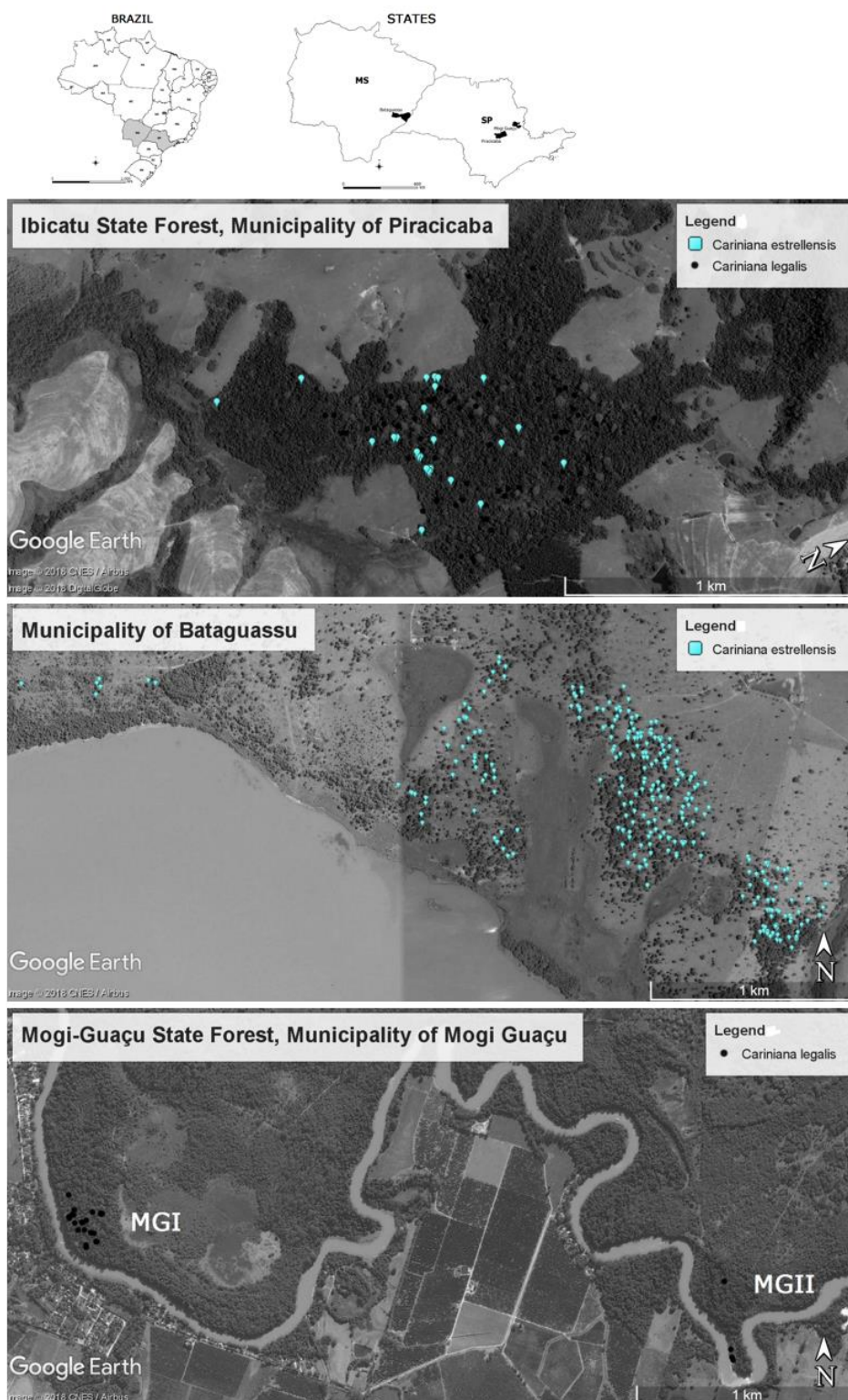
3.1.2 Bataguassu

The Bataguassu site covers 448.2 ha, consists of forest fragments and isolated trees (21° 38'00" S, 52° 14'02" W, 273.3 m asl), and is located in the city of Bataguassu, Mato Grosso do Sul State, Brazil, near the Pardo River (Figure 1). The region is characterized as a transition zone between the Savanna and Atlantic Forest biomes (IBGE, 2016) and is isolated, surrounded by monoculture crops (sugarcane and Eucalyptus) and pasture. The predominant soil in the region is dark red Oxisols of medium texture and low natural fertility. The climate is tropical humid with rainy summers and dry winters, an average temperature of 23.1°C, and annual rainfall ranging from 1,200 to 1,500 mm (INSTITUTO BRASILEIRO DE GEOGRAFIA E ESTATÍSTICA- IBGE, 2016). All 284 *C. estrellensis* trees (0.63 trees/ha) found in the landscape were georeferenced (GPS-Garmin), measured for DBH, sampled (foliar or cambial tissue), estimated for age based on the annual mean DBH increment, and genotyped (Table 7, Figure 2). The DBH of *C. estrellensis* ranged from 21 to 147 cm (mean 65.6 cm) and the estimated age ranged from 36 to 241 years (mean of 108 years).

3.1.3 Mogi-Guaçu

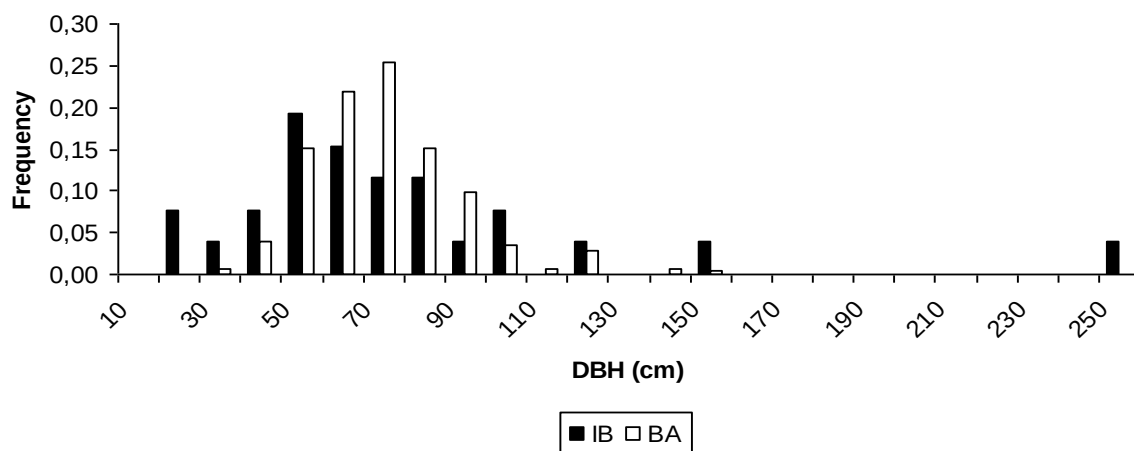
The Mata da Figueira (MGI) is a small, 7.2 ha, riparian forest fragment in the semi-deciduous plateau and part of the Mogi-Guaçu Ecological Station (22°16'S 47°11' W, mean altitude of 600 m asl). Located approximately 2.9 km from MGI is a cluster of four reproductively mature *C. legalis* trees, demonimated MGII (Figure 1). MGI and MGII are isolated from other populations by at least 4 km and are located approximately 75 km from Ibicatu. The climate is the same as that described for Ibicatu. All *C. legalis* trees in MGI and MGII were sampled (bark cambium), mapped (GPS III-Garmin, USA), measured for DBH, estimated for age based on annual mean DBH increment, and genotyped (Table 7, Figure 3). MGI contains 22 *C. legalis* trees and MGII contains 4 trees, for a total of 26 trees (3.6 trees/ha), with DBH ranging from 21 to 144 cm (mean 68 cm), and estimated age ranging from 27 to 144 years, with a mean of 83 years.

Figure 1- Spatial distribution of *Cariniana estrellensis* and *Cariniana legalis* trees sampled in the Ibicatu State Forest, Sao Paulo State, Brazil.



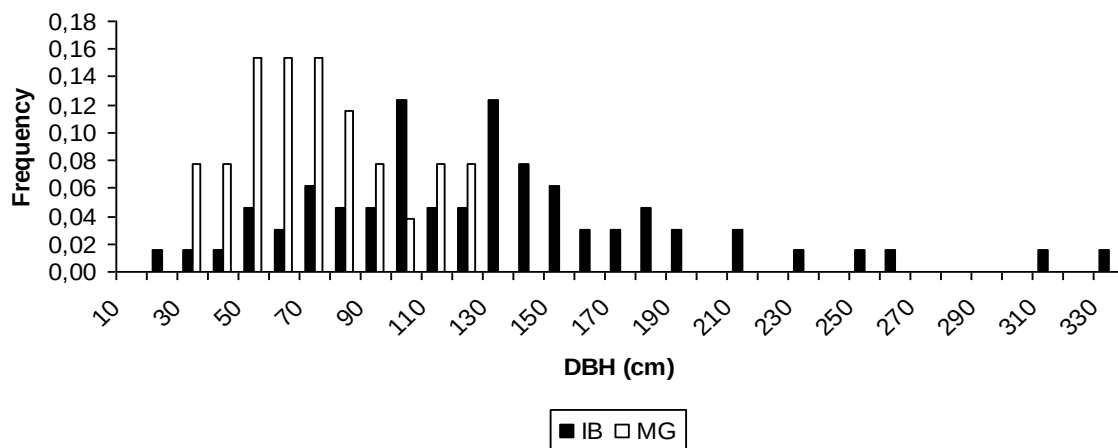
Source: Google Earth, (2018).

Figure 2- DBH frequency distribution for *Cariniana estrellensis* trees sampled in Ibicatu (IB) and Bataguassu (BA).



Source: Prepared by author.

Figure 3- DBH frequency distribution for *Cariniana legalis* trees sampled in Ibicatu (IB) and Mogi-Guaçu (MG).



Source: Prepared by author.

3.2 DNA EXTRACTION AND MICROSATELLITE AMPLIFICATION

The DNA extraction of *C. estrellensis* and *C. legalis* was carried out using the method described by Doyle and Doyle (1990). *Cariniana estrellensis* was genotyped for nine microsatellite loci (SSR) and *C. legalis* was genotyped for seven SSR loci (Table 8). Details on amplification and genotyping of the selected loci for *C. estrellensis* are given in Guidugli et al. (2009) and Tambarussi et al. (2013a). For *C. legalis*, details are described in Tambarussi et al. (2013a). All loci used for both species present Mendelian inheritance, an absence of genetic linkage, and genotypic linkage equilibrium (TAMBARUSSI et al., 2013b; KUBOTA et al., 2017).

Table 8- Microsatellite loci used for *Cariniana estrellensis* and *Cariniana legalis*.

	Primers	Reference
<i>Cariniana estrellensis</i>		
Ibicatu	Ce07, Ce18	Guidugli et al., 2009
Ibicatu	Cle01, Cle04, Cle05, Cle08, Cle09, Cle10, Cle12	Tambarussi et al., 2013a
Bataguassu	Ce01, Ce02, Ce04, Ce09, Ce10, Ce11, Ce13, Ce14, Ce18	Kubota et al., 2017
<i>Cariniana legalis</i>		
Ibicatu	Cle01, Cle04, Cle05, Cle08, Cle09, Cle10, Cle12	Tambarussi et al., 2013a
Mogi-Guaçu	Cle01, Cle04, Cle05, Cle08, Cle09, Cle10, Cle12	Tambarussi et al., 2013a

3.3 DATA ANALYSIS

3.3.1 Genetic diversity and inbreeding

Genetic diversity was quantified at the population level. In order to determine if there are differences based on tree age, the population was divided into two groups, 50% of trees with low DBH and the other 50% with high DBH. Genetic diversity indices estimated were: total number of alleles per locus (k), allelic richness (R), and observed (H_o) and expected (H_e) heterozygosity according to Hardy-Weinberg equilibrium. Inbreeding was quantified using the fixation index (F) and the statistical significance of F values were tested using

Monte Carlo permutation of alleles between individuals. All estimates were carried out using the FSTAT software (GOUDET, 1995). In order to test the indices for differences between samples, we used an unpaired t-test. The genetic differentiation (G_{st}) between the species was also estimated using the standardized genetic differentiation (G'_{st}) for microsatellite loci (HEDRICK, 2005) and the seven common loci between species (Cle01, Cle04, Cle05, Cle08, Cle09, Cle10 and Cle12). All of these estimates were carried out using the FSTAT software (GOUDET, 1995).

3.3.2 Estimates of group coancestry and variance effective size

Group coancestry (Θ) for the total sample of trees in each population was estimated as:

$$\Theta = \frac{\sum_{i=1}^n 0.5(1 + F_i) + \sum_{i=1}^n \sum_{j \neq i}^n \theta_{ij}}{n^2},$$

where n is the sample size, F_i is the inbreeding coefficient of the i -th individual, and θ_{ij} is the pairwise coancestry coefficient between the i -th and j -th individuals (LINDGREN et al., 1997). The θ_{ij} value was estimated using the Nason coancestry estimator (LOISELLE et al., 1995). The F_i and θ_{ij} indices were estimated using the Spagedi 1.3 software (HARDY; VEKEMANS, 2002). As the Θ index was derived from the inbreeding coefficient (ranging from 0 to 1) and true pairwise coancestry coefficient (ranging from 0 to 1), and we estimated F_i and θ_{ij} using coefficients of correlation (ranging from -1 to 1), all values lower than zero were assumed as zero. Furthermore, estimates of inbreeding and coancestry from gene markers may be biased due to the occurrence of null alleles, allele dropout, and genotyping errors (MORAES et al., 2013). F_i values lower than 0.125, the minimum inbreeding expected for mating between two half-sib individuals, were also assumed as zero, and values greater than 0.25, the minimum inbreeding expected for mating between two full-sib individuals, were assumed as 0.25. θ_{ij} values lower than 0.125, the minimum coancestry coefficient expected between two half-sib individuals, were also assumed as zero, and θ_{ij} values higher

than 0.25, the minimum coancestry coefficient expected between two full-sibs, were assumed as 0.25. The variance effective population size was calculated following Cockerham (1969) as $N_e = 0.5/\Theta$ and the relationship between N_e and the sample size (n) was calculated as N_e/n . The loss of observed heterozygosity per generation based on N_e and due to genetic drift was estimated using a model that assumes one locus with two alleles in random mating populations with discrete generations (not overlapping), $H_{o(t)}/H_{o(0)} = [1 - (1/2N_e)]^t$, and the decrease in the heterozygosity in generation t as $H_{o(t)} = H_{o(0)}[1 - (1/2N_e)]^t$ (FRANKEL; SOULE, 1981), where $H_{o(0)}$ and $H_{o(t)}$ are actual heterozygosity and heterozygosity in generation t , respectively.

3.3.3 Analysis of intrapopulation spatial genetic structure

The intrapopulation spatial genetic structure (SGS) was estimated based on the mean coancestry coefficient (θ_{ij}) between pairwise trees within distance classes, using the Nason coancestry estimator (LOISELLE et al., 1995) and Spagedi 1.3 software (HARDY; VEKEMANS, 2002). The statistical significance of θ_{ij} values was calculated by comparing the limits of the confidence interval at 95% probability of θ_{ij} for each distance class, calculated by Monte Carlo permutations of individuals between distance classes. Due to the differences in number of sampled trees and population density between populations, four distance classes were used for *C. estrellensis* (0–75, 75–150, 150–250, and 250–983 m) and for *C. legalis* (0–50, 50–100, 100–200, and 200–600 m). To compare SGS between species and populations, the Sp statistic (VEKEMANS; HARDY, 2004) was calculated as $Sp = -b_k/(1 - \theta_l)$, where θ_l is the coancestry coefficient calculated between all pairs of individuals in the first distance class and b_k is the slope of regression of the coancestry coefficient on the logarithm of spatial distance between trees. To test for significance of SGS, the spatial position of each individual was permuted 1000 times to obtain the frequency distribution of b_k under the null hypothesis that θ_{ij} and $\ln(d_{xy})$ are uncorrelated.

3.3.4 Estimating historical gene dispersal

Historical gene dispersal (σ_g) for each population was estimated assuming that the SGS follows the isolation by distance pattern at equilibrium (HARDY et al., 2006). The effective neighborhood population size (Nb) was estimated as $Nb = (1 - \theta_1)/b_k$ (VEKEMANS; HARDY, 2004), where b_k is the regression slope within a distance class of $\sigma_g < d_{ij} < 20\sigma_g$. Due to the fact that this estimate of Nb is dependent on the effective density (D_e) (HARDY et al., 2006), D_e was estimated as $D_e = D/2$ and $D_e = D/10$, where D is the actual population density (VEKEMANS; HARDY, 2004). The lower and upper bounds for the 95% confidence interval (95% CI) of Nb were estimated by jackknifing data over each locus (HARDY et al., 2006). The 95% CI of σ_g was estimated following Hardy et al. (2006). All analyses were carried out using the Spagedi 1.3 software (HARDY; VEKEMANS, 2002).

3.3.5 Parentage analysis

Combined non-exclusion probability of the first parent (P_1), combined non-exclusion probability of identity (Q_i), and realized pollen and seed dispersal in both species and all populations were carried out by parentage analysis (maternity and paternity), using the software CERVUS 3.0 (MARSHALL et al., 1998; KALINOWSKI; TAPER; MARSHALL, 2007). Cryptic gene flow (C_{gf}) was estimated as described in Dow and Ashley (1996). Parentage (maternity and paternity) analyses were based on the single exclusion method.

In order to identify parents for all sampled trees, all sampled individuals within populations were used as candidate parents. However, to accept a candidate parent as the true parent, we adopted the following approach: i) self-assignments were excluded; ii) positive assignment for descendants was accepted if there was a maximum of two mismatches between the descendant and the assigned putative parent or among the trio: descendant, first, and second assigned parent; iii) as *C. estrellensis* starts fruiting at 10 years of age, which corresponds to a DBH > 7 cm and *C. legalis* starts fruiting at approximately 20 years of age and a DBH > 20 cm (CARVALHO, 2003), putative *C. estrellensis* parents with less than 10

years differences in relation to the descendant tree, and putative *C. legalis* parents with less than 20 years differences in relation to the descendant tree were discarded.

To confirm positive assignments, the θ_{xy} was estimated between descendant and assigned putative parents, as well as between assigned parents and trees assigned to the same putative parents, as described above. The expected θ_{xy} value for parent-sib pairs is 0.25, between half-sibs is 0.125, and full-sibs is 0.25. Realized pollen dispersal distance was estimated as the distance between two putative parents when two parents (probable mother and father) were assigned. In cases where at least one putative parent was assigned, realized seed dispersal distance was estimated assuming that the sole assigned parent is the mother. When two putative parents were assigned, realized seed dispersal distance was based on the mean distance between the offspring and first and second parent. The minimum, maximum, and median pollen and seed dispersal distances were also calculated using the Euclidean distance between two points. Self-fertilization (s) was accepted only in cases where there was no mismatching between tested descendant and the assigned putative parent. Following Tambarussi et al. (2017), to estimate the rate of mating among related trees (t_r), assigned parents with $\theta_{xy} \geq 0.1$ were assumed to be genetically related. Effective pollination neighbor area (A_{ep}) corresponds to the circular area in which 63% of pollen donors that fertilized a mother tree are expected to be located; this was calculated based on Levin (1998) and the effective pollination radius (r_{ep}) based on Austerlitz and Smouse (2001).

4 RESULTS

4.1 GENETIC DIVERSITY AND INBREEDING

For *C. estrellensis* in IB and BA, we found a total of 46 and 75 alleles, respectively, and for *C. legalis* in IB and MG, we found a total of 100 and 97 alleles, respectively (Table 9). The observed (H_o) and expected (H_e) heterozygosity were similar between *C. estrellensis* (IB: $H_o = 0.71$; $H_e = 0.66$; BA: $H_o = 0.65$; $H_e = 0.69$) and *C. legalis* (IB: $H_o = 0.81$; $H_e = 0.86$; MG: $H_o = 0.82$; $H_e = 0.89$) populations. The results for fixation index (F) were significantly ($P < 0.05$) higher than zero for *C. estrellensis* of BA ($F = 0.06$) and *C. legalis* of IB ($F = 0.06$), indicating inbreeding. According to the unpaired t-test, comparing 50% of trees with $<DBH$ and $>DBH$, the allelic richness (R), H_o , H_e and F were not significantly different (Table 10). However, F values of *C. estrellensis* in BA (0.06) and *C. legalis* in IB (0.09) were significantly higher than zero in trees with $< DBH$, suggesting the occurrence of inbreeding. Genetic differentiation (G'_{st}) between species ($G'_{st} = 0.550 \pm 0.058$, mean $\pm$ standard error) indicates that genetic diversity is mainly distributed among rather than within species.

Table 9- Genetic diversity and inbreeding in sampled *Cariniana estrellensis* and *Cariniana legalis* trees.

Sample	<i>n</i>	<i>k</i>	<i>R</i> (SE)	<i>H_o</i> (SE)	<i>H_e</i> (SE)	<i>F</i> (SE)
<i>Cariniana estrellensis</i>	310	144				
Ibicatu	26	46	-	0.71 (0.06)	0.66 (0.03)	-0.07 (0.08)
50%< DBH	13	37	3.95 (0.30)	0.71 (0.07)	0.64 (0.03)	-0.11 (0.10)
50%> DBH	13	44	4.68 (0.24)	0.70 (0.06)	0.69 (0.02)	-0.01 (0.08)
Bataguassu ¹	284	75	-	0.65 (0.03)	0.69 (0.02)	0.06 (0.08)*
50%< DBH	142	74	4.98 (0.67)	0.64 (0.05)	0.68 (0.05)	0.06 (0.04)*
50%> DBH	142	65	5.01 (0.63)	0.66 (0.06)	0.69 (0.05)	0.05 (0.05)
<i>Cariniana legalis</i>	91	130				
Ibicatu ²	65	100	-	0.81 (0.02)	0.86 (0.01)	0.06 (0.02)*
50%< DBH	32	86	7.80 (0.47)	0.75 (0.04)	0.83 (0.03)	0.09 (0.07)*
50%> DBH	33	89	8.62 (0.53)	0.87 (0.03)	0.88 (0.02)	0.01 (0.05)
Mogi-Guaçu ²	26	97	-	0.82 (0.07)	0.89 (0.01)	0.08 (0.07)
50%< DBH	12	79	9.85 (0.68)	0.82 (0.08)	0.92 (0.01)	0.10 (0.08)
50%> DBH	14	85	9.58 (0.68)	0.85 (0.06)	0.89 (0.02)	0.04 (0.06)

n is the sample size; *k* is the total number of alleles across all loci; *R* is the allelic richness for 10 genotypes in *C. estrellensis* and nine in *C. legalis*; *H_o* is the observed heterozygosity; *H_e* is the expected heterozygosity;

F is the fixation index; SE is the standard error; ¹Kubota (2017); ²Tambarussi et al. (2015); *P< 0.05.

Source: Prepared by author.

Table 10- Probability (P) of unpaired t-test between pairwise samples with 50% of trees with lower DBH vs 50% with higher DBH in *Cariniana estrellensis* and *Cariniana legalis*.

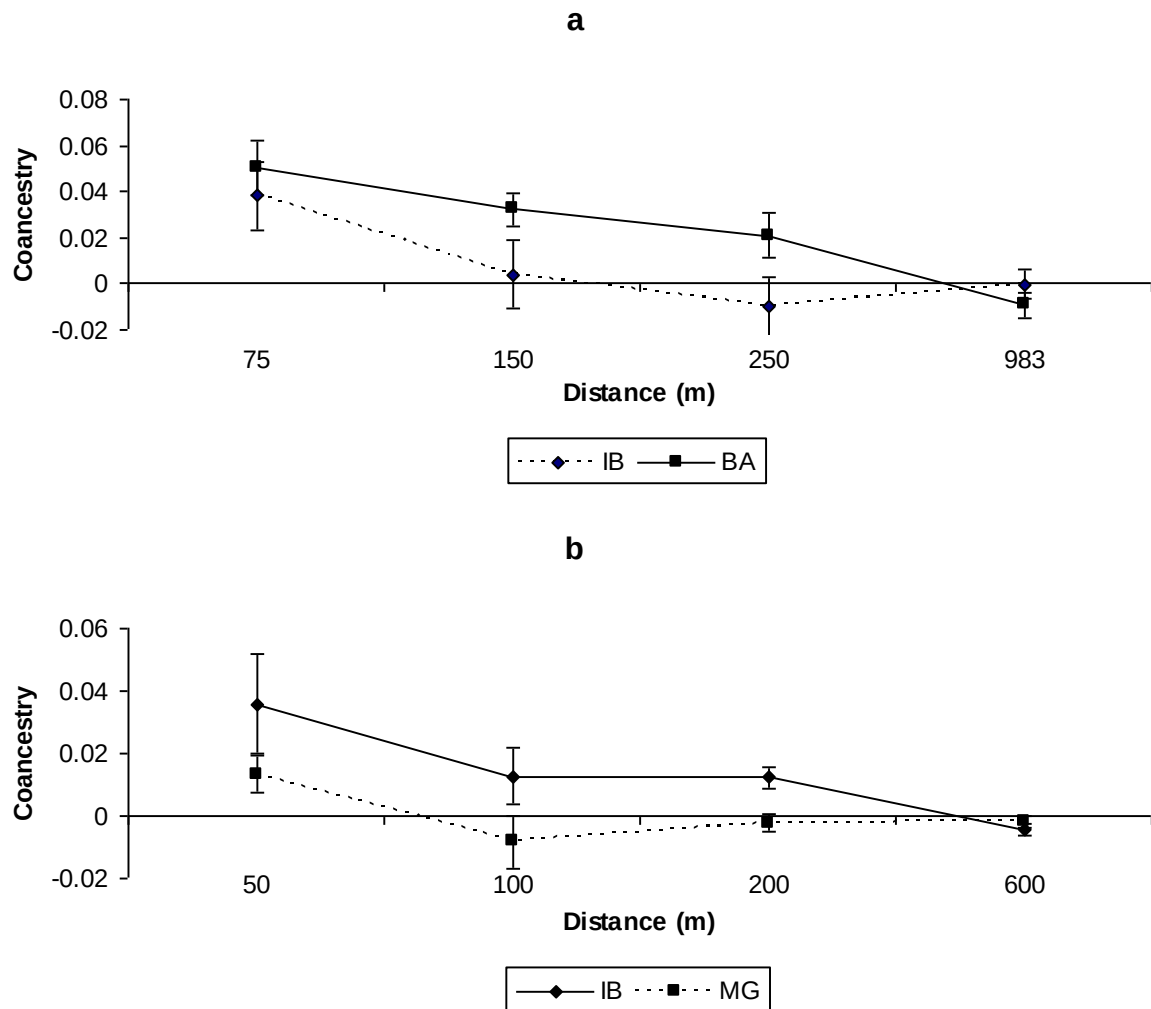
		<i>R</i>	<i>H_e</i>	<i>H_o</i>	<i>F</i>
<i>Cariniana estrellensis</i>					
Ibicatu	<50 vs ≥ 50%	0.079	0.189	0.913	0.473
Bataguassu	<50 vs ≥ 50%	0.974	0.902	0.852	0.923
<i>Cariniana legalis</i>					
Ibicatu	<50 vs ≥ 50%	0.266	0.124	0.030	0.240
Mogi-Guaçu	<50 vs ≥ 50%	0.785	0.250	0.740	0.542

R is the allelic richness for nine genotypes; *H_o* is the observed heterozygosity; *H_e* is the expected heterozygosity; *F* is the fixation index.

4.2 INTRAPOPULATION SPATIAL GENETIC STRUCTURE

Significant spatial genetic structure (SGS) was detected for *C. estrellensis* up to approximately 115 m in IB and 350 m in BA (Figure 4). For *C. legalis*, SGS was significant up to approximately 250 m in IB and 60 m in MG (Figure 4). Beyond these distances, the mean pairwise coancestry coefficient decreased to non-significant or significantly lower than zero, indicating a typical pattern of isolation by distance. The intensity of SGS measured by the S_p -statistic was significant, but not significantly different between populations of each species (Table 11). Based on restricted b_k , the historical gene dispersal distance (σ_g) produced a maximum of 8.5 m and a Nb of 46 for *C. estrellensis* in IB and in BA the maximum was 140 m with a Nb of 78. For *C. legalis* in IB, we found a maximum σ_g of 54 m and a Nb of 152 and in MG, the maximum σ_g was 28 m and Nb was 155, assuming $D_e = D/10$.

Figure 4- Correlogram of coancestry coefficient (θ_{ij}) in four distance classes between *Cariniana estrellensis* trees located in Ibicatu and Bataguassu (a) and *Cariniana legalis*, located in Ibicatu and Mogi-Guaçu (b).



Source: Prepared by author.

Table 11- Estimates of spatial genetic structure indices for trees of both species in the studied populations.

	<i>Cariniana estrellensis</i>		<i>Cariniana legalis</i>	
	Ibicatu	Bataguassu	Ibicatu	Mogi-Guaçu
Trees/ha	0.36	0.063	0.93	3.6
First distance class (m)	0–75	0–25	0–100	0–63
Coancestry: θ_1	0.038*	0.127*	0.019*	0.004*
Regression slope: b_k	$-0.019 \pm 0.010^*$	$-0.028 \pm 0.018^*$	$-0.015 \pm 0.008^*$	$-0.019 \pm 0.010^*$
Distance where b_k was estimated (m)	0–200	0–600	0–200	0–150
Sp -statistic: $\pm$ SE	$0.020 \pm 0.011^*$	$0.033 \pm 0.022^*$	$0.015 \pm 0.007^*$	$0.019 \pm 0.006^*$
D_e	0.36	0.00063	0.0093	0.036
$Nb \pm$ SE	21 ± 22	48 ± 86	54 (41–70)	149 ± 150
$\sigma \pm$ SE (m) ($D_e = D/2$)	2.2 ± 0.9	78 ± 52	21 (19–24)	19.8 ± 8.8
D_e	0.05	0.000315	0.000451	0.015
$Nb \pm$ SE	46 (42–51)	$78 \pm$ NC	152 (62)	155 (109–201)
$\sigma \pm$ SE (m) ($D_e = D/10$)	8.5 (8.1–9.0)	$140 \pm$ NC	54 (10)	28 (24–33)

θ_1 is the mean pairwise coancestry coefficient in first distance class; b_k is the regression slope of θ_1 on log of spatial distance; Sp is the intensity of spatial genetic structure; $\pm$ 2SE is the standard error. * $P < 0.05$.

4.3 EFFECTIVE POPULATION SIZE

The group coancestry coefficient (Θ) was low among all pairwise *C. estrellensis* (0.03473–0.00236) and *C. legalis* (0.00747–0.01375) trees suggesting that in random mating, the expected inbreeding from mating among related trees is very low ($< 5\%$, Table 12). The variance effective population size (N_e) shows that the 26 and 284 *C. estrellensis* trees of IB and BA correspond to 10 and 119 unrelated and non-inbred individuals or a N_e/n of 0.37 and 0.42, respectively. For *C. legalis*, the estimated N_e suggests that of the 65 and 26 trees of IB and MG, 33 and 15 are unrelated and non-inbred individuals or a N_e/n of 0.5 and 0.57, respectively. The estimated loss of heterozygosity after 50 generations ($H_{o(t=50)}$), based on actual N_e , indicates that the observed heterozygosity for *C. estrellensis* in IB and BA is expected to be only 7.7% ($H_{o(t)} = 0.055$) and 81.0% ($H_{o(50)} = 0.527$), respectively, of the actual ($H_{o(0)}$: IB= 0.71; BA= 0.65). For *C. legalis* in IB and MG, the observed heterozygosity

is expected to be 46.6% ($H_{o(t)} = 0.378$) and 18.4% ($H_{o(50)} = 0.151$), respectively, of the actual ($H_{o(0)}$: IB= 0.81; MG= 0.82).

Table 12- Group coancestry (Θ), variance effective size (N_e) and expected decrease in heterozygosity after 50 generations ($H_{o(t=50)}$) by genetic drift for samples of *Cariniana estrellensis* and *Cariniana legalis*; n is the sample size; H_o is the actual observed heterozygosity; $H_{o(exp)}$ is the expected values for H_o after 50 generations due to genetic drift.

Sample	n	Θ	N_e	N_e / n	$H_{o(t=50)}$	H_o	$H_{o(exp)}$
<i>Cariniana estrellensis</i>							
Ibicatu	26	0.03473	9.5	0.37	0.077	0.71	0.06
Bataguassu ¹	284	0.00236	118.5	0.42	0.810	0.65	0.53
<i>Cariniana legalis</i>							
Ibicatu ²	65	0.00747	32.5	0.50	0.466	0.81	0.38
Mogi-Guaçu ²	26	0.01375	14.8	0.57	0.184	0.82	0.15

¹Kubota (2017); ²Tambarussi et al. (2015); *P< 0.05. SE is the standard error.
Source: Prepared by author.

4.4 PARENTAGE ANALYSIS

For all trees sampled, the combined non-exclusion probability of the first parent (P_1) was higher in *C. estrellensis* (IB= 0.045008; BA= 0.025563) than in *C. legalis* (IB= 0.002699; MG= 0.000383). This resulted in a cryptic gene flow (C_{gf}) higher in *C. estrellensis* (IB= 0.698; BA= 0.999) than *C. legalis* (IB= 0.161; MG= 0.010) populations, indicating a high probability that pollen and seed flow in *C. estrellensis* may be biased (Table 13). However, the combined non-exclusion probability of identity (Q_i) was lower for both *C. estrellensis* populations (IB= 0.00000002; BA= 0.0000054) than for *C. legalis* (IB= 0.00044367; MG= 0.00030133), indicating that all adults present different genotypes, which is favourable for the assignment of parents in parentage analysis.

Table 13- Combined non-exclusion probability of the first parent (P_1), cryptic gene flow (C_{gf}), and the combined non-exclusion probability of identity (Q_i) for samples of *Cariniana estrellensis* and *Cariniana legalis*.

	P_1	n	C_{gf}	Q_i
<i>Cariniana estrellensis</i>				
Ibicatu	0.045008	26	0.698	0.00000002
Batagassu	0.025563	284	0.999	0.00000540
<i>Cariniana legalis</i>				
Ibicatu	0.002699	65	0.161	0.00044367
Mogi-Guaçu	0.000383	26	0.010	0.00030133

At least one putative parent was found for 16 and 123 *C. estrellensis* trees of IB and BA, respectively, and for 25 and 10 *C. legalis* trees of IB and MG, respectively. These results suggest a respective seed immigration rate of 38.5 and 56.7% for *C. estrellensis*, and for *C. legalis* of 61.5% for both populations (Table 14). Two putative parents within the sample areas were detected for 5 and 28 *C. estrellensis* trees of IB and BA, respectively, and for 5 *C. legalis* tree of IB, suggesting a rate of pollen flow of 80.1 and 90.1% for *C. estrellensis*, and for *C. legalis* of 92.3 and 100%. No trees were themselves assigned as the parent tree, indicating an absence of realized self-fertilization. In general, mean coancestry coefficient between trees (θ_{xy}) and assigned putative parents was lower than expected for *C. estrellensis* in IB (0.18) and for *C. legalis* in IB (0.22) and MG (0.10). Assuming a minimum coancestry coefficient of 0.1 ($\theta_r \geq 0.1$) to determine parents as related individuals, we found two pairs in IB ($\theta_r = 0.17$) and 11 pairs in BA ($\theta_r = 0.29$) for *C. estrellensis*, and three pairs ($\theta_r = 0.20$) in IB for *C. legalis* to be related parents (Table 14). Thus, the realized mating among related trees (t_r) for *C. estrellensis* in IB was 0.125 and in BA was 0.089 and in *C. legalis* in IB it was 0.120. The pairwise coancestry coefficient between assigned trees with at least one common parent ranged from -0.01 to 0.15. The mean fixation index (F) for assigned trees with at least one parent ranged from -0.14 to 0.13, assigned trees with two parents ranged from -0.01 to 0.09, and for assigned trees with related parents ranged from -0.12 to 0.14. The mean distance between related parents for *C. estrellensis* ranged from 615 to 398 m and for *C. legalis* the distance was 312 m.

4.5 POLLEN AND SEED DISPERSAL DISTANCE

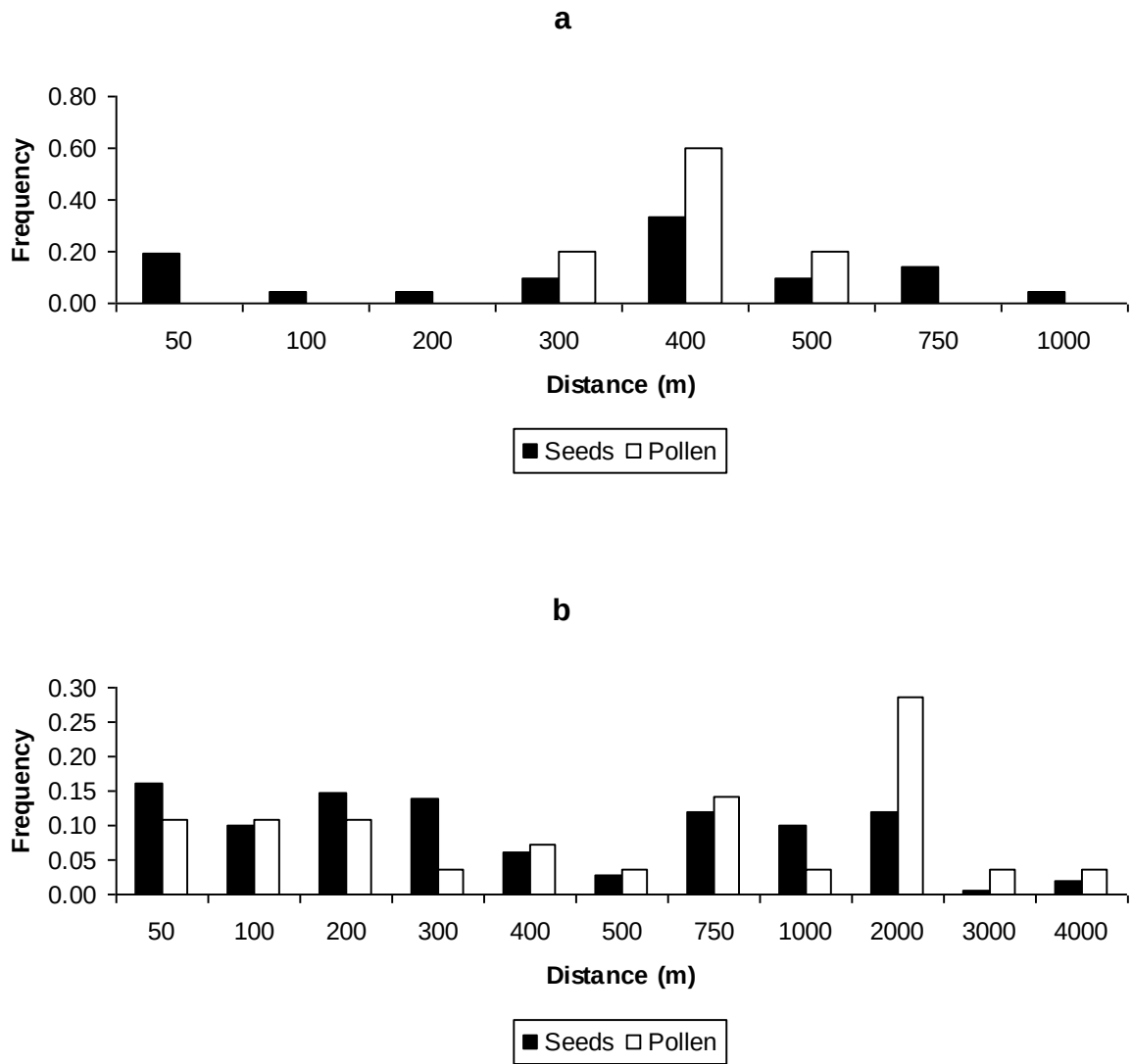
The pollen dispersal distance for *C. estrellensis* ranged from 10 to 3309 m, with a mean of 338 and 850 m in IB and BA, respectively. For *C. legalis*, the pollen dispersal distance ranged from 183 to 385 m, with a mean of 312 m in IB (Table 14, Figure 5). For *C. estrellensis*, the median pollen dispersal distance was lower (IB= 330 m, BA= 516 m) than the mean, indicating a pattern of isolation by distance. However, for *C. legalis* the median (322 m) was higher than the mean, indicating a random pollen dispersal pattern. The effective pollination area (A_{ep}) ranged from 3.9 to 476 ha for *C. estrellensis* and for *C. legalis* it was 3.2 ha, indicating an effective pollination radius (r_{ep}) ranging from 111 to 1,231 m for *C. estrellensis* and 101 m for *C. legalis* (Table 14). Seed dispersal distance for *C. estrellensis* ranged from 2 to 3483 m, with a mean of 308 m in IB, and in BA the minimum was 452 m and maximum was 615 m. For *C. legalis* seed dispersal distance ranged from 14 to 851 m, with a mean minimum and maximum of 338 and 393 m, respectively in IB, and in MG it was 72 m. The median seed dispersal distance was lower than the mean for the BA population of *C. estrellensis* and for both *C. legalis* populations, indicating a pattern of isolation by distance.

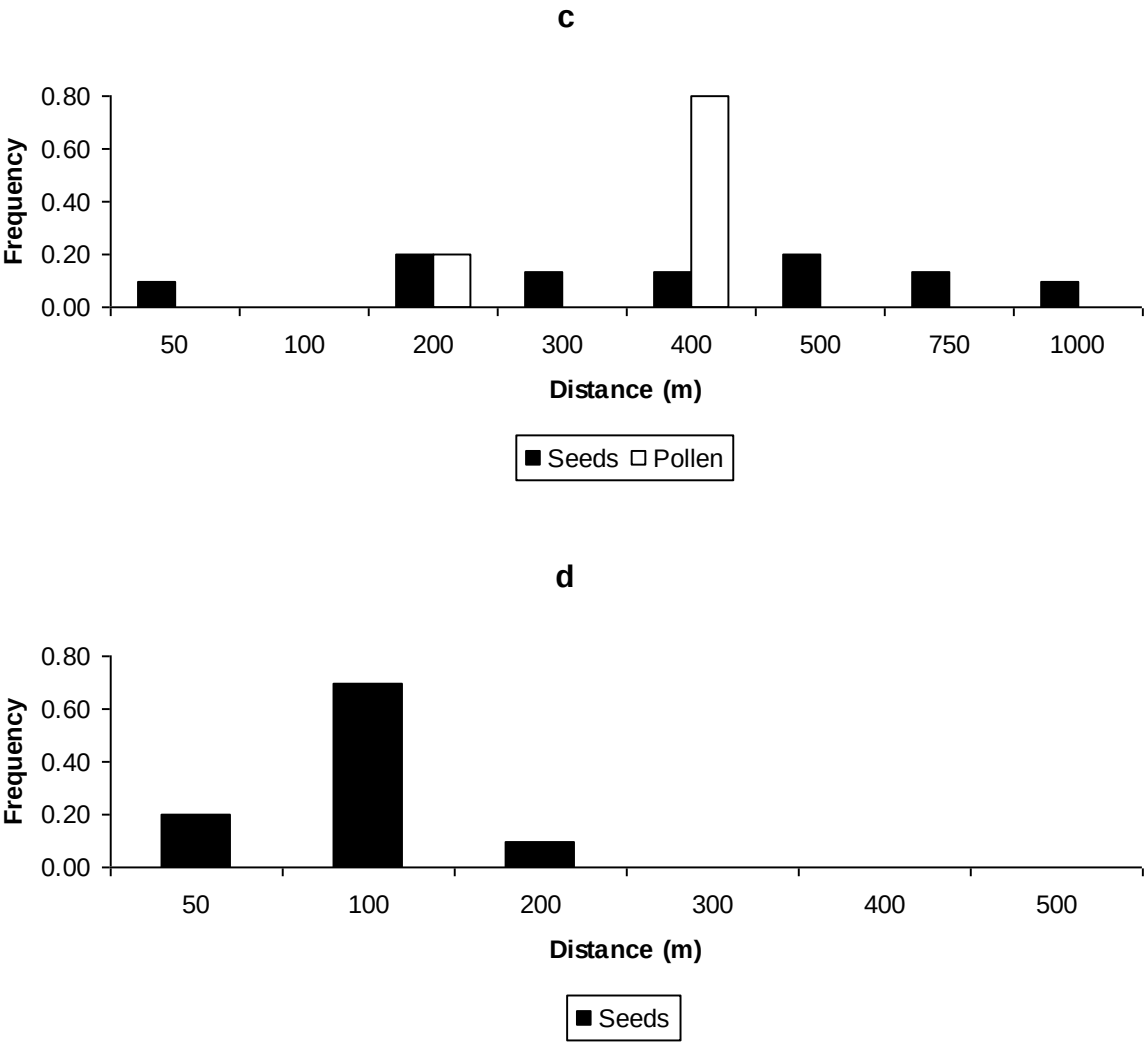
Table 14- Pollen and seed flow and dispersal distance, pairwise coancestry (θ_{xy}) and fixation index (F) for *Cariniana estrellensis* in Ibicatu (IB) and Bataguassu (BA) and *Cariniana legalis* in Ibicatu (IB) and Mogi-Guaçu (MG).

	<i>Cariniana estrellensis</i>				<i>Cariniana legalis</i>			
	IB		BA		IB		MG	
	Pollen	Seeds	Pollen	Seeds	Pollen	Seeds	Pollen	Seeds
Sample size: n	26	26	284	284	65	65	26	26
Number of unassigned trees (%)	21 (80.1)	10 (38.5)	256 (90.1)	161 (56.7)	60 (92.3)	40 (61.5)	26 (100)	16 (61.5)
Number of assigned trees	5	16	28	123	5	25	0	10
Mean distance (SD) m	338 (88)	308 (227)	850 (888)	452 (594)/615 (697)	312 (80)	338 (230)/393 (236)	-	72 (28)
Minimum/Maximum distance (m)	226/465	4/878	10/3309	2/3483	183/385	14/851	-	24/131
Median: Minimum/Maximum (m)	330	325	516	233/340	322	300/397	-	67
Effective pollination neighbor area: A_{ep} (ha)	3.9	-	476	-	3.2	-	-	-
Effective pollination radius: r_{ep} (m)	111	-	1231	-	101	-	-	-
Coancestry								
Assigned trees and parents (SD)	0.18 (0.04)	-	0.25 (0.00)	-	0.22 (0.01)	-		0.10 (0.04)
Between relative parents: $\theta_r \geq 0.1$ (SD)	0.17 (0.06)	-	0.29 (0.04)	-	0.20 (0.03)	-		-
Mating among relatives: t_r	0.125	-	0.089	-	0.120	-		-
One parent in common (SD)	0.15 (0.02)	-	0.02 (0.02)	-	0.08 (0.02)	-		0.01 (0.03)
Fixation index: F								
Assigned trees (SD)	-0.14 (0.05)	-	0.02 (0.02)	-	0.10 (0.2)	-		0.13 (0.04)
Assigned trees both parents (SD)	-0.01 (0.06)	-	0.07 (0.03)	-	0.09 (0.07)	-		
Inbreeds assigned for θ_r (SD)	-0.12 (0.06)	-	0.08 (0.03)	-	0.14 (0.07)	-		-

SD is the standard deviation.

Figure 5- Frequency distribution of seed and pollen dispersal distance in *Cariniana estrellensis* of Ibicatu (a) and Bataguassu (b) and *Cariniana legalis* of Ibicatu (c) and Mogi-Guaçu (d).





Source: Prepared by author.

5 DISCUSSION

5.1 GENETIC DIVERSITY

Genetic diversity is mainly distributed between species ($G_{st}' = 0.550$) rather than within species. Observed (H_o) and expected (H_e) heterozygosity were similar between populations of the species. The indices of heterozygosity, and particularly H_e are known to not be affected by sample size, due to the fact that they are dependent on gene frequencies. Thus, these indices are not the most effective in investigating processes that affect genetic diversity, such as forest fragmentation and logging (SEBBENN et al., 2008). However, for *C. legalis* in IB and *C. estrellensis* in BA, the fixation index (0.09 and 0.06, respectively) was significantly higher than zero in trees with low DBH, suggesting a reduction in levels of inbreeding as trees move from younger to older life stages, as well as mortality of inbred trees at early stages of growth due to inbreeding depression.

5.2 MATING SYSTEM AND INBREEDING

All assigned trees of both species were the result of outcrossing. This is consistent with previous analyses of open-pollinated *C. estrellensis* seeds (GUIDUGLI et al., 2016), suggesting selection against selfed individuals or self-incompatibility. In contrast, self-fertilization has been reported in studies on *C. legalis* based on open-pollinated seeds (4.3–17%, TAMBARUSSI et al., 2016) and juveniles established in provenance and progeny tests (1–9.9%, SEBBENN et al., 2001). This suggests stronger selection against selfed *C. legalis* individuals in natural populations than in experimental trials. However, realized mating among related individuals (t_r) was detected for both species (8.9–12.5%). In previous studies of *C. estrellensis*, no t_r was found based on open-pollinated seeds (GUIDUGLI et al., 2016), but for *C. legalis* mating among relatives has been detected in samples of open-pollinated seeds (4.4–26.6%, TAMBARUSSI et al., 2016) and in juveniles in experimental trials (5.9–9.1%, SEBBENN et al., 2001). These results further suggest selection against inbred individuals especially at early stages for *C. legalis*; however, in natural populations as well as in trials, inbred individuals may survive for a long time.

As no selfing was detected by parentage analysis, the inbreeding found in populations of both species can be attributed to mating between relatives. Both *C. estrellensis* and *C.*

legalis are subject to inbreeding depression. Kubota (2017) detected stronger inbreeding depression for survival in *C. estrellensis* at the seedling stage (8 months of age) for individuals produced from self-fertilization (2.6%) than from mating among relatives (0.2%). Tambarussi et al. (2017) also found greater inbreeding depression for survival in *C. legalis* seedlings produced from self-fertilization (3.9-36%) than from mating among relatives (0.2–30.4%). The stronger inbreeding depression for selfing than mating among related trees is supported by the absence of selfed trees in our study populations, with inbred individuals originated from mating among relatives surviving up to 91 years of age in *C. estrellensis* and 122 years of age in *C. legalis*.

Selfing results in inbreeding of at least 50% ($100\%(0.5(1 + F_m))$, where F_m is the inbreeding in the mother) and mating among related individuals results in inbreeding equal to the coancestry between related parents ($F_r = \theta_r$); for example, if the parents are full-sibs ($\theta_{fs} = 0.25$), inbreeding of 25% is expected in their descendants. Thus, inbreeding originating from mating among related individuals is expected to result in lower homozygosis for identical by descent alleles than from selfing. As deleterious genes that produce inbreeding depression generally occur at low frequencies, mating among related individuals has low probability to be combined in the homozygosis stage and, consequently, some mating among related individuals do not result in inbreeding depression. Furthermore, the expression of inbreeding depression has been reported (KUBOTA, 2017) as stronger in early stages of tree development, which can explain the decreased levels of inbreeding among older trees. The fact that inbreeding in early stages was only detected for *C. legalis* in IB and for *C. estrellensis* in BA may be explained by the fact that the genetic load or the occurrence and frequency of deleterious alleles is variable between populations and individuals due to the life histories of mutation in the populations.

5.3 INTRAPOPULATION SPATIAL GENETIC STRUCTURE

Populations of both species presented spatial genetic structure (SGS), indicating that there is high probability that trees located within these distances are genetically related. A decrease in the mean pairwise coancestry coefficient with an increase in the distance between trees indicates a gene dispersal pattern of isolation by distance (IBD). This pattern is consistent with that expected for natural tree populations (HARDY et al., 2006; DEGEN; SEBBENN, 2014). SGS is mainly determined by seed and pollen dispersal (HARDY et al.,

2006; BORN et al., 2008). However, the absence of SGS beyond the detected distances does not mean that at these distances individuals are unrelated; some trees may be related but they are not grouped, and they can mate if pollen vectors visit such trees, as detected herein. The mean distance between assigned trees and related parents was greater than the SGS distance detected: for *C. estrellensis* it ranged from 398 to 615 m, and for *C. legalis* it was 312 m. Another factor that we must consider is that the study populations are located in an extensively fragmented forest landscape and deforestation in the area may have modified the original SGS due to logging.

The SGS intensity measured by the S_p -statistic was similar between populations and species (ranging from 0.015 to 0.033). This can be explained by the fact that both species have similar dispersal vectors: pollen by bees and seeds by wind. The S_p -statistic was lower than the estimates for other wind pollinated species using SSR markers, such as *Dicorynia guianensis* (0.100), and higher than the estimates for *Jacaranda copaia* (0.015) using RAPD (HARDY et al., 2006).

5.4 GENE FLOW

The results for both species suggest greater levels of pollen (80.1–100%) than seed immigration into the populations (38.5–61.5%). The coefficient of coancestry expected between parents and sibs is 0.25, or on average 25% of genes of parents and descendants are identical by descent. Mean pairwise coancestry coefficient between trees and assigned putative parents was lower than expected for both *C. estrellensis* (0.18–0.25) and *C. legalis* (0.10–0.22). The differences between the estimated and expected values (0.25) are due to difficulties in estimating kinship using genetic markers (CARVALHO et al., 2010). However, when several loci are used simultaneously, the mean value of loci tends to the expected value. Thus, we can consider that the estimates obtained herein reflect the expected relationship between parents and descendants. This may also explain the lower expected values for *C. legalis* which is likely an artefact of the sampling as the number of loci used (7 loci) was lower than for *C. estrellensis* (9 loci).

Nevertheless, the estimates of pairwise coancestry between parents and descendants were greater than zero, supporting the hypothesis that these individuals are indeed related, and the trees assigned to parents are likely correct. The majority of *C. estrellensis* and *C. legalis* trees that were not assigned a mother or father are remnants of the pre-fragmentation era (<

100 years) in the study populations. Thus, these results may be explained by the fact that parent trees were logged from the area around or within the forest fragments, died before sampling, or the trees originated from seed immigration from populations located outside of the sample areas. The results also demonstrate that the populations are not genetically isolated due to the occurrence of pollen and seed flow from outside the study populations. Pollen and seed flow introduces new alleles into a population, enabling increases in genetic diversity and effective population size.

5.5 POLLEN DISPERSAL DISTANCE

Both species are mainly pollinated by bees, which have the potential for long distance pollen dispersal (GHAZOUL, 2005). Realized pollen dispersal for *C. estrellensis* reached longer distance (3309 m) than for *C. legalis* (IB= 385 m). Mean realized pollen dispersal distance for *C. estrellensis* was greater in BA (850 m) than in IB (338 m) and that detected for *C. legalis* in IB (312 m). The same pattern was observed for the effective pollination area (A_{ep}) and effective pollination radius (r_{ep}) for the populations of the species (Table 14). However, it is important to note that these results are likely underestimates due to pollen immigration or mortality of pollen parents. In both populations of *C. estrellensis*, pollen was dispersed in a pattern of isolation by distance (IBD), with a higher frequency of pollination occurring between trees in closer proximity than more distant trees. However, in IB for *C. legalis* the pattern was random. This random pattern may be due to the underestimation of pollen dispersal distance due to pollen immigration, death or logging of the pollen parents.

The distances and realized patterns of pollen dispersal for both species can be attributed to many factors, such as sample design and types of individuals sampled, pollen dispersal vectors, flowering phenology, self-incompatible systems, inbreeding depression, among others. Studies carried out in small areas will result in lower mean and maximum dispersal distances than in larger areas. This can explain the longer pollen dispersal distance detected for *C. estrellensis* in BA, where the study area was larger (448.2 ha) than in IB (72 ha) for both species. Furthermore, as the sampling in this study did not include seeds, the results for both species represent the realized pollen dispersal and not the effective pollen dispersal, which occurs at fertilization. Based on samples of open-pollinated seeds of *C. estrellensis* from BA, effective pollen dispersal reached up to 3519 m, with a mean of 597 m, and also followed an IBD pattern (KUBOTA, 2017). Similarly, Guidugli et al. (2016) studied

a population of *C. estrellensis* in an eight ha forest fragment and detected a mean pollen dispersal of 146.9 m. Based on samples of open-pollinated seeds of *C. legalis*, pollen reached up to 922 m in IB, with a mean of 352 m and also followed an IBD pattern (TAMBARUSSI et al., 2015). We can see that the effective and realized maximum, mean, and pattern of pollen dispersal do not differ widely. The minimal differences can be due to many factors that can occur between fertilization and the current life cycle of the sampled trees, such as inbreeding depression, random mortality, disease, predation, and logging, which can change the effective pattern of pollen dispersal in relation to that detected here, the realized pollen dispersal pattern.

Ghazoul (2005) notes that fragmented populations can be sustained if pollinators are able to travel long distances. The results of this study for *C. estrellensis* and *C. legalis*, which are mainly pollinated by bees, confirm this expectation. Our results suggest that, currently, there are favorable conditions for maintaining the genetic diversity of the studied populations, thus indicating their utility as sites for *in situ* conservation of these vulnerable species.

5.6 SEED DISPERSAL DISTANCE

Seed dispersal in *C. estrellensis* also reached long distances in the BA population (3483 m). The explanation for this result is the same as that discussed for pollen; the ability to measure gene dispersal depends on the sample design and as the sample area of BA was larger than the other studied populations of both species, we were able to detect longer seed dispersal distances. This also explains why mean seed dispersal distance for *C. estrellensis* was longer in BA (452–615 m) than in IB (308 m) and for *C. legalis* it was greater in IB (338–393 m) than MG (72 m). However, the seed dispersal pattern was isolation by distance.

The maximum seed dispersal was greater than pollen dispersal in all populations of *C. estrellensis* and in IB for *C. legalis*. This can be explained by the fact that for both species, seeds are dispersed by wind and pollen dispersed mainly by bees, both of which are vectors with the potential for long distance dispersal. Furthermore, aggregation of regenerants near to the parent trees can result in high mortality rates among juveniles due to predation, thus leading to lower levels of aggregation at advanced life stages (JANZEN, 1970), which may result in longer average seed dispersal distances.

For both species, the historical gene dispersal distance (σ_g), based on the model of equilibrium between immigration and genetic drift, resulted in lower gene dispersal distance

than that estimated from parentage analysis (*C. estrellensis*: 8.5–78 m; *C. legalis*: 20–54 m). The differences between the methods can be explained by the fact that parentage analysis is a direct method to determine gene dispersal, while the historical gene dispersal distance, measured by σ_g , is an indirect method that is heavily dependant on the distance at which the regression analysis is carried out. Furthermore, the model of equilibrium between immigration and genetic drift produced an effective population neighbour size (N_b) in *C. estrellensis* (BA= 78, IB= 46) and *C. legalis* (IB= 152, MG= 155) that is generally higher than the census number of the population. This indicates an overestimation, which is likely because our data does not fit the assumption of the model of equilibrium between immigration and genetic drift. Thus, the parentage analysis results are more robust to explain the gene dispersal in the species' populations.

5.7 FINAL CONSIDERATIONS

Cariniana estrellensis and *C. legalis* are Neotropical trees that are vulnerable to extinction and the results reported herein on pollen and seed flow and dispersal will inform strategies aimed at their *in situ* and *ex situ* conservation. First, for *in situ* conservation, the results show that the studied populations of both species are not reproductively isolated due to pollen flow from outside the study areas. However, it is important to maintain connectivity of the studied populations with other reproductive populations that were not included in this study to ensure continuation of gene flow. Thus, other forest fragments and trees of the species surrounding the forest fragments must be preserved.

The variance effective population size (N_e) was lower than census size (N) in all populations. This is related to the occurrence of SGS and inbreeding. Lower N_e than N has also been reported for other trees of the Atlantic Forest (BITTENCOURT; SEBBENN; 2007; GAINO et al., 2010; MORAES; SEBBENN, 2011; TAMBARUSSI et al., 2015; SPOLADORE et al., 2017). Furthermore, with the exception of the *C. estrellensis* population in BA (N_e = 119), the other populations (*C. estrellensis*: IB= 10; *C. legalis*: IB= 33, MG= 15) showed a N_e that is lower than that suggested (N_e = 70) for short term genetic conservation to avoid the effects of genetic drift, such as the occurrence of inbreeding (CABALLERO et al., 2016). If the N_e is low, the genetic drift in the populations will quickly decrease heterozygosity, resulting in a decrease in population fitness (KALINOWSKI; WAPLES,

2002; CABALLERO et al., 2016). The loss of heterozygosity after 50 generations ($H_{o(t=50)}$) based on actual N_e was higher in populations with low N_e (7.7–46.6%) than with higher N_e (*C. estrellensis*: BA= 81.0%). However, as both species present overlapping generations, the loss in heterozygosity is expected to be greater than that observed using this model due to the occurrence of mating between related trees. To avoid inbreeding depression due to genetic drift in small populations, for *in situ* conservation the N_e must be increased to at least 70. The N_e can be increased for *C. estrellensis* in IB and *C. legalis* in IB and MG through the introduction of about 60, 40, and 55 non-inbred and unrelated individuals, respectively. The introduced individuals must originate from other populations of the species within the same region to avoid other possible genetic problems, including outbreeding depression (SEBBENN, 2006). For practical reasons, following the recommendation of Spoladore et al. (2017), we suggest the introduction at least 150 individuals to mitigate against the possible mortality of the introduced trees due to random mortality, predation, disease, and other factors.

The results for SGS provide fundamental information to develop strategies for seed collection for *ex situ* conservation, environmental reforestation, and tree breeding, as SGS defines the distance at which related individuals are likely to occur. Based on the results discussed herein, the distance between trees identified for seed collection must be population specific: for *C. estrellensis* the distance in BA is at least 350 m apart and 115 m apart in IB; for *C. legalis* the distance is at least 250 m in IB and 60 m in MG. The use of seeds that are inbred or from genetically related families, due to related mothers, must be avoided for conservation purposes because it will decrease the effective size of the sampled progeny arrays.

6 CONCLUSIONS

1. Genetic diversity is mainly distributed between species than within species;
2. Populations of both species present spatial genetic structure and near neighbor trees are likely to be genetically related;
3. The extend of SGS is similar between populations of both species;
4. Younger *C. estrellensis* trees from Bataguassu population present greater inbreeding than larger trees and young *C. legalis* trees from Ibicatu population present less heterozygosity and greater inbreeding than large trees due to inbreeding depression;
5. In natural populations of both species, inbreeding depression is stronger for selfed trees than from those originated from mating among related individuals;
6. The spatial isolation of populations of both species did not result in reproductive isolation due to pollen and seed immigration from other populations;
7. Estimates of pollen and seed dispersal distance are dependent on the sample design, with a greater ability to estimate long distances in large rather than small sample areas;
8. The realized dispersal distance of pollen and seeds for both species reached long distances, but in general followed a pattern of isolation by distance.

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