Chanthorn, W., **Wiegand, T.**, **Getzin, S.**, Brockelman, W.Y., Nathalang, A. (2018):
Spatial patterns of local species richness reveal importance of frugivores for tropical forest diversity
J. Ecol. **106** (3), 925 – 935

http://dx.doi.org/10.1111/1365-2745.12886

DR. WIRONG CHANTHORN (Orcid ID : 0000-0002-9854-2179)

Article type : Research Article

Handling Editor: Mark Rees

Spatial patterns of local species richness reveal importance of frugivores for tropical forest diversity

Wirong Chanthorn[1,*], Thorsten Wiegand[2,3], Stephan Getzin[2], Warren Y. Brockelman[4,5] and Anuttara Nathalang[4]

[1]Department of Environmental Technology and Management, Faculty of Environment, Kasetsart University, Ngamwongwan road, Bangkok 10900, Thailand;[2]Helmholtz Centre for Environmental Research–UFZ, Dept of Ecological Modeling, PF 500136, DE-04301 Leipzig, Germany;[3]German Centre for Integrative Biodiversity Research (iDiv) Halle-Jena-Leipzig, Deutscher Platz 5e, 04103 Leipzig, Germany;[4]Ecology Laboratory, BIOTEC, 113 Science Park, Paholyothin Road, Klong Luang, Pathum Thani 12120, Thailand;[5]Institute of Molecular Biosciences, Mahidol University, Salaya, Phutthamonthon 4 road, Nakhon Pathom 73170, Thailand.

*Correspondence author. E-mail: fsciwrc@ku.ac.th

Running headline: Spatial patterns of tree local species richness

Summary

1. Seed dispersal by frugivores, particularly primates, plays an important role in structuring and maintaining tree diversity in tropical forests. However, little is known about the effect of frugivores on the diversity of saplings and large trees.

2. We used detailed census data from the fully mapped 30-ha Mo Singto forest dynamics plot in Thailand together with spatial point pattern analysis to find out if the local species richness of small (dbh <10 cm) and large (dbh ≥10 cm) trees in the neighbourhood of large trees of 52 focal species was larger or smaller than expected by an appropriate null model.

3. We then used binary data (+ or 0) on the seed dispersal network at the Mo Singto plot to test the hypothesis that the major primate frugivores, rather than other arboreal frugivores, generated patterns of locally increased species richness around their preferred diet species (i.e., accumulator effects).

4. More than half of the focal species showed accumulator effects with respect to species richness of small trees (< 10 cm in diameter), but accumulator effects with respect to large trees were weak and not consistent with those of small trees. Primate-dispersed focal species (but not hornbill- or other smaller bird-dispersed species) showed significantly larger positive effect sizes than the remaining focal species.

5. *Synthesis.* Our analysis suggested that primates—as major drivers of contagious seed dispersal—generate species-rich seed rain around their preferred food-tree species, which results in significantly larger local species richness of saplings. This is likely a consequence of heterospecific seed rain that reduces negative density dependence, and the presence of the accumulator pattern which persists at least until the large-size stage. Hence, extirpation of primates may result in significant changes in the diversity and spatial structure of tropical forests.

Key-words: gibbon, individual species–area relationship, macaque, Mo Singto plot, point pattern analysis, spatial contagious seed dispersal.

Introduction

Animal seed dispersers play an important role in structuring and maintaining tree diversity of tropical forests (Levine & Murrell 2003; Beckman & Rogers 2013). Mutually beneficial interactions between plants and animals reflect coevolution between plant life histories and animal behaviours (Gomez & Verdu 2012). One striking example of mutual plant-animal interactions is seed dispersal by primates, which provide important dispersal service for a variety of large-seeded trees and lianas in tropical forests (Chapman & Russo 2011; Gomez & Verdu 2012; Bufalo *et al.* 2016; Corlett 2017). Primates are often generalist frugivores able to feed on several kinds of fruit at once (Wrangham *et al.* 1994; McConkey 2000; Andresen 2002; Albert *et al.* 2013a), and some species drop them in a restricted home range (McConkey 2000; Russo 2005). This behaviour is likely to generate spatial patterns of seed deposition that can have important implication for the dynamics of the forest.

In addition to helping seeds escape from the detrimental effects of negative density dependent processes, such as conspecific competition or Janzen-Connell effects (Janzen 1970; Connell 1971), primates may also generate spatial patterns of seeds that have effects on forest dynamics and species coexistence. Contagious seed dispersal, defined as the greater tendency for seed arrival in some sites while others receive fewer seeds (Schupp *et al*. 2002), can arise if animals favour specific areas (such as those under fruiting or fruit-processing trees, display sites, latrines or resting sites) where they defecate seeds in large numbers (Wenny 2001; Schupp *et al.* 2002; Carlo & Morales 2008; Viswanathan *et al.* 2015). Recently, this phenomenon has been reported in a community-wide study of seeds and seedling stages in the Barro Colorado plot in Panama (Wright *et al.* 2016). Spatially contagious seed dispersal has the potential to mediate species coexistence in two ways. Firstly, it limits recruitment to some sites even when species are abundant, thereby generating recruitment limitation (i.e., failure to have viable juveniles at all available sites; Hurtt & Pacala 1995; Hubbell *et al.* 1999). Recruitment limitation can be a powerful force for maintaining diversity in species-rich communities because it allows many sites to be won by "forfeit" by species that are not the best competitors for the site (Tilman 1994; Hurtt & Pacala 1995; Schupp *et al.* 2002; Schupp *et al.* 2010). Secondly, contagious multi-species seed rain may reduce conspecific negative density dependence, and ultimately enhance the coexistence of seedlings and saplings (Janzen 1970; Connell 1971).

Primates, especially gibbons, macaques, and many species of New World monkeys, are recognized as important dispersers of seeds of a large variety of trees and lianas throughout the humid tropics (McConkey 2000; Chapman & Russo 2011; Gomez & Verdu 2012; Albert et al. 2013a; Bufalo *et al.* 2016; Brockelman et al. 2017; Corlett 2017). They can generate distinct spatial patterns of seedlings and saplings that may last into the adult stage (Russo & Augspurger 2004; Russo *et al*. 2006; Stoner *et al*. 2007). Primates may spend prolonged times at their favourite food trees which are also used for feeding, social interactions, sleeping or vocalizing (McConkey 2000; Andresen 2002; Russo & Augspurger 2004). Many primates are generalist frugivores that usually consume a variety of different fruits in a single day, and tend to defecate an average of 2–4 species of seeds per single defecation event (Wrangham *et al.* 1994; McConkey 2000; Andresen 2002; Albert *et al.* 2013a). An intensive study of the foraging of gibbons in Thailand has revealed than an adult will consume an average of 9–12 species during a 5-day period (Suwanvecho *et al.* in press). The same study has also found that a gibbon group makes numerous repeated visits to the same preferred food sources, which increases the chance that diverse seeds will be deposited under the same trees. Such spatially contagious seed dispersal should result in higher local species richness of seedlings and saplings around these trees (Russo 2005; Stevenson 2011; Punchi-Manage *et al.* 2015). Although the effect of seed dispersal on the spatial pattern of tree species is well documented (e.g., Seidler & Plotkin 2006), few studies have linked seed dispersal to potential negative or positive species' co-occurrence patterns in tropical tree communities, or explored how fruit and seed consumers (e.g., gibbons) affect local co-occurrence of tree species (but see Stevenson 2011; Punchi-Manage *et al.* 2015).

One approach to finding out if local species richness of saplings (and large trees) is indeed increased around preferred species is to analyse the spatial patterns of species richness using the "individual species-area relationship", or *ISAR* (Wiegand & Moloney 2014). The *ISAR* function is the mean species richness within distance *r* of the individuals of a given focal species *f* (Wiegand *et al.* 2007; Wiegand & Moloney 2014). Comparison of the observed *ISAR* function with that of multiple realizations of a suitable null model (where the focal species locations are compared to random locations in the plot) reveals if a focal species is surrounded by local species assemblages of lower or higher than expected species richness. Combined with data on seed dispersal networks, this technique allows us to determine if animal seed disperser activity leaves signatures in the species richness surrounding tree species that are preferred by primate frugivores. In our study we expected significantly higher local species richness of saplings around large trees of preferred species (i.e., they are "accumulator species"). We also expect that this signal should be weaker or absent for the larger size classes of trees (but see Russo & Augspurger 2004). This is because many of the original focal trees might not have started reproducing before the larger surrounding trees germinated, and might already have died by the time surrounding trees grew up. Additionally, many other processes may intervene until a small tree finally reaches large size.

Here we test the hypothesis that disperser activity generates patterns of increased local species richness of saplings around preferred food tree species of animal seed dispersers. We were interested in the assemblage of arboreal frugivores, especially those which reach fruits as soon as they are ripe. To test our hypothesis, we apply the *ISAR* methodology to data of the 30-ha Mo Singto forest plot located in a pristine tropical forest of Thailand where tree seeds are dispersed by large arboreal mammal (especially primate) and bird species. In a first analysis we determine for 52 abundant focal species the local species richness of all small trees (dbh < 10 cm) around the large trees (dbh ≥ 10 cm) of a given focal species. Due to the diverse and complex seed dispersal network on and around the Mo Singto plot we hypothesize that accumulator effects should prevail and that the strength of accumulator effects should differ among groups of focal species preferred by different animal dispersers. We expect that large-bodied animals such as primates or hornbills should create spatially contagious seed dispersal because their large gape width and relative high body mass (McConkey *et al.* 2002; Kitamura *et al.* 2004) enable them to co-disperse many of their preferred seed species. Finally, we assess the local species richness of all large trees around the large trees of the focal species to test if an accumulator signal in the species richness of saplings persists into the community of large trees; we expect that it will not for reasons given above.

Materials and methods

STUDY AREA AND TREE DATA

The study was conducted in the 30-ha Mo Singto forest dynamics plot (MST); 600 m × 500 m, in size, a ForestGEO plot of the Centre for Tropical Forest Science (CTFS) network (Brockelman *et al*. 2017). The plot is located at 101°22′ E and 14°26′ N with an altitude range of 725–815 m asl in the central landscape of Khao Yai National Park, part of a UNESCO world heritage site. The dry season lasts from November to April, but there are some thunderstorms occurring during March to April. Average annual precipitation is ca. 2,000 mm and the average annual minimum–maximum temperature range is 19°–28° C (Brockelman *et al.* 2017).

We used data from the 2010 census of the Mo Singto plot where all trees with diameter at breast height (dbh) ≥1 cm were tagged, identified and mapped inside the 30-ha plot. We divided all trees into two size classes, large (dbh ≥10 cm; assumed to be adults) and small (dbh 1– <10 cm; assumed to be saplings). To obtain sufficient statistical power for our focal species we selected as focal species only species with more than 50 large-sized individuals, which was true for 52 of 263 tree species in the plot.

ANIMAL SEED DISPERSERS

Khao Yai National Park still contains a high diversity of largely frugivorous arboreal mammal and bird species, including gibbons (*Hylobates lar* and *H. pileatus*), macaques (*Macaca leonina*), civets (five species), bears (*Ursus thibetana, Helarctos malayanus*), hornbills (four species) and other smaller frugivorous birds such as barbets, orioles, pigeons, mynas and bulbuls (Lynam *et al.* 2006). Gibbons (Whittington & Treesucon 1991; McConkey & Brockelman 2011; McConkey *et al.* 2015; Brockelman *et al.* 2017), macaques (Albert *et al.* 2013a), deer (Chanthorn & Brockelman 2008; Brodie *et al.* 2009), bears (Ngoprasert *et al.* 2011), hornbills (Kitamura *et al.* 2002, Kitamura *et al*. 2004) and smaller birds (Sankamethawee *et al.* 2011; Khamcha *et al.* 2014) are all potentially important seed dispersers in the Mo Singto area of Khao Yai Park. The most probable seed dispersers of tree species in the Mo Singto plot are shown in Table S1 based on extensive observations of Kitamura *et al*. (2002) and Brockelman *et al.* (2017).

We selected four groups of seed dispersers: gibbons, macaques, hornbills (four species) and smaller birds, and categorized them for each tree species as dispersing or non-dispersing. Dispersal effectiveness been evaluated only for relatively few species in detail. We therefore used a binary network with realized links as an approximation. A recent study by Corso *et al.* (2015) showed that, despite widespread belief, the loss of information in binary networks was not significant for most network properties. Terrestrial mammals such as civets, deer, bears and elephants also feed on many of the same tree species as primates and birds, but except for a few tree species, their dispersal service within the forest may be limited because they usually deposit seeds in large clumps (deer, bears), often eat the seeds instead of swallowing them (squirrels, deer), have a less diverse fruit diet, or carry the seeds out of the forest (sambar deer, elephants, civets) (Chanthorn & Brockelman 2008; Nakashima *et al.* 2010; McConkey & Brockelman 2011). Bats may also disperse some fruit species, but we lack basic data on their activity in our study area, and they are likely to be more important as seed dispersers in open areas and second-growth forests (Muscarella & Fleming 2007).

SUMMARY FUNCTION

The *ISAR* (individual species area relationship) is a summary function based on point pattern theory (Wiegand & Moloney 2014) that quantifies the spatial structure of the local species richness around individuals of a focal species based on point pattern data. The $ISAR_f(r)$ is defined as the mean number of species found within the neighbourhoods of radius r around the individuals of a focal species f (Wiegand *et al.* 2007). The *ISAR* function can be expressed as the sum of a well-known summary point pattern function, the bivariate nearest neighbour distribution function $D_{fi}(r)$ (Wiegand & Moloney 2014) that give the probability that species i is present in the neighbourhood with radius r around focal species f:

$$ISAR_f(r) = \sum_{i=1, i \neq f}^{S} D_{fi}(r) \tag{1}$$

where the sum is over all species except the focal species *f* and *S* is the total number of species found in the plot. The maximum radius of the neighbourhoods *r* used in this study was 50 m. We applied the *ISAR* to estimate local species richness of (i) small trees around large individuals of the focal species (L-S analysis) and (ii) large trees around large individuals of the focal species (L-L analysis).

NULL MODEL

Our null hypothesis is that local species richness around large trees of a focal species cannot be distinguished from that of random locations in the plot. The simplest model to test this null hypothesis would be complete spatial randomness (also called homogeneous Poisson process) that relocates the individuals of the focal species independently to random locations within the entire plot. However, this point process does not conserve the observed spatial autocorrelation of focal species and may lead to overestimation of significant effects (it makes the simulation envelopes too narrow; Wiegand & Moloney 2014). We therefore used techniques of pattern reconstruction (Wiegand *et al.* 2013; Wiegand & Moloney 2014: sections 4.3.3.3 and 4.3.3.4) to generate the null model patterns that relocate individuals of the focal species to random locations within the entire plot, but retain the observed spatial autocorrelation in the focal species (see e.g., Wang *et al.* 2016).

The pattern reconstruction null model is the point pattern implementation of the common species area relationship (SAR; Shimatani & Kubota 2004). It tests if the focal species is located in areas of lower or higher local species richness than expected by the SAR.

This null model is sensitive to effects of the environment (that may, e.g., generate patches with lower or higher than average species richness or by causing variation in density leading to such patches), effects of enhanced seed dispersal service close to preferred tree species (which may increase local species richness of seedlings and saplings), and to effects of interactions with individuals of other tree species which may modulate the small-scale placement of trees (e.g., due to competition for space) (Wiegand & Moloney 2004; Wiegand *et al.* 2007; Punchi-Manage *et al.* 2015; Tsai *et al.* 2015; Chacón-Labella *et al.* 2016). We expect that the effects of seed dispersal service close to preferred tree species and those of plant-plant interactions will operate over small spatial scales (< 50 m). In contrast, gradients in environmental conditions (above 50 m) will be noticed by departures from this null model at larger distances.

GOODNESS-OF-FIT TESTS

The standard method to detect significant departures from the null model is use of "pointwise" simulation envelopes that are, for example, the fifth lowest or highest values of the *ISAR* function of the 199 null model simulations (Wiegand & Moloney 2004; Wiegand *et al.* 2007; Wiegand *et al.* 2016; Figure 1b). If the observed *ISAR* function is at neighbourhood *r* above the pointwise simulation envelopes we have an accumulator species (a species neighboured by more species than expected; e.g., Figure 1b). Conversely, if the observed *ISAR* function is below the pointwise envelopes we have a repeller species (a species neighboured by fewer species than expected). This test has for a fixed neighbourhood distance *r* a significance level of $\alpha = 0.05$. However, because of the problem of multiple inference (Loosmore & Ford 2006) the true error level α will be smaller if we look at a range of neighbourhoods. We expect the effects of contagious seed dispersal to be strongest below and immediately outside the crowns of the individuals of the preferred tree species. We therefore test significant departures from the *ISAR* function for the 1−30 m distance interval that encompasses this range, but show for selected analyses results of up to 50 m.

To avoid the problem of simultaneous inference we used a maximum absolute deviation (MAD) test that reduces the scale-dependent information (over an appropriate distance interval, here 1−30 m) into a single test statistic (Myllymäki *et al.* 2016; Wang *et al.* 2016; Wiegand *et al.* 2016). In a first step of this test we standardize the *ISAR* functions to obtain standardized effect sizes (*SES*; also called *z*-score):

$$SES_f^i(r) = \frac{obs_f^i(r) - \exp_f(r)}{sd_f(r)} \qquad (2)$$

where $i = 0$ for the observed data and $i = 1, ...199$ for the simulated data, the $obs^i_f(r)$ is the *ISAR* function of the observed data ($i = 0$) or the null model data ($i = 1, ...199$), the $exp_f(r)$ is the mean of the *ISAR* function of the 199 simulations of the null model and $sd_f(r)$ the corresponding standard deviation. The pointwise simulation envelopes of the transformed summary functions $SES^i_f(r)$ approximate for all distances r values of z_α and $–z_\alpha$, where z_α is the critical value of α (i.e., 1.96 for $\alpha = 0.05$; Figure 1C; Wiegand *et al.* 2016). This works under the mild condition that the distribution of the *ISAR* functions of the null model simulations approximates a normal distribution for fixed values of r (Wiegand *et al.* 2016).

Because the standarization (eq. 2) yields pointwise simulation envelopes of constant width (Figure 1C), it makes sense to reduce the scale-dependent information of the transformed summary functions $SES^i_f(r)$ into a single test statistic $S^i_{\max}$, being its maximal absolute value (over distance interval 1−30 m). The tenth largest value of the $S^i_{\max}$ ($i = 1$,

…199) is then the upper global envelope G^+, and $-G^+$ the lower global envelope. We can reject the null model with exact significance level α if $SES_f^0(r) > G^+$ or $SES_f^0(r) < G^-$ for one or more distances r within the interval (Wiegand *et al.* 2016).

To get comparable estimates of effect sizes that consider multiple inferences, we normalize the standardized *ISAR* function of the observed data to:

$$SES_f^*(r) = \frac{SES_f^0(r)}{G^+} \tag{3}$$

Following normalization, an accumulator species shows at one or more neighbourhoods r values of $SES_f^*(r) > 1$, and a repeller species $SES_f^*(r) < -1$. More importantly, the absolute value of $SES_f^*(r)$ is a multiple-inference corrected effect size that describes the strength of departures from the null model at neighbourhood r in a standardized way (Wang *et al*. 2016).

To obtain for a given focal species a measure of the strength of positive and negative departures from the null model we estimated for each focal species f the indices $S_f^+ = \max_{r=1,..30}[SES_f^*(r)]$ and $S_f^- = \min_{r=1,..30}[SES_f^*(r)]$, the maximal positive and the minimal negative values of the multiple-testing corrected standardized effect size $SES_f^*(r)$ of the observed summary *ISAR* function, taken over the 1−30 m interval. We then used a *t*-test to compare the mean of the values of S_f^+ among species belonging to different groups of dispersers (i.e., gibbon dispersed vs. non-gibbon dispersed, macaques vs. non-macaques, hornbills vs. non-hornbills, and smaller birds vs. others). This simple analysis reveals which focal species associated with a given group of seed dispersers shows the largest difference in the average strength of accumulator effects when compared with that of the remaining focal species. We also conducted the analogous analyses for focal species with negative repeller effects (measured by S_f^-). Because we lack systematic data on the effectiveness of the different dispersers for the different focal tree species, we cannot conduct here more sophisticated analyses.

Results

THE SPECIES RICHNESS OF SAPLINGS AROUND LARGE TREES

Nephelium melliferum and *Garcinia benthamii* are examples of species with a strong signal of positive departure (Figure 1a-c). The MAD test revealed that 27 (52%) of all focal species departed positively from the null model, but only three species negatively (Figure 2a). Strong negative departures were shown by the two canopy species *Sloanea sigun* and *Mastixia pentandra*. Mixed departures occurred only for the species *Mastixia pentandra* with significant negative departures at small neighbourhoods and positive departures at larger neighbourhoods (Figure 2a). The frequency of positive departures declined with neighbourhood radius (Figure 2a; Figure S1); only four out of 52 species showed significant departures at the >40 m neighbourhood (Figure 2a). This suggests that larger-scale environmental gradients did not interfere in our analysis.

The *t*-test showed that the strength of positive effects of a focal species f (i.e., the index S_f^+) was significantly larger for gibbon-dispersed species than for species not dispersed by gibbons (with mean values of 1.39 vs. 0.96, Table 1a). The same significant tendency occurred for macaque-dispersed species (mean strength of 1.46 vs. 1.01; Table 1a). The mean strength of positive effects was at all neighbourhoods r larger for the group of macaque (or gibbon) dispersed species than for non-macaque (or non-gibbon) species (Figure S2a). At the same time the mean strength of negative effects was at all neighbourhoods smaller for macaque (or gibbon) dispersed species than for non-macaque (or gibbon) species (Figure S2c). However, the mean strength of positive and negative effects of species dispersed by hornbills (and small-bodied birds) did not differ from those not dispersed by hornbills (or small-bodied birds) (Table 1a; Figures S2b, d). Our results therefore suggest that the activity of large-bodied dispersers such as the gibbon or macaque contribute disproportionally to the frequent accumulator effects at the Mo Singto plot. These effects were for most focal species limited within the typical crown area (approximately <10–15 m), but extended for a few species up to 50 m (Figure 2a).

THE SPECIES RICHNESS OF LARGE TREES AROUND LARGE TREES

The MAD test revealed that 13 focal species departed positively from the null model and 13 species negatively. Mixed departures did not occur (Figure 2b). Negative effects occurred mostly at smaller distances (< 10m) and positive departures at intermediate distances of 13 to 20 m (Figure 2b; Figure S1); only two out of 52 species showed significant departures at the >40 m neighbourhoods (Figure 2b). This suggests again that larger-scale environmental gradients did not interfere in our analysis.

The *t*-tests showed no differences between species with different groups of dispersers (Table 1b). Thus, the few accumulator effects in the local species richness of large trees around large trees of a focal species were not correlated with the specific disperser groups as found for small trees. Accordingly, the mean strength of positive effects in the L-L analysis was in general smaller than for the L-S analysis but larger for negative effects (cf. Table 1b and 1a). Of the 27 significant accumulator species in the L-S analysis only five were among the 13 significant accumulator species in the L-L analysis. There was also no relationship between the strength of positive effects in the L-S and the L-L analysis (Figure S4). However, the two strong repeller species in the L-S analysis (*S. sigun* and *M. pentandra*; Figure 2a) were even stronger repellers in the L-L analysis (Figure 2b).

Discussion

In this study, we analysed data from the tropical forest of the Mo Singto plot, Thailand, to test the hypothesis that patterns of locally increased species richness of saplings may emerge around preferred trees of animal seed dispersers. We combined here spatial analysis of detailed forest inventory data of the Mo Singto plot with qualitative data on the associated binary tree-frugivore interaction network. This is the best we can do to test our hypothesis, given that it is not possible to track seed dispersal of many tree species by many frugivorous species in a detailed way as well as tracking the fate of the dispersed seeds until the large tree class. Another simplification is our assumption that trees all mature at 10 cm in dbh; this is at best a rough estimate of a mean tendency.

THE ROLE OF PRIMATE SEED DISPERSAL

Our results suggest that large-bodied primate seed dispersers such as gibbons and macaques shape patterns of local species richness of saplings in the Mo Singto plot. Focal tree species with seeds dispersed by large primates showed on average stronger accumulator effects than tree species not dispersed by large primates. Accumulator effects were more frequent close to the stem and declined with increasing distance from the stem. According to these findings, we propose the hypothesis of “primate-mediated diversity facilitation” via spatially contagious seed dispersal, which can explain why species that are frequently visited by large primates show higher species richness of saplings in their neighbourhoods. The mechanism is that they forage on a variety of fruits from many tree species, particularly those identified here as accumulator species, and visit those species more often than the others (Asensio *et al.* 2011;

Jose-Dominguez *et al.* 2015; Suwanvecho *et al.* in press). The movement and daily life rhythm of gibbons (or other arboreal primates) are oriented around those trees and change over the year depending primarily on their preferred food species (McConkey & Chivers 2007; Asensio *et al.* 2011). Brockelman *et al.* (2014) and Suwanvecho *et al.* (in press) have shown that highly preferred individual trees of heavily used species such as *Nephelium melliferum*, *Polyalthia simiarum* and *Garcinia benthamii* are visited repeatedly (more than 10 times) during their fruiting seasons. Consequently, primates disperse seeds of a number of minor food species together with seeds of their main food species mostly in areas surrounding their favourite trees. This mechanism has the potential to generate patches of higher seedling and sapling density in the neighbourhood of the stems of their preferred tree species (i.e., over the canopy and somewhat beyond).

The seeds of several focal species are dispersed by several groups of animals. For example, accumulator effects of tree species such as *Bridelia insulna, Cinnamomum subavenium* and *Syzygium syzygioides* that are co-dispersed by primates and birds (Table S1) could be enhanced by complementary effects of shared seed dispersers in the network. Several studies have reported contagious seed dispersal mediated by birds (Kwit *et al.* 2004; Carlo & Morales 2008; Viswanathan *et al.* 2015). Although birds can swallow entire seeds, they play a secondary role in generating accumulation effects because their smaller body size and short retention time in the gut limit their ability to carry many mixed-species seeds. Primates play a crucial role in seed dispersal of large and small seeds, but that large seeds are inaccessible to small frugivores (Chapman & Russo 2011; McConkey & Brockelman 2011; Bufalo *et al.* 2016). The gibbons and macaques were shared dispersers. However, we expect that a gibbon is relatively more important as a major driver of the accumulator effect because only the gibbons have relatively small, exclusive territories inside the forest, whereas macaques typically show larger scale movements across many habitats including those used by humans (Albert *et al.* 2013b; Jose-Dominguez *et al.* 2015). Because of this, gibbons are more regular and frequent visitors to individual preferred trees than are macaques (Suwanvecho *et al.* in press).

More generally, patches with locally increased densities of seeds (i.e., spatially contagious seed dispersal; Schupp *et al.* 2002) are likely to occur if frugivores direct seeds towards other fruiting plants and habitats. Examples of such behaviour include bellbirds (*Procnias tricarunculata*) in tropical forests in Costa Rica which distributed more seeds under song perches in canopy gaps where they had a better survival than underneath the parent tree (Wenny & Levey 1998), and Peruvian spider monkeys (*Ateles paniscus*) which dispersed large numbers of seeds underneath their sleeping sites resulting in strong clumping that persisted to the sapling stage (Russo & Augspurger 2004). Animal seed dispersal, however, will only translate into an advantage for the dispersed plant if conditions at the new site are more favourable than those underneath the canopy of the parent plant (directed seed dispersal; Howe & Smallwood 1982; Wenny 2001; Schupp *et al.* 2002). The major assumption of this mechanism is that zones of high species richness have to be away from areas where negative density-dependent effects are strong. Our results showed that the strongest accumulator effects occurred at scales beyond the canopy of single tree (>10 m). These distances are relatively favourable for trees because of less NDD from conspecific species (Caughlin *et al.* 2015) and natural enemies (Comita *et al.* 2014). Additionally, the contagious seed dispersal increases heterospecific seed rain and consequently the heterospecific neighbourhood of seedlings, thereby reducing NDD due to natural enemies (Wright *et al.* 2016).

We expected that increased species richness in the neighbourhood of preferred tree species might also persist into larger size classes of older trees, but that this effect would be weaker. Indeed, we found that significant increases in richness were more frequent in small trees around large trees (L-S; 27 species) than in large trees around large trees (L-L; 13 species), with relatively little overlap among the accumulator species (Figures 2 & S1). We also found no difference in the strength of positive effects between focal species that are gibbon-dispersed (or macaque-dispersed) when compared to the rest of the focal species. We explain this lack of effect for large trees by the fact that most of the trees responsible for the effects on the current generation of large trees are likely to have died in the previous few decades, and those trees present may not have started reproducing when the peripheral trees germinated. Also, large trees are exposed for a longer time to processes that can dilute or mask the signal.

The emergence of small-scale negative repeller effects in the analysis of large trees (Figure 2b) can be explained by competition for space because large trees physically occupy more space that preempts other large trees. This reduces the number of large trees in the close neighbourhood of other large trees and may translate into lower species richness in the crown areas of large trees (Wiegand *et al.* 2007; Perry *et al.* 2009; Punchi-Manage *et al.* 2015). However, the strong and consistent repeller effects *Slonea sigun* and *Matixea pentandra* in the L-S and L-L analysis can be explained by specific species traits *S. sigun* may repel individuals of other species by vegetative root expansion, and *M. pentandra* shows particular seed dispersal by bears that deposit seeds in large piles (>50 seeds; Chanthorn pers. obs.).

The locally increased species richness found in the sapling community around large trees persisted for the community of large trees only in neighbourhoods just outside the range of competition for individual space. This pattern is similar to the findings of Punchi-Manage *et al.* (2015) in an *ISAR* analysis of the Sinharaja forest plot in Sri Lanka. However, these authors found, in contrast to our results, a signal of dispersal mode (animal versus wind) in the strength of positive effects only for the L-L analysis, but not for small saplings around large trees as in our study. They explained this by a recent decline in animal seed dispersal service (Harrison *et al.* 2013) that was visible for saplings but not yet for large trees. In contrast, animal seed dispersers are still common at our study site in the central landscape of Khao Yai National Park (Kitamura *et al.* 2002; Lynam *et al.* 2006; Brockelman *et al.* 2017). In addition, the signal of primate dispersal in the local species richness of large trees may be diluted by the large array of processes that may intervene until a small tree finally reaches large size.

CONSEQUENCES FOR COEXISTENCE

Negative density dependence is an underlying mechanism of species coexistence in tropical forest through Janzen-Connell effects (Janzen 1970; Connell 1971) by preventing hyperabundant species from outcompeting other species (Terborgh, 2012). The contagious multi-species seed rain of animal seed dispersers may allow the coexistence of seedlings and saplings in the neighbourhood of their preferred trees and reduce the effects of conspecific density dependence proposed by Janzen (1970) and Connell (1971). Primates that swallow most or all seeds are particularly good at moving the seeds away from their parental trees and dropping them in neighbourhoods richer in heterospecifics (Schupp *et al.* 2002; McConkey & Chivers 2007). Furthermore, seed dispersal by primates under their preferred trees will create spatially heterogeneous seed shadows. The result of this aggregated dispersal will be that large areas may be devoid of seeds of the species involved and create opportunities for colonization by seeds from other dispersal networks (Wenny 2001; Schupp *et al.* 2002). The co-dispersal of several tree species by primates may generate additional heterogeneity in seed-fall at different spatial and temporal scales. As a consequence, seedlings and saplings of a given species may be surrounded by largely unpredictable sets of competitors which may further dilute the outcome of deterministic competition with heterospecifics (Punchi-Manage *et al.* 2015).

Because our study was conducted at the local scale of the 30-ha plot and all accumulator species are old-growth species (none is a long-lived pioneer species), there should be little effect of the species pool or environmental heterogeneity on the observed increases of species richness in the neighbourhood of the accumulator species. It is interesting that all accumulator tree species are "old-growth" forest species, and do not include long-lived pioneer species that have persisted on parts of the plot some unknown time since disturbance (Brockelman et al. 2017). This is not surprising because gibbons, which do not leave the forest, are the main dispersers of old-growth forest species. Persisting individuals of long-lived pioneer species, although fed on by gibbons, are mainly dispersed by a variety of ground-mobile mammals such as deer and bears (e.g., Chanthorn & Brockelman 2008; Brodie et al. 2009). Macaques are 'half-way' dispersers that feed mostly in the old-growth forest but also utilize more open habitats. Thus, an accumulator mechanism based on primate-dispersed species will primarily affect alpha diversity in relatively mature forests.

The theory of contagious seed dispersal does not have to account for or depend on environmental heterogeneity, as originally proposed by Schupp *et al*. (2002). It is a purely disperser-centred mechanism, and does not even depend on how the adult trees are distributed. The case for its existence—based on *ISAR* analysis—is, however, not air-tight. It is still conceivable that confounding factors related to the environment such as existence of a bias in the locations of the focal species with respect to local species richness affect the results, or that tree characteristics other than fruit production differentially attract dispersers. Further analyses controlling for such effects are needed to strengthen our hypothesis that attractor effects are influenced by dispersers. This may include, for example, comparing local species richness around individual trees of a focal species with differing fruit production or attractiveness to animal dispersers, or conducting more detailed studies of seed rain by primate dispersers.

Conclusions

In this study we have shown that the individual species-area relationship *ISAR* reveals subtle effects in the local species richness around individual tree species. In particular, it allowed us to detect in a species-rich tropical forest locally higher species richness of saplings in the neighbourhood of preferred food species of gibbons and macaques. This suggests that animal seed dispersers impact the small-scale spatial structure of tree communities. However, in other cases when seed dispersal is not directed towards particular plant species, but may occur in a more diffuse manner inside the home ranges of the animals (e.g., Holbrook & Smith 2000) or is directed towards specific microsites such as forest gaps (Schupp *et al.* 1989), signatures of seed dispersal would be more difficult to detect in patterns of local species richness. Given the inherent dificulties of detecting such patterns, we can expect that enhanced local species richness caused by seed dispersing animals should be a common phenomenon in tropical forests that still have intact animal communities. In many tropical forests, extirpation of primates is therefore predicted to cause changes in the future structure and dynamics of forests.

Authors’ contributions

W.C., T.W. and S.G. designed the study and analyses. W.C. and T.W. analysed the data. W.Y.B. and A.N. conceived the Mo Singto plot census and seed dispersal data. W.C. wrote the first draft of the manuscript, and T.W., S.G. and W.Y.B. substantially contributed to writing the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

Acknowledgements

The authors thank the Department of National Parks, Wildlife and Plant Conservation for permission to work in Khao Yai and their staff for cooperation. S.G. and the visiting of W.C. in Germany were funded by the European Research Council (ERC) Advanced Grant SpatioDiversity (grant number 233066) to T.W. We also thank Matteo Detto, Sabrina Russo and Florian Hartig for commenting our manuscript. Finally, we thank the Cluster and Program Management Office and the Bioresources Technology Development Unit of National Science and Technology Development Agency (Thailand) who have supported funding for the tree census and database management of the Mo Singto plot.

Data Accessibility

The dataset for tree census in 2010 is available from the repository of the center for tropical forest science-forest global earth observatory (CTFS-ForestGEO): http://www.ctfs.si.edu/site/Mo+Singto. The data of large-large and large-small analyses is available from the Zenodo digital repository: https://doi.org/10.5281/zenodo.1005115 (Chanthorn, 2017).

References

Albert, A., Hambuckers, A., Culot, L., Savini, T. & Huynen, M. C. (2013a) Frugivory and seed dispersal by northern pig-tailed macaques (*Macaca leonina*), in Thailand. *International Journal of Primatology,* **34,** 170-193.

Albert, A., Huynen, M. C., Savini, T. & Hambuckers, A. (2013b) Influence of food resources on the ranging pattern of northern pig-tailed macaques (*Macaca leonina*). *International Journal of Primatology*, **34,** 696-713.

Andresen, E. (2002) Primary seed dispersal by red howler monkeys and the effect of defecation patterns on the fate of dispersed seeds. *Biotropica*, **34,** 261-272.

Asensio, N., Brockelman, W. Y., Malaivijitnond, S. & Reichard, U. H. (2011) Gibbon travel paths are goal oriented. *Animal Cognition*, **14,** 395-405.

Beckman, N. G. & Rogers, H. S. (2013) Consequences of seed dispersal for plant recruitment in tropical forests: Interactions within the seedscape. *Biotropica*, **45,** 666-681.

Brockelman, W. Y., Nathalang, A. & Maxwell, J. F. (2017) *Mo Singto Plot: Flora and Ecology*. National Science and Technology Development Agency and Department of National Parks, Wildlife and Plant Conservation, Bangkok.

Brockelman, W. Y., Nathalang, A., Greenberg, D. B. & Suwanvecho, U. (2014) Evolution of small-group territoriality in gibbons. *Primates and Cetaceans: Field Research and Conservation of Complex Mammalian Societies* (eds J. Yamagiwa & L. Karczmarski), pp. 213-230. Springer Japan, Tokyo.

Brodie, J. F., Helmy, O. E., Brockelman, W. Y. & Maron, J. L. (2009) Functional differences within a guild of tropical mammalian frugivores. *Ecology*, **90,** 688-98.

Bufalo, F. S., Galetti, M. & Culot, L. (2016) Seed dispersal by primates and implications for the conservation of a biodiversity hotspot, the Atlantic forest of South America. *International Journal of Primatology*, **37,** 333-349.

Carlo, T. A. & Morales, J. M. (2008) Inequalities in fruit-removal and seed dispersal: consequences of bird behaviour, neighbourhood density and landscape aggregation. *Journal of Ecology*, **96,** 609-618.

Caughlin, T. T., Ferguson, J. M., Lichstein, J. W., Zuidema, P. A., Bunyavejchewin, S. & Levey, D. J. (2015) Loss of animal seed dispersal increases extinction risk in a tropical tree species due to pervasive negative density dependence across life stages. *Proceedings of the Royal Society B-Biological Sciences,* **282**.

Chacón-Labella, J., de la Cruz, M. & Escudero, A. (2016) Beyond the classical nurse species effect: diversity assembly in a Mediterranean semi-arid dwarf shrubland. *Journal of Vegetation Science*, **27,** 80-88.

Chanthorn, W. & Brockelman, W. Y. (2008) Seed dispersal and seedling recruitment in the light-demanding tree *Choerospondias axillaris* in old-growth forest in Thailand. *Scienceasia,* **34,** 129-135.

Chanthorn, W (2017). Results of L-S and L-L analyses. Zenodo. http://doi.org/10.5281/zenodo.1005115

Chapman, C. A. & Russo, S. E. (2011) Primate seed dispersal: Linking behavioral ecology with forest community structure. *Primates in perspective* (ed C. J. Campbell), pp. 510-525. Oxford University Press, New York.

Comita, L. S., Queenborough, S. A., Murphy, S. J., Eck, J. L., Xu, K. Y., Krishnadas, M., Beckman, N. & Zhu, Y. (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.

Connell, J. H. (1971) On the role of natural enemies in preventing competitive exclusion in some marine animals and in rain forest trees. *Dynamics of numbers in populations* (eds P. J. den Boer & G. R. Gradwell), pp. 298-312 Centre for Agricultural Publications and Documentation, Proceedings for the Advanced Study Institute, Osterbeek, Wageningen, Netherlands.

Corlett, R. T. (2017) Frugivory and seed dispersal by vertebrates in tropical and subtropical Asia: An update. *Global Ecology and Conservation,* **11,** 1-22.

Corso, G., Torres Cruz, C. P., Pinto, M. P., de Almeida, A. M. & Lewinsohn, T. M. (2015) Binary versus weighted interaction networks. *Ecological Complexity,* **23,** 68-72.

Gomez, J. M. & Verdu, M. (2012) Mutualism with plants drives primate diversification. *Systematic Biology,* **61,** 567-577.

Harrison, R. D., Tan, S., Plotkin, J. B., Slik, F., Detto, M., Brenes, T., Itoh, A. & Davies, S. J. (2013) Consequences of defaunation for a tropical tree community. *Ecology Letters***,** **16**, 687-694.

Holbrook, M. K. & Smith, B. T. (2000) Seed dispersal and movement patterns in two species of *Ceratogymna* hornbills in a West African tropical lowland forest. *Oecologia,* **125,** 249-257.

Hubbell, S. P., Foster, R. B., O'Brien, S. T., Harms, K. E., Condit, R., Wechsler, B., Wright, S. J. & de Lao, S. L. (1999) Light-gap disturbances, recruitment limitation, and tree diversity in a neotropical forest. *Science,* **283,** 554-7.

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

Janzen, D. H. (1970) Herbivores and the number of tree species in tropical forests. *American Naturalist,* **104** 501-528.

Jose-Dominguez, J. M., Huynen, M. C., Garcia, C. J., Albert-Daviaud, A., Savini, T. & Asensio, N. (2015) Non-territorial macaques can range like territorial gibbons when partially provisioned with food. *Biotropica,* **47,** 733-744.

Khamcha, D., Savini, T., Westcott, D. A., McKeown, A., Brockelman, W. Y., Chimchome, V. & Gale, G. A. (2014) Behavioral and social structure effects on seed dispersal curves of a forest-interior bulbul (Pycnonotidae) in a tropical evergreen forest. *Biotropica,* **46,** 294-301.

Kitamura, S., Yumoto, T., Poonswad, P., Chuailua, P. & Plongmai, K. (2004) Characteristics of hornbill-dispersed fruits in a tropical seasonal forest in Thailand. *Bird Conservation International,* **14,** S81-S88.

Kitamura, S., Yumoto, T., Poonswad, P., Chuailua, P., Plongmai, K., Maruhashi, T. & Noma, N. (2002) Interactions between fleshy fruits and frugivores in a tropical seasonal forest in Thailand. *Oecologia,* **133,** 559-572.

Kwit, C., Levey, D. J. & Greenberg, C. H. (2004) Contagious seed dispersal beneath heterospecific fruiting trees and its consequences. *Oikos,* **107,** 303-308.

Levine, J. M. & Murrell, D. J. (2003) The community-level consequences of seed dispersal patterns. *Annual Review of Ecology Evolution and Systematics,* **34,** 549-574.

Loosmore, N. B. & Ford, E. D. (2006) Statistical inference using the G or K point pattern spatial statistics. *Ecology,* **87,** 1925-1931.

Lynam, A. J., Round, P. D. & Brockelman, W. Y. (2006) *Status of birds and large mammals in Thailand's Dong Phayayen - Khao Yai forest complex* Wildlife Conservation Society and Biodiversity Research and Training (BRT) Program, Bangkok.

McConkey, K. R. (2000) Primary seed shadow generated by gibbons in the rain forests of Barito Ulu, central Borneo. *American Journal of Primatology,* **52,** 13-29.

McConkey, K. R., Aldy, F., Ario, A. & Chivers, D. J. (2002) Selection of fruit by Gibbons (*Hylobates muelleri* x *agilis*) in the rain forests of Central Borneo. *International Journal of Primatology,* **23,** 123-145.

McConkey, K. R. & Brockelman, W. Y. (2011) Nonredundancy in the dispersal network of a generalist tropical forest tree. *Ecology,* **92,** 1492-1502.

McConkey, K. R., Brockelman, W. Y., Saralamba, C. & Nathalang, A. (2015) Effectiveness of primate seed dispersers for an "oversized" fruit, *Garcinia benthamii*. *Ecology,* **96,** 2737-2747.

McConkey, K. R. & Chivers, D. J. (2007) Influence of gibbon ranging patterns on seed dispersal distance and deposition site in a Bornean forest. *Journal of Tropical Ecology,* **23,** 269-275.

Muscarella, R. & Fleming, T. H. (2007) The role of frugivorous bats in tropical forest succession. *Biological Reviews,* **82,** 573-590.

Myllymäki, M., Mrkvička, T., Grabarnik, P., Seijo, H. & Hahn, U. (2017) Global envelope tests for spatial processes. *Journal of the Royal Statistical Society: Series B (Statistical Methodology)***, 79**, 381-404.

Nakashima, Y., Inoue, E., Inoue-Murayama, M. & Abd Sukor, J. R. (2010) Functional uniqueness of a small carnivore as seed dispersal agents: a case study of the common palm civets in the Tabin Wildlife Reserve, Sabah, Malaysia. *Oecologia,* **164,** 721-730.

Ngoprasert, D., Steinmetz, R., Reed, D. H., Savini, T. & Gale, G. A. (2011) Influence offruit on habitat selection of Asian bears in a tropical forest. *Journal of Wildlife Management,* **75,** 588-595.

Perry, G. L. W., Enright, N. J., Miller, B. P. & Lamont, B. B. (2009) Nearest-neighbour interactions in species-rich shrublands: the roles of abundance, spatial patterns and resources. *Oikos,* **118,** 161-174.

Punchi-Manage, R., Wiegand, T., Wiegand, K., Getzin, S., Huth, A., Gunatilleke, C. V. S. & Gunatilleke, I. (2015) Neighborhood diversity of large trees shows independent species patterns in a mixed dipterocarp forest in Sri Lanka. *Ecology,* **96,** 1823-1834.

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. & Augspurger, C. K. (2004) Aggregated seed dispersal by spider monkeys limits recruitment to clumped patterns in Virola calophylla. *Ecology Letters,* **7,** 1058-1067.

Russo, S. E., Portnoy, S. & Augspurger, C. K. (2006) Incorporating animal behavior into seed dispersal models: Implications for seed shadows. *Ecology,* **87,** 3160-3174.

Sankamethawee, W., Pierce, A. J., Gale, G. A. & Hardesty, B. D. (2011) Plant-frugivore interactions in an intact tropical forest in north-east Thailand. *Integrative Zoology,* **6,** 195-212.

Schupp, E. W., Howe, H. F., Augspurger, C. K. & Levey, D. J. (1989) Arrival and Survival in Tropical Treefall Gaps. *Ecology,* **70,** 562-564.

Schupp, E. W., Jordano, P. & Gomez, J. M. (2010) Seed dispersal effectiveness revisited: a conceptual review. *New Phytologist,* **188,** 333-353.

Schupp, E. W., Milleron, T. & Russo, S. E. (2002) Dissemination limitation and the origin and maintenance of species-rich tropical forests. *Seed Dispersal and Frugivory: Ecology, Evolution and Conservation* (eds D. J. Levey, W. R. Silva & M. Galetti), pp. 19-33. CABI Publishing, Wallingford, Oxfordshire, UK.

Seidler, T. G. & Plotkin, J. B. (2006) Seed dispersal and spatial pattern in tropical trees. *Plos Biology,* **4,** 2132-2137.

Shimatani, K. & Kubota, Y. (2004) Quantitative assessment of multispecies spatial pattern with high species diversity. *Ecological Research,* **19,** 149-163.

Stevenson, P. R. (2011) The Abundance of large ateline monkeys is positively associated with the diversity of plants regenerating in Neotropical forests. *Biotropica,* **43,** 512-519.

Suwanvecho, U., Brockelman, W. Y., Nathalang, A., Santon, J., Matmoon, U., Somnuk, R., Mahannop, N. (2017) High interannual variation in the diet of tropical forest frugivore (*Hylobates lar*). *Biotropica* in press.

Terborgh, J. (2012) Enemies maintain hyperdiverse tropical forests. *The American Naturalist,* **179,** 303-314.

Tilman, D. (1994) Competition and biodiversity in spatially Structured habitats. *Ecology*, **75,** 2-16.

Tsai, C. H., Lin, Y. C., Wiegand, T., Nakazawa, T., Su, S. H., Hsieh, C. H. & Ding, T. S. (2015) Individual Species-area relationship of woody plant communities in a heterogeneous subtropical monsoon rainforest. *Plos One,* **10**, e0124539.

Viswanathan, A., Naniwadekar, R. & Datta, A. (2015) Seed dispersal by avian frugivores: Non-random heterogeneity at fine scales. *Biotropica,* **47,** 77-84.

Wang, X. G., Wiegand, T., Kraft, N. J. B., Swenson, N. G., Davies, S. J., Hao, Z. Q., Howe, R., Lin, Y. C., Ma, K. P., Mi, X. C., Su, S. H., Sun, I. F. & Wolf, A. (2016) Stochastic dilution effects weaken deterministic effects of niche-based processes in species rich forests. *Ecology,* **97,** 347-360.

Wenny, D. G. (2001) Advantages of seed dispersal: A re-evaluation of directed dispersal. *Evolutionary Ecology Research*, **3,** 51-74.

Wenny, D. G. & Levey, D. J. (1998) Directed seed dispersal by bellbirds in a tropical cloud forest. *Proceedings of the National Academy of Sciences*, **95,** 6204-6207.

Whittington, C. L. & Treesucon, U. (1991) Selection and treatment of food plants by white-handed gibbons (*Hylobates lar*) in Khao Yai National Park, Thailand. *Natural History Bulletin of Siam Society*, **39,** 111-122.

Wiegand, T., Grabarnik, P. & Stoyan, D. (2016) Envelope tests for spatial point patterns with and without simulation. *Ecosphere,* **7,** e01365 .

Wiegand, T., Gunatilleke, C. V. S., Gunatilleke, I. & Huth, A. (2007) How individual species structure diversity in tropical forests. *Proceedings of the National Academy of Sciences of the United States of America,* **104,** 19029-19033.

Wiegand, T., He, F. & Hubbell, S. P. (2013) A systematic comparison of summary characteristics for quantifying point patterns in ecology. *Ecography,* **36,** 092-103.

Wiegand, T. & Moloney, K. A. (2004) Rings, circles, and null-models for point pattern analysis in ecology. *Oikos,* **104,** 209-229.

Wiegand, T. & Moloney, K. A. (2014) *Handbook of Spatial Point-Pattern Analysis in Ecology*. Boca Raton: CRC Press.

Wrangham, R. W., Chapman, C. A. & Chapman, L. J. (1994) Seed dispersal by forest chimpanzees in Uganda. *Journal of Tropical Ecology,* **10,** 355-368.

Wright, S. J., Calderon, O., Hernandez, A., Detto, M. & Jansen, P. A. (2016) Interspecific associations in seed arrival and seedling recruitment in a Neotropical forest. *Ecology,* **97,** 2780-2790.

Figures & Table

FIGURE 1. The *ISAR* methodology. (A) Observed *ISAR* function of all focal species (grey lines) for the L-S analysis and that of the accumulator species *Nephelium melliferum* (NEPHME; top) and *Garcinia benthamii* (GARCBE; bottom) (red lines). For better display we subtracted for all focal species the expectation $SAR(r)$ of the null model. (B) The pointwise simulation envelopes (lines) for the species *N. melliferum* (top) *and G. benthamii* (bottom), being the 5th lowest and highest values of the $ISAR_f(r)$ - $SAR(r)$ of the 199 simulations of the null model. (C) Same as B), but for standardized effect sizes (Z-scores). Note that the pointwise simulation envelopes approximate values of 1.96 and -1.96. The global envelopes are shown as green lines.

FIGURE 2. Summary of the results for the L-S (a) and L-L analysis (b). The figure shows for different focal species (rows; for full species names see Table S1) the multiple testing-corrected effect size $SES_f^*(r)$ (eq. 3) from the pattern reconstruction null model. Accumulator effects are indicated by green, repeller effects by red and non-significance is indicated by blue. Dark green and red indicates large effects ($SES_f^*(r)$ >1.5 and $SES_f^*(r) < -1.5$). The symbols on the right show the results of the goodness-of-fit test over the 1−30 m distance interval: ** ($p < 0.01$), * ($p < 0.05$), ($p < 0.1$). Note that each graph omits about 30 species that did not show significant effects. Seed dispersal modes are also showed on the next right, i.e. B is smaller birds (excluding hornbills), P is primates, F is all arboreal frugivores, O is unknown animals, A is abiotic vectors, W is wind (see more detail in Supporting information, Table S1).

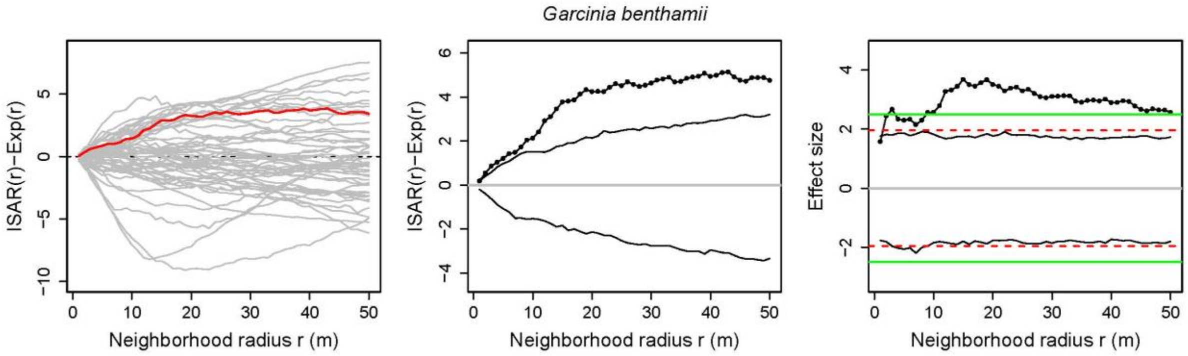
Table 1. Comparison of the strength of positive and negative effects of large focal species on the neighbourhood species richness of small (a) and large trees (b) dispersed by different seed

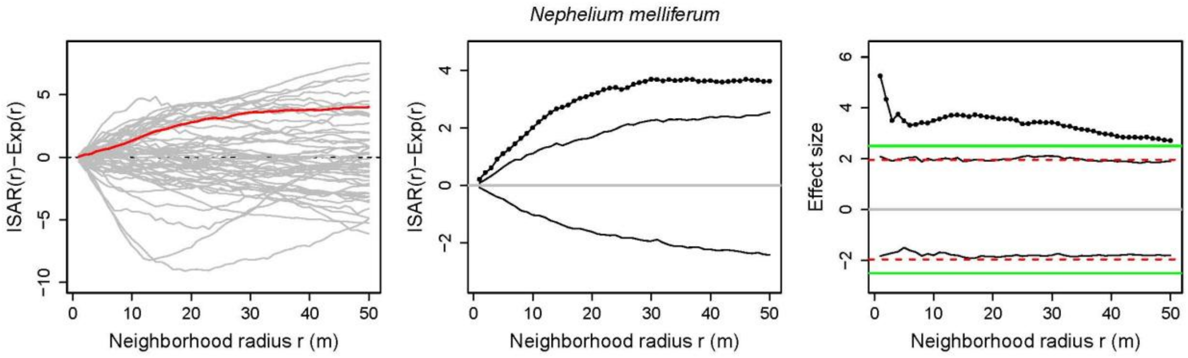
dispersers. To measure the strength of positive and negative effects of a given focal species we used the maximal positive (S_f^+) and minimal negative (S_f^-) values of its multiple-testing corrected standardized effect size $SES_f^*(r)$, taken over the 1-30m interval. We then conducted a *t*-test to compare the mean of S_{f}^+ and S_{f}^+ among species with different groups of dispersers (see also Figure S2).

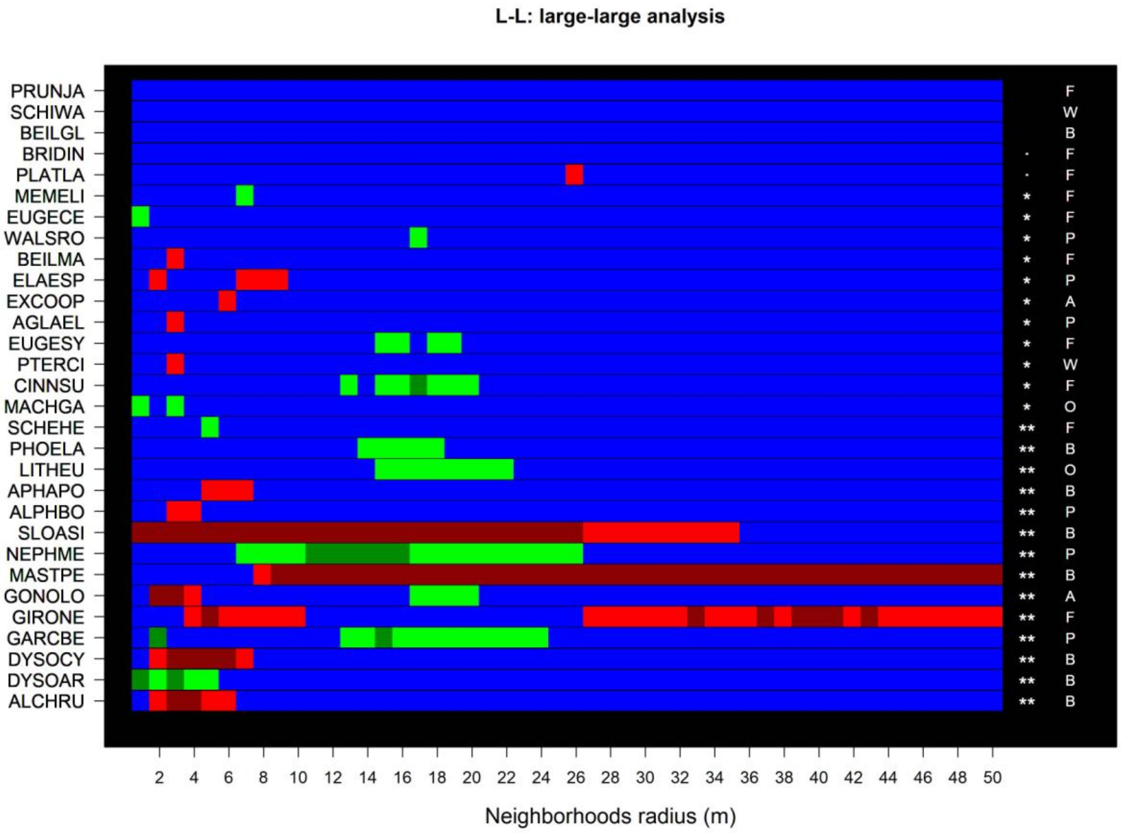
Table 1.

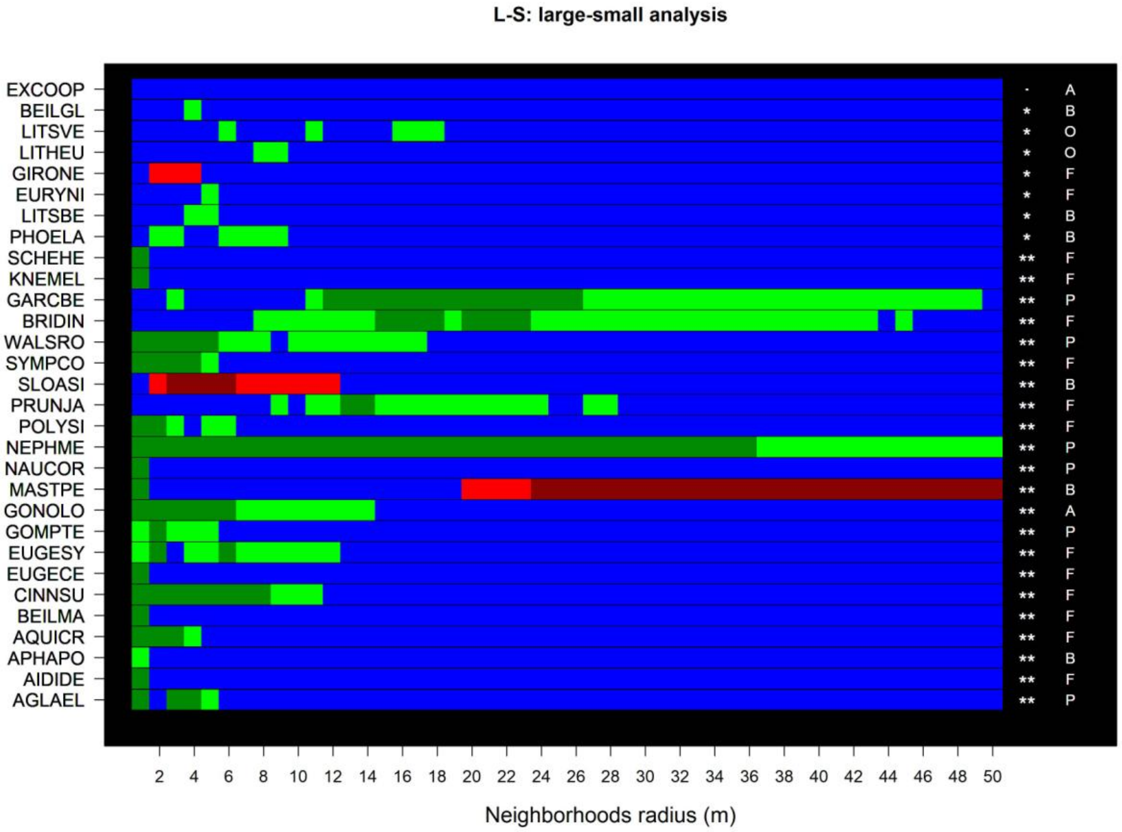
Disperser	Positive departures			Negative departures		
a) L-S analysis	Mean strength	t-value	p-value	Mean strength	t-value	p-value
Gibbon	1.39	2.40	**0.0208**	0.45	-0.81	0.4246
Non-gibbon	0.96			0.56		
Macaque	1.46	2.47	**0.0174**	0.46	-0.53	0.6004
Non-macaque	1.01			0.54		
Hornbills	1.33	1.14	0.2603	0.31	-1.87	0.0717
Non-hornbills	1.11			0.59		
Small birds	1.21	0.18	0.8599	0.55	0.35	0.7309
Others	1.18			0.50		
b) L-L analysis	Mean strength	t-value	p-value	Mean strength	t-value	p-value
Gibbon	0.77	1.15	0.2568	0.68	-1.19	0.2387
Non-gibbon	0.63			0.88		
Macaque	0.76	0.71	0.4785	0.71	-0.65	0.5212
Non-macaque	0.68			0.82		

Hornbills	0.65	-0.56	0.5813	0.91	1.20	0.2377
Non-hornbills	0.72			0.70		
Small birds	0.68	-0.37	0.7114	0.80	0.24	0.8107
Others	0.73			0.76		


Garcinia benthamii


Nephelium melliferum


L-L: large-large analysis


L-S: large-small analysis