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Spatial genetic structure and mating system in forest tree populations from seasonally dry tropical forests: a review

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Abstract

Gene dispersal processes shape demographic and microevolutionary dynamics of tree species. Gene dispersal patterns can be studied by spatially explicit methods. Spatial genetic structure (SGS), summarized in the S_p statistic, provides indirect estimates of gene dispersal across generations for a known or assumed population effective density. S_p is modulated by exogenous and endogenous factors including the mating system that can be assessed using outcrossing rates (t_m). Knowledge on t_m and S_p are particularly important for the conservation of species in fragmented biomes such as seasonally dry tropical forests (SDTF). The main aim of this review was to evaluate putative drivers of S_p and t_m , and their consequences for gene dispersal in tree species from SDTF. We reviewed 59 genetic studies on SDTF tree species published between 2000 and 2020 and extracted data on propagule dispersal, successional stages, seasonality, mating system, population density, landscape features, type of molecular markers, pairwise kinship in the first distance class (F_1), S_p statistic, mean gene dispersal distance (σ_g), and multilocus outcrossing rates (t_m). S_p was significantly associated with the mating system where $S_p(\text{outcrossing}) > S_p(\text{mixed-mating})$, and population density where S_p was higher in high-density populations. Outcrossing rate was significantly associated with the type of propagule dispersal, where t_m was higher in populations of plants pollinated by wind, and in those with animal-mediated seed dispersal, $t_m(\text{zoochory}) > t_m(\text{anemochory}) > t_m(\text{autochory})$, and with successional stage where $t_m(\text{late-successional}) > t_m(\text{pioneer})$. These factors are relevant to inform management actions in conservation and restoration projects. Thus, the knowledge on the determinants of gene dispersal processes can help to rescue SDTF through sustainable management.

Keywords Gene dispersal · Neotropical forests · Outcrossing rates · Plant dispersal ecology · Population density · Spatial genetic structure

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Alejandra Lorena Goncalves and María Victoria García contributed equally to this work.

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Introduction

Gene dispersal processes shape demographic and microevolutionary dynamics of plant populations (Richardson et al. 2014). The relative contributions of propagule dispersal to overall gene dispersal depend on the movement of biparentally inherited genes by seeds and paternally inherited genes by pollen. The distances at which propagules are effectively dispersed can be inferred from spatially explicit genetic analyses, specifically, (1) from spatial patterns of parent–offspring relationships and (2) from the spatial genetic structure in populations (Chybicki and Burczyk 2010; Vekemans and Hardy 2004) conditional on the availability of population effective density information. Genetic information on parent–offspring relationships lets us characterize the spatial configuration of family units, whereas the spatial structure

of genetic relatedness within populations informs us about demographic-evolutionary dynamics of tree species.

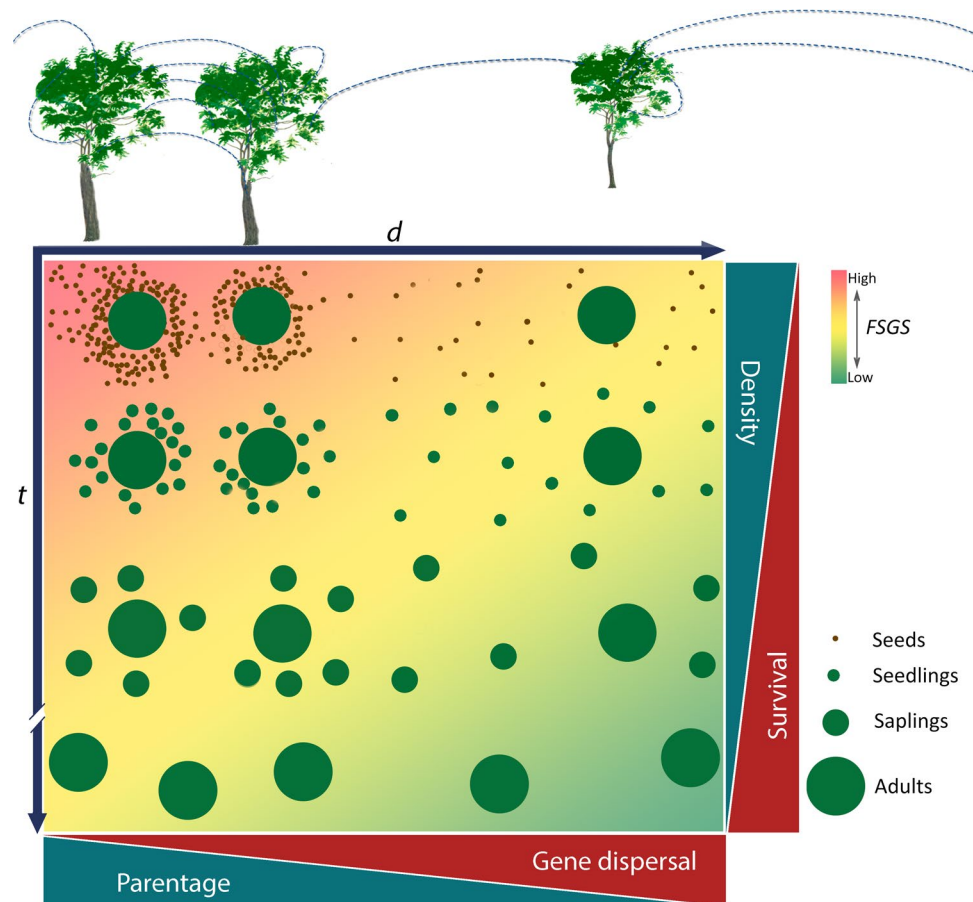
Mating systems, propagule dispersal, and spatial genetic structure are determined by evolutionary and ecological factors and can change over both spatial and temporal scales (Finkeldey 2002; García et al. 2017; Nason and Hamrick 1997). The spatio-temporal variation of outcrossing rates and pollen-mediated dispersal distances can be a consequence of changes in population density and pollinator abundance across the species distribution range and among flowering events (Ward et al. 2005). The movement patterns of seeds and pollen and subsequent complex spatial patterns in offspring mortality affect the gene and genotypic structures of the offspring generation (Gillet et al. 2005), which shape the fine-scale spatial genetic structure (FSGS) through time (Hampe et al. 2010; Hardy et al. 2006; Lowe et al. 2018) (Fig. 1).

Gene dispersal distances can be inferred from genetic data conditional on a set of assumptions using spatially explicit methods. Parent–offspring or parentage analysis can provide information on the mating system and on gene dispersal for a given cohort or generation, and is therefore referred to as a method that provides direct estimates of gene dispersal, whereas FSGS integrates the processes of

dispersal and mortality across generations, and yields therefore indirect estimates of gene dispersal (Oddou-Muratorio and Klein 2008).

Gene dispersal within tree populations is driven by the movement of seeds away from the mother trees and by the movement of pollen among trees. Seed dispersal—as the link between the end of reproduction and the beginning of vegetative growth—is an essential event for the persistence of plant populations by shaping the spatial configuration of sites where individuals establish (Hampe et al. 2010; Hamrick et al. 1993; Wang and Smith 2002). Species whose seeds are deposited near the maternal plant (e.g., gravity or wind dispersal) or species whose seeds are deposited in clumps or patches should have a stronger FSGS than species whose seeds are dispersed by mobile animals (Chung and Epperson 2000; Hamrick et al. 1993). Also, abiotically dispersed and pioneer species in general have a stronger spatial aggregation and a stronger FSGS than late-successional species (Dalling et al. 2002; Lowe et al. 2018). These pioneer species show reduced survival of seeds and seedlings at high conspecific densities (Ghazoul 2005). Population density is also relevant to pollination, which often constrains seed production (Vekemans and Hardy 2004). The movements of pollinators—builders of plant

Fig. 1 Schematic representation of fine-scale spatial genetic structure (FSGS) on different life stages in the space–time complex. Pollination events (dotted lines), time (t), and distance (d) are represented



dispersal networks—configure pollen-mediated gene dispersal (Fenster 1991). Dense aggregations of plants tend to attract more pollinators (Ghazoul 2005). However, cross-fertilization within stands may primarily occur between the nearest flowering trees (Adams 1992; Dick et al. 2008). Spatial aggregation could be reinforced by associations with patchy habitats or it could be disrupted by density-dependent mortality effects (Hampe et al. 2010) (Fig. 1).

Fragmented forest tree populations can show altered patterns of mating and dispersal. Habitat fragmentation affects the mating system of remnant populations by promoting reproductive isolation (Young et al. 1996). Restricted gene dispersal could lead to geographically clustered genetic diversity. This disruption of gene dispersal can have multiple consequences such as more structured and less cohesive gene pools and the increase of isolation by distance over broader areas (Jordano 2017). Fragmentation is also a disruptive process of plant-pollinator interactions (Amorim et al. 2021; Bennett et al. 2020). The cost of dispersal is expected to be a strong selective force in fragmented habitats (Cheptou et al. 2008). Fragmentation can impact gene dispersal if the fragment boundary limits or truncates dispersal (Diniz et al. 2019; Sebbenn et al. 2011) or if fragmentation enhances dispersal distances (Fuchs and Hamrick 2010; White et al. 2002). Thus, pollination success could be positively correlated with local conspecific density in continuous forests (Ghazoul 2005) while in fragmented habitats, pollinators may expand the genetic connectivity, thereby linking forest fragments (Dick et al. 2008) (Fig. 1).

The mating system of forest tree populations has a strong impact on the genetic relatedness of the offspring (Degen and Sebbenn 2014). Parentage analyses allow a direct estimation of gene dispersal parameters based on multilocus genotype data of a population of potential parents of studied seeds or seedlings (Hamrick and Trapnell 2011; Smouse et al. 2001). These direct methods provide a measure of contemporary gene dispersal by the application of a mixed mating model (Ritland and Jain 1981) and can estimate multilocus outcrossing rates, selfing rates, and the proportion of mating among relatives in one or few flowering seasons, dispersal distances and the contribution of pollination from outside the study plot. For example, high rates of outcrossing detected in tropical rainforest tree species (average multilocus outcrossing rate $t_m = 0.88$) were explained as a consequence of self-incompatibility mechanisms (Bawa et al. 1985). Ward et al. (2005) reported that self-fertilization rates were inversely correlated with population density in Neotropical trees from rainforests, thus suggesting more selfing at low density. Similarly, outcrossing rates in fragmented plant populations showed a significant overall decrease compared to those in continuous populations (Aguilar et al. 2008) indicating that small isolated populations

may experience mate limitation and loss of genetic diversity through increased inbreeding (Aguilar et al. 2008).

Another approach to estimate dispersal parameters is based on the spatial genetic structure: it allows an indirect estimation of gene dispersal parameters, based on the regression of genetic relatedness versus geographical distance among individuals within populations (Luximon et al. 2014; Vekemans and Hardy 2004), conditional on effective population density. The FSGS can be quantified using the Sp statistic defined as $Sp = -b_F / (1 - F_1)$, where F_1 is the mean kinship coefficient F_{ij} between all individuals i and j belonging to a first distance interval and b_F is the regression slope of all F_{ij} on the sampling distances r_{ij} or $\ln(r_{ij})$ (Vekemans and Hardy 2004). This indirect method provides a measure of the historical gene dispersal, i.e., an average of this value over several or dozens of generations of the population's past (Austerlitz et al. 2004). Significant effects of the mating system, pollen and seed dispersal vectors, and plant population density on Sp statistics were detected (Vekemans and Hardy 2004). The FSGS patterns within populations also depend on the degree of overlap between “gene shadows” of adjacent individuals, i.e., the overlap of seed and pollen-mediated gene dispersal events around each parent (Hardy et al. 2006). The degree of overlap between “gene shadows” is directly proportional to density and gene dispersal distances. It implies that a specific level of FSGS can be obtained under higher density and lower dispersal distance, or vice versa (Hardy et al. 2006). Thus, taking into account the relevance of the landscape structure on population density, spatial genetic structure, and dispersal distances, we still lack insight into how these factors affect forest tree species from one of the most fragmented Neotropical forest ecosystems, the seasonally dry tropical forests (SDTF).

Across Latin America and the Caribbean, SDTF are distributed into 12 highly threatened floristic groups (DRYFLOR 2016; Särkinen et al. 2011) (Fig. 2). These forests have a relevant biological value in terms of their highly endemic flora (DRYFLOR 2016) dominated by woody species of the families Leguminosae, Bignoniaceae, and Anacardiaceae (Prado 2000). The SDTF are a mosaic of a few large forest fragments and multiple small and disturbed fragments with crucial importance for the connectivity and persistence of the forest (Särkinen et al. 2011). These forests are in a critical state because they have suffered from recent anthropogenic fragmentation (DRYFLOR 2016).

This review builds upon previous reviews and syntheses of genetic diversity (Hamrick and Godt 1996), mating systems (Ward et al. 2005), and fine-scale spatial genetic structure (Hardy et al. 2006) of forest tree species. The main aim of this review is to evaluate the underlying factors of spatial genetic structure and outcrossing rates, and their consequences for gene dispersal in keystone tree species from seasonally dry tropical forests. Therefore, this review

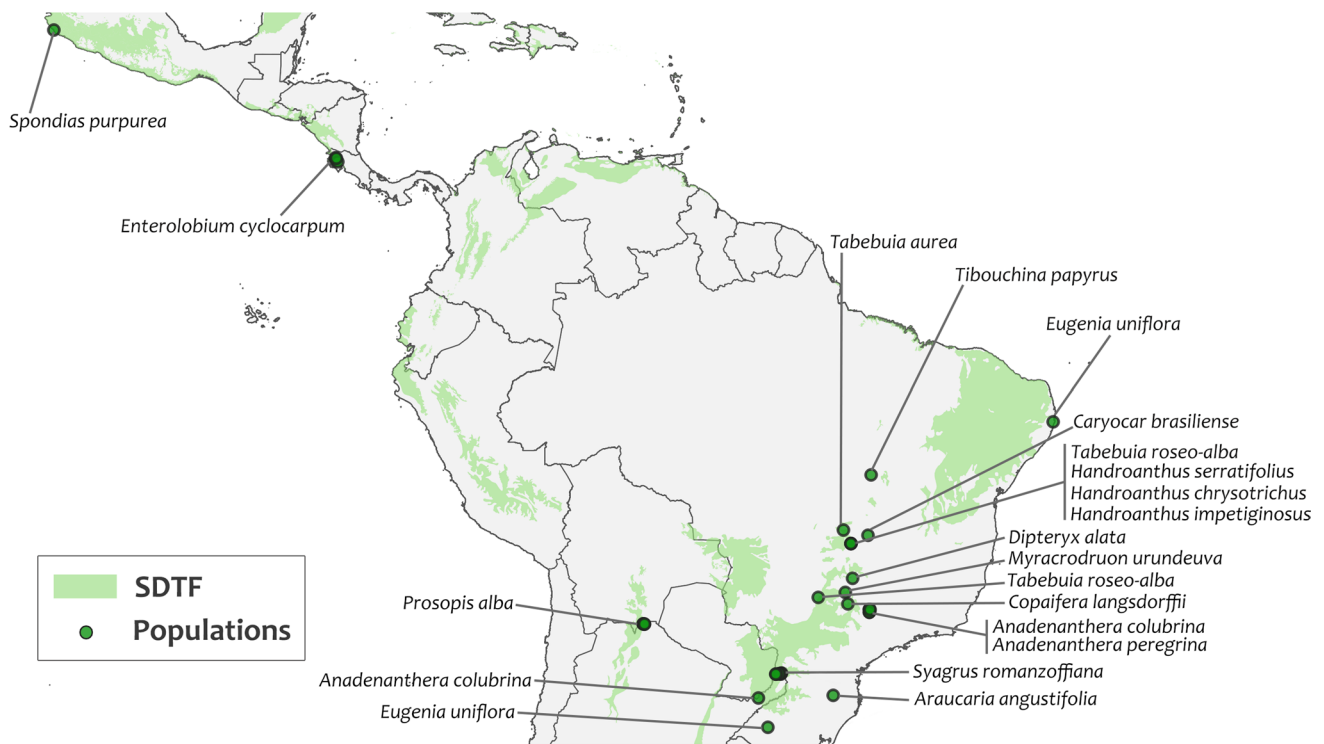


Fig. 2 Sampling sites of forest tree populations from seasonally dry tropical forests (SDTF) analyzed in the studies considered in this review. Schematic SDTF distribution based on DRYFLOR (2016)

provides a framework to contextualize future studies of forest tree species from this biome, weighing the different factors that influence gene dispersal distances of woody plants at local and regional scales, which is relevant to understand evolutionary processes, impacts, and ecosystem responses, in order to provide useful information for conservation strategies and sustainable management.

Materials and methods

Compilation of database

A comprehensive literature review of gene dispersal, spatial genetic structure, and mating system in forest tree populations from seasonally dry tropical forests was undertaken by searching and accessing peer-reviewed literature from the Scopus database, for articles listed until December 2020. The keywords: “seasonally dry tropical forest” AND “tree species” AND “gene dispersal” were considered. Therefore, this review is drawn from published papers in journals with diverse scopes to provide an up-to-date account of the present status of this active research area. For each study, we considered the following variables on population and species characteristics (see categories and further precisions below): pollination syndrome, body size of pollinators, distances of

pollen movement, seed dispersal syndrome, seed dispersers, the morphology of diaspores, distances of seed movement, successional stage, seasons of blooming and fruiting, mating system, population density, and landscape features. We focused on the following estimated indices: (1) FSGS parameters: F_1 , the pairwise kinship in the first distance class, the Sp statistic, and σ_g , which represents half the mean squared gene dispersal distance in two-dimensional space (Vekemans and Hardy 2004) and (2) mating system parameters: t_m , the multilocus outcrossing rate (Ritland 2002) (Table 2).

We studied 50 populations of forest tree species that largely occur in SDTF, with some extending into the rain or dry forests (Fig. 2). The species were taxonomically resolved and belonged to 14 different genera and eight families. The Bignoniaceae and Leguminosae families were the most widely represented, as in the SDTF (Table 1).

For pollination syndrome, three categories were considered: anemogamous, entomophilous, and bat-pollinated. Within entomophilous species, the type of pollinating insect was recorded by body size as follows: small bees, medium size bees, and large bees based on the O’Connell et al. (2018) estimations. For seed dispersal syndromes, seven categories were considered: autochory, anemochory, autochory-zoochory, zoochory by birds, zoochory by bats, zoochory by livestock, and zoochory by rodents, while dispersal distances were evaluated based on the Vittoz and Engler

Table 1 Biological information of SDTF forest tree species analyzed in this review

Species	Fam ¹	Pollination		d1	Seed dispersal			Phenology			Mating system ⁸	Ref	
		L1 ²	L2		L3 ³	L4 ⁴	L5 ⁵	d2	L6 ⁶	L7 ⁷			L8 ⁷
<i>Anadenanthera colubrina</i>	Leg	e	Small bees	300–2760	Au	–	DP	<50	Pi	Early WS	DS	m (M)	[1–3]
<i>Anadenanthera peregrina</i>	Leg	e	Bees	402–1953	Au	–	DP	<50	Pi	Early WS	DS	m (M)	[3,4]
<i>Araucaria angustifolia</i>	Ara	Ab	Wind	83–131	Au-Zo	Ro, Bi	P	20–75	Lt	DS	WS	d	[5,6]
<i>Caryocar brasiliense</i>	Car	z	Bats		Zo	Bi	Dr	400–1500	Lt	WS	DS	m (O)	[7,8]
<i>Copaifera langsdorffii</i>	Leg	e	Small bees, bees	300–2760	Zo	Bi	FA	40–120	It	WS	DS	m (O)	[9–12]
<i>Dipteryx alata</i>	Leg	e	Bees	402–1953	Zo	Ro, Ba	Dr	400–1500	Lt	WS	DS	m (M)	[13–15]
<i>Enterolobium cyclocarpum</i>	Leg	e	Bees	402–1953	Zo	Ma, Ca, Ho	IP	400–1500	It	DS	DS	m (M)	[38]
<i>Eugenia uniflora</i>	Myrt	e	Bees	402–1953	Zo	Bi	IP	400–1500	Pi	WS	WS	m (M)	[16]
<i>Handroanthus chrysotrichus</i>	Big	e	Large bees	388–2207	An	–	Dr	40–150	Pi	DS	DS	m (M)	[20,21]
<i>Handroanthus impetiginosus</i>	Big	e	Large bees	388–2207	An	–	DP	40–150	Pi	DS	DS	m (O)	[22]
<i>Handroanthus serratifolius</i>	Big	e	Large bees	388–2207	An	–	DP	40–150	Pi	DS	DS	m (O)	[21,23]
<i>Myracrodruon urundeuva</i>	Ana	e	Bees	402–1953	An	–	W	40–150	Pi	DS	DS	d	[24–26]
<i>Prosopis alba</i>	Leg	e	Bees	402–1953	Zo	Lv	W	400–1500	Pi	WS	WS	m (M)	[27–29]
<i>Spondias purpurea</i>	Ana	e	Small bees, wasps	300–2760	Zo	Ma, Bi	IP	400–1500	Lt	DS	DS	d	[37]
<i>Syagrus romanzoffiana</i>	Are	e	Bees, beetles	402–1953	Zo	Ro	Dr	400–1500	Pi	WS	DS	m (O)	[30–32]
<i>Tabebuia aurea</i>	Big	e	Large bees	388–2207	An	–	Dr	40–150	Lt	DS	DS	m (M)	[17–19]
<i>Tabebuia roseo-alba</i>	Big	e	Large bees	388–2207	An	–	DP	40–150	Pi	DS	DS	m (M)	[23,33]
<i>Tibouchina papyrus</i>	Mel	e	Large bees	388–2207	An	–	DP	40–150	Pi	Late WS	DS	m (M)	[34–36]

Abbreviations:

- ¹ Fam, family; Ana, Anacardiaceae; Ara, Araucariaceae; Are, Arecaceae; Big, Bignoniaceae; Car, Caryocaraceae; Leg, Leguminosae; Mel, Melastomataceae; Myr, Myrtaceae
 - L, level; L1, pollen dispersal vector; L2, pollinators; L3, seed dispersal vector; L4, seed dispersers; L5, morphology of diaspores; L6, successional stage; L7, blooming; L8, fruiting
 - d, range of distances; d1, pollen movement; d2, seed movement
 - ² e, entomophily; z, zoophily; a, anemophily
 - ³ Au, autochory; An, anemochory; Zo, zoochory
 - ⁴ Bi, birds; Ro, rodents; Ba, bats; Ma, mammals; Ca, cattle; Ho, horses; Lv, livestock
 - ⁵ DP, dehiscent pods; P, pinion; Dr, drupe; FA, fleshy appendage; IP, indehiscent pods; W, winged
 - ⁶ Pi, pioneer; It, intermediate; Lt, late successional
 - ⁷ DS, dry season; WS, wet season
 - ⁸ d, dioecious; m, monoecious (M, mixed mating system); O, outcrossing
- References: 1: Araújo et al. 2004; 2: Borges et al. 2017; 3: Feres 2013; 4: Costa et al. 2003; 5: Bittencourt and Sebbenn 2008; 6: Sant'Ana et al. 2013; 7: Hay et al. 2000; 8: Collevatti et al. 2011; 9: Herrero-Jáuregui et al. 2009; 10: Sebbenn et al. 2011; 11: Manoel et al. 2012; 12: Tarazi et al. 2013; 13: Oliveira and Sigrist 2008; 14: Ragusa-Netto 2017; 15: Gomes dos Santos et al. 2018; 16: Coelho et al. 2007; 17: Barros 2001; 18: Ragusa-Netto 2005; 19: Braga and Collevatti 2011; 20: Bittencourt and Moraes 2010; 21: Mendes-Rodrigues et al. 2012; 22: Bittencourt 2017; 23: Gandolphii and Bittencourt 2010; 24: Nunes et al. 2008; 25: Gaino et al. 2010; 26: Calvo Rodriguez et al. 2017; 27: Bessega et al. 2012; 28: Bessega et al. 2017; 29: Roser et al. 2017; 30: Guimarães et al. 2005; 31: Beghini et al. 2013; 32: Giombini et al. 2017; 33: Feres et al. 2012; 34: Ribeiro Montoro and Dos Santos 2008; 35: Collevatti et al. 2010a; 36: de Souza Lima et al. 2015; 37: Cristóbal-Pérez et al. 2020; 38: Gonzales et al. 2010

Table 2 Fine-scale spatial genetic structure, density, gene dispersal, and mating system of populations of forest tree species from SDTF analyzed in this review

Species	SDTF ¹	Genetic marker	Np	Spatial genetic structure		Density (trees/ha)	Gene dispersal		Ref	Mating system		Ref
				F ₁	Sp		σ_g (De = D/2)	σ_g (De = D/4)		Mean σ_g	t _m	
<i>Anadenanthera colubrina</i> (CSJ)	MI	M	2	0.059	0.0090	8.6	NC	10.89	17	0.49	n/a	[39]
<i>Anadenanthera colubrina</i> (RP)	CB	M	2	0.136	0.0090	20	n/a	n/a	n/a	0.62	0.47	[3]
<i>Anadenanthera peregrina</i> (RP)	CB	M	1	0	0.0000	20	n/a	n/a	n/a	0.91	0.68	[3]
<i>Araucaria angustifolia</i>	MI	A	1	0.076	n/a	7.7	n/a	n/a	n/a	0.96	0.19	[41,42]
<i>Araucaria angustifolia</i>	MI	M	1	0.001	0.0026	n/a	n/a	n/a	n/a	1	n/a	[44]
<i>Araucaria angustifolia</i> (FV)	MI	M	1	0.004	0.0090	n/a	n/a	n/a	n/a	1	n/a	[44]
<i>Araucaria angustifolia</i> (NG)	MI	M	1	0.017	0.0160	n/a	n/a	n/a	n/a	0.99	n/a	[5]
<i>Araucaria angustifolia</i> (PD)	MI	M	1	0.017	0.0150	n/a	n/a	n/a	n/a	1	n/a	[44]
<i>Araucaria angustifolia</i> (RG)	MI	M	1	0.038	0.0120	n/a	n/a	n/a	n/a	0.99	n/a	[5]
<i>Araucaria angustifolia</i> (AL)	CB	M	1	0.149	0.0116	12.2	n/a	n/a	n/a	0.89	n/a	[45]
<i>Caryocar brasiliense</i> (ANV)	CB	M	1	0.146	0.0090	10	n/a	n/a	n/a	1	0.21	[46]
<i>Caryocar brasiliense</i> (FAL)	CB	M	1	0.146	0.0090	8	n/a	n/a	n/a	1	0.09	[46]
<i>Caryocar brasiliense</i> (JA)	CB	A	1	n/a	0.0082	n/a	n/a	n/a	n/a	1	n/a	[46]
<i>Caryocar brasiliense</i> (PNB)	CB	M	1	0.146	0.0090	9	n/a	n/a	n/a	1	0.14	[46]
<i>Caryocar brasiliense</i> (URU)	CB	M	2	0.146	0.0090	10	n/a	n/a	n/a	1	0.19	[46]
<i>Copaifera langsdorffii</i>	CB	M	1	0.071	0.0259	23.3	n/a	n/a	n/a	1	0.84	[11]
<i>Dipteryx alata</i>	CB	M	1	0.059	0.0172	27	n/a	n/a	n/a	0.71	n/a	[49]
<i>Enterolobium cyclocarpum</i> (AG)	CN	I	1	n/a	n/a	n/a	n/a	n/a	n/a	0.9	0.32	[50]
<i>Enterolobium cyclocarpum</i> (CA)	CN	I	1	n/a	n/a	n/a	n/a	n/a	n/a	0.89	n/a	[50]
<i>Enterolobium cyclocarpum</i> (PV)	CN	A	1	0.321	n/a	n/a	n/a	n/a	n/a	n/a	n/a	–
<i>Enterolobium cyclocarpum</i> (SLM)	CN	A	1	0.064	n/a	n/a	n/a	n/a	n/a	n/a	n/a	–
<i>Enterolobium cyclocarpum</i> (SR)	CN	A	1	0.165	n/a	n/a	n/a	n/a	n/a	n/a	n/a	–
<i>Enterolobium cyclocarpum</i> (TA)	CN	I	1	n/a	n/a	n/a	n/a	n/a	n/a	0.91	n/a	[50]
<i>Enterolobium cyclocarpum</i> (TE)	CN	I	1	n/a	n/a	n/a	n/a	n/a	n/a	0.81	n/a	[50]
<i>Eugenia uniflora</i>	CA	AF	5	n/a	0.0120	n/a	n/a	n/a	n/a	n/a	n/a	–
<i>Handroanthus chrysotrichus</i>	CB	M	1	0.045	0.0118	0.13	2.74	n/a	n/a	n/a	n/a	–
<i>Handroanthus impetiginosus</i>	CB	M	1	0.058	0.0125	0.07	2.66	n/a	n/a	1	n/a	[54]
<i>Handroanthus serratifolius</i>	CB	M	1	0.108	0.0128	0.33	2.97	n/a	n/a	n/a	n/a	–
<i>Myracrodruon urundeuva</i>	CB	M	1	0.059	0.0269	1.08	n/a	n/a	n/a	1	0.1	[25]
<i>Prosopis alba</i> (CD)	SP	M	1	0.011	0.0050	n/a	66.26	79.51	162.3	0.72	0.81	[56]
<i>Spondias purpurea</i> (I)	MX	M	1	0.053	0.0128	3.23	n/a	n/a	n/a	1	n/a	[58]
<i>Spondias purpurea</i> (II)	MX	M	1	0.077	0.0108	n/a	n/a	n/a	n/a	1	n/a	[58]
<i>Spondias purpurea</i> (III)	MX	M	1	0.05	0.0105	n/a	n/a	n/a	n/a	1	n/a	[58]
<i>Syagrus romanzoffiana</i> (DI)	MI	M	1	0.125	0.0310	15	n/a	n/a	n/a	0.98	n/a	[32]

Table 2 (continued)

Species	SDTF ¹	Genetic marker	Np	Spatial genetic structure		Density (trees/ha)	Gene dispersal			Ref	Mating system		Ref
				F ₁	Sp		σ _g (De = D/2)	σ _g (De = D/4)	σ _g (De = D/8)		t _m	rp	
<i>Syagrus romanzoffiana</i> (D3)	MI	M	1	0.1	0.0290	15	n/a	n/a	n/a	[32]	0.98	b	[32]
<i>Syagrus romanzoffiana</i> (P3)	MI	M	1	0.07	0.0260	15	n/a	n/a	n/a	[32]	0.92	b	[32]
<i>Tabebuia aurea</i> (HF)	CB	M	1	0.025	0.0060	6.5	n/a	n/a	n/a	[19]	0.8	d	[19]
<i>Tabebuia aurea</i> (MF)	CB	M	1	0.025	0.0060	6.5	n/a	n/a	n/a	[19]	0.58	d	[19]
<i>Tabebuia roseo-alba</i> (RP)	CB	M	1	0.033	n/a	n/a	n/a	n/a	n/a	[33]	0.84	0.12	a
<i>Tabebuia roseo-alba</i> (SE)	CB	M	1	0.048	n/a	n/a	n/a	n/a	n/a	[33]	0.96	0.1	a
<i>Tabebuia roseo-alba</i>	CB	M	1	0.048	0.0034	n/a	n/a	n/a	n/a	[53]	0.96	a	[53]
<i>Tibouchina papyrus</i>	CB	M	1	0.032	0.0085	84.9	n/a	n/a	n/a	[35]	n/a	a	–

Abbreviations:

¹SDTF floristic groups: MI, Misiones; CB, Central Brazil; CN, Central America-Northern South America; CA, Caatinga; SP, Subandean Piedmont; MX, Mexico

Genetic marker: M, microsatellites; A, allozymes; I, isozymes; AF, amplified fragment length polymorphism; Np, number of population samples analyzed; F₁, kinship coefficient between adjacent individuals; Sp, Sp statistic; σ_g, gene dispersal distance for different estimated; De, effective density; D, census population density; t_m, outcrossing rates; rp, correlated paternity

²Approximation of population density (trees/ha)

³Estimation methods of outcrossing rates: a, mixed mating model; b, inbreeding coefficient; c, mating system; d, paternity analyses

References: 3: Feres 2013; 5: Bittencourt and Sebbenn 2008; 6: Sant'Ana et al. 2013; 10: Sebbenn et al. 2011; 11: Manoel et al. 2012; 19: Braga and Collevatti 2011; 25: Gaiño et al. 2010; 32: Giombini et al. 2017; 33: Feres et al. 2012; 35: Collevatti et al. 2010a; 39: Gonçalves et al. 2019; 40: Gonçalves et al. 2021; 41: Mantovani et al. 2006; 42: Patreze and Tsai 2010; 43: Stefenon et al. 2008; 44: Sousa et al. 2005; 45: Collevatti et al. 2010b; 46: Collevatti et al. 2001a, b; 47: Collevatti and Hay 2011; 48: de Melo et al. 2012; 49: Tarazi et al. 2010; 50: Rocha and Aguilar 2001; 51: Gonzales et al. 2010; 52: Lowe et al. 2018; 53: Collevatti et al. 2014; 54: Bittencourt and Semir 2005; 55: Moraes et al. 2012; 56: Bessega et al. 2000; 57: Bessega et al. 2016; 58: Cristóbal-Pérez et al. 2020

(2007) estimations. The successional stage and seasonality of blooming and fruiting allowed us to classify species in pioneer, intermediate, and late-successional. For the mating system, we identified three categories: monoecious species with mixed mating system, monoecious species with outcrossing, or dioecious species. Population densities were categorized based on the information reported in original publications as low, medium, or high density, and considering the number of trees per hectare if available. The landscapes in which the study sites are located were classified as continuous or fragmented forests, urban areas, or pastures. The floristic groups Misiones, Central Brazil, Central America-Northern South America, Caatinga, Subandean Piedmont, and Mexico where populations are located were also considered. All of these categories were employed as predictor variables of the Sp statistic and of t_m .

Data analysis

The Sp statistic and t_m outcrossing rates were analyzed among groups defined based on the traits of forest tree populations from the SDTF biome to detect differences between or among categories of each variable. The Shapiro–Wilk W test was used to evaluate the normality of residuals, which was systematically rejected. The Kruskal–Wallis test was performed for the analysis of multi-group comparisons. The non-parametrical Kruskal–Wallis test results in high statistical power for non-symmetrical distributions (Van Hecke 2010). Therefore, the medians among groups were compared to identify the biological and ecological factors that have strong influences on the Sp statistic and on t_m outcrossing rates. Fisher's least significant difference and the Bonferroni correction criteria were used to assess significant differences of post hoc comparisons.

Results

The Sp statistic and/or t_m are reported for a total of 43 populations of 18 forest tree species from SDTF (Table 2). With an average of 0.0117 ± 0.0077 , the minimum Sp statistic detected was 0.0026 in *Araucaria angustifolia*, a species for which the patterns of FSGS were not significantly different from a random distribution of genotypes, while the highest Sp statistic detected was 0.0310 in a highly fragmented population of *Syagrus romanzoffiana*. On the other hand, with an average of 0.92 ± 0.13 , the t_m values ranged from 0.49 in a population of *Anadenanthera colubrina*, which showed a patchy distribution, to 1.00 in dioecious and in certain outcrossed populations such as *Caryocar brasiliense* and *Handroanthus impetiginosus* (Table 2). On average, Sp was up to three times higher in species exhibiting a mixed mating system with a predominance of self-fertilization

[$Sp(Tibouchina papyrus) = 0.0085$ and $Sp(Anadenanthera colubrina) = 0.0090$] than in species exhibiting a mixed mating system with a predominance of cross-fertilization [$Sp(Tabeuia roseo-alba) = 0.0034$] (Table 2).

The analyzed traits allowed defining and contrasting different groups through the shared and exclusive characteristics that may explain similarities and discontinuities. The Kruskal–Wallis test performed using Sp statistic and t_m values as effects showed that plant mating system and population density significantly influence patterns of FSGS (Table 3). Sp was significantly associated with the mating system where $Sp(\text{monoecious-outcrossing}) = 0.0161 > Sp(\text{dioecious}) = 0.0128 > Sp(\text{monoecious mixed-mating}) = 0.0080$, and population density where $Sp(\text{high density}) = 0.0152 > Sp(\text{low density}) = 0.0138 > Sp(\text{medium density}) = 0.0073$ (Table 3). Outcrossing rate was significantly associated with the type of propagule dispersal where t_m was higher in populations of plants pollinated by wind ($t_m = 0.9897$), and in those with animal-mediated seed dispersal, $t_m(\text{autochory-zoochory}) = 0.9897 > t_m(\text{anemochory}) = 0.8814 > t_m(\text{autochory}) = 0.5545$, the mating system where $t_m(\text{dioecious}) = 0.9938 > t_m(\text{monoecious outcrossing}) = 0.9850 > t_m(\text{monoecious mixed-mating}) = 0.7974$, and successional stage, where $t_m(\text{late-successional}) = 0.9400 > t_m(\text{intermediate}) = 0.9169 > t_m(\text{pioneer}) = 0.8751$. Regarding different categories of these factors, the strongest effect on t_m was attributed to the mating system, to seed and pollen dispersal vectors, and to successional stage, which showed statistically significant differences among groups (Table 3).

Discussion

The role of gene dispersal on plant demography and microevolution of forest tree populations from SDTF biome was analyzed by assessing plant mating systems and spatial genetic structure. The underlying factors that significantly influenced the spatial genetic structure were the mating system and population density, whereas the underlying factors that significantly influenced outcrossing rates were pollen and seed dispersal, and successional stage. The extent to which the variation of these factors impacts the gene dispersal configuration of forest tree species from SDTF is relevant knowledge to restore this anthropogenically disturbed biome.

Outcrossing and mating among relatives

Plant mating patterns are affected by floral sexuality and compatibility relations (Bullock 2009). Also, patterns of gene dispersal have implications for mating systems, inbreeding levels, and the maintenance of genetic diversity (Dick et al. 2008). Tree species from SDTF are highly

Table 3 Effects of different biological and ecological factors on FSGS (S_p) and outcrossing rates (t_m)

Factor	S_p			H statistic	p value	t_m			H statistic	p value
	n	Mean	SD			n	Mean	SD		
<i>Pollination</i>				9.0189	0.1083				11.6950*	0.0392
Small bees/bees	6	0.0110	0.0092			7	0.7850	0.1925		
Wind	5	0.0109	0.0054			6	0.9897	0.0171		
Bats	6	0.0093	0.0012			6	0.9818	0.0445		
Bees/moths/beetles	3	0.0114	0.0013			7	0.9303	0.0726		
Large bees	9	0.0111	0.0068			7	0.8780	0.1531		
Bees/beetles	3	0.0287	0.0025			3	0.9800	0.0173		
<i>Seed dispersal</i>				11.7040	0.0689				21.0680*	0.0018
Anemochory	9	0.0098	0.0078			8	0.8814	0.142		
Autochory	2	0.0090	0.0000			2	0.5545	0.0912		
Autochory-zoochory	5	0.0109	0.0054			6	0.9897	0.0171		
Zoochory by bats	1	0.0172	0.0000			1	0.7110	0.0000		
Zoochory by birds	11	0.0116	0.005			11	0.9891	0.0327		
Zoochory by livestock	1	0.0050	0.0000			5	0.8586	0.0584		
Zoochory by rodents	3	0.0287	0.0025			3	0.9800	0.0173		
<i>Successional stage</i>				2.2404	0.3262				6.1027*	0.0473
Pioneer	14	0.0141	0.0100			12	0.8751	0.1666		
Intermediate	1	0.0259	0.0000			6	0.9169	0.0697		
Late	17	0.0102	0.0037			18	0.9400	0.1210		
<i>Mating system</i>				6.5520*	0.0378				23.6950*	7.16E-06
Dioecious	9	0.0128	0.0065			10	0.9938	0.0138		
Monoecious—mixed mating system	11	0.0080	0.0047			14	0.7974	0.1472		
Monoecious—outcrossing	12	0.0161	0.0090			12	0.9850	0.0317		
<i>Density</i>				11.9710*	0.0025				1.2937	0.5237
High density	14	0.0152	0.0096			16	0.9371	0.1126		
Low density	8	0.0138	0.0054			9	0.9458	0.0700		
Medium density	10	0.0073	0.0021			11	0.8561	0.1803		
<i>Landscape</i>				0.9633	0.6178				5.7444	0.0566
Continuous forests	14	0.0114	0.0056			16	0.9768	0.0339		
Fragmented forests	14	0.0138	0.0088			15	0.8627	0.1655		
Urban area-pastures	4	0.0109	0.0109			5	0.8706	0.1551		
<i>Site</i>				5.3079	0.2571				8.4577	0.0762
Caatinga	1	0.0120	0.0000			0	—	—		
Central Brazil	18	0.0109	0.0068			18	0.9034	0.1386		
Central America-Northern South America	0	—	—			4	0.8780	0.0452		
Misiones	9	0.0166	0.0099			10	0.9368	0.1578		
Mexico	3	0.0114	0.0013			3	1.0000	0.0000		
Subandean Piedmont	1	0.0050	0.0000			1	0.7810	0.0000		

*Significant values (p value < 0.05). *SD*, standard deviation

dependent on animals for different features of their reproduction and regeneration. Since anthropogenic disturbance has rapid effects on the abundance of pollinators and seed dispersers, the biotically dispersed tree species could be more vulnerable to anthropogenic changes than abiotically dispersed tree species (Auffret et al. 2017).

Plant mating systems are often described by the “mixed mating model,” where a fraction of progeny are derived from self-fertilization and the remainder derived from outcrossing (Ritland 2002). The SDTF species included in this review were characterized by high outcrossing rates with an average value near unity. Around 74–77% of

previously studied species from dry forests were considered self-incompatible (Bullock 2009).

High outcrossing rates, as a central feature of the mating system (Goodwillie et al. 2005; Lowe et al. 2005; Ward et al. 2005), contribute to far-ranging gene dispersal in SDTF populations, causing a decrease in the mean FSGS levels. Highly mobile pollinators that transport pollen further across the landscape can promote mating between genetically distant individuals, causing high outcrossing rates and high rates of multiple paternity (Wessinger 2021). Also, outcrossing rates in monoecious trees, such as *Tabebuia roseo-alba*, depend on the intensity of self-incompatibility mechanisms, protogyny and protandry, foraging behavior of pollinators, and selective abortion of selfed fruits or seeds (Feres et al. 2012). *Prosopis alba*, *T. aurea*, and *T. roseo-alba* are predominantly or completely outcrossing monoecious species (Braga and Collevatti 2011; Gandolphi and Bittencourt 2010; Roser et al. 2017). This mating system results in lower levels of FSGS than in species that include a significant proportion of selfing or correlated mating.

Usually, the studied SDTF populations belonged to monoecious tree species with mixed mating systems (Table 3). As a consequence, even though some tree species have been described as predominantly outcrossing, they may have restricted dispersal. This is the case of *A. colubrina*, in which restricted gene dispersal has been estimated in populations from Central Brazil and Misiones (Feres 2013; Gonçalves et al. 2019, respectively). *Anadenanthera colubrina*, *A. peregrina*, and *Tibouchina papyrus* share characteristics such as pioneer successional stage, gravity-mediated short-distance seed dispersal, spatially clustered recruitment of related seedlings, and sapling recruitment near to the mother trees. The correlation between the extent of seed and pollen dispersal should be stronger when most mating events occur between near neighbors (Hardy et al. 2006). In this way, limited foraging distances of pollinating insects within the forest fragments, and overall short distances of seed dispersal, high tree densities, and mixed mating systems influence gene dispersal patterns of these species. Gene dispersal patterns within populations of *A. colubrina* were characterized by short gene dispersal distances ($\sigma_g = 5\text{--}17$ m) and a significant FSGS (Gonçalves et al. 2019).

The statistically significant influence of the mating system on FSGS and outcrossing rates denotes the relevance of this biological factor on gene dispersal distances. Gene dispersal distances detected in *Handroanthus chrysotrichus*, *H. impetiginosus*, and *H. serratifolius* populations (Bignoniaceae) from Central Brazil were strongly contrasted among species ($\sigma_g = 6$; $\sigma_g = 23$; and $\sigma_g = 77$ m) (Collevatti et al. 2014). This fact was attributed to differences in the mating system, which was, respectively, mixed-mating, self-incompatible, and outcrossed for these species (Collevatti et al. 2014).

Population density in fragmented forests

Research on plant dispersal ecology should account for spatial scale and heterogeneity, temporal scale, and system complexity (Robledo-Arnuncio et al. 2014). The distribution of forest patches and the population density are relevant factors to FSGS in SDTF forest tree species. Neotropical SDTF populations showed on average a weak FSGS ($Sp = 0.01$) compared to the structure detected by Vekemans and Hardy (2004) in other plant populations ($Sp = 0.03$), such as in forest tree populations from tropical rainforests ($Sp = 0.02$) (Dick et al. 2008; Hardy et al. 2006). Intermediate population densities that characterize several of the studied SDTF populations, in general, are related to fragmented forests within landscape matrices that are permeable to dispersal among patches. In contrast, low population densities that characterize late-successional tree species from continuous rainforests, in general, are related to higher inbreeding in spatially isolated trees (Dick et al. 2008).

In the present review, the weakest FSGS was detected in populations with an intermediate reported density. Based on Sp values, *P. alba* populations from the Subandean Piedmont showed one of the lowest FSGS ($Sp = 0.0050$) (Bessega et al. 2016) compared with the other studied populations. High gene dispersal distances ($\sigma_g = 66\text{--}162$ m) were explained as a consequence of the influence of livestock providing seed dispersal in fragmented forests. Also, the breakdown of nearest-neighbor mating in populations with intermediate densities could contribute to the decrease of FSGS. However, in the context of isolation by distance, there is a limit to gene dispersal. In our review, isolated populations of *Myracrodruon urundeuva* (Gaino et al. 2010) together with *Dipteryx alata* from small remnant forests in Central Brazil (Collevatti et al. 2010a) and *Syagrus romanzoffiana* from disturbed areas in Misiones (Giombini et al. 2017) showed the strongest FSGS compared with the other species from SDTF ($Sp = 0.0172\text{--}0.0310$). These populations showed restricted pollen and seed dispersal both in high and low densities in highly fragmented landscapes.

Despite the high number of FSGS studies on forest tree populations from SDTF, scarce direct information on gene dispersal distances was found. This lack could be a consequence of the difficulty in defining the effective density parameter because this parameter depends on the variance of reproductive events between individuals. In long-lived tree species, the average number of individuals that contribute offspring to the next generation may be difficult to estimate (Ridley 2003).

Under isolation by distance, dispersal-drift equilibrium can be assumed to characterize gene dispersal distances of forest tree populations from SDTF. For the inference of σ_g , the iterative procedure suggested by Vekemans and Hardy (2004) and Hardy et al. (2006) highlights that assumptions

regarding De/D are critical. Thus, in the absence of independent data on effective density, a range of effective density values (De) can be considered (D , $D/2$, $D/4$, $D/8$, and $D/10$) to obtain an empirical confidence interval on σ_g (Vekemans and Hardy 2004). New detailed parentage analyses assessing how reproductive success varies among individuals and through time will provide reliable estimates of the range of De/D ratios for tropical trees, and can also provide direct gene dispersal estimates (Hardy et al. 2006).

Distances and patterns of pollen and seed dispersal

In a changing world, understanding the potential gene dispersal rates of Neotropical SDTF species will allow us to predict whether plant populations can become connected through pollen movement, which may contribute to the exchange of adaptive genetic variation exchange, or whether seed movement allows for migration into, and colonization of new suitable habitats. Long-distance seed dispersal and/or extensive pollen flow typically lead to weak or non-detectable FSGS (Gonzales et al. 2010).

As previously explained, the outcrossing rates and pollen and seed-mediated gene dispersal are sensitive to ecological factors and show variation over both spatial and temporal scales. Several studies have addressed the pollen dispersal distances of Neotropical trees (Hamrick and Murawski 1990; Latouche-Hallé et al. 2004; Lowe et al. 2005; Nason and Hamrick 1997). In those studies, insect-mediated pollination has prevailed compared to other types of pollination. The effects of biotic pollination syndrome are frequently associated with mixed mating systems (Aide 1986; Goodwillie et al. 2005). Spatio-temporal variation of pollinator guilds can produce different gene dispersal patterns (Dick et al. 2008; Kenta et al. 2004). As a consequence of pollen dispersal occurring at high distances in low-density forest tree populations (Ward et al. 2005), the patchy habitats could promote further-ranging pollen movement in disturbed areas (Bessega et al. 2016). Gonzales et al. (2010) analyzed the impacts of landscape disturbance on FSGS of *Enterolobium cyclocarpum* populations from the Central America-Northern South America SDTF floristic group and detected higher levels of kinship in the first distance intervals in forest populations from protected areas than in populations from pasture areas. In populations of this species, Rocha and Aguilar (2001) reported spatial and temporal variation in their outcrossing rates over two consecutive years. Similarly, in *T. aurea* populations from Central Brazil, a temporal analysis of gene dispersal allowed detecting a high variation in pollen dispersal distances and in breeding structure between flowering seasons in fragmented forests (Braga and Collevatti 2011), while the authors attributed weak FSGS ($Sp=0.0060$) to long-distance seed dispersal. Similar FSGS values were detected within tree *Entandrophragma*

cylindricum populations from African rainforests (Monthe et al. 2017), as a consequence of far-ranging gene dispersal distances ($\sigma_g = 1,078\text{--}1,500$ m). In such cases, a high extent of pollen-mediated gene dispersal could frequently hamper the estimation of the gene dispersal range (Savolainen et al. 2007).

The sampling scale is a key aspect to consider at the beginning of gene dispersal studies of Neotropical forest tree populations. Following the recommendations provided by Hardy et al. (2006), for the inference of σ_g , an appropriate sampling scheme is required, which should include pairs of individuals separated by distances ranging from $\sim 10\text{--}50$ m (neighbors) to $\sim 10\text{--}20$ km (20 times σ_g estimates, which are typically on the order of 500–1000 m). A wide distance range also allows us to evaluate the linearity of the kinship curve considering the spatial population distribution in a large area (Vekemans and Hardy 2004).

The spatially clustered recruitment of offspring is a predominant pattern in SDTF forest tree populations probably because of regeneration near mother trees, or alternatively, near resting places of animal dispersers. Clustered recruitment and moderate FSGS ($Sp=0.0090\text{--}0.0149$) was detected in zoochorous forest tree species, such as *Eugenia uniflora* populations from Misiones and Caatinga floristic groups (Lowe et al. 2018), *Araucaria angustifolia* from Misiones (Stefenon et al. 2008), *Spondias purpurea* from Mexico (Cristóbal-Pérez et al. 2020), and *Caryocar brasiliense* from Central Brazil (Collevatti et al. 2001a, b; Collevatti et al. 2010b). All of these species develop fruits that are attractive to dispersers such as drupes and fleshy appendages and show seed dispersal mediated by birds. In *Copaifera langsdorffii* populations from Central Brazil, also dispersed by birds, saplings recruited within a fragmented population were all assigned to mothers located within the same population (Sebbenn et al. 2011), suggesting restricted seed dispersal, whereas gene dispersal among patches was attributed to far-ranging pollen dispersal (Manoel et al. 2012, 2021). Genetic studies in other Neotropical trees are in agreement with a pattern of narrow-ranging seed dispersal vs. far-ranging pollen dispersal, e.g., species with seed dispersal mediated by gravity and zoochory such as *Bertholletia excelsa*, *Genipa americana*, *Hymenaea stigonocarpa*, and *Ilex paraguariensis* (Baldoni et al. 2020; de Vasconcelos Melo et al. 2021; Moreno et al. 2021; Seoane et al. 2019), and others with seed dispersal mediated by anemochory such as *Swietenia macrophylla* (Silva de Oliveira et al. 2020). Together, these studies suggest that SDTF species maintain connectivity between anthropogenically fragmented populations, and that in many cases, despite adaptations to long-distance dispersal via zoochory, it appears to be pollen dispersal that assures the genetic connectivity between fragments.

In plants dispersed by zoochory, the spatial distribution of saplings is related to the behavior of seed dispersal vectors

(Gelmi-Candusso et al. 2017). The strong FSGS detected in *D. alata* and *S. romanzoffiana* populations could be a consequence of seed dispersal ensured by scatter-hoarding rodents. Hardy et al. (2006) also described a strong FSGS and low gene dispersal distances in other Neotropical forest tree species dispersed by rodents, such as *Vouacapoua americana*, *Carapa procera*, and *Moronobea coccinea* ($\sigma_g \leq 200$ m).

Our results are in agreement with some previous reviews that inform the differences of FSGS among populations are associated with the mating system, population density, pollination, seed dispersal, and successional stage of forest tree species (e.g., Gelmi-Candusso et al. 2017; Hardy et al. 2006; Lowe et al. 2018; Nathan and Muller-Landau 2000; Ward et al. 2005).

Future directions and prospects for integration

Most of the knowledge built around gene dispersal in forest trees involves heterogeneous landscapes, across which authors seek to detect genetic discontinuities that reflect major factors that may influence the genetic structure and mating systems of species. The effects of the anthropogenic fragmentation of SDTF on gene dispersal depend on the spatial genetic structure and the outcrossing rates prior to disturbance. Thus, analyzing the factors that determine gene dispersal is a key tool to define the optimal minimum distances between mother trees used as seed trees for reforestation.

The spatio-temporal patterns of tree populations retain signatures of ecological and evolutionary processes such as dispersal of propagules, establishment, competition, genetic drift, gene flow, fragmentation, and population expansions (Robledo-Arnuncio et al. 2014). Thus, the integrated analysis from the spatial genetic patterns of different life stages within populations and the genetic structure among distant populations can help to reveal the importance of underlying processes that shape the spatio-temporal dynamics of gene dispersal in forest tree species from SDTF. Our results reveal the value of considering several biological and ecological factors such as population density, mating system, and pollen and seed dispersal when designing sampling strategies for seed collection in conservation, breeding, and environmental restoration projects.

The conservation and sustainable use of genetic diversity is a valuable strategy to counteract the fast climate change. In this way, gene dispersal studies will contribute to the characterization of SDTF for the conservation of its genetic resources. In this context resounds the urgent need for the implementation of conservation areas to protect SDTF and their high floristic and genetic diversity. Thus, the

knowledge on gene dispersal processes can help to rescue SDTF, maintain population connectivity and genetic variability, preserving optimal conditions for natural processes through sustainable management.

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Data availability Data are available from the FIGSHARE repository (Goncalves et al. 2022). Dataset not peer-reviewed. Goncalves et al. (2022). Data from “Spatial genetic structure and mating system in forest tree populations from Seasonally Dry Tropical Forests: a review”. V1. figshare. [Dataset]. <https://doi.org/10.6084/m9.figshare.18128774.v1>.

Declarations

Conflict of interest The authors declare no competing interests.

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