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Interspecific associations in seed arrival and seedling recruitment in a Neotropical forest

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Abstract. Contagious seed dispersal refers to the tendency for some sites to receive many dispersed seeds while other sites receive few dispersed seeds. Contagious dispersal can lead to interspecific associations in seed arrival, and this in turn might lead to interspecific associations in seedling recruitment. We evaluate the extent of spatially contagious seed arrival, the frequency of positive interspecific associations in seed arrival, and their consequences for seedling recruitment at the community level in a tropical moist forest. We quantified seed arrival to 200 passive seed traps for 28 yr of weekly censuses and seedling recruitment to 600 1-m^2 quadrats for 21 yr of annual censuses on Barro Colorado Island, Panama. We assessed whether spatially contagious seed dispersal was more important among zoochorous species than among anemochorous species, increased in importance with similarity in fruiting times, and led to interspecific associations in seed arrival and seedling recruitment. We controlled adult seed source associations statistically to evaluate predicted relationships. We found that spatially contagious seed arrival was widespread among zoochorous species, but also occurred among anemochorous species when the strong, consistent trade winds were present. Significant interspecific associations in seed arrival were more likely for pairs of species with zoochorous seeds and similar fruiting times and persisted through seedling recruitment. Thus, interspecifically contagious seed dispersal affects local species composition and alters the mixture of interspecific interactions through the seed, germination, and early seedling stages in this forest. Future investigations should consider the implications of interspecific association at the regeneration stages documented here for later life stages and species coexistence.

Key words: anemochory; Barro Colorado Island; contagious seed dispersal; fruiting phenology; seed production; seed rain; seedling recruitment; zoochory.

Introduction

Interspecific interactions structure natural communities. Among sessile organisms, dispersal outcomes set the template for subsequent interspecific interactions, with important implications for local species composition, coexistence, and species richness. While theory focuses on the failure of species to arrive at some sites and its implications (Sale 1977, Hurtt and Pacala 1995, Nathan and Muller-Landau 2000), another possible outcome includes dispersal hotspots where propagules of different species arrive together. Dispersal hotspots and interspecific associations in propagule arrival will increase the frequency of interspecific interactions with implications for community structure.

Spatially contagious seed dispersal refers to the tendency for some sites to receive many dispersed seeds while other sites receive few dispersed seeds (Schupp et al. 2002, 2010, Kwit et al. 2004). Seeds arrive (or fail to arrive) in particular places for many reasons. Heterogeneity of the upper canopy surface affects turbulence and the deposition of wind-dispersed seeds (henceforth, anemochorous seeds; Bohrer et al. 2008). Branches and lianas provide perches, pathways, and obstructions that influence the resting places and movements of bats, birds, and arboreal mammals and the deposition of animal-dispersed seeds (henceforth, zoochorous seeds; e.g., Wehncke et al. 2003). The lower vegetation obstructs and redirects falling seeds. And, seed-hoarding animals often cache fallen seeds near distinctive objects (e.g., Jansen and Forget 2001). These mechanisms all contribute to spatially contagious seed arrival. More anemochorous seeds land where down drafts prevail, more zoochorous seeds land beneath favored perches, and fewer seeds land beneath obstructing vegetation.

Spatially contagious seed arrival might lead to positive interspecific associations in seed arrival when seeds of different species are dispersed in similar ways and at similar times. Frugivores might be the most potent agent of interspecific seed arrival association. As frugivores move among fruiting plants, seeds acquired at one plant are often deposited beneath a second fruiting plant (e.g., Howe 1980, 1981, Howe and Vande Kerckhove 1981, Loiselle 1990, Herrera et al. 1994, Poulin et al. 1999, Clark et al. 2004, Kwit et al. 2004, Garcia et al. 2007, Blendinger et al. 2011, White and Vivian-Smith 2011, Carlo et al. 2013, Viswanathan et al. 2015). Dispersal

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between plants mediated by frugivores becomes likely for synchronously fruiting zoochorous species. Consistent winds might cause spatially persistent turbulence and spatially contagious seed arrival among anemochorous species. Where wind characteristics change seasonally, interspecific associations in seed arrival become likely among synchronously fruiting anemochorous species. Both dispersal mode and the timing of fruiting are likely to contribute to interspecific associations in seed arrival.

Whether interspecific associations of seed arrival persist into later life stages depends on how the initial spatial distribution of seed arrival is modified as seeds and newly established seedlings interact with local biotic and abiotic environments and survive or die. Associations in seed arrival will be weakened at later stages if generalist seed predators and/or competition among seedlings reduce survival where seeds of many species are deposited (Loiselle 1990, Kwit et al. 2004, Russo 2005). Alternatively, associations in seed arrival will be reinforced at later stages if survival is greater where seeds of many species are deposited or for seeds deposited beneath heterospecifics (Herrera et al. 1994, Garcia et al. 2007, Carlo and Tewksbury 2014). Negative and positive outcomes dependent on associations with other species have been termed associational susceptibility and resistance, respectively, and are well documented for plant–herbivore interactions (reviewed by Barbosa et al. 2009).

Here, for the first time, we evaluate the extent of spatially contagious seed arrival, the frequency of positive interspecific associations in seed arrival, and their consequences for seedling recruitment at the community level. Our analyses are for the species-rich tropical forest of Barro Colorado Island, Panama and draw on 28 yr of seed arrival and 21 yr of seedling recruitment data for several hundred fixed locations. We test for interspecifically contagious seed arrival at the community level by evaluating the hypothesis that spatial variation in the number of species arriving simultaneously is greater than expected by chance for all seed plants, as well as for zoochorous and anemochorous species separately. We then use pairwise combinations of up to 187 well-represented species to evaluate five hypotheses (arrows in Fig. 1). First, we ask whether similarity of seed dispersal mode influences interspecific associations in seed arrival (henceforth, seed-arrival associations), predicting that zoochorous species tend to have positive seed-arrival associations (arrow 1, Fig. 1). Second, we explore whether synchronicity of seed production (henceforth, fruiting associations) influences seed-arrival associations, predicting positive relationships between fruiting and seed-arrival associations for pairs of zoochorous species and also for pairs of anemochorous species (arrow 2). Third, we evaluate the consequences for spatial associations in seedling recruitment (henceforth, recruit associations), predicting positive relationships between seed-arrival and recruit associations (arrow 3). Finally, recognizing that spatial associations among reproductive adults (henceforth, source associations) must also affect seed-arrival and recruit associations (arrows 4 and 5, respectively), we control for source associations statistically to evaluate the relationships represented by arrows 1, 2, and 3. Because all pairwise combinations of species are considered, we evaluate these hypotheses within the permutation framework provided by Mantel correlation and partial correlation analyses. We find evidence consistent with each hypothesis. Spatially contagious seed dispersal leads to interspecific associations of seed arrival and seedling recruitment in this tropical forest.

METHODS

We documented seed arrival and seedling recruitment in the mature tropical moist forest of the 50-ha Forest Dynamics Plot (FDP) on Barro Colorado Island (BCI), Panama (9°9′ N, 79°51′ W). Annual rainfall and

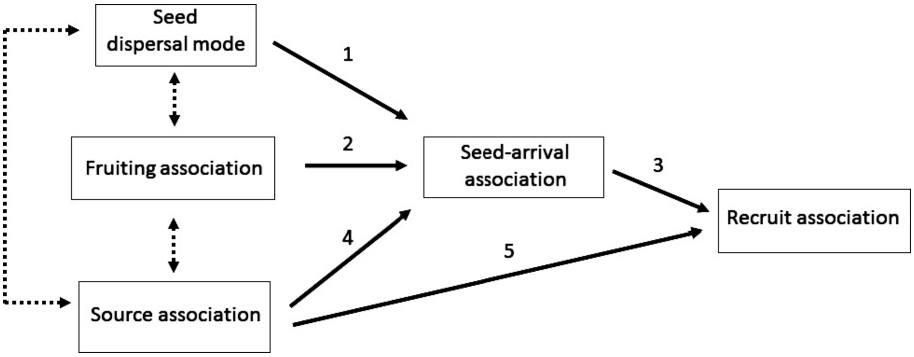

FIG. 1. A conceptual model of contagious seed dispersal and its consequences, showing relationships among seed dispersal mode, temporal associations in seed production (or fruiting associations), and spatial associations in seed arrival, seedling recruitment, and adult source locations. We predict zoochorous species will have positive seed-arrival associations (arrow 1), fruiting and seed-arrival associations will be positively related for both zoochorous and anemochorous species (arrow 2), and seed-arrival and recruit associations will be positively related (arrow 3). We also recognize that spatial associations in adult source locations will influence spatial associations in seed arrival and seedling recruitment (arrows 4 and 5, respectively). Covariances among exogenous variables (dashed double-headed arrows) are expected to be insignificant.

temperature average 2,600 mm and 27°C, respectively (Windsor 1990, Leigh 1999). Strong northeast trade winds characterize the dry season (January into May), while variable weak winds characterize the wet season (Windsor 1990, Wright et al. 2008). In the FDP, all free-standing, woody plants larger than 1 cm in diameter at 1.3 m height (DBH) have been identified, mapped and measured for DBH in 1982, 1985, and every five years thereafter (Condit 1998, Hubbell et al. 1999; http://ctfs.si.edu/webatlas/datasets/bci). We used the 2010 census to evaluate adult source associations and earlier censuses to evaluate consistency of source associations.

To quantify seed arrival, we conducted 1,456 weekly censuses of 200 passive traps between January 1987 and December 2014 (Wright et al. 2005*b*). Each trap consisted of a square, 0.5-m^2 PVC frame supporting an open-topped, 1-mm mesh bag ~0.8 m above the ground. Traps were located at 13.5-m intervals on alternating sides of preexisting trails and randomly between 4 and 10 m from the trail. We identified and counted capsules and mature (endosperm filled) and damaged (by insects or vertebrates) seeds and fruit at each trap in each census. Capsules provide evidence of reproduction after seeds are gone. Capsules refer to a fruit part that vertebrates never consume and are true capsules for dehiscent species and pedicels or bracts for indehiscent species. We estimated the number of seeds falling into each trap at each census as the number of undamaged seeds plus the product of the number of undamaged, mature fruit and species-specific mean seed-to-fruit ratios.

To quantify seedling recruitment, we conducted 21 annual censuses of all woody seedlings (no lower size threshold) in 600 1-m^2 seedling plots between January and April each year from 1994 through 2014 (Wright et al. 2005*b*). We tagged, identified, and measured all seedlings that recruited since the previous census starting in 1995. The seedling plots were located 2 m from the three sides of each seed trap that face away from the nearby trail. Henceforth, we will refer to a seed trap and its three associated seedling plots as a "station."

We assigned dispersal modes to each species based on diaspore morphology and extensive observations of BCI seed dispersal (Muller-Landau 2005, Hardesty 2005). Dispersal modes were zoochorous, anemochorous, and explosively dispersed. Data S1 includes the full dispersal mode data set.

Community-level contagious seed arrival

To evaluate whether seed arrival was contagious at the community level, we compared observed and 999 randomized variances of number of seed species over the 200 traps. We performed the randomization separately for each weekly census with 10 or more species, where the 10 species criterion ensured a reasonable opportunity for randomized and observed variances to differ. Species co-occur more often than expected by chance if observed variances are larger than 950 randomized variances (one-tailed test) for a reasonably large percentage of censuses (>5%).

We performed two randomizations of the variance of the number of species present (Data S2). In the first, species were randomly assigned to their observed number of traps for each census. This first randomization broke up any spatial pattern caused by limited dispersal, which causes neighboring traps to receive seeds from the same nearby sources. To maintain the observed spatial autocorrelation of seed fall into neighboring traps, the second randomization assigned species to traps by shifting the observed trap records by a random number of trap locations for each species. This second randomization preserved most of the observed spatial autocorrelation because the 200 stations are numbered sequentially along the trails with just six breaks where trails leave the FDP. We repeated both randomizations for all 446 seed species captured, for the 305 zoochorous species only and for the 118 anemochorous species only.

For anemochorous species, we also used these randomizations to evaluate the hypothesis that contagious seed arrival is related to seasonal changes in wind conditions. We placed censuses into a two-by-two contingency table defined by wind conditions (strong, consistent, trade winds from January through May vs. weak, intermittent winds from June through December) and by the outcome of the randomization (significant vs. insignificant) and used a Fisher Exact Test to evaluate the prediction that contagious anemochorous seed arrival is associated with the trade winds.

Pairwise association metrics

To evaluate the hypotheses presented in Fig. 1, we calculated fruiting, seed-arrival, recruit, and adult source associations for each pair of species. We included species with 100 or more seed/fruit records for fruiting and seed-arrival associations. Let n_{jct} equal the number of seeds of species j captured in census c and trap t. We quantified fruiting associations for species i and j as

$$P_{ij} = \Sigma_c \left(p_{ic} \times p_{jc}\right)^{0.5}, \tag{1}$$

where $p_{jc} = \Sigma_t\, n_{jct}/\Sigma_c\, \Sigma_t\, n_{jct}$ or the proportion of all seeds of species j captured in census c. P_{ij} is the geometric mean proportion of seeds of species i and j collected in the same census.

We quantified seed-arrival associations using a randomization that maintained the observed temporal variation in seed production. A co-arrival consisted of a trap–census combination with two species present as seeds, mature fruit, or capsules. We summed observed co-arrivals over the 291,200 (200 × 1,456) trap–census combinations for each pair of species. We then shuffled traps randomly for one species and summed randomized co-arrivals over the 291200 randomized trap–census combinations 999 times. The number of times observed co-arrivals exceeded its randomized value served as our metric of seed-arrival association. We also calculated the geometric mean proportion of seeds captured in the same trap and census ($\Sigma_c \Sigma_t [p_{ict} \times p_{jct}]^{0.5}$). Results were qualitatively similar for co-arrivals and proportions ($r = 0.808$). We present results for co-arrivals because co-arrivals provide a test for significant pairwise interspecific seed-arrival associations.

Fruiting and seed-arrival associations are sensitive to the length of census intervals. For example, the value of P_{ij} increases monotonically with interval length. We calculated fruiting and seed-arrival associations for intervals of one and four weeks. The 1-week interval corresponds to our weekly censuses. The 4-week interval aligns with intraspecific synchrony of seed production on BCI, where >75% of annual seed fall occurs within one or two consecutive months for most species in most years (Zimmerman et al. 2007). Our results were qualitatively similar for both intervals, and we present results for 4-week intervals in the main text and for 1-week intervals in supplemental material (Appendix S1: Fig. S1 and Tables S1–S4).

We quantified recruit associations with a second randomization for species with 30 or more recruits. We pooled the three seedling plots for each station and calculated the proportion of recruits of species s recorded at station st ($p_{s,\mathrm{st}}$) and the observed geometric mean proportion of recruits recorded at the same station for species i and j ($\Sigma_{\mathrm{st}} [p_{i,\mathrm{st}} \times p_{j,\mathrm{st}}]^{0.5}$). We then shifted stations around a one-dimensional torus by a different random number of stations 999 times and calculated randomized values. The number of times the observed geometric mean proportion exceeded its randomized value served as our metric of recruit association.

We quantified source associations as bivariate Ripley's K values for free-standing species with 30 or more reproductive trees. Individuals were considered to be reproductive if their DBH exceeded $\mathrm{DBH}_{\max}/2$, where $\mathrm{DBH}_{\max}$ is the largest species-specific DBH observed for the 50-ha plot and another 154 ha of mapped forest plots located within 30 km of BCI. Half $\mathrm{DBH}_{\max}$ explains 81% of the interspecific variation in species-specific reproductive DBH size thresholds observed among BCI trees (Wright et al. 2005*a*, Visser et al. 2016). We excluded climbers because reproductive size thresholds are unknown and fruit can be produced far from mapped stems (Putz 1984). The Ripley's K value for species i and j and distance d ($K_{ij}[d]$) equals the average number of individuals of species j within distance d of an individual of species i standardized by the density of individuals of species j. For stationary spatial processes, $K_{ij}(d) = K_{ji}(d)$ (Dixon 2002). For independent spatial processes, the expected value of $K_{ij}(d)$ is $\pi \times d^2$ regardless of the underlying univariate spatial processes, and the variance of $L_{ij}(d) = [K_{ij}(d)/\pi]^{0.5}$ is approximately constant (Dixon 2002). We calculated $L_{ij}(d)$ for d of 10, 20, … 160 m with the Kmulti function and isotropic edge correction in the spatstat R package (Baddeley and Turner 2005). We verified that $K_{ij}(d) \approx K_{ji}(d)$ and that $L_{ij}(d)$ is distributed around its expected value of d with approximately constant variance. $L_{ij}(30)/30$ served as our measure of source association (see *Results: Pairwise association metrics* for choice of $d = 30$ m).

We converted categorical dispersal modes into a final dichotomous similarity matrix to evaluate the prediction that pairs including two zoochorous species tend to have larger, positive seed-arrival associations (arrow 1 in Fig. 1) than do pairs including one or two non-zoochorous species.

Mantel correlation analyses

We used simple and partial Mantel correlation analyses to evaluate predictions represented by numbered arrows in Fig. 1. Mantel correlation analyses use permutations to accommodate problematic distributions and dependence among observations when all pairwise comparisons are evaluated (Legendre and Fortín 1989). Simple Mantel correlations evaluate the relationship between two matrices of pairwise metrics. Partial Mantel correlations evaluate the relationship between two matrices of pairwise metrics while holding a third matrix constant. We performed simple and partial Mantel correlation analyses for the four triplets of pairwise metrics connected by solid arrows and dashed covariances in Fig. 1. The first triplet included dispersal mode and fruiting and seed-arrival associations (arrows 1 and 2 and the corresponding dashed line in Fig. 1). The second triplet included fruiting, source, and seed-arrival associations (arrows 2 and 4 and the corresponding dashed line). The third triplet included dispersal mode and source and seed-arrival associations (arrows 1 and 4 and the corresponding dashed line). The final triplet included seed-arrival, recruit, and source associations (arrows 3, 4, and 5). The predictions in Fig. 1 are sustained if solid arrows correspond to significant simple and partial Mantel correlations and dashed lines correspond to insignificant values. We also used simple Mantel correlation analyses to evaluate the relationship between fruiting and seed-arrival associations for pairs of zoochorous species only and anemochorous species only. We performed these analyses with the mantel and mantel.partial functions in the vegan R package (Oksanen et al. 2015).

RESULTS

We captured 1,556,163 seeds and fruits of 446 species and recorded 51,815 seedling recruits of 370 species. The 2010 FDP census included 210,826 trees of 302 species. Species number declines from seeds/fruits to recruits to the FDP census because seeds/fruits include all seed species, recruits only include woody species, and the FDP census only includes free-standing, woody species with DBH ≥ 1 cm.

Community-level contagious seed arrival

Randomizations to evaluate interspecifically contagious seed arrival at the community level were performed for 1,454, 1,426, and 523 weekly censuses with 10 or more species captured for all seed, zoochorous species, and anemochorous species, respectively. The observed variance among traps in the number of species captured was greater than 950 of the 999 randomized variances for 21.0%, 33.9%, and 12.6% of censuses for all seed, zoochorous species, and anemochorous species, respectively, for the first randomization (Fig. 2). Values were similar for the second randomization: 19.7%, 33.5%, and 8.6%, respectively. Thus, interspecifically contagious seed arrival is widespread and is most strongly expressed among zoochorous species, as predicted.

For anemochorous species, censuses with significant variance in the number of species captured were concentrated between January and May when the strong northeast trade winds prevail (14.4% of censuses with 10 or more anemochorous species) and were rare between June and December when winds are variable and intermittent (3.5% of censuses; Fig. 2C, Fisher Exact Test, $P = 0.00387$). Among anemochorous species, interspecifically contagious seed dispersal occurred seasonally when the northeast trades bring strong, consistent winds.

Pairwise association metrics

We calculated fruiting and seed-arrival associations for all pairwise combinations of 187 species with 100 or more seed/fruit records (17,391 species pairs). The fruiting association metric had a truncated normal distribution (Fig. 3A) and was larger than 0.25 for 30.2% of species pairs for 4-week intervals. In other words, over 28 years, a remarkable 5,252 species pairs dispersed more than 25% of their seeds in single 4-week intervals.

A uniform distribution of seed-arrival associations is expected under our randomization. The observed distribution was distorted by 6,660 species pairs with zero observed co-arrivals for 4-week census intervals. The two species involved in most of these pairs rarely produced seeds in the same 4-week interval ensuring zero or near zero co-arrivals. The distribution of seed-arrival associations for the remaining species pairs was approximately uniform, but with an excess of large values (Fig. 3B). Significant positive seed-arrival associations (observed number of co-arrivals larger than 950 randomized values) characterized 10.8% of the remaining species pairs for four-census intervals, providing the first evidence for positive interspecific associations in seed arrival.

We calculated recruit associations for all pairwise combinations of 108 species with 30 or more recruits (5,778 species pairs). We used a second randomization to quantify recruit associations so a null, uniform distribution is again expected. The observed distribution was approximately uniform, but with an excess of small and especially large values (Fig. 3C). Significant positive recruit associations (observed number of co-occurrences larger than 950 randomized values) characterized 13.1%

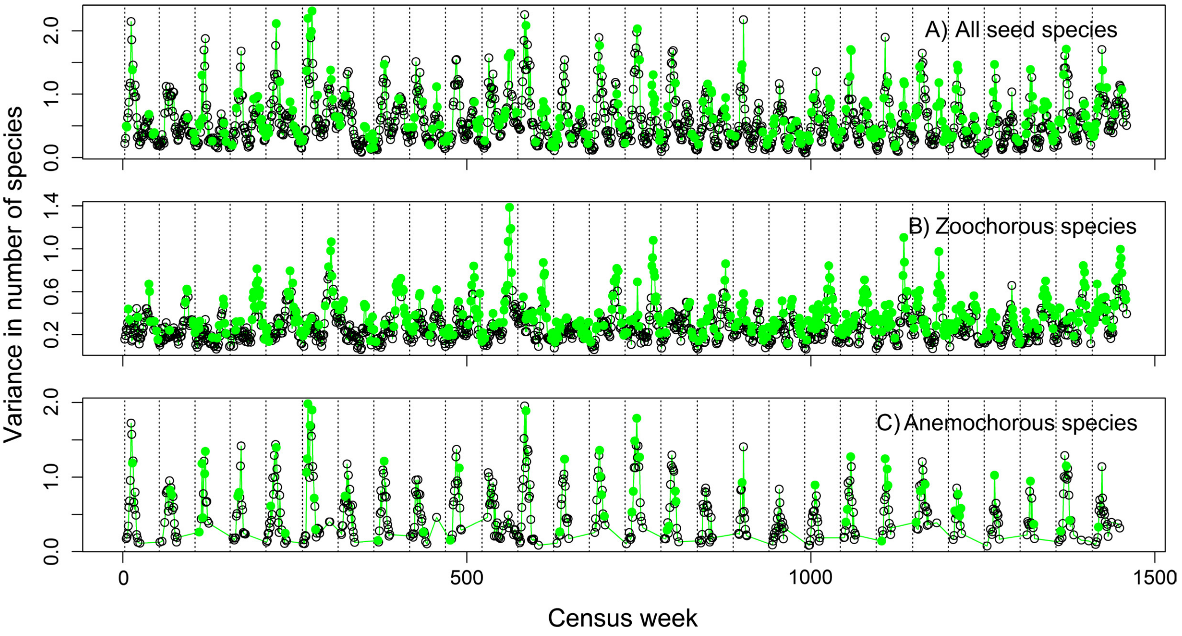

FIG. 2. Evidence for community-wide contagious seed dispersal in the seed rain in the tropical moist forest of Barro Colorado Island, Panama. Panels present the variance in the number of species captured by 200 seed traps for each weekly census with 10 or more seed species for (A) all species ($n = 1,454$ censuses), (B) zoochorous species only ($n = 1,426$ censuses), and (C) anemochorous species only ($n = 523$ censuses). Solid green symbols represent censuses for which the observed variances were larger than 950 randomized variances, which provides evidence for interspecifically spatially contagious seed arrival (i.e., different species tend to arrive and fail to arrive at the same locations). Open black symbols represent censuses with insignificant variances. Dashed vertical lines represent the first census in each calendar year (1987–2014). [Color figure can be viewed in the online issue, which is available at wileyonlinelibrary.com.]

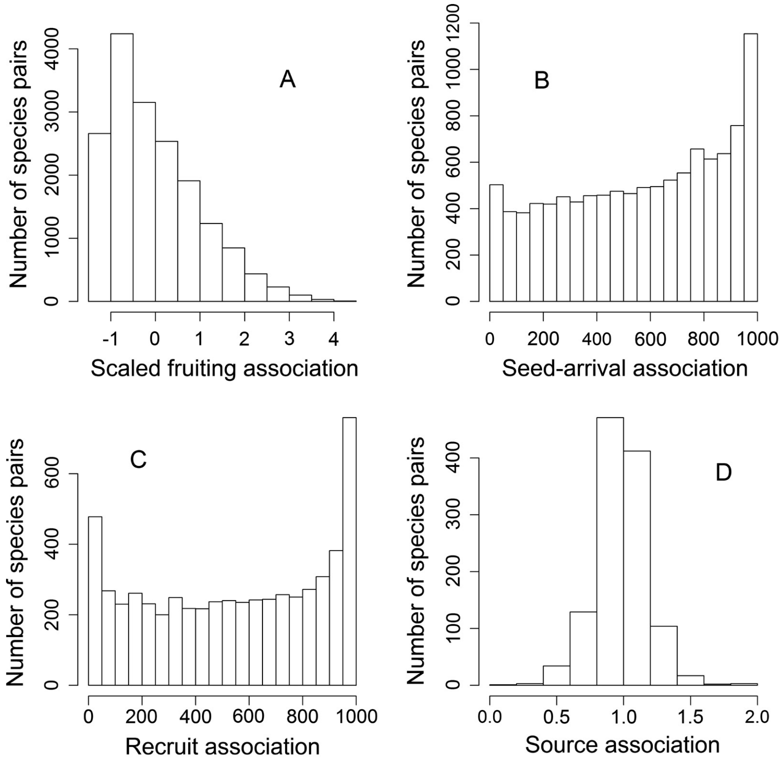

FIG. 3. Distributions of pairwise association or similarity metrics. (A) The fruiting association metric is the geometric mean proportion of seeds dispersed in the same 4-week interval and is scaled to distinguish small values. (B and C) The seed-arrival and recruit association metrics are the number of randomizations for which the observed number of co-arrivals was larger than its randomized value. Values larger than 950 indicate significant positive pairwise associations. (D) The source association metric is the bivariate Ripley's *K* value calculated for reproductive adults at a 30-m spatial scale and standardized to an expected value of 1. Values cluster around 1, suggesting that heterospecific adults were distributed independently for many species pairs.

of species pairs, providing the first evidence for positive interspecific associations in recruitment.

We calculated adult source associations for all pairwise combinations of 49 species with 30 or more adults in the 2010 census of the 50-ha plot (1,176 species pairs). We chose $d = 30$ m and $L_{ij}(30)$ as our measure of source association because this spatial scale had the largest Mantel correlation with seed-arrival associations ($r = 0.180$, $P < 0.001$). This choice maximizes the contribution of source associations in subsequent analyses (arrow 4 in Fig. 1). The distribution of $L_{ij}(30)/30$ was centered on its expected value of 1 (Fig. 3D), which suggests that heterospecific adults were distributed independently for most species pairs (as shown by Wiegand et al. 2012). We evaluated the consistency of adult source associations through time by comparing values for the six censuses of the 50-ha

TABLE 1. Relationships among dispersal mode, fruiting associations, and seed-arrival associations (arrows 1 and 2 and the corresponding dashed line in Fig. 1) on Barro Colorado Island, Panama.

	Simple					
	Seed-arrival association		Fruiting association		Dispersal mode	
Partial	Correlation	*P*	Correlation	*P*	Correlation	*P*
Seed-arrival association			0.282	<0.001	0.0872	<0.001
Fruiting association	0.286	<0.001			−0.0267	0.751
Dispersal mode	0.0988	<0.001	−0.0536	0.940		

Notes: Simple and partial Mantel correlations and associated probabilities are presented above and below the diagonal, respectively. The partial Mantel correlations evaluate relationships between the variables in the appropriate row and column headings while holding the third variable constant. Four consecutive weekly censuses were pooled to calculate temporal and seed-arrival associations.

TABLE 2. Relationships among fruiting, source, and seed-arrival associations (arrows 2 and 4 and the corresponding dashed line in Fig. 1) on Barro Colorado Island, Panama.

	Simple					
	Seed-arrival association		Fruiting association		Source or adult association	
Partial	Correlation	*P*	Correlation	*P*	Correlation	*P*
Seed-arrival association			0.317	<0.001	0.224	<0.001
Fruiting association	0.316	<0.001			0.0425	0.091
Source or adult association	0.222	<0.001	−0.0309	0.868		

Notes: Simple and partial Mantel correlations and associated probabilities are presented above and below the diagonal, respectively. The partial Mantel correlations evaluate relationships between the variables in the appropriate row and column headings while holding the third variable constant. Four consecutive weekly censuses were pooled to calculate temporal and seed-arrival associations.

plot that overlap our seed censuses (Appendix S2: Fig. S1). Adult source associations were reasonably well correlated ($r > 0.50$) after 25 years (1985 vs. 2010) despite slow changes associated with tree deaths and growth into the reproductive size class (Appendix S2: Fig. S1).

Mantel correlation analyses

We evaluated the relationship between fruiting and seed-arrival associations for pairs of zoochorous and for pairs of anemochorous species, using 124 zoochorous and 59 anemochorous species with 100 or more seed/fruit records. Fruiting associations were significantly, positively correlated with seed-arrival associations for zoochorous species (Mantel $r = 0.338$, $P < 0.001$) and for anemochorous species (Mantel $r = 0.272$, $P < 0.001$) for four-census intervals. Mantel correlation coefficients were similar for single-census intervals (Mantel $r = 0.372$ and 0.292, respectively, $P < 0.001$). Thus, seed-arrival associations increased with synchrony of seed production in both zoochorous and anemochorous species.

We evaluated relationships among dispersal mode, fruiting associations and seed-arrival associations (arrows 1 and 2 and the corresponding dashed line in Fig. 1) for 124 zoochorous, 59 anemochorous and four ballistically dispersed species with 100 or more seed/fruit records (187 species total). Simple and partial Mantel correlations had similar values and were highly significant ($P < 0.001$) for the relationships represented by arrows 1 and 2 in Fig. 1 and were insignificant for the covariance represented by the corresponding dashed line (Table 1 and Appendix S1: Table S1). Thus, dispersal mode and fruiting associations made independent, significant contributions to seed-arrival associations. Species pairs comprised of two zoochorous species had significantly larger seed-arrival associations than did species pairs including one or two non-zoochorous species.

We evaluated relationships among fruiting, source, and seed-arrival associations (arrows 2 and 4 and the corresponding dashed line in Fig. 1) for the subset of 44 zoochorous, three anemochorous and two ballistically dispersed species that also had 30 or more adults in the 50-ha plot (49 species total). Simple and partial Mantel correlations had nearly identical values and were highly significant ($P < 0.001$) for relationships represented by arrows 2 and 4 in Fig. 1 and were insignificant for the covariance represented by the corresponding dashed line (Table 2 and Appendix S1: Table S2). Thus, fruiting associations and source associations made independent, significant, positive contributions to seed-arrival associations.

We evaluated relationships among dispersal mode, source associations, and seed-arrival associations (arrows 1 and 4 and the corresponding dashed line in Fig. 1) for the same 49 species used in the previous Mantel correlation analysis. Simple and partial Mantel correlations had nearly identical values and were highly significant ($P < 0.001$) for the relationship represented by arrow 4 in Fig. 1, were positive but insignificant for the relationships represented by arrow 1 ($P = 0.166$ and $P = 0.112$ for simple and partial Mantel correlations), and were insignificant for the corresponding covariance (Table 3 and Appendix S1: Table S3). The relationship between dispersal mode and seed-arrival associations (arrow 1 in Fig. 1) was significant in a previous analysis including 187 species (Table 1 and Appendix S1: Table S1). The insignificant outcome for the subset of 49 species that also have 30 or more adults in the 50-ha plot probably reflects the small number of non-zoochorous species ($n = 5$ species). We conclude that dispersal mode and source associations made independent, significant, positive contributions to seed-arrival associations.

We evaluated relationships among seed-arrival, source, and recruit associations (arrows 3, 4, and 5 in Fig. 1) for 37 zoochorous, three anemochorous, and two explosively dispersed species with 30 or more adults, 30 or more recruits, and 100 or more seed/fruit records (42 species total). Simple Mantel correlations were highly significant ($P < 0.001$) for all three relationships (Table 4 and Appendix S1: Table S4). Partial Mantel correlation coefficients were also highly significant ($P < 0.001$) but were consistently smaller than the corresponding simple Mantel correlation coefficients (Table 4 and Appendix S1:

Table 3. Relationships among dispersal mode, source association, and seed-arrival association (arrows 1 and 4 and the corresponding dashed line in Fig. 1) on Barro Colorado Island, Panama.

	Simple					
	Seed-arrival association		Source or adult association		Dispersal mode	
Partial	Correlation	*P*	Correlation	*P*	Correlation	*P*
Seed-arrival association			0.224	<0.001	0.0605	0.166
Source or adult association	0.226	<0.001			−0.0197	0.717
Dispersal mode	0.0666	0.112	−0.0342	0.863		

Notes: Simple and partial Mantel correlations and associated probabilities are presented above and below the diagonal, respectively. The partial Mantel correlations evaluate relationships between the variables in the appropriate row and column headings while holding the third variable constant. Four consecutive weekly censuses were pooled to calculate seed-arrival association.

Table S4). This implies that source associations contributed positively to seed-arrival associations, and source and seed-arrival associations both contributed positively to recruit associations.

Finally, we evaluated the relationship between seed-arrival and recruit associations (arrow 3 in Fig. 1) a second time for the much larger number of species with 30 or more recruits and 100 or more seed/fruit records (108 species). Simple Mantel correlations were 0.236 ($P < 0.001$) for four-census intervals and 0.196 ($P < 0.001$) for single-census intervals, indicating that seed-arrival associations persisted as recruit associations.

Discussion

Interspecifically contagious seed dispersal, with some sites receiving many dispersed seeds of many species while other sites receive few dispersed seeds of any species (Schupp et al. 2002, Kwit et al. 2004), is well known for particular pairs of species or small groups of species (reviewed by Schupp et al. 2010). We evaluated contagious seed arrival and its consequences for seedling recruitment at the community level for the first time, using 1.56 million seed or fruit arrivals recorded in 28 yr of weekly censuses of 200 0.5-m^2 seed traps and 51,815 seedling recruits recorded in 21 annual censuses of 600 1-m^2 plots at Barro Colorado Island (BCI), Panama. We found strong evidence for spatially contagious seed arrival at the community level and positive interspecific associations in seed arrival and seedling recruitment.

Community-wide seed arrival

Community-wide contagious seed arrival characterized zoochorous species throughout our 28-yr study (Fig. 2B). This finding extends earlier studies that documented contagious seed deposition associated with frugivores along travel routes, at preferred perches and at fruiting plants (e.g., Howe 1980, 1981, Howe and Vande Kerckhove 1981, Loiselle 1990, Herrera et al. 1994, Clark et al. 2004, Kwit et al. 2004, Russo and Augspurger 2004, Garcia et al. 2007, Blendinger et al. 2011, White and Vivian-Smith 2011, Fedriani and Wiegand 2014, Viswanathan et al. 2015). While previous studies focused mostly on zoochorous species, we also documented community-wide contagious seed dispersal among anemochorous species during the first months of the year when the strong, northeast trade winds prevail (Fig. 2C). This finding is perhaps unexpected by ecologists but was anticipated by atmospheric models in which consistent winds interact with heterogeneous canopy heights to alter local probabilities of deposition of anemochorous seeds (Bohrer et al. 2008, Trakhtenbrot et al. 2014).

Table 4. Relationships among source, seed-arrival, and recruit associations (arrows 3, 4, and 5 in Fig. 1) on Barro Colorado Island, Panama.

	Simple					
	Recruit association		Seed-arrival association		Source or adult association	
Partial	Correlation	*P*	Correlation	*P*	Correlation	*P*
Recruit association			0.237	<0.001	0.228	<0.001
Seed-arrival association	0.201	<0.001			0.199	<0.001
Source or adult association	0.190	<0.001	0.154	<0.001		

Notes: Simple and partial Mantel correlations and associated probabilities are presented above and below the diagonal, respectively. The partial Mantel correlations evaluate relationships between the variables in the appropriate row and column headings while holding the third variable constant. Four consecutive weekly censuses were pooled to calculate seed-arrival association.

Interspecific associations

Interspecific associations were strong and robust. Positive, interspecific associations in seed arrival were associated with similar fruiting times and dispersal modes (arrows 1 and 2 in Fig. 1, Table 1), and associations documented for seed arrival persisted through to seedling recruitment (arrow 3 in Fig. 1, Table 4). Interspecific associations of reproductive adults made significant contributions to the positive, interspecific associations in seed arrival and seedling recruitment (arrows 4 and 5 in Fig. 1, Tables 2 and 4). When reproductive adult associations were controlled statistically, however, significant relationships remained between seed arrival associations and similarity of fruiting times and dispersal modes (Tables 2 and 3) and between seed arrival and recruit associations (Table 4). Thus, fruiting times and dispersal modes influenced seed-arrival associations and seed arrival influenced recruit associations independently of adult source associations.

Implications

Contagious seed dispersal and positive, interspecific associations in seed arrival and recruitment are statistically significant, widespread, and predictable; however, their quantitative contribution to species composition and coexistence is unknown. We believe their contribution will prove to be important due to the well-documented effects of the Janzen-Connell mechanism (Janzen 1970, Connell 1971). The largest numbers of zoochorous (anemochorous) seeds fall to the ground beneath (just downwind from) their seed mother. Of those seeds that are dispersed away from their seed mother, some will land beneath a fruiting heterospecific and some will land away from any fruiting plant but in close proximity to a heterospecific seed. Most seeds that fall near their seed mother are killed by host-specific pests associated with the mother tree and her nearby seeds and seedlings (reviewed by Comita et al. 2014). The much smaller number of seeds that fall to the ground near heterospecifics will tend to escape these local concentrations of host-specific pests and to survive (for examples, see Herrera et al. 1994, Garcia et al. 2007, Carlo and Tewksbury 2014). This mechanism will enhance the importance of interspecifically contagious seed arrival and interspecific associations in seedling recruitment.

This mechanism is clearly evident during plant regeneration in the BCI forest. Spatial variation in conspecific seed arrival is extreme (Wright et al. 2005*b*), the fruiting plant directly overhead dominates local seed rain (Harms et al. 2000), pervasive conspecific density-dependent mortality during the seed-to-seedling transition reduces local dominance to levels typical of adult trees (Harms et al. 2000), and significant conspecific density-dependent mortality continues until trees reach at least 10 cm in DBH (Zhu et al. 2015). Conspecific density-dependent mortality will tend to preserve interspecific association observed for seed arrival and seedling recruitment.

In the extreme case, seed-arrival associations might persist into the adult stage. We are aware of just one example from a Danish forest where 18 native zoochorous species tend to co-occur in natural "orchards" (Lazaro et al. 2005). Tropical forests are likely candidates for similar "orchards" because more than 80% of tree species are zoochorous (Gentry 1983, Muller-Landau and Hardesty 2005) and contagious dispersal of zoochorous species is widespread (Fig. 2B); however, significant pairwise interspecific associations are rare among adult trees on BCI (Fig. 3D; Wiegand et al. 2012). A next step will be to evaluate how the interspecific associations in seedling recruitment documented here affect onward performance and the implications for later life stages and species coexistence.

Future directions

Previous studies of contagious seed dispersal have focused on hotspots of seed arrival; however, interspecific associations in seed arrival also imply relatively cold spots where relatively few seeds arrive (Herrera et al. 1994, Carlo et al. 2013). The characteristics of cold spots might be as interesting as the better-studied hotspots. For example, anemochorous seeds arrive in diminished numbers in low-canopy tree fall gaps on BCI (Puerta-Piñero et al. 2013) as predicted by models of atmospheric turbulence (Bohrer et al. 2008). Long-lived, understory vegetation might also contribute to cold spots by redirecting falling seeds away from some locations and toward others. Sterile trees, males of dioecious species and species with dry, well-defended diaspores might also represent cold spots avoided by frugivores and granivores. In contrast, the most rewarding fruits attract frugivores, and reproductive adults of species with rewarding fruits might be hotspots for contagious seed dispersal and positive, interspecific associations in seed arrival. Future exploration of the site characteristics and species traits that determine interspecific associations in seed deposition will provide additional insight into the early regeneration of plant communities (Carlo and Tewksbury 2014).

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LITERATURE CITED

Baddeley, A., and R. Turner. 2005. spatstat: an R package for analyzing spatial point patterns. Journal of Statistical Software 12:1–42.

Barbosa, P., J. Hines, I. Kaplan, H. Martinson, A. Szczepaniec, and Z. Szendrei. 2009. Associational resistance and associational susceptibility: having right or wrong neighbors. Annual Review of Ecology, Evolution, and Systematics 40:1–20.

Blendinger, P. G., J. G. Blake, and B. A. Loiselle. 2011. Composition and clumping of seeds deposited by frugivorous birds varies between forest microsites. Oikos 120:463–471.

Bohrer, G., G. G. Katul, R. Nathan, R. L. Walko, and R. Avissar. 2008. Effects of canopy heterogeneity, seed abscission and inertia on wind-driven dispersal kernels of tree seeds. Journal of Ecology 96:569–580.

Carlo, T. A., and J. J. Tewksbury. 2014. Directness and tempo of avian seed dispersal increases emergence of wild chiltepins in desert grasslands. Journal of Ecology 102:248–255.

Carlo, T. A., D. Garcia, D. Martinez, J. M. Gleditsch, and J. M. Morales. 2013. Where do seeds go when they go far? Distance and directionality of avian seed dispersal in heterogeneous landscapes. Ecology 94:301–307.

Clark, C. J., J. R. Poulsen, E. F. Connor, and V. T. Parker. 2004. Fruiting trees as dispersal foci in a semi-deciduous tropical forest. Oecologia 139:66–75.

Comita, L. S., S. A. Queenborough, S. J. Murphy, J. L. Eck, K. Xu, M. Krishnadas, N. Beckman, and Y. Zhu. 2014. Testing predictions of the Janzen-Connell hypothesis: a meta-analysis of experimental evidence for distance- and density-dependent seed and seedling survival. Journal of Ecology 102:845–856.

Condit, R. 1998. Tropical forest census plots. Springer-Verlag and R. G. Landes Company, Berlin, Germany.

Connell, J. H. 1971. On the role of natural enemies in preventing competitive exclusion in some marine animals and in rain forest trees. Pages 298–312 *in* P. J. den Boer and G. Gradwell, editors. Dynamics of numbers in populations. Center for Agricultural Publication and Documentation, Wageningen, the Netherlands.

Dixon, P. M. 2002. Ripley's K function. Pages 1796–1803 *in* A. H. El-Shaarawi and W. W. Piegorsch, editors. Encyclopedia of environmetrics. John Wiley & Sons, Chichester, UK.

Fedriani, J. M., and T. Wiegand. 2014. Hierarchical mechanisms of spatially contagious seed dispersal in complex seed-disperser networks. Ecology 95:514–526.

Garcia, D., I. Martinez, and J. R. Obeso. 2007. Seed transfer among bird-dispersed trees and its consequences for post-dispersal seed fate. Basic and Applied Ecology 8:533–543.

Gentry, A. H. 1983. Dispersal ecology and diversity in neotropical forest communities. K. Kubitzki, editor. Dispersal and distribution: an international symposium. Paul Parey, Hamburg, Germany.

Harms, K. E., S. J. Wright, O. Calderon, A. Hernandez, and E. A. Herre. 2000. Pervasive density-dependent recruitment enhances seedling diversity in a tropical forest. Nature 404:493–495.

Herrera, C. M., P. Jordano, L. Lopezsoria, and J. A. Amat. 1994. Recruitment of a mast-fruiting, bird-dispersed tree—bridging frugivore activity and seedling establishment. Ecological Monographs 64:315–344.

Howe, H. F. 1980. Monkey dispersal and waste of a Neotropical fruit. Ecology 61:944–959.

Howe, H. F. 1981. Dispersal of a Neotropical nutmeg (*Virola sebifera*) by birds. Auk 98:88–98.

Howe, H. F., and G. A. Vande Kerckhove. 1981. Removal of wild nutmeg (*Virola surinamensis*) crops by birds. Ecology 62:1093–1106.

Hubbell, S. P., R. B. Foster, S. T. O'Brien, K. Harms, R. Condit, B. Wechsler, S. J. Wright, and S. L. De Lao. 1999. Light-gap disturbances, recruitment limitation, and tree diversity in a neotropical forest. Science 283:554–557.

Hurtt, G. C., and S. W. Pacala. 1995. The consequences of recruitment limitation: reconciling chance, history and competitive differences between plants. Journal of Theoretical Biology 176:1–12.

Jansen, P. A., and P. M. Forget. 2001. Scatter-hoarding rodents and tree regeneration in French Guiana. Pages 275–288 *in* F. Bongers, P. Charles-Dominique, P. M. Forget, and M. Théry, editors. Nouragues: dynamics and plant-animal interactions in a neotropical rainforest. Kluwer Academic Publishers, Dordrecht, the Netherlands.

Janzen, D. H. 1970. Herbivores and the number of tree species in tropical forests. American Naturalist 104:501–528.

Kwit, C., D. J. Levey, and C. H. Greenberg. 2004. Contagious seed dispersal beneath heterospecific fruiting trees and its consequences. Oikos 107:303–308.

Lazaro, A., S. Mark, and J. M. Olesen. 2005. Bird-made fruit orchards in northern Europe: nestedness and network properties. Oikos 110:321–329.

Legendre, P., and M. Fortín. 1989. Spatial pattern and ecological analysis. Vegetatio 80:107–138.

Leigh Jr., E. G. 1999. Tropical forest ecology: a view from Barro Colorado Island. Oxford University Press, Oxford, UK.

Loiselle, B. A. 1990. Seeds in droppings of tropical fruit-eating birds—importance of considering seed composition. Oecologia 82:494–500.

Muller-Landau, H. C., and B. D. Hardesty. 2005. Seed dispersal of woody plants in tropical forests: concepts, examples and future directions. Pages 267–309 *in* D. F. R. P. Burslem, M. A. Pinard, and S. E. Hartley, editors. Biotic interactions in the tropics: their role in the maintenance of species diversity. Cambridge University Press, Cambridge, UK.

Nathan, R., and H. C. Muller-Landau. 2000. Spatial patterns of seed dispersal, their determinants and consequences for recruitment. Trends in Ecology & Evolution 15:278–285.

Oksanen, J., F. G. Blanchet, R. Kindt, P. Legendre, P. R. Minchin, R. B. O'Hara, G. L. Simpson, P. Solymos, M. H. H. Stevens, and H. Wagner. 2015. vegan: community ecology package. R package version 2.3-0. http://CRAN.R-project.org/package=vegan

Poulin, B., S. J. Wright, G. Lefebvre, and O. Calderon. 1999. Interspecific synchrony and asynchrony in the fruiting phenologies of congeneric bird-dispersed plants in Panama. Journal of Tropical Ecology 15:213–227.

Puerta-Piñero, C., H. C. Muller-Landau, O. Calderón, and S. J. Wright. 2013. Seed arrival in tropical forest tree fall gaps. Ecology 94:1552–1562.

Putz, F. E. 1984. The natural history of lianas on Barro Colorado Island, Panama. Ecology 65:1713–1724.

Russo, S. E. 2005. Linking seed fate to natural dispersal patterns: factors affecting predation and scatter-hoarding of *Virola calophylla* seeds in Peru. Journal of Tropical Ecology 21:243–253.

Russo, S. E., and C. K. Augspurger. 2004. Aggregated seed dispersal by spider monkeys limits recruitment to clumped patterns in *Virola calophylla*. Ecology Letters 7:1058–1067.

Sale, P. F. 1977. Maintenance of high diversity in coral reef communities. American Naturalist 111:337–359.

Schupp, E. W., T. Milleron, and S. E. Russo. 2002. Dissemination limitation and the origin and maintenance of species-rich tropical forests. Pages 19–33 *in* D. J. Levey, W. R. Silva, and M. Galetti, editors. Seed dispersal and frugivory: ecology, evolution and conservation. CAB International, Wallingford, UK.

Schupp, E. W., P. Jordano, and J. M. Gomez. 2010. Seed dispersal effectiveness revisited: a conceptual review. New Phytologist 188:333–353.

Trakhtenbrot, A., G. G. Katul, and R. Nathan. 2014. Mechanistic modeling of seed dispersal by wind over hilly terrain. Ecological Modelling 274:29–40.

Visser, M. D., M. Bruijning, S. J. Wright, H. C. Muller-Landau, E. Jongejans, L. C. Comita, and H. de Kroon. 2016. Functional traits as predictors of vital rates across the life-cycle of tropical trees. Functional Ecology 30:168–180.

Viswanathan, A., R. Naniwadekar, and A. Datta. 2015. Seed dispersal by avian frugivores: non-random heterogeneity at fine scales. Biotropica 47:77–84.

Wehncke, E. V., S. P. Hubbell, R. B. Foster, and J. W. Dalling. 2003. Seed dispersal patterns produced by white-faced monkeys: implications for the dispersal limitation of neotropical tree species. Journal of Ecology 91:677–685.

White, E., and G. Vivian-Smith. 2011. Contagious dispersal of seeds of synchronously fruiting species beneath invasive and native fleshy-fruited trees. Austral Ecology 36:195–202.

Wiegand, T., A. Huth, S. Getzin, X. Wang, Z. Hao, C. V. S. Gunatilleke, and I. A. U. N. Gunatilleke. 2012. Testing the independent species' arrangement assertion made by theories of stochastic geometry of biodiversity. Proceedings of the Royal Society B 279:3312–3320.

Windsor, D. M. 1990. Climate and moisture variability in a tropical forest: long-term records from Barro Colorado Island, Panama. Smithsonian Institution Press, Washington, D.C., USA.

Wright, S. J., M. A. Jaramillo, J. Pavon, R. Condit, S. P. Hubbell, and R. B. Foster. 2005*a*. Reproductive size thresholds in tropical trees: variation among individuals, species and forests. Journal of Tropical Ecology 21:307–315.

Wright, S. J., H. C. Muller-Landau, O. Calderon, and A. Hernandez. 2005*b*. Annual and spatial variation in seedfall and seedling recruitment in a neotropical forest. Ecology 86:848–860.

Wright, S. J., A. Trakhtenbrot, G. Bohrer, M. Detto, G. G. Katul, N. Horvitz, H. C. Muller-Landau, F. A. Jones, and R. Nathan. 2008. Understanding strategies for seed dispersal by wind under contrasting atmospheric conditions. Proceedings of the National Academy of Sciences USA 105:19084–19089.

Zhu, Y., L. S. Comita, S. P. Hubbell, and K. Ma. 2015. Conspecific and phylogenetic density-dependent survival differs across life stages in a tropical forest. Journal of Ecology 103:957–966.

Zimmerman, J. K., S. J. Wright, O. Calderon, M. A. Pagan, and S. Paton. 2007. Flowering and fruiting phenologies of seasonal and aseasonal neotropical forests: the role of annual changes in irradiance. Journal of Tropical Ecology 23: 231–251.

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