

Effects of zoochory on the spatial genetic structure of plant populations

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Abstract

Spatial genetic structure (SGS) of plants results from the nonrandom distribution of related individuals. SGS provides information on gene flow and spatial patterns of genetic diversity within populations. Seed dispersal creates the spatial template for plant distribution. Thus, in zoochorous plants, dispersal mode and disperser behaviour might have a strong impact on SGS. However, many studies only report the taxonomic group of seed dispersers, without further details. The recent increase in studies on SGS provides the opportunity to review findings and test for the influence of dispersal mode, taxonomic affiliation of dispersers and their behaviour. We compared the proportions of studies with SGS among groups and tested for differences in strength of SGS using *Sp* statistics. The presence of SGS differed among taxonomic groups, with reduced presence in plants dispersed by birds. Strength of SGS was instead significantly influenced by the behaviour of seed dispersal vectors, with higher SGS in plant species dispersed by animals with behavioural traits that result in short seed dispersal distances. We observed high variance in the strength of SGS in plants dispersed by animals that actively or passively accumulate seeds. Additionally, we found SGS was also affected by pollination and marker type used. Our study highlights the importance of vector behaviour on SGS even in the presence of variance created by other factors. Thus, more detailed information on the behaviour of seed dispersers would contribute to better understand which factors shape the spatial scale of gene flow in animal-dispersed plant species.

KEYWORDS

animal behaviour, fine-scale spatial genetic structure, plant–animal interactions, seed dispersal, seed dispersal distance, *Sp* statistic

1 | INTRODUCTION

Fine-scale spatial genetic structure (SGS) is the nonrandom spatial distribution of related individuals within a population (Hamrick & Loveless, 1986; Vekemans & Hardy, 2004). SGS in plants results primarily from gene flow via pollen and seed dispersal. A number of additional factors, such as environmental conditions, the plant's life history traits, morphology and demographics, might also influence the presence and strength of SGS by affecting the pattern and spatial scale of gene flow, and the seedling survival rate (Hamrick & Godt, 1996; Hardy et al., 2006). Pollination and seed dispersal differ

in strength and scale of their effect on gene flow (Hardy et al., 2006). While pollen grains carry only the paternal set of chromosomes, seeds carry the combined set from both parents and thereby contribute twice as much to overall gene flow. The contribution of pollen (σ_p) and seed (σ_s) dispersal variance to the overall parent-offspring dispersal variance (σ_g^2) can thus be expressed as $\sigma_g^2 = \frac{1}{2} \sigma_p^2 + \sigma_s^2$ (Crawford, 1984). Furthermore, seed dispersal creates the spatial template for recruitment and the resulting genotype distribution of future generations (Howe & Miriti, 2004). While pollen dispersal can compensate for genetic drift within populations and counteract genetic differentiation among populations (Howe & Miriti,

2004) by homogenizing spatial genetic patterns on large scales (Isagi, Kanazashi, Suzuki, Tanaka, & Abe, 2004), seed dispersal is generally regarded to have a stronger effect on small-scale genetic patterns (Hamilton, 1999). In fact, the analysis of SGS can shed light on the patterns of seed dispersal (Hamrick & Trapnell, 2011; Slatkin, 1985) and allow for an approximation of dispersal distances (Heuertz, Vekemans, Hausman, Palada, & Hardy, 2003).

Postdispersal processes that affect seed germination and establishment can influence SGS as well, and have to be considered for the interpretation of SGS patterns. These processes include seed and seedling predation, pathogen attacks, and intra- and interspecific competitions for nutrients and light. Density-dependent mortality, and host-specific predation or pathogens, can reduce SGS by increasing mortality with increasing density of conspecific seedlings (Connell, 1971; Janzen, 1970). Similarly, random demographic thinning with increasing age of cohorts can also reduce SGS (Schroeder, Tran, & Dick, 2014). Conversely, micro-geographic environmental heterogeneity might favour survival of locally well-adapted and potentially related genotypes, resulting in the aggregation of quantitative traits within populations (Scotti, González-Martínez, Budde, & Lagüe, 2015; Yeaman & Jarvis, 2006). In such cases, the importance of the spatial scale of gene flow for evolutionary processes becomes evident. While large-scale gene flow can increase local genetic diversity and provide a diverse gene pool for adaptation under high selective pressure, in sites with low-to-intermediate selective pressure it can instead counteract adaptation. In this case, restricted gene flow facilitates local adaptation (Savolainen, Pyhäjärvi, & Knürr, 2007; Scotti et al., 2015). This scenario might also result in high levels of biparental inbreeding (in absence of self-incompatibility), resulting in a reduction of genetic diversity within the population (Ellstrand & Elam, 1993) and, in the long-term, of fitness and adaptability (Lankau, 2009). Therefore, the presence of spatial patterns in genetic variation is also an important prerequisite for evolutionary processes (Rundle & Nosil, 2005; Sokal & Wartenberg, 1983).

In this review, we focus on the influence of seed dispersal by animals (zoochory) on SGS.

1.1 | Zoochory and spatial patterns of seed dispersal

Zoochorous seed dispersal occurs through three different mechanisms. Seeds can be (a) swallowed, transported inside the guts of frugivores and deposited through defecation or regurgitation (endozoochory); (b) actively carried in hands, mouths, bills or mandibles and dropped after the edible part of the fruit has been removed (synzoochory) or (c) transported passively attached to skin, fur or feathers (epizoochory) (Howe & Smallwood, 1982). Animals can act as primary seed dispersers when they deposit seeds after having removed fruits from the plant, or as secondary dispersers when already dispersed seeds are moved further on (Wang & Smith, 2002). As zoochorous seed dispersal is an interaction between animals and fruits/seeds, it is plausible that the behaviour of animal dispersal vectors influences patterns of seed dispersal (Cortes &

Uriarte, 2013; Russo, Portnoy, & Augspurger, 2006; Sasal & Morales, 2013). Generally, the behaviour of vectors, for example frequency of visits to fruiting plants, quality and quantity of fruit and seed handling, plays a role in determining seed dispersal efficacy (Schupp, 1993; Schupp, Jordano, & Gómez, 2010). More specifically, spatial patterns of seed dispersal are directly related to the vector's movement patterns which in turn are affected by intrinsic (vector-specific) and extrinsic (ecological/environmental) factors (Laundré, Hernandez, & Ripple, 2010; Patterson, Thomas, Wilcox, Ovaskainen, & Matthiopoulos, 2008). Intrinsic factors include body size, nutrient requirements and dietary strategies, physiological condition, social organization, and mating system (e.g., Jordano, García, Godoy, & García-Castaño, 2007; Karubian, Durães, Storey, & Smith, 2012; Lichti, Steele, & Swihart, 2017; Wehncke, Valdez, Domínguez, Valdez, & Dominguez, 2004). Extrinsic factors include seasonal and interannual variation in fruit abundance, the spatial distribution of feeding, sleeping, resting and singing sites, and predation risk (e.g., Abedi-Lartey, Dechmann, Wikelski, Scharf, & Fahr, 2016; Julliot, 1997; Perea, González, San Miguel, & Gil, 2011; Wenny & Levey, 1998). Although the influence of behaviour of seed dispersal vectors on spatial patterns of seed dispersal has been empirically studied and theoretically modelled for a long time (Bialozyt, Flinkerbusch, Niggemann, & Heymann, 2014; Bialozyt, Luettmann, et al., 2014; Cortes & Uriarte, 2013; Cousens, Hill, French, & Bishop, 2010; Estrada & Coates-Estrada, 1984; Fleming & Williams, 1990; Jordano & Herrera, 1995; Russo et al., 2006; Sasal & Morales, 2013), its implications for SGS of plant populations have come under intensive study only recently.

1.2 | Spatial genetic structure analysis

SGS is analysed by genotyping georeferenced plant individuals and by assessing changes in genetic relatedness with spatial distance. For genotyping, a variety of different marker types has been used, but in the last few years, most SGS studies have used microsatellites whose high variability allows to distinguish kinship even between closely related individuals. The relatedness between pairs of individuals can be calculated with a number of kinship coefficients (e.g., Burgman & Williams, 1995; Loiselle, Sork, Nason, & Graham, 1995; Sokal & Oden, 1978). Following the recommendations of Vekemans and Hardy (2004), most recent studies employ the coefficient published by Loiselle et al. (1995) which has proven to be more robust than other coefficients if rare alleles occur in the data set (e.g., Ritland, 1996; Rousset, 2000). This is frequently the case when highly variable microsatellites are used. For spatial autocorrelation analysis, the kinship coefficient of pairs of individuals is averaged in predefined distance classes and tested for significance by permutations within in each distance class. Alternatively, for a one-value measure of SGS, Vekemans and Hardy (2004) introduced the S_p statistics. It is calculated by regressing pairwise genetic relatedness over the logarithm of pairwise spatial distance. S_p value is calculated as $S_p = -\hat{b}_F / 1 - \hat{F}_{(1)}$, with \hat{b}_F as the slope of the linear regression, and $\hat{F}_{(1)}$ as the mean kinship coefficient of the first distance class which

comprises closest neighbours. Thus, S_p values primarily depend on the rate of decrease of pairwise kinship over distance. By providing a numerical value for the strength of SGS that is largely independent of sampling scheme and of arbitrarily chosen distance classes, it allows for the comparison of SGS between populations and species (Vekemans & Hardy, 2004).

Previous reviews used the S_p statistics to compare SGS among plant groups in order to determine the influence of different factors on SGS. For example, Nazareno, Alzate-Marin, and Pereira (2013) showed a relationship between plant sexual system and the strength of SGS. Vekemans and Hardy (2004) found significant effects of breeding system, life form and plant population density, but no significant effects of pollination mechanism or of seed dispersal on SGS. Dick, Hardy, Jones, and Petit (2008) compared SGS of plant species focusing on gene dispersal distances and climate region. While mean S_p values did not differ between tropical and temperate regions, a significant difference was found between wind- and animal-pollinated species in temperate regions, and among seed dispersal vectors (birds, bats and primates versus gravity, wind, water and rodents) in tropical regions. However, none of these reviews focused on the effects of animal seed dispersal on SGS.

1.3 | Aims of this review

The number of studies on SGS in animal-dispersed plant species has increased as a result of methodological advances. This includes plant species whose seeds are dispersed endo- or synzoochorously by vectors from different taxonomic groups and with different behavioural traits. Thus, it is timely to review the effect of zoochorous seed dispersal on the occurrences and strength of SGS.

In our review, we address the following questions:

1. *Does seed dispersal mode (endozoochory vs. synzoochory) influence the occurrence and strength of SGS?* We expect seeds transported in guts to be dispersed over longer distances than seeds carried in hands, mouths, bills or mandibles (Herrera & Jordano, 1981; Howe, 1989; Vander Wall & Beck 2012; Wehncke, Hubbell, Foster, & Dalling, 2003). Under this expectation, SGS should occur more frequently and be stronger (i.e., S_p values higher) in synzoochorously compared to endozoochorously dispersed plant species.
2. *Does taxonomic affiliation of the seed dispersal vector influence the occurrence and strength of SGS?* As the major groups of seed dispersal vectors (bats, birds, primates, rodents and ants) vary in their morphological features of physiology and mobility, we expect differences in the occurrence frequency and strength of SGS between these (C  rtes & Uriarte, 2013; Ness, Bronstein, Andersen, & Holland, 2004). More specifically, we expect plant species dispersed by highly mobile animals (bats, birds) to be less likely to show SGS and have weaker SGS compared to less mobile taxa.
3. *Does the behaviour of seed dispersal vectors influence the occurrence and strength of SGS?* While vectors from different

taxonomic groups differ in various basic aspects of their biology, they may nevertheless show functionally similar behaviour, such as hoarding of seeds by rodents and birds or dropping of seeds at specific roosting sites by birds and bats. Specifically, we expect plant species dispersed by vectors that move over large distances immediately after feeding or that cache seeds far away from food sources to be less likely to show SGS or have weaker SGS compared to animals that remain close to fruiting plants after feeding or discard seeds while feeding. Furthermore, as vector behaviours also determine seed dispersal distances, we expect S_p values to be related to observed seed dispersal distances.

4. *Which additional factors have an influence on occurrence and strength of SGS of zoochorous plants?* Other factors besides seed dispersal have been previously seen to influence SGS of plant species, but the number of animal-dispersed species was low in these studies (Dick et al., 2008; Nazareno et al., 2013; Vekemans & Hardy, 2004). In line with previous reviews, we examine the effect of pollination mechanism (animal vs. wind), climate region (temperate vs. tropical), plant life form, sexual and breeding system, population density and genetic marker type used (AFLP, Allozymes, ISSR, Microsatellites and RAPD) on the strength of SGS.

2 | METHODS

2.1 | Compilation of database

We queried Web of ScienceTM for articles listed until July 2017, describing SGS of zoochorously dispersed plant species (query: "spatial genetic structure" or "population genetic structure" + "seed dispersal" or "frugivory" or "endozoochory" or "synzoochory" or "ants" or "bats" or "birds" or "primates" or "rodents"). Additionally, we included studies on animal-dispersed plant species analysed in previously published reviews on SGS. For each study, we extracted data on plant characteristics (habitat, plant population density, pollination mechanism, sexual system, etc.), and data on the analytical methods (marker type used) from the publication itself or from the publications referenced therein. We also noted the presence or absence of SGS and, if provided, its strength in terms of S_p values (Table 1). The presence or absence of SGS was based on whether the authors identified significant SGS through one of the following three methods: (i) spatial autocorrelogram based on permutations, (ii) the slope of the linear regression over the pairwise distance matrix or (iii) significance of S_p statistics. Strength of SGS was assessed by the S_p statistics whenever values were provided or when we could obtain the regression slope and first distance class kinship coefficient values for its calculation. We calculated the mean of all analysed populations if more than one population of the same species was analysed in the same or different studies and if there was no indication seed dispersal systems differed. In cases where seed dispersers differed between studied populations of the same plant species, we considered them separately. As many publications did not provide detailed information on the animal species that acted as seed dispersal

TABLE 1 Information on zoochorously dispersed plant species included in this review

Species (Family)	Plant life form ^a	Climate region ^b	Breeding system ^c	Pollinator ^d	Dispersal mechanism ^e	Dispersal vectors ^f	Disperser behavioural category ^g	Marker type ^h	SGS ⁱ	Sp ^j	References
<i>Adansonia digitata</i> (Bombacaceae)	T	Tr-d	m(SI)	A	Endo	Ba	C	AFLP	Y	0.022	Kyndt et al. (2009)
<i>Araucaria angustifolia</i> (Araucariaceae)	T	Tr-w	d	W	Syn	Bi	E	Mi	Y	0.006	Stefenon et al. (2008), Sant'Anna et al. (2013)
<i>Attalea phalerata</i> (Arecaceae)	T	Tr-w	m(n/a)	A	Endo	P	B	Mi	Y	0.024	Choo et al. (2012)
<i>Baillonella toxisperma</i> (Sapotaceae)	T	Tr-w	m(M)	A	Endo	P, Ro, E	n/a ^k	Mi	Y	0.010	Duminil, Abessolo, et al. (2016)
<i>Cabralea canjerana</i> (Meliaceae)	T	Tr-w	d	A	Endo	Bi	n/a	Mi	N	n/a	Tavares De Oliveira Melo et al. (2014)
<i>Carapa guianensis</i> (Meliaceae)	T	Tr-w	m(SI)	A	Syn	Ro	D	Mi	Y	0.005	Cloutier et al. (2007), Dick et al. (2008)
<i>Carapa procera</i> (Meliaceae)	T	Tr-w	m(M)	A	Syn	Ro	D	RAPD	Y	0.028	Hardy et al. (2006)
<i>Castanopsis sclerophylla</i> (Fagaceae)	T	Te	m(O)	W	Syn	Ro	D	Mi	Y	0.005	Wang et al. (2011)
<i>Ceratiola ericoides</i> (Ericaceae)	S	Tr-d	d	W	Endo	Bi	n/a	Al	N	n/a	Trapnell et al. (2008)
<i>Chrysophyllum sanguinolentum</i> (Sapotaceae)	T	Tr-w	m(n/a)	A	Endo	P	n/a	AFLP, RAPD	Y	0.015	Hardy et al. (2006)
<i>Cinnamomum insularimontanum</i> (Lauraceae)	T	Te	m(n/a)	A	Endo	Bi	A	Al	N	n/a	Chung et al. (2003)
<i>Clusia lechleri</i> (Clusiaceae)	T	Tr-w	d	A	Endo	Bi	A	Mi	N	n/a	Quevedo et al. (2013)
<i>Clusia sphaerocarpa</i> (Clusiaceae)	T	Tr-w	d	A	Endo	Bi	A	Mi	N	n/a	Quevedo et al. (2013)
<i>Dicorynia guianensis</i> (Leguminosae)	T	Tr-w	d	A	Endo	Bi	A	Mi	N	n/a	Quevedo et al. (2013)
<i>Dioscorea japonica</i> (Dioscoreaceae)	E	Te	d	A	Endo	Ro	D	RAPD	Y	0.019	Hardy et al. (2006)
<i>Dysoxylum malabaricum</i> (Meliaceae)	T	Tr-w	m(M)	A	Syn	Ro	D	Mi	Y	0.014	Mizuki et al. (2010)
<i>Erythrophloeum suaveolens</i> (Fabaceae)	T	Tr-w	m(M)	A	Endo	Bi	B		N	n/a	Bodare et al. (2017)
<i>Fagus crenata</i> (Fagaceae)	T	Te	m(SI)	W	Syn	Ro	n/a	Mi	Y	0.006	Duminil, Dainou, et al. (2016)
<i>Fagus sylvatica</i> (Fagaceae)	T	Te	m(O)	W	Syn	Bi	D	Mi	Y	0.003	Oddou-Muratorio et al. (2010)
<i>Ficus citrifolia</i> (Moraceae)	E	Tr-w	m(O)	A	Endo	Ba	C	Mi	Y	0.013	Heer et al. (2015)
<i>Ficus cyrtophylla</i> (Moraceae)	E	Tr-w	m(O)	A	Endo	Ba	n/a	Mi	Y	0.007	Nazareno et al. (2013)
<i>Ficus exasperata</i> (Moraceae)	T	Tr-w	d	A	Endo	Bi	B	Mi	N	0.029	Zhou & Chen (2010)
<i>Ficus eximia</i> (Moraceae)	T	Te	d	A	Endo	Bi	n/a	Mi	Y	0.035	Dev et al. (2011)
<i>Ficus hispida</i> (Moraceae)	T	Tr-w	m(O)	A	Endo	Ba	n/a	Mi	Y	0.006	Nazareno et al. (2013)
<i>Ficus insipida</i> (Moraceae)	T	Te	d	A	Endo	Ba	n/a	Mi	Y	0.031	Dev et al. (2011) ^m
<i>Ficus obtusifolia</i> (Moraceae)	E	Tr-w	m(O)	A	Endo	Ba	C	Mi	Y	0.004	Heer et al. (2015)
<i>Ficus pumila</i> (Moraceae)	E	Te	d	A	Endo ^j	Ba, Bi*	n/a	Mi	Y	0.074	Wang et al. (2009)
<i>Ficus yoponensis</i> (Moraceae)	T	Tr-w	m(O)	A	Endo	Ba	C	Mi	Y	0.008	Heer et al. (2015)
<i>Globba lancangensis</i> (Zingiberaceae)	H	Te	m(n/a)	A	Syn	A	n/a	ISSR	Y	n/a	Zhou et al. (2007)

(Continues)

TABLE 1 (Continued)

Species (Family)	Plant life form ^a	Climate region ^b	Breeding system ^c	Pollinator ^d	Dispersal mechanism ^e	Dispersal vectors ^f	Disperser behavioural category ^g	Marker type ^h	SGS ⁱ	Sp ^j	References
<i>Manilkara maxima</i> (Sapotaceae)	T	Tr-w	m(O)	A	Endo	Ba, Bi, P	n/a	Mi	Y	0.015	Ganzhorn et al. (2015)
<i>Milicia excelsa</i> (Moraceae)	T	Te	d	W	Endo	Ba	A	Mi	Y	0.005	Bizoux et al. (2009)
<i>Moronebea coccinea</i> (Clusiaceae)	T	Tr-w	m(n/a)	A	Syn	Ro	D	RAPD	Y	0.053	Hardy et al. (2006)
<i>Neolitsea sericea</i> (Lauraceae)	T	Te	d	A	Endo	Bi	A	Al	N	n/a	Chung, Chung, Oh, et al. (2000)
<i>Notholithocarpus densiflorus</i> (Fagaceae)	S	Te	m(O)	A	Syn	Bi	E	Mi	Y	0.010	Dodd et al. (2013)
<i>Oenocarpus bataua</i> (Arecaceae)	T	Tr-w	m(n/a)	n/a	Endo	Bi	n/a	Mi	Y	n/a	Karubian et al. (2010)
<i>Olea europaea</i> (Oleaceae)	T	Te	m(SI)	W	Endo	Bi	n/a	Mi	Y	0.005	Beghè et al. (2017)
<i>Parkia panurensis</i> (Fabaceae)	T	Tr-w	m(n/a)	A	Endo	P	n/a	Mi	Y	n/a	Bialozyt, Luettmann, et al. (2014)
<i>Pinus pumila</i> (Pinaceae)	T	Te	m(n/a)	W	Syn	Bi	n/a	Al	Y	n/a	Tani et al. (1998)
<i>Polygala reinii</i> (Polygalaceae)	S	Te	n/a	A	Syn	A	D	Al	Y	0.026	Nakagawa (2010)
<i>Pouteria reticulata</i> (Sapotaceae)	T	Tr-w	d	A	Endo	Bi, P	A	Mi	Y	0.006	Schroeder et al. (2014)
<i>Protium spruceanum</i> (Burseraceae)	T	Tr-w	d	n/a	Endo	Bi	n/a	Al	N	0.011	Vieira et al. (2012)
<i>Prunus africana</i> (Rosaceae)	T	Tr-w	m(SI)	A	Endo	Bi, P	B	Mi	Y	0.014	Berens et al. (2014) ^{jm}
<i>Prunus avium</i> (Rosaceae)	T	Te	m(SI)	A	Endo	Bi	A	Mi	Y	0.009	Schueler et al. (2006)
<i>Psychotria acuminata</i> (Rubiaceae)	S	Tr-w	m(SI)	A	Endo	Bi	C	AFLP	Y	0.036	Theim et al. (2014)
<i>Psychotria hoffmannseggiana</i> (Rubiaceae)	S	Tr-w	m(SI)	A	Endo	Bi	C	AFLP	Y	0.023	Theim et al. (2014)
<i>Psychotria horizontalis</i> (Rubiaceae)	S	Tr-w	m(SI)	A	Endo	Bi	C	AFLP	Y	0.015	Theim et al. (2014)
<i>Psychotria marginata</i> (Rubiaceae)	S	Tr-w	m(SI)	A	Endo	Bi	C	AFLP	Y	0.046	Theim et al. (2014)
<i>Psychotria nervosa</i> (Rubiaceae)	S	Tr-w	m(n/a)	A	Endo	Bi	n/a	Al	N	0.012	Dewey & Heywood (1988), Vekemans & Hardy (2004)
<i>Psychotria officinalis</i> (Rubiaceae)	S	Tr-w	m(SI)	A	Endo	Bi	A	Al	Y	0.010	Loiselle et al. (1995), Vekemans and Hardy (2004)
<i>Pulmonaria officinalis</i> (Boraginaceae)	H	Te	m(SI)	A	Syn	A	D	Mi	Y	0.004	Meeus et al. (2013)
<i>Quercus ellipsoidalis</i> (Fagaceae)	T	Te	m(SI)	W	Syn	Bi	E	Mi	Y	0.011	Lind-Riehl & Gailing (2015)
<i>Quercus ilex</i> (Fagaceae)	T	Te	m(SI)	W	Syn	Bi	E	Mi	N	0.004	Soto et al. (2007)
<i>Quercus lobata</i> (Fagaceae)	T	Tr-d	m(SI)	W	Syn	Bi	E	Mi	Y	0.005	Sork et al. (2015)
<i>Quercus mongolica</i> (Fagaceae)	T	Te	m(SI)	W	Syn	Bi	n/a	Al	Y	n/a	Chung & Chung (2004)
<i>Quercus petraea</i> (Fagaceae)	T	Te	m(SI)	W	Syn	Ro	D	Mi	Y	0.008	Streiff et al. (1998), Vekemans & Hardy (2004)
<i>Quercus robur</i> (Fagaceae)	T	Te	m(SI)	W	Syn	Bi	E	Mi	Y	0.003	Streiff et al. (1998), Vekemans & Hardy (2004)
<i>Quercus rubra</i> (Fagaceae)	T	Te	m(SI)	W	Syn	Bi	E	Mi	Y	0.005	Lind-Riehl & Gailing (2015)
<i>Rhus javanica</i> (Anacardiaceae)	T	Te	d	A	Endo	Bi	n/a	Mi	Y	0.015	Chung, Epperson, et al. (2000), Vekemans & Hardy (2004)

(Continues)

TABLE 1 (Continued)

Species (Family)	Plant life form ^a	Climate region ^b	Breeding system ^c	Pollinator ^d	Dispersal mechanism ^e	Dispersal vectors ^f	Disperser behavioural category ^g	Marker type ^h	SGS ⁱ	Sp ^j	References
<i>Schinus molle</i> (Anacardiaceae)	T	Tr-d	d	A	Endo	Bi	B	AF	Y	0.021	Lemos et al. (2015)
<i>Sclerolaena diacantha</i> (Chenopodiaceae)	S	Tr-d	m(M)	W	Syn	A	n/a	Al	Y	n/a	Peakall & Beattie (1995)
<i>Sextonia rubra</i> (Laureaceae)	T	Tr-w	m(n/a)	A	Endo	Bi	A	Mi, RAPD	N	0.006	Hardy et al. (2006)
<i>Simarouba amara</i> (Simaroubaceae)	T	Tr-w	d	A	Endo	Ba, Bi, P	n/a	AFLP, Mi	Y	0.008	Hardesty, Dick, Kremer, Hubbell and Bermingham, (2005), Dick et al. (2008)
<i>Sorbus torminalis</i> (Rosaceae)	T	Te	m(Sl)	A	Endo	Bi	B	Mi	Y	0.014	Jankowska-Wroblewska et al. (2016), Oddou-Muratorio, Demesure-Musch, Pélissier and Gouyon 2004
<i>Symphonia globulifera</i> (Clusiaceae)	T	Tr-w	m(O)	A	Endo	Ba, P, R, AM, T	A	Mi	Y	0.011	Torroba-Balmori et al. (2017)
	T	Tr-w	m(O)	A	Endo	Bi, P, SR	B	Mi	Y	0.025	Torroba-Balmori et al. (2017)
	T	Tr-w	m(O)	A	Endo	Ba, AM, SR	n/a	Mi, RAPD	Y	0.017	Hardy et al. (2006)
<i>Trillium grandiflorum</i> (Melanthiaceae)	H	Te	m(Sl)	A	Syn	A	n/a	Al	Y	0.025	Kalisz et al. (2001), Vekemans & Hardy (2004)
<i>Trillium maculatum</i> (Melanthiaceae)	H	Te	n/a	n/a	Syn	A	D	Al	N	n/a	Walker et al. 2009)
<i>Viola michelii</i> (Myristicaceae)	T	Tr-w	d	A	Endo	Bi, P, AM	n/a	AFLP, RAPD	Y	0.015	Hardy et al. (2006)
<i>Voucapoua americana</i> (Fabaceae)	T	Tr-w	m(M)	A	Syn	Ro	D	Mi, RAPD	Y	0.028	Dutech et al. (2002) ^m , Hardy et al. (2006)

^aE: epiphyte or hemi-epiphyte; H: herb; S: shrub; T: tree.^bTr-d: tropical-dry; Tr-w: tropical-wet/moist; Te: temperate.^cd: dioecious; m: monoecious (M: mixed mating system, O: outcrossing, Sl: self-incompatible).^dA: animal (insect or vertebrate); W: wind.^eEndo: endozoochory, Syn: synzoochory.^fA: ants; Ba: bats; Bi: birds; P: primates; Ro: rodents; Mix: including various taxa (AM: nocturnal arboreal mammals, E: elephants, SR: small ruminants, T: tapirs).^gsee Table 2.^hAFLP: amplified fragment length polymorphism; Al: allozymes; ISSR: inter-sequence short repeats; Mi: microsatellites; RAPD: random amplified polymorphic DNA.ⁱY: SGS present; N: SGS absent.^jMean Sp values for adults of all populations of that species or specific study.^kInformation not available.^lAbsent seed dispersers *Ficus pumila*.^mSp value calculated from published results.

vectors or on vector behaviour, we extracted pertinent information from publications referenced in the studies. For our analysis, we only considered studies on adult life stage of the plant as we were ultimately interested in the long-term effects of animal seed dispersal in SGS. In total, we obtained data for SGS in adult plants of 68 zoochorously dispersed species.

2.2 | Statistical analyses

First, we examined the effect of seed dispersal mode (endozoochory or synzoochory) on the presence and strength of SGS in plant species. Epizoochorously dispersed species were underrepresented; therefore, we excluded them from the analysis (Williams & Guries, 1994; Bonnin, Ronfort, Wozniak, & Olivieri, 2001; Rico & Wagner 2016). Second, we tested whether the presence and strength of SGS in plant species were related to the taxon of the seed dispersers (ants, bats, birds, primates, rodents). We assigned plant species for which more than one animal taxon was described as seed disperser to the category “mix” (not included in the analysis). Third, we tested for the effect of seed disperser behaviour on SGS. For this, whenever this information was available in the respective publications or in literature referenced therein, we assigned dispersers to five categories according to behavioural traits (Table 2). Fourth, we compared *Sp* values between groups of zoochorous plants that differed in pollination mechanism, climatic region, sexual and breeding system, and genetic marker used. Finally, we correlated *Sp* values with observed seed dispersal distance and plant population density using the Spearman rank correlation.

To determine whether dispersal mode, disperser taxa and behaviour had a statistically significant influence on the occurrence of SGS in plant populations, we used the `PROP.TEST()` function in R which tests for the null hypothesis that the proportion of studies with presence of SGS is equal across all categories. For testing the influence of different categories of dispersal vectors on SGS, we first identified outliers with the modified Thompson tau test (Thompson, 1985) and based on the results, excluded two studies from the subsequent

analysis [*Moronobea coccinea* (Hardy et al., 2006) and *Ficus pumila* (Wang et al., 2009)]. *Moronobea coccinea* was variably described as rodent or gravity-dispersed by Hardy et al. (2006) and Dick et al. (2008), respectively. Similarly, *F. pumila* was described as bat-, ant- and rodent-dispersed, but studied in an urban area without seed dispersers, where most fruits fell to the ground without further removal. Therefore, in both cases, seeds might have been mainly gravity-dispersed which would explain the high *Sp* values. Second, we examined whether the assumptions for an ANOVA were met, namely, the normal distribution of residuals and homogeneity of variance, which we tested with Shapiro–Wilk test and a Barlett's K-squared test. Both assumptions were met after log-transformation of *Sp* values, which were then used for further analysis.

We conducted Factorial ANOVAS to analyse the influence of seed dispersal (mode, taxa and behaviour) on the strength of SGS using the `AOV()` function in R (RStudio 2016). In each model, we included additional factors previously considered as relevant for SGS (i.e., pollination mechanism, climate region, plant life form, sexual and breeding system, and marker type) to account for potential interactions with seed dispersal. In cases where significant differences between categories were detected, we performed a Tukey post hoc comparison using the `TUKEYHSD()` function.

We then analysed, separately, the main effects of these additional factors on SGS strength using again a Factorial ANOVA. In addition, to maintain comparability with previous reviews, we also tested each factor separately with either a one-way ANOVA or a *t* test, depending on the number of levels.

Finally, to analyse the correlation of *Sp* values with plant population density and observed seed dispersal distance, we conducted the Spearman rank correlation. For cases where populations of the same plant species were analysed, we used the `GEOM_SMOOTH()` function to visualize intraspecific differences of the effect of plant population density and marker type use on the strength of SGS. For statistical analysis and its graphical representation, we used the R packages “STATS,” “DOBY,” “USERFRIENDLYSCIENCE,” “GGPLOT2” and “GGPUBR”

TABLE 2 Categorization of seed dispersers based on feeding and post-feeding behavioural traits. Seed dispersers were assigned to a given category if they were described as having one or more behavioural traits of the respective category

	Feeding/foraging behaviour	Postfeeding behaviour
Category A	Swallows seeds at source Spits/Regurgitates seeds after transport Short-feeding bouts	Moves away from source after feeding High mobility
Category B	Spits/regurgitates seeds at source High loss of fruits while foraging Long-feeding bouts	Remains close to source after feeding Low mobility
Category C	Swallows seeds at source	Low or high mobility Passive accumulation of seeds i.e. consistently used roosting, perching or lekking sites
Category D	Takes fruits/seeds and feeds away from source	Active accumulation of seeds through caching or hoarding Low mobility For example rodents, ants
Category E	Takes fruits/seeds and feeds away from source	Active accumulation of seeds through caching or hoarding High mobility For example scatter-hoarding birds

(Højsgaard & Halekoh, 2016; Kassambara, 2017; Peters, 2017; R Core Team 2016; RStudio, 2016; Wickham, 2009).

3 | EFFECT OF SEED DISPERSAL MODE ON SGS

Seed dispersal mode (endozoochory or synzoochory) had a marginally significant influence on the occurrence of SGS: synzoochorous plants tended to have SGS more frequently compared to endozoochorous plant species (Table 3; $\chi^2(1) = 3.1$, $p = .058$). Strength of SGS differed significantly between endozoochorously and synzoochorously dispersed plant species (ANOVA, $F(1,18) = 7.04$, $p = .016$) with lower Sp values in synzoochorously dispersed species compared to endozoochorously dispersed species. However, the effect of seed dispersal mode on SGS strength was significantly dependent on marker type used (ANOVA, $F(1,18) = 4.49$, $p = .048$). Therefore, with the available data, we cannot disentangle the effects of seed dispersal mode and marker type used.

4 | EFFECT OF SEED DISPERSER TAXONOMIC GROUP ON SGS

The proportion of plant species with SGS varied significantly between dispersers from different taxonomic groups ($\chi^2(5) = 14.894$, $p = .011$; Table 3). This difference could be attributed to the much lower proportion of plant species dispersed by birds that showed SGS (Table 3). However, the strength of SGS did not differ between taxonomic groups (ANOVA, $F(4,16) = 0.17$, $p = .94$; Figure 1b, Table 4). No interaction effects were found with the additional factors. Our results suggest seed dispersal by birds reduces the

likelihood of SGS occurrence, but when present, strength is comparable to that produced by other seed disperser groups. High variance in Sp values within categories indicates other factors that we could not account for affected the strength of SGS within the taxonomic groups.

5 | EFFECT OF SEED DISPERSER BEHAVIOUR ON SGS

The occurrence of SGS differed significantly among behavioural groups of seed dispersers ($\chi^2(4) = 11.9$, $p = .018$; Table 3). Plant species dispersed by vectors of category A were less likely to have SGS compared to other groups. These dispersers were characterized by having short-feeding bouts or travel faster and longer away from the source plant. Sp values were also significantly different between categories (ANOVA: $F(4,12) = 4.35$, $p = .02$; Figure 1c, Table 4), without significant interaction effects of the additional factors. SGS was the weakest for plant species dispersed by highly mobile animals which move away from source plants immediately after feeding (category A), and which accumulate seeds in widely distributed caches (category E, see below). In contrast, Sp values were the highest for plants dispersed by animals with short-range movement and behaviours that maintain individuals around fruit sources after feeding or that increase the rate of fruit or seed droppings around sources (category B), and for plants with dispersers that accumulate seeds in roosts (category C).

The Tukey post hoc test indicated that only categories C and E differed significantly in the strength of SGS ($p = .044$), and that the difference between B and E was marginally significant ($p = .071$). Thus, if seeds were accumulated either actively in roosts, or passively in close vicinity to the maternal plant, SGS was higher than in plants whose seeds were actively distributed to caches by scatter-hoarding birds.

One noticeable result was the high variance in Sp values within plants from category C and D (Figure 1c, Table 4). In both cases, seeds are accumulated, either in roosts by flying animals (category C), or in caches by scatter hoarding mammals or in ant mounds (category D). In contrast, SGS was generally low in species dispersed by scatter-hoarding birds (E). In all three cases, the strength of SGS likely depends on (i) the number of seeds taken from each source plant, (ii) the number of seeds accumulated in a single cache or roosting site, (iii) the number of source plants for a single caching site and (iv) the distance between source plant(s) and the caching or roosting sites. Although the respective studies did not report whether dispersers tended to accumulate seeds from a few or many source plants, research shows scatter hoarding birds fly for long distances after fruit and seed collection, transporting a small number of seeds in their beaks (Lovette & Fitzpatrick, 2016), which results in a wide distribution of dispersed seeds and could potentially reduce SGS. For example, blue jays carry a mean of 2.2 acorns from the same tree at a time, and travel on average 1.1 km before depositing seeds in widely distributed caches (Darley-Hill & Johnson, 1981). In

TABLE 3 The presence of SGS in zoochorously dispersed plant species. We report the number and percentage of plant species with SGS for which we obtained information on seed dispersal mode, seed disperser group and/or seed disperser behaviour

	Category	# of plant species studied	# (%) of plant species with SGS
Seed dispersal mode	Endozoochory	42	31 (74)
	Synzoochory	26	24 (92)
Seed disperser taxonomy	Ants	6	5 (83)
	Bats	7	7 (100)
	Birds	32	20 (63)
	Primates	4	4 (100)
	Rodents	10	10 (100)
Seed disperser behaviour	Category A	10	5 (50)
	Category B	7	5 (71)
	Category C	9	9 (100)
	Category D	13	12 (92)
	Category E	8	7 (88)



FIGURE 1 Comparison of Sp values of plant species with (a) different dispersal modes: dispersal through defecation or regurgitation (endozoochory) versus dispersal through actively carried seeds (synzoochory), (b) different taxonomic groups of dispersal vectors and (c) different behavioural categories of dispersal vectors. In (c), bars with different superscripts differ at $p < .05$ (Tukey post hoc test). Horizontal lines are median values, boxes indicate 25% and 75% quartiles

TABLE 4 Comparison of the strength of SGS, via Sp statistics, among the seed disperser categories for seed dispersal mode, seed disperser taxonomy and seed disperser behaviour. Mean Sp , median, standard deviation (SD) and the number of studies (N) are given for each category. Significance was tested with a Factorial ANOVA

		Sp mean	Sp median	SD	N
Seed dispersal mode	Endozoochory	0.0164	0.0145	0.0108	29
	Synzoochory	0.0144	0.0102	0.0129	19
	ANOVA, $F(1,18) = 7.04$, $p = .02$				
Seed disperser taxonomy	Ants	0.0182	0.0250	0.0122	3
	Bats	0.0149	0.0098	0.0108	9
	Birds	0.0156	0.0120	0.0122	18
	Primates	0.0151	0.0151	0.0073	4
	Rodents	0.0185	0.0163	0.0152	10
	ANOVA, $F(4,16) = 0.17$, $p = .94$				
Seed disperser behaviour	Category A	0.0084	0.0094	0.0026	5
	Category B	0.0195	0.0212	0.0053	5
	Category C	0.0221	0.0221	0.0136	9
	Category D	0.0178	0.0163	0.0146	12
	Category E	0.0075	0.0058	0.0039	7
	ANOVA, $F(4,12) = 4.35$, $p = .02$				

contrast, category D comprised ground-dwelling rodents and ants which frequently stay near source plants after collecting seeds. For example, rodents transport fallen seeds of Holm oaks (*Quercus ilex*) over short distances (median = 1.5 m) before depositing them in caches (Gómez, Puerta-Piñero, & Schupp, 2008), thus increasing the potential for formation of SGS. Category C included studies of Paletropical and Neotropical bats that often deposit seeds beneath feeding roosts and birds with roosting behaviour. We expect seed dispersal by birds with lekking behaviour or primates with recurrent sleeping or resting sites to result in similar dispersal patterns, but we did not find studies on strength of SGS for these. The high variance in category C might be further explained by factors previously

shown to influence seed deposition by bats: spatial distribution of resources, body size, social structure and feeding competition (Heithaus, Fleming, & Opler, 1975). In all cases where seeds are passively or actively accumulated, the number of source plants, and potentially also the distance to source plants, can be determined with genetic markers providing information on how hoarding and roosting behaviour shape SGS (García, Jordano, Arroyo, & Godoy, 2009; Godoy & Jordano, 2001; Hamrick & Trapnell, 2011).

The spatial distribution of resources, body size, social structure and feeding competition likely influence dispersal patterns in all behavioural categories. Therefore, the differences we detected between behaviour categories, despite these additional influencing factors, make the detected differences even more notable. Our results confirm SGS strength is strongly dependent on how animals feed, whether they deposit seeds around fruit source and whether they stay close to the fruit sources after feeding or gathering seeds, which directly influences seed deposition patterns and seed dispersal distance. In fact, based on the few studies that provided estimates or observations of seed dispersal distances ($N = 13$), we found a trend towards lower Sp values with longer seed dispersal distances (Spearman rank correlation, $r_s = -.320$, $p = .113$, Fig. S1).

Several studies analysed in this review did not supply Sp statistics but nevertheless provide strong indications for effects of animal behaviour on SGS. (i) Trapnell, Schmidt, and Hamrick (2008) studied two populations of the shrub *Ceratiola ericoides*, whose seeds are dispersed by frugivorous birds in sand dunes. The population where the surrounding tree community offered safe perching sites for birds had higher mean kinship coefficients between neighbouring shrub individuals than the population where forest cover was reduced. In the latter, birds flew away more rapidly after collecting fruits as a strategy to reduce predation risk. (ii) The trees *Neolitsea sericea* and *Cinnamomum insularimontanum* are mainly dispersed by frugivorous birds that tend to leave the fruiting tree immediately after the collection of single fruits (Chung, Chung, Chung, & Epperson, 2000; Chung, Chung, Oh, & Epperson, 2000; Chung, Nason, Epperson, &

Chung, 2003). No SGS was detected in populations of these trees. (iii) Seeds of *Ficus hispida* are mainly dispersed by large green pigeons (*Treron capellei*), solitary fig specialists that frequently drop fruits while feeding (Birdlife International 2001; Lambert, 1989). In an autocorrelation analysis, adult *F. hispida* showed high kinship coefficient values within the first distance class (Dev, Kjellberg, Hos-saert-McKey, & Borges, 2011). (iv) Seeds of the palm *Oenocarpus bataua* are dispersed by umbrella birds (*Cephalopterus penduliger*). Male umbrella birds had individual-specific leks to which they returned constantly after feeding. They spent 80% of their time at their leks and deposited there 50% of the ingested seeds. This created a diverse pool of seeds within the leks, with five times more seed sources than outside the leks. SGS within leks was weaker than in the surrounding areas (Karubian et al., 2012). (v) The same plant species, *Oenocarpus bataua*, is also dispersed by white-bellied spider monkeys (*Ateles belzebuth*). These monkeys used sleeping sites repeatedly which resulted in an accumulation of seeds, but only from the few palms on which they fed before retiring to sleep. Consequently, seed source diversity beneath sleeping sites was low and SGS significant. (Karubian, Ottewell, Link, & Di Fiore, 2015).

Secondary seed dispersal, that is subsequent movement of the seeds after its primary deposition, can also influence SGS strength by increasing seed dispersal distances and further modifying the spatial patterns of seed dispersal (Gallegos, Hensen, & Schleuning, 2014; Hämäläinen et al., 2017; Hirsch, Kays, & Jansen, 2012; Mizuki & Takahashi, 2009). A study on agoutis showed a large number of seeds were stolen from caches and transported further, which resulted in final dispersal distances of >100 m (Jansen et al., 2012). This suggests secondary seed dispersal might be more efficient than previously considered, and thus might have a nontrivial influence on SGS.

6 | ADDITIONAL FACTORS INFLUENCING SGS OF ZOOCHOROUSLY DISPERSED SPECIES

In our data set of zoochorously dispersed plant species, among the additional factors, we found only pollination mechanism (ANOVA: $F(1,20) = 5.92$, $p = .02$) and marker type used (ANOVA: $F(3,20) = 4.23$, $p = .02$) had a significant influence on the strength of SGS (Table 5). Plant species pollinated by animals had higher Sp values than wind-pollinated species (Fig. S2). A similar trend of pollination on SGS has been seen before for temperate species (Dick et al., 2008), but not for species from diverse climatic regions (Vekemans & Hardy, 2004) (Table S1). We found no effect of sexual system, nor breeding system, in contrast to previous reviews (Nazareno et al., 2013; Vekemans & Hardy, 2004); however, our results showed high variance within categories and a low number of self-compatible species. Like previous findings, we did not detect a difference in the strength of SGS between plants growing in different climatic regions (Dick et al., 2008). Neither did we detect differences among plant life forms, but our data set consisted mainly of tree species so the results cannot be

TABLE 5 Effects of additional factors (i.e., factors other than seed dispersal) on the strength of SGS

		Sp mean	Sp median	SD	N
Pollination mechanism	Animal	0.0183	0.0150	0.0117	37
	Wind	0.0066	0.0051	0.0041	11
ANOVA, $F(1,20) = 0.39$, $p = .02$					
Plant life form	Epiphyte	0.0183	0.0140	0.0113	3
	Herbs	0.0146	0.0146	0.0147	2
	Shrub	0.0237	0.0230	0.0135	7
	Tree	0.0138	0.0100	0.0108	36
ANOVA, $F(3,20) = 2.31$, $p = .11$					
Sexual system/ Breeding system	Monoecious (Mixed)	0.0179	0.0187	0.0099	5
	Monoecious (Outcrossing)	0.0120	0.0100	0.0078	10
	Monoecious (Self-incompatible)	0.0140	0.0103	0.0119	19
	Dioecious	0.0156	0.0145	0.0106	10
ANOVA, $F(3,20) = 2.06$, $p = .14$					
Climate region	Temperate	0.0129	0.0102	0.0096	21
	Tropical	0.0177	0.0150	0.0127	27
ANOVA, $F(1,20) = 2.91$, $p = .10$					
Markers	AFLP	0.0231	0.0212	0.0110	9
	Allozyme	0.0203	0.0250	0.0086	3
	Microsatellite	0.0123	0.0094	0.0094	35
	RAPD	0.0184	0.0150	0.0076	6
ANOVA, $F(3,20) = 0.85$, $p = .02$					

compared to other studies. Jump, Rico, Coll, and Peñuelas (2012) suspected that the use of different markers might impact the strength of SGS. In our data set, studies using microsatellites resulted in significantly lower Sp values compared to studies using AFLPs (Fig. S3a). However, when we restricted the comparison of plant species investigated in parallel with two different marker types, we could not confirm the finding by Jump et al. (2012) (Fig. S3b). The potential interaction effect of pollination and marker type used was accounted for on all our analysis by testing for interactions using the Factorial ANOVA.

Contrary to what we expected, plant population density showed no correlation with strength of SGS (Spearman rank correlation, $r_s = -.01$, $p = .48$, Fig. S4a). Furthermore, when we compared populations from the same plant species with different adult plant densities through a generalized linear regression, there was no clear pattern (Fig. S4b). Eight out of fifteen plant species showed a decrease in Sp value with an increase in plant population density, while seven out of fifteen showed an increase in Sp values.

The list of additional factors that might potentially influence SGS in the surveyed studies, but were present in too few studies to include in the analysis, included fruit availability and plant distribution (Bizoux et al., 2009; Trapnell et al., 2008), management situation of plant populations (Lind-Riehl & Gailing, 2015), habitat

fragmentation (Vieira, Fajardo, de Souza, Reis, & de Carvalho, 2012; Wang, Compton, & Chen, 2011), urbanization level of study site (Wang et al., 2009), specific microhabitat requirements limiting germination success (Chung et al., 2003; Heer et al., 2015) and plant life history, such as masting events or high fruiting yields (Lind-Riehl & Gailing, 2015; Vieira et al., 2012), clonality (Dodd, Mayer, Nettel, & Afzal-Rafii, 2013) or plant life form (Heer et al., 2015). Many of these factors influence directly or indirectly foraging behaviour of the seed dispersal vectors.

The available evidence on our study shows zoochorous seed dispersal has an important impact on spatial distribution of genotypes at local scales.

7 | FUTURE DIRECTIONS

In many studies that analyse spatial genetic structure of zoochorous plants, behaviour of seed dispersal vectors was neglected. Our study provides evidence that vector behaviour impacts SGS via shaping seed dispersal patterns (Stiles, 2000). These patterns can be highly consistent over time (Heymann et al., 2017), increasing the probability of an effect of seed dispersal on SGS. Anthropogenic disturbances that might modify vector behaviour are thus likely to influence seed dispersal patterns and in turn SGS (Jones, Duke-Sylvester, Leberg, & Johnson, 2017; McConkey & O'Farrill, 2015). Our results emphasize the need for future studies on population genetics of animal-dispersed plants to include ecological and behavioural observations of dispersal vectors as a key for understanding gene flow and spatial distribution of genetic diversity.

Focal observations of fruiting trees (Jordano & Godoy 2002; Donatti et al., 2011) can provide data on number and identity of dispersers present in the area, and their behaviour during and immediately after feeding. Furthermore, focal-animal sampling (Morales, García, Martínez, Rodríguez-Pérez, & Herrera, 2013) or radio-tracking dispersers or seeds (Holbrook & Smith, 2000; Levey & Sargent 2000; Pons & Pausas, 2007) can determine whether seed dispersers deposit seeds in clusters or clumps. If so, molecular markers can be used to determine the number of maternal source plants, and potentially, also their location (Agrawal, Agrawal, Tandon, & Raina, 2013; Heymann et al., 2012).

Our analyses were based on studies that examine SGS in adult plants; however, the scale and strength of SGS may change over life stages (e.g., Bialozyt, Flinkerbusch, et al., 2014; Bialozyt, Luettmann, et al., 2014). Future studies relating seed dispersal to SGS in zoochorously dispersed plants should consistently include earlier life stages (seedlings, saplings). Although seedlings are not fully representative of seed dispersal shadows, as surviving seedlings passed the bottlenecks of seed and seedling mortality due to predators and pathogens, they are still more likely to reflect the initial spatial template created by seed dispersers. Furthermore, our analysis showed that besides seed disperser behaviour, pollination mechanism and marker type used can have a significant effect on SGS. Therefore, future studies on the effect of animal seed dispersal on SGS should

consider the impact of pollination on SGS, and take caution when comparing studies that use different marker types. Overall, our results show SGS is strongly dependent on plant–animal interaction. Consequently, a more integrative approach between plant and animal ecology is needed to fully comprehend its formation and strength in zoochorous plants.

Although not widely acknowledged, the analyses of SGS can also have practical implications for conservation (Escudero, Iriondo, & Torres, 2003). The spatial extent of SGS can be used to identify the scale over which seeds should be collected and planted to optimize genetic diversity of recruits in managed forest regeneration (Cruse-Sanders & Hamrick, 2004; Jin, He, & Lu, 2003; Melo Júnior et al., 2015; Ramos et al., 2016; Yao, Zhang, Ye, & Huang, 2011). Understanding the impact of zoochorous seed dispersal on SGS may help to integrate frugivore behaviour in forest conservation and management strategies.

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AUTHOR CONTRIBUTIONS

T.A.G.C., E.W.H. and K.H. designed and wrote the manuscript. T.A.G.C. and K.H. did the bibliographic research. T.A.G.C. analysed the data and prepared figures and tables.

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SUPPORTING INFORMATION

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