

Stochastically driven adult–recruit associations of tree species on Barro Colorado Island

Stephan Getzin, Thorsten Wiegand and Stephen P. Hubbell

Proc. R. Soc. B 2014 **281**, 20140922, published 16 July 2014

Supplementary data

["Data Supplement"](#)

<http://rspb.royalsocietypublishing.org/content/suppl/2014/07/15/rspb.2014.0922.DC1.html>

References

[This article cites 45 articles, 4 of which can be accessed free](#)

<http://rspb.royalsocietypublishing.org/content/281/1790/20140922.full.html#ref-list-1>



This article is free to access

Subject collections

Articles on similar topics can be found in the following collections

[ecology](#) (1704 articles)

[theoretical biology](#) (96 articles)

Email alerting service

Receive free email alerts when new articles cite this article - sign up in the box at the top right-hand corner of the article or click [here](#)



Cite this article: Getzin S, Wiegand T, Hubbell SP. 2014 Stochastically driven adult–recruit associations of tree species on Barro Colorado Island. *Proc. R. Soc. B* **281**: 20140922.
<http://dx.doi.org/10.1098/rspb.2014.0922>

Received: 16 April 2014

Accepted: 19 June 2014

Subject Areas:

ecology, theoretical biology

Keywords:

Berman test, habitat association, life trait, pattern reconstruction, point pattern analysis, segregation

Author for correspondence:

Stephan Getzin

e-mail: stephan.getzin@ufz.de

Electronic supplementary material is available at <http://dx.doi.org/10.1098/rspb.2014.0922> or via <http://rsob.royalsocietypublishing.org>.

Stochastically driven adult–recruit associations of tree species on Barro Colorado Island

Stephan Getzin¹, Thorsten Wiegand¹ and Stephen P. Hubbell^{2,3}

¹Department of Ecological Modelling, Helmholtz Centre for Environmental Research—UFZ, Permoserstrasse 15, Leipzig 04318, Germany

²Department of Ecology and Evolutionary Biology, University of California, Los Angeles, CA 90095, USA

³Smithsonian Tropical Research Institute, Apartado 0843-03092, Balboa, Ancon, Republic of Panama

The spatial placement of recruits around adult conspecifics represents the accumulated outcome of several pattern-forming processes and mechanisms such as primary and secondary seed dispersal, habitat associations or Janzen–Connell effects. Studying the adult–recruit relationship should therefore allow the derivation of specific hypotheses on the processes shaping population and community dynamics. We analysed adult–recruit associations for 65 tree species taken from six censuses of the 50 ha neotropical forest plot on Barro Colorado Island (BCI), Panama. We used point pattern analysis to test, at a range of neighbourhood scales, for spatial independence between recruits and adults, to assess the strength and type of departure from independence, and its relationship with species properties. Positive associations expected to prevail due to dispersal limitation occurred only in 16% of all cases; instead a majority of species showed spatial independence ($\approx 73\%$). Independence described the placement of recruits around conspecific adults in good approximation, although we found weak and noisy signals of species properties related to seed dispersal. We hypothesize that spatial mechanisms with strong stochastic components such as animal seed dispersal overpower the pattern-forming effects of dispersal limitation, density dependence and habitat association, or that some of the pattern-forming processes cancel out each other.

1. Introduction

Plants can only move during their seed stage; once germinated, they cannot escape interactions with their biotic and abiotic neighbourhood. Understanding the spatial association between adult plants and their offspring is therefore critical to get insights on plant population and community dynamics [1]. However, the different stages from seed dispersal to the sapling stage are often difficult to study, especially in tropical forests. For example, seed limitation in tropical forests is pervasive [2], and seed arrival of most tropical tree species is sparse and patchy [3]. The template generated by primary seed dispersal is then modified by secondary seed dispersal [4], post-dispersal processes such as seed predation [5], microhabitat requirements for establishment [6] and density-dependent survival [7]. The spatial adult–offspring association, in turn, can be relatively easily studied in large plots of fully mapped forest communities [8] such as those sampled within the network of the Center for Tropical Forest Science (CTFS) [9,10]. This association constitutes the (medium-term) accumulated outcome of all processes and mechanisms from seed production at the parent tree up to the point where the offspring has reached a certain size threshold (e.g. 1 cm diameter at breast height to enter the census called in the following ‘recruits’). We therefore expect that the spatial adult–recruit association should conserve imprints of past processes and be a useful ‘ecological archive’

from which we may obtain hints on the relative importance of underlying processes and the type of population and community dynamics [8,11].

Various mechanisms have the potential to result in distinct spatial associations between adults and conspecific recruits. Our *a priori* hypothesis is that recruits should be positively associated with adults because of dispersal limitation [12,13] where seeds are dispersed in their majority close to their parents. However, even if a species shows strong dispersal limitation, the resulting adult–recruit association may be more complex because recruits (which are mostly saplings) can stay for decades below sizes of 1 cm diameter at breast height (DBH) waiting for conditions becoming favourable for growing [14]. In this case, a substantial proportion of their parents may have already died and we may rather observe association patterns of the ‘partial overlap’ type [15–17], where recruits aggregate around parents that are still alive, but recruits without living parents are locally segregated from the current adults. Similar patterns of partial overlap can also emerge under dispersal limitation if species exhibit intraspecific spatial variation in seed production. However, seed dispersal by bats, non-volant mammals, birds or wind can contribute to independent or segregated adult recruit associations. For example, the behaviour of large frugivores that defecate seeds in masses, or central-place foragers that move seeds from a wide area to nests, may cause aggregated recruit patterns [18] that are largely decoupled or spatially independent from the locations of the parent trees [8]. By contrast, wind-dispersed species may show less likely seedling clumping than animal-dispersed species [3], making spatially segregated adult–recruit patterns more probable. Another prominent mechanism that has the potential to generate positive adult–recruit associations is association of species with a certain topographic habitat feature such as slope [19,20] or soil type [21,22]. However, if particular associations with environmental covariates change from recruits to adults [20,23,24], this can generate partial overlap or segregation patterns.

Finally, although dispersal limitation [13] or shared habitat association lets us expect a close adult–recruit association, propagules falling close to fruiting adults only rarely produce saplings because species-specific predators and pathogens make the direct neighbourhood of a parent tree inhospitable for the survival of seedlings. This mechanism, known as Janzen–Connell effect [25,26], or negative plant–soil feedback mediated by soil biota [27], can counteract positive associations at smaller neighbourhood scales and may lead to independence or segregation [13]. It is clear, however, that the processes and mechanisms described above will each operate at distinct spatial scales and that an analysis of adult–recruit association therefore needs to explicitly account for spatial scale. Thus, habitat associations, seed dispersal and negative density dependence have strong potential to generate distinct scale-dependent spatial association patterns in the adult–recruit relationship.

Recent advances in spatial point pattern analysis [28,29] combined with the availability of large fully mapped plots of tropical forest [9,10] have produced an inspiring new perspective on the structure of hyperdiverse communities [15–17] and allow us to quantify adult–recruit patterns for a large number of species even in species-rich forests. This provides unique opportunities for testing whether positive adult–recruit associations do indeed prevail and for deriving hypotheses on the relative importance and the interplay of the various processes and mechanisms listed above. The spatial association

between the adult and recruit generation also has important consequences for the type of community dynamics and species coexistence. For example, strong positive spatial associations, where recruits are tightly clustered around the adult trees, yield intraspecific aggregation and interspecific segregation, which can enhance the local coexistence in plant communities by increasing the importance of intraspecific competition relative to interspecific competition [30,31].

A fundamental first task in quantifying the spatial adult–recruit association is testing for statistical independence between the spatial distribution of the recruits from that of the adults and quantifying the magnitude of departures from independence. If this null hypothesis is rejected, we can then continue to quantify the spatial association patterns in more detail [32] and relate it to species properties. However, as already noted by Lotwick & Silverman [33], implementing a null model of independence is complicated because it must break the possible spatial association between the two patterns while conserving the statistical properties of the observed univariate spatial patterns [34], such as the observed spatial autocorrelation [33].

In this study, we used techniques of spatial point pattern analysis [17,28,29] to quantify the intraspecific adult–recruit associations for more than 60 species over six censuses in the 50 ha forest dynamics plot on Barro Colorado Island (BCI), Panama. We structured our analysis into three parts. First, patterns generated by pattern reconstruction [35,36] served as null expectation to test whether recruits are spatially independent from the adults. Second, we updated the classification scheme developed by Wiegand *et al.* [17,32] to more closely characterize the magnitude and types of potential departures from independence at different neighbourhood scales around adult trees. Finally, we tested for statistical relationships between the type of adult–recruit association and species properties such as shared associations to topographic habitat variables, shade-tolerance guild or dispersal mode. We used the results of our comprehensive analysis to derive hypotheses on the relative importance of processes that determine the spatial distribution patterns of recruits and discuss the consequences of our findings for population and community dynamics.

2. Material and methods

(a) Study area

The tropical forest at BCI, Panama (9°10' N, 79°51' W) is a seasonally moist tropical forest that hosts more than 300 tree and shrub species. Rainfall averages 2600 mm yr⁻¹, with a pronounced dry season. Investigations were carried out with data from the 50 ha forest dynamics plot, which consists of mainly old-growth lowland moist forest. Elevation ranges from 120 to 155 m above mean sea level. The plot was established in 1982 and all trees with at least 1 cm DBH have been mapped, tagged and measured every 5 years since 1985. Details on the plot are provided by Condit [9] and Losos & Leigh [10].

We used the data from the six 1982, 1985–2010 census combinations [37]. We included all living trees, but excluded shrub and liana species, and divided them into the two non-overlapping life stages recruits and adult trees. Adults were defined based on a species-specific DBH threshold for reproductive size provided by Hubbell *et al.* [37], and recruits were all trees that entered the census for the first time (i.e. crossed the 1 cm DBH threshold during the last 5 years). To compare the patterns of recruits with those of their potential parent trees, we used the

adult trees from the previous census. To obtain sufficient sample sizes, we restricted our analysis for a given census to species that had at least 50 adults and at least 50 recruits. We obtained for the different census periods datasets for 40–53 different species, representing a total of 65 species.

(b) Testing for independence between adults and recruits (analysis 1)

To detect potential association patterns in the placement of recruits around adult trees, we used the null model of independence [29]. Because the adults are antecedent to the recruits, we keep the adult locations fixed but randomize the locations of the recruits. To conserve the spatial autocorrelation structure [33,34] in the independence test, we used non-parametric techniques of pattern reconstruction to create stochastic replicates of the observed recruit patterns that are used in the null model [29,35,36]. Pattern reconstruction uses optimization techniques (for details, see the electronic supplementary material, appendix A) to reconstruct a point pattern based on the information provided by several summary statistics calculated from the observed pattern [36,38]. The spatial structure of the reconstructed patterns very closely matches that of the observed patterns.

To evaluate departures between the observed data and the stochastic realizations of the null model, we need summary statistics that are able to quantify the observed and simulated spatial patterns. Illian *et al.* [39] and Wiegand *et al.* [36] recommend using several summary statistics of different nature to test for potential departures from a null model. This is especially important for ‘real-world’ patterns, which often show aspects of heterogeneity (see below). Here, we use the bivariate K -function $K_{12}(r)$ and the bivariate distribution function of the nearest-neighbour distances $D_{12}(r)$ [39] for this purpose. The $K_{12}(r)$ can be defined as the mean number of recruits within neighbourhoods with radius r around the adult trees divided by the mean density λ_2 of recruits in the plot, but in analysis 1 we used the transformation $L_{12}(r) = (K_{12}(r)/\pi)^{0.5} - r$ to stabilize the variance [33]. The $D_{12}(r)$ gives the proportion of adult trees that have at least one recruit within distance r .

We estimated simulation envelopes from 199 simulations of the independence null model. A departure from the null model at a given neighbourhood distance r around adult trees was indicated if a given summary statistic of the observed data (i.e. $D_{12}(r)$ or $K_{12}(r)$) was outside the simulation envelopes being the fifth lowest and highest values of the summary statistic estimated from the simulations of the null model. However, because the simulation envelope test is prone to type I error inflation, we used a goodness-of-fit test (GoF) [40] to determine the overall fit of the null model over the distance interval 1–250 m. Significant departure occurred if the GoF was significant with a 2.5% error rate for at least one of the two summary statistics (in the ‘worst’ case of independence of the two summary statistics this yields a joint error rate of $\approx 5\%$).

(c) The type of the adult–recruit association pattern (analysis 2)

The GoF test provides only a binary assessment of the spatial adult–recruit association and does not convey information on the magnitude of effects and the type of departures. The goals of this analysis were therefore to determine how the recruits (pattern 2) of a given species were distributed within neighbourhoods of con-specific adults (pattern 1), and how strongly they departed from independence. In case of homogeneous patterns (i.e. the spatial configuration of recruits around adults is the same all over the plot and only subject to stochastic fluctuation, which follows the same laws within the entire plot [39]), we would have only

two possible types of departure attraction and segregation, and departures in $D_{12}(r)$ and $K_{12}(r)$ would be highly correlated. However, the spatial configuration of recruits around adults may show high variability and spatial trends. For example, some adults may have many neighbouring recruits but others very few. In this case, $D_{12}(r)$ and $K_{12}(r)$ will show contrasting results [29,32]. We therefore updated the classification scheme developed by Wiegand *et al.* [32] and used the standardized effect sizes of $D_{12}(r)$ and $K_{12}(r)$ to classify the type and strength of departures from independence

$$\left. \begin{aligned} P(r) &= \frac{(D_{12}(r) - E[D_{12}(r)])}{SD[D_{12}(r)]} \\ \text{and } M(r) &= \frac{(K_{12}(r) - E[K_{12}(r)])}{SD[K_{12}(r)]}, \end{aligned} \right\} \quad (2.1)$$

where the operators $E[\cdot]$ and $SD[\cdot]$ indicate the expectation and standard deviation of the summary statistic at neighbourhood r under independence, respectively.

The location of each species within the two-dimensional classification space (figure 1a,b) conveys information on the significance and strength of the adult–recruit relationship. Because the distribution of $P(r)$ and $M(r)$ is approximately the standard normal distribution, the box delimited by values of $-2.33, 2.33$ (which correspond to a p -value of 0.025 for two summary statistics individually) approximates the area where the null hypothesis cannot be rejected, and a given species departs more strongly from independence the farther away it is located from the box. However, the quadrant of the scheme where the species is located provides additional information on the type of departure. In addition to independence, four other types of spatial association patterns are possible for each neighbourhood r [32]:

- **Type 0: ‘independence’**: neither $K_{12}(r)$ nor $D_{12}(r)$ show significant departures from independence (figure 1f).
- **Type I: ‘segregation’**: recruits occur consistently less within neighbourhoods with radius r around adult trees than expected under independence ($M(r) < 0, P(r) < 0$; figure 1d).
- **Type II: ‘partial overlap’**: recruits occur on average more often within the neighbourhoods of adult trees than expected [$M(r) \geq 0$], but a notable proportion of adult trees have less nearest recruit neighbours than expected ($P(r) < 0$; figure 1c). This type occurs only for heterogeneous patterns.
- **Type III: ‘mixing’**: recruits occur consistently more often within the neighbourhood of adult trees than expected ($M(r) \geq 0, P(r) \geq 0$; figure 1e).
- **Type IV**: This association type corresponds to ($M(r) < 0, P(r) \geq 0$) and is predicted to occur only rarely [32] (if adult trees are highly clustered and few recruits are close to the adult clusters).

To explore how the proportion of these association types changed with the neighbourhood r around the adult trees, we used all species for which the GoF test indicated significant departures from independence, and counted for each association type and neighbourhood radius r the number of cases where the observed value of the summary statistic was located outside the simulation envelopes [17]. All other cases were added to the independence type.

(d) Relationships between association type and species properties (analysis 3)

In case that analysis 1 indicated departures from independence, we were interested to find hints on potentially underlying mechanisms to facilitate formulation of hypotheses. An obvious hypothesis for positive associations (i.e. mixing or partial overlap) is shared habitat association. Several methods exist to test for this, with the most popular being a torus translation test

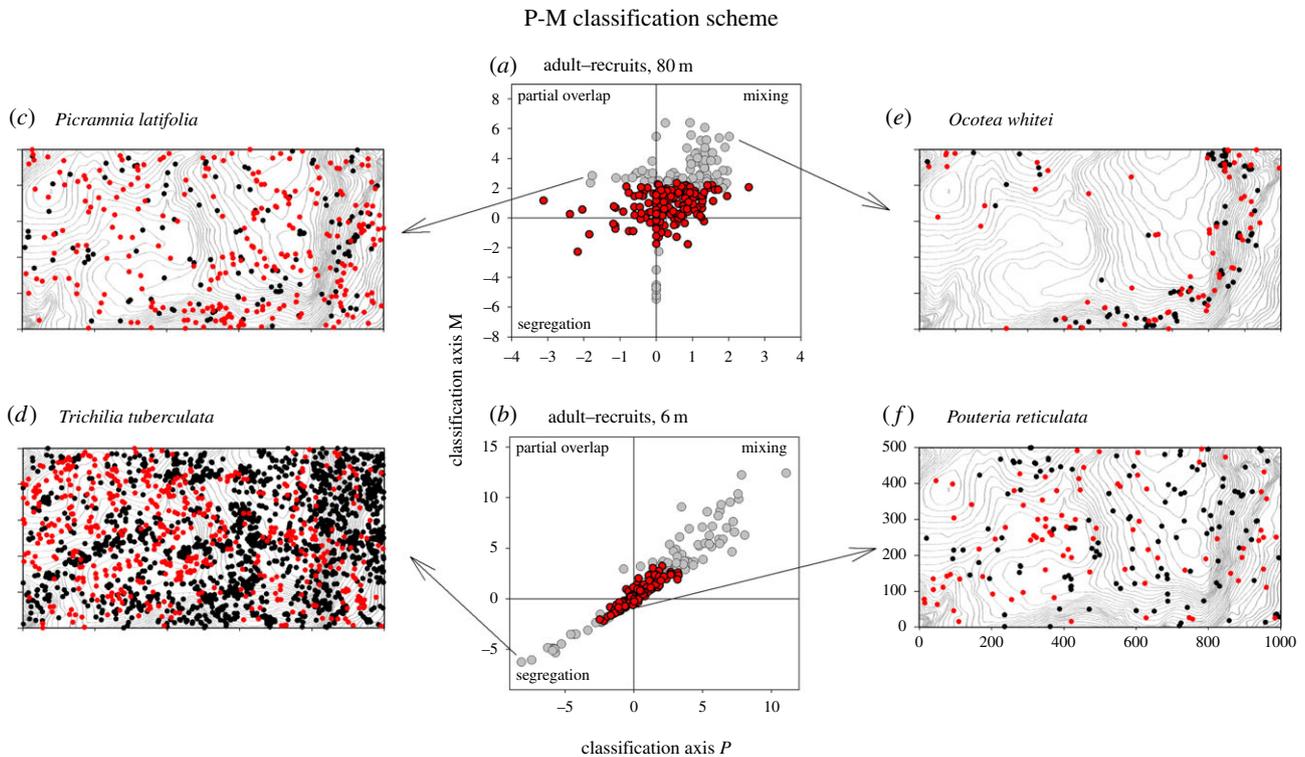


Figure 1. Classification of adult–recruit associations at the 1000 m × 500 m BCI forest dynamics plot. (a) Allocation of the adult–recruit associations of all analysed species for all six censuses and a large-scale neighbourhood radius of $r = 80$ m (significant cases: grey circles; non-significant cases: red circles). (b) The same as (a) but for a small-scale neighbourhood of $r = 6$ m. Axis P is positive (negative) if there are on average more (fewer) recruits at the scale r from adults than expected, and axis M is positive (negative) if the probability that an adult has its nearest recruit neighbour within distance r is larger (smaller) than expected. (c) Example for partial overlap at large scale (red circles, adults; black circles, recruits) of the species *Picramnia latifolia*. (d) Example for small-scale segregation of the species *Trichilia tuberculata*. (e) The large-scale mixing of *Ocotea whitei* reflects their consistent habitat association to covariates such as slope and TWI. (f) Example of a species whose adult–recruit association cannot be distinguished from independence at small scales. The grey contour lines in the back of the four maps show the elevation of the BCI plot.

[19] where associations of a species pattern with *a priori* defined discrete habitat types is investigated. However, we used here the Berman test [41], which tests association to continuous topographic habitat variables. Topographic variables are considered good surrogates for unavailable more direct environmental variables and were successful in detecting species assemblages at the BCI forest that agreed [20] with previous assumptions [19]. We used here the six spatial covariates of Kanagaraj *et al.* [20]: elevation (Elv), slope (S), aspect (Asp), convexity (Con), topographical wetness index (TWI) and vertical distance to streams (VDS) at a spatial resolution of 5 m × 5 m quadrats.

We used the Berman test [41] to test for spatial independence of the recruit and adult pattern of the 65 species from the six (continuous) topographic covariates. The Berman test is based on the mean S_{obs} of the covariate values $v(x_i)$ at the locations x_i of the trees of a given pattern, which are then compared with the corresponding S_{sim} values obtained from repeated simulations of a suitable null model. Significant departures from the null model are assessed by the test statistic $Z_1 = (S_{\text{obs}} - \mu) / \sigma$, where μ is the mean value of S_{sim} under the null model and σ^2 the corresponding variance [41]. The null distribution of this test statistic is approximately the standard normal distribution. To consider the spatial autocorrelation (clustering) of the recruit and adult patterns [41], we used the null model of pattern reconstruction as applied in analysis 1 (for details, see the electronic supplementary material, appendix B).

To test whether the five association types were statistically related with species properties, we used a permutation test proposed by Hothorn *et al.* [42]. We conducted the permutation test separately for small (i.e. 2–10 m) and large neighbourhoods (60–100 m). We selected these distances because they represent neighbourhoods where deviations from independence were most interesting

(i.e. segregation peaked at smallest scales while mixing peaked between 60 and 100 m; cf. figure 2) and because they reflect contrasting scales of direct tree–tree interaction effects at small and influences from habitat at large scales. The permutation test reveals whether the association type depended statistically on the individual categories of the life traits ‘shade-tolerance guild’ and ‘dispersal agent’ (for details, see the electronic supplementary material, appendix C, and tables C1 and C2).

We approximated the null distribution of independence of association between the categorical data based on Monte Carlo re-sampling techniques with 10 000 permutations to assess H_0 at $\alpha = 0.05$, and determined the *maxT*-statistic and the associated *p*-value [42]. Finally, we also present a standardized linear statistic that can be interpreted similarly to Pearson residuals for the independence hypothesis [42]. In this standardized contingency table, large positive or negative values highlight deviation from independence in favour of a positive or negative association between both variables, respectively. The permutation tests were executed with the R software package *coin* [42], whereas the spatial pattern analysis was done with the software PROGRAMITA [29] (which can be accessed at www.Programita.org).

3. Results

(a) Testing for independence between adults and recruits (analysis 1)

The GoF test over the 1–250 m distance interval revealed that the proportion of species with independent adult–recruit association made up 71.4%, 54.7%, 70.0%, 61.0%, 69.8% and

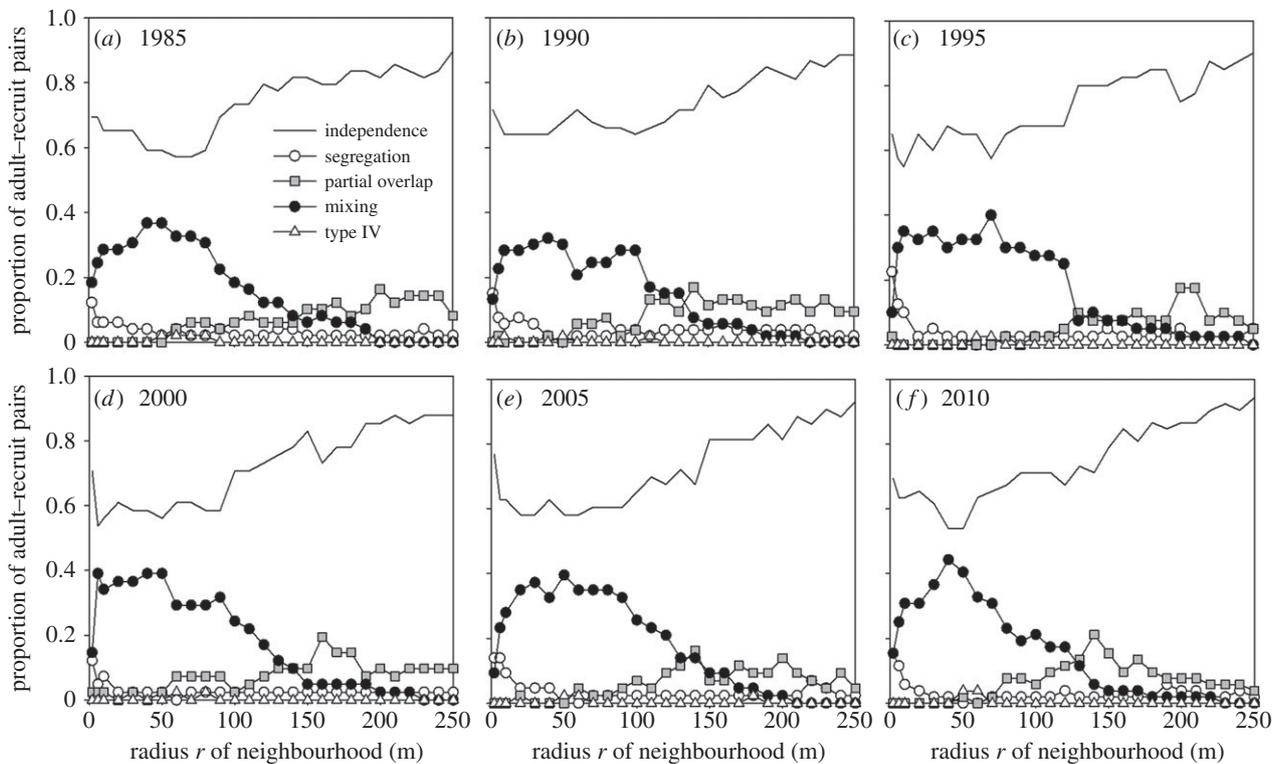


Figure 2. (a–f) Spatial pattern analysis of adult–recruit associations and their scale-dependent changes. The most common type was ‘independence’ between adults and recruits, followed by ‘mixing’, ‘partial overlap’ and ‘segregation’.

71.2% of the adult–recruit pairs in the 1985–2010 censuses, respectively (66.4% for all censuses combined). However, if we consider the proportion of independence for individual neighbourhood radii (i.e. cases where the species had a non-significant GoF test, or both summary statistics were inside the simulation envelope at neighbourhood r), adult–recruit pairs showed a peak of independence at the smallest neighbourhood (2 m) and a steady increase towards larger scales from approximately 100 m onwards (figure 2). Averaged over all spatial scales 1–250 m and summarized for all six censuses, independence was the most common type, which accounted on average for 73.2% of all cases.

Independence between recruits and adults was little affected by temporal variation in maturation or senescence of the potential parent cohort. GoF tests for independence of recruits of the 2010 census and adults of the six earlier censuses revealed independence for 63.3–73.3% of the adult–recruit pairs (see the electronic supplementary material, appendix D and figure D1).

(b) The type of the adult–recruit association pattern (analysis 2)

Averaged over all 1–250 m neighbourhoods, and summarized for all six censuses, ‘mixing’ and ‘partial overlap’ were, with 16.4% and 6.5%, the second and third most common association types, respectively. Mixing mostly dominated the significant deviations from independence at the first 130 m, having its peak at large scales between 60 and 100 m (figure 2). ‘Segregation’ occurred on average only in 3.6% of all cases. The plots of the P – M scheme showed that although there are a few outlier species, most of the species fall within or close to expectation under independence (figure 1a,b).

(c) Relationships between association type and species properties (analysis 3)

Analysis with the Berman test revealed that the dependency of the species distribution patterns on topographic covariates was relatively weak (electronic supplementary material, figure E1 and appendix E). We also found that shared habitat association of adults and recruits occurred at small neighbourhoods (2, 6 and 10 m) for 23–46% (average 36.6%) of the species that showed mixing (electronic supplementary material, appendix E). The same analysis was also done for large neighbourhoods where mixing peaked (60, 80 and 100 m; figure 2). We found in 27–57% (average 44.3%) of the cases consistent association of adults and recruits to the topographic covariates may have caused the mixing at large scales (electronic supplementary material, appendix E). Thus, even though topography had stronger effects on the positive association type, it contributed to adult–recruit mixing in fewer than half of the cases.

The permutation test suggested relationships between life-history strategies and the spatial association pattern of recruits around adults. According to the large positive values of the contingency table, shade-tolerant species (S) tended to show at small scales only segregation but no mixing or partial overlap, whereas gap species (G) tended to show no segregation but partial overlap and mixing (table 1a). At larger scales, shade-tolerant species tended to show also segregation but no independence (table 1a). Individual dispersal agents showed mostly weak or inconsistent relationships with spatial association types (electronic supplementary material, appendix C and table C2). However, the permutation tests for a single category (comprising bats, birds and mammals) revealed at small scales the highly significant result that animal-dispersed species are positively related to independence, species with explosive seed dispersal to mixing (but

Table 1. Results of the permutation tests of independence between life-history strategies and spatial patterns at small- (2–10 m) and large-scale (60–100 m) distance intervals. $p < 0.05$ indicates that the four types of adult–recruit association depend on the life-history strategies. Large positive or negative values in the standardized contingency table highlight deviation from independence in favour of a positive or negative association between spatial patterns and the individual categories of the life traits (left column): light demanding gap specialist (G), intermediate (I) and shade-tolerant (S) species, animal, explosive (Exp) and wind-dispersed species. For details, see Results section and electronic supplementary material, appendix C.

	independence	segregation	partial overlap	mixing	independence	segregation	partial overlap	mixing
(a)	shade-tolerance guild: small scale				shade-tolerance guild: large scale			
G	0.01	−3.32	1.52	1.53	1.72	−1.73	−0.94	−0.84
I	0.82	−0.53	−0.67	−0.52	2.33	−1.22	−1.34	−1.47
S	−0.54	3.17	−0.85	−0.96	−2.97	2.26	1.67	1.67
	$maxT = 3.3239, p = 0.0156$				$maxT = 2.9715, p = 0.035$			
(b)	dispersal agent: small scale				dispersal agent: large scale			
animal	5.88	−7.13	−1.45	−1.20	−2.99	0.96	1.52	2.16
Exp	−4.36	−1.48	2.75	5.51	0.11	−0.60	−0.95	0.52
wind	−3.93	10.32	−0.41	−2.99	3.76	−0.73	−1.16	−3.21
	$maxT = 10.3226, p < 2.2 \times 10^{-6}$				$maxT = 3.7559, p = 0.0068$			

not independence) and wind-dispersed species to segregation (table 1b). At large scales, effects were relatively weak.

4. Discussion

In this study, we conducted a comprehensive analysis of the spatial association of newly recruited saplings at the BCI forest relative to their potential parents. We found that the spatial pattern of recruits was in approximately three-quarters of the cases independent from the adult trees, but showed in 16% of the cases the expected positive associations, in 7% partial overlap, and only in 4% segregation. The remarkable prevalence of independence between recruit and adult patterns can mean that (i) there is real independence, (ii) stochastic effects overpower a potential biological signal in the data or (iii) the test is not sensitive enough. We reduced the risk of (iii) by using the pattern reconstruction implementation of independence and by using two summary statistics simultaneously. Option (i) is in contrast to expectations from many of the distance-dependent processes that are known to operate in tropical forests and have a strong potential to create smaller-scale (i.e. less than 50 m) association patterns during the transition from seeds to recruits. We expected that dispersal limitation [2,13], one of the cornerstones of neutral theory [43], should result for most species in smaller-scale positive associations where recruits are clustered around adults. Additionally, shared or opposed habitat association should result in positive or negative small- or larger-scale association, respectively, and Janzen–Connell effects should result in smaller-scale segregation between recruits and adults [5,19,23].

Our first analysis revealed that an overwhelming majority of species showed independence between adults and recruits. We therefore could not expect to find in our subsequent analyses strong relationships between association types and species properties. Although shared habitat association of recruit and adult trees is a candidate mechanism for creating positive ‘mixing’ association, we found that fewer than half of the species with mixing showed consistent associations to topographic habitat variables for both adults and recruits.

Additionally, we confirmed earlier studies showing that habitat preference changed often between different life stages within the same species so that over time recruits or adults lost or attained habitat dependency [20,23]. The particularly strong fluctuations in habitat association of the recruit communities over the six censuses (electronic supplementary material, figure E1a) suggest that potential habitat associations were strongly masked by unpredictable chance events in dispersal (i.e. stochasticity; option (ii)). In contrast to a recent study by Baldeck *et al.* [44] that was based on the proportion of community compositional variation in fixed scale 20 m × 20 m subplots, the significances of the habitat associations in our study were little dependent on sample size (see the electronic supplementary material, appendix E and table E).

The hypothesis on the strong stochastic component of dispersal (option (ii)) is supported by our permutation test (table 1), which showed that animal-dispersed species tended to show independence. Most of the 65 study species are dispersed by animals, but BCI hosts 24 species of non-volant mammals, 20 species of bats and 86 species of birds that may jointly disperse seeds of one and the same species [3]. While individual dispersal agents show (rather weak) relationships with spatial association types (see the electronic supplementary material, appendix C and table C2), the joint outcome of differences in spatial movement behaviour of these taxa has the potential to create strong stochasticity in the resulting dispersal patterns that diffuses deterministic adult–recruit associations. While some of this stochasticity may be reduced by more detailed data and more refined models of disperser behaviour, a substantial proportion of variability will remain due to the inherent stochasticity of the complex dispersal process [45,46], similar to long-term weather forecasts. We hypothesize that this complexity is a major cause of the surprising dominance of independent associations between adults and recruits on BCI.

An alternative explanation for the high incidence of independence found here is that some of the pattern-forming processes cancel out each other (i.e. option (i)). For example, highly aggregated seed distributions typical of dispersal kernels [3,47] may be removed by Janzen–Connell effects or more general density-dependent mortality. This is in

accordance with recent findings by Terborgh *et al.* [13] and others [48] that showed that undispersed seeds (i.e. seeds that fell beneath the crown of conspecific fruiting adults) contribute little or nothing to sapling recruitment and that newly recruited saplings occurred at locations independent from that of reproductive conspecifics. Another explanation for the high incidence of independence would be that recruits emerged only decades after seed dispersal and that most of their parents had already died. However, we could reject this hypothesis at least for a 30-year interval when comparing the recruits of the last census with the adults of all earlier censuses (see the electronic supplementary material, appendix D and figure D1). Clearly, independence could also be a result of lack of analytical power of our method (option (iii)) because the datasets for some very few species are based on 50 adults and 50 recruits. However, we found that significant adult–recruit associations did not primarily depend on the sample sizes, although significant effects tended to be slightly more frequent for larger sample sizes at the smallest neighbourhood of $r = 2$ m (see the electronic supplementary material, appendix F and table F4). Additionally, the BCI plot provides already an incredibly large dataset for our analysis and if we cannot statistically detect more significant effects in this dataset, we have to conclude from a practical standpoint that stochastic effects overpower deterministic effects at the BCI forest, if the latter were present to a large extent (i.e. option (ii)). This is our main hypothesis for the observed lack of spatial dependence between recruits and adults. As outlined above, the highly stochastic animal dispersal process is a promising candidate mechanism for overpowering deterministic spatial structure. The high incidence of statistically independent adult–recruit associations is an intriguing result that requires an explanation, but we have to leave the more detailed search for the underlying mechanisms to further studies. The question of whether strong pattern-forming processes and mechanisms cancel out each other or are overpowered by stochastic processes has important implications for our understanding of the dynamics of species-rich forests.

5. Conclusion

We found that the outcome of the multiple and complex processes that determine the location and survival of recruits resulted in the majority of cases in spatial independence between recruits and their potential parents, and that habitat and species traits left in relatively few cases a detectable signal of non-independence. What are the consequences of our findings for long-term dynamics and coexistence in diverse

tropical forests? Overall, it is interesting to see that the cumulative outcome of several directed processes results in associations that mostly cannot be distinguished statistically from independence. That means that the recruit community is in space largely decoupled from the adult community. Although it may be tempting to interpret the independent adult–recruit relationship in favour of neutral theory, such a conclusion is premature because neutral theory does not explicitly consider a recruit community [43] and therefore cannot be directly compared with our analysis.

The finding that the recruit community is spatially decoupled from the adult community means that the forest will remain diverse in the long term because the next adult generation is likely to be placed at somewhat different locations than the current one. This is a mechanism that avoids high local densities of particular species and therefore acts, similarly to Janzen–Connell effects, as a stabilizing mechanism [49]. Independent placement of offspring relative to the parents may prevent species from developing, over evolutionary time, distinctive life-history strategies, because at the end stochasticity determines the final survival location [50]. Indeed, most species on BCI have not extreme but intermediate light requirements and lifestyles [51].

Our results suggest several avenues for future work. Repeating the analyses for forests where animal seed dispersal is less important or where dispersers went extinct [52] would enable researchers to test the hypothesis of stochastic animal dispersal, and it would be important to include forests that show a larger degree of environmental heterogeneity than the BCI plot. Finally, conducting analyses for forests with different species richness can show whether prevalence of independence is related to species richness (i.e. the dilution hypothesis [17,53]). Assessing what is different in forests with different prevalence in spatial patterns should allow us to reach a broader understanding of the relative importance of processes for the adult–recruit relationship and forest dynamics.

Acknowledgement. We thank Torsten Hothorn for advice on the permutation tests and two anonymous reviewers for critical comments on the manuscript.

Funding statement. The BCI forest dynamics research project was made possible by National Science Foundation grants to S.P.H., support from the Center for Tropical Forest Science, the Smithsonian Tropical Research Institute, the John D. and Catherine T. MacArthur Foundation, the Mellon Foundation, the Celera Foundation and numerous private individuals, and through the hard work of over 100 people from 10 countries over the past decades. The plot project is part of the Center for Tropical Forest Science, a global network of large-scale demographic tree plots. S.G. and T.W. were supported by ERC advanced grant no. 233066 to T.W.

References

1. Condit R, Hubbell SP, Foster RB. 1992 Recruitment near conspecific adults and the maintenance of tree and shrub diversity in a neotropical forest. *Am. Nat.* **140**, 261–286. (doi:10.1086/285412)
2. Hubbell SP, Foster RB, O'Brien ST, Harms KE, Condit R, Wechsler B, Wright SJ, de Lao SL. 1999 Light-gap disturbances, recruitment limitation, and tree diversity in a neotropical forest. *Science* **283**, 554–557. (doi:10.1126/science.283.5401.554)
3. Muller-Landau HC, Wright SJ, Calderon O, Condit R, Hubbell SP. 2008 Interspecific variation in primary seed dispersal in a tropical forest. *J. Ecol.* **96**, 653–667. (doi:10.1111/j.1365-2745.2008.01399.x)
4. Jansen PA, Bongers F, Hemerik L. 2004 Seed mass and mast seeding enhance dispersal by a neotropical scatter-hoarding rodent. *Ecol. Monogr.* **74**, 569–589. (doi:10.1890/03-4042)
5. Beckman NG, Neuhauser C, Muller-Landau HC. 2012 The interacting effects of clumped seed dispersal and distance- and density-dependent mortality on seedling recruitment patterns. *J. Ecol.* **100**, 862–873. (doi:10.1111/j.1365-2745.2012.01978.x)
6. Svenning JC. 1999 Microhabitat specialization in a species-rich palm community in Amazonian Ecuador. *J. Ecol.* **87**, 55–65. (doi:10.1046/j.1365-2745.1999.00329.x)

7. Harms KE, Wright SJ, Calderon O, Hernandez A, Herre EA. 2000 Pervasive density-dependent recruitment enhances seedling diversity in a tropical forest. *Nature* **404**, 493–495. (doi:10.1038/35006630)
8. Wiegand T, Martinez I, Huth A. 2009 Recruitment in tropical tree species: revealing complex spatial patterns. *Am. Nat.* **174**, E106–E140. (doi:10.1086/605368)
9. Condit R. 1998 *Tropical forest census plots: methods and results from Barro Colorado Island, Panama, and a comparison with other plots*, p. 211. Berlin, Germany: Springer.
10. Losos EC, Leigh EG. 2004 *Tropical forest diversity and dynamism: findings from a large-scale plot network*, p. 645. Chicago, IL: University of Chicago Press.
11. McIntire EJB, Fajardo A. 2009 Beyond description: the active and effective way to infer processes from spatial patterns. *Ecology* **90**, 46–56. (doi:10.1890/07-2096.1)
12. Plotkin JB, Chave JM, Ashton PS. 2002 Cluster analysis of spatial patterns in Malaysian tree species. *Am. Nat.* **160**, 629–644. (doi:10.1086/342823)
13. Terborgh J, Alvarez-Loayza P, Dexter K, Cornejo F, Carrasco C. 2011 Decomposing dispersal limitation: limits on fecundity or seed distribution? *J. Ecol.* **99**, 935–944. (doi:10.1111/j.1365-2745.2011.01836.x)
14. Montgomery RA, Chazdon RL. 2002 Light gradient partitioning by tropical tree seedlings in the absence of canopy gaps. *Oecologia* **131**, 165–174. (doi:10.1007/s00442-002-0872-1)
15. Bagchi R *et al.* 2011 Spatial patterns reveal negative density dependence and habitat associations in tropical trees. *Ecology* **92**, 1723–1729. (doi:10.1890/11-0335.1)
16. Detto M, Muller-Landau HC. 2013 Fitting ecological process models to spatial patterns using scalewise variances and moment equations. *Am. Nat.* **181**, E68–E82. (doi:10.1086/669678)
17. Wiegand T, Huth A, Getzin S, Wang XG, Hao ZQ, Gunatilleke CVS, Gunatilleke IAUN. 2012 Testing the independent species' arrangement assertion made by theories of stochastic geometry of biodiversity. *Proc. R. Soc. B* **279**, 3312–3320. (doi:10.1098/rspb.2012.0376)
18. Passos L, Oliveira PS. 2002 Ants affect the distribution and performance of seedlings of *Clusia criuva*, a primarily bird-dispersed rain forest tree. *J. Ecol.* **90**, 517–528. (doi:10.1046/j.1365-2745.2002.00687.x)
19. Harms KE, Condit R, Hubbell SP, Foster RB. 2001 Habitat associations of trees and shrubs in a 50-ha neotropical forest plot. *J. Ecol.* **89**, 947–959. (doi:10.1046/j.0022-0477.2001.00615.x)
20. Kanagaraj R, Wiegand T, Comita LS, Huth A. 2011 Tropical tree species assemblages in topographical habitats change in time and with life stage. *J. Ecol.* **99**, 1441–1452. (doi:10.1111/j.1365-2745.2011.01878.x)
21. Zhang LW, Mi XC, Shao HB, Ma KP. 2011 Strong plant-soil associations in a heterogeneous subtropical broad-leaved forest. *Plant Soil* **347**, 211–220. (doi:10.1007/s11104-011-0839-2)
22. John R *et al.* 2007 Soil nutrients influence spatial distributions of tropical tree species. *Proc. Natl Acad. Sci. USA* **104**, 864–869. (doi:10.1073/pnas.0604666104)
23. Comita LS, Condit R, Hubbell SP. 2007 Developmental changes in habitat associations of tropical trees. *J. Ecol.* **95**, 482–492. (doi:10.1111/j.1365-2745.2007.01229.x)
24. Lai JS, Mi XC, Ren HB, Ma KP. 2009 Species-habitat associations change in a subtropical forest of China. *J. Veg. Sci.* **20**, 415–423. (doi:10.1111/j.1654-1103.2009.01065.x)
25. Connell JH. 1971 On the role of natural enemies in preventing competitive exclusion in some marine animals and in rain forest trees. In *Dynamics of populations* (eds PJ den Boer, GR Gradwell), pp. 298–312. Wageningen, The Netherlands: PUDOC.
26. Janzen DH. 1970 Herbivores and the number of tree species in tropical forests. *Am. Nat.* **104**, 501–528. (doi:10.1086/282687)
27. Mangan SA, Schnitzer SA, Herre EA, Mack KML, Valencia MC, Sanchez EI, Bever JD. 2010 Negative plant–soil feedback predicts tree-species relative abundance in a tropical forest. *Nature* **466**, U752–U710. (doi:10.1038/nature09273)
28. Perry GLW, Miller BP, Enright NJ. 2006 A comparison of methods for the statistical analysis of spatial point patterns in plant ecology. *Plant Ecol.* **187**, 59–82. (doi:10.1007/s11258-006-9133-4)
29. Wiegand T, Moloney KA. 2014 *A handbook of spatial point pattern analysis in ecology*. New York, NY: Chapman and Hall/CRC.
30. Stoll P, Prati D. 2001 Intraspecific aggregation alters competitive interactions in experimental plant communities. *Ecology* **82**, 319–327. (doi:10.1890/0012-9658(2001)082[0319:IAACII]2.0.CO;2)
31. Raventos J, Wiegand T, De Luis M. 2010 Evidence for the spatial segregation hypothesis: a test with nine-year survivorship data in a Mediterranean shrubland. *Ecology* **91**, 2110–2120. (doi:10.1890/09-0385.1)
32. Wiegand T, Gunatilleke S, Gunatilleke N. 2007 Species associations in a heterogeneous Sri Lankan dipterocarp forest. *Am. Nat.* **170**, E77–E95. (doi:10.1086/521240)
33. Lotwick HW, Silverman BW. 1982 Methods for analyzing spatial processes of several types of points. *J. R. Stat. Soc. B Met.* **44**, 406–413.
34. Dixon P. 2002 Ripley's K-function. In *Encyclopedia of environmetrics* (eds AH El-Shaarawi, WW Piergorsch), pp. 1796–1803. New York, NY: John Wiley and Sons Ltd.
35. Jacquemyn H, Brys R, Honnay O, Roldan-Ruiz I, Lievens B, Wiegand T. 2012 Nonrandom spatial structuring of orchids in a hybrid zone of three *Orchis* species. *New Phytol.* **193**, 454–464. (doi:10.1111/j.1469-8137.2011.03913.x)
36. Wiegand T, He FL, Hubbell SP. 2013 A systematic comparison of summary characteristics for quantifying point patterns in ecology. *Ecography* **36**, 92–103. (doi:10.1111/j.1600-0587.2012.07361.x)
37. Hubbell SP, Condit R, Foster RB. 2005 Barro Colorado Forest census plot data. See <http://ctfs.amarb.harvard.edu/webatlas/datasets/bci/>.
38. Tscheschel A, Stoyan D. 2006 Statistical reconstruction of random point patterns. *Comput. Stat. Data Anal.* **51**, 859–871. (doi:10.1016/j.csda.2005.09.007)
39. Illian J, Penttinen A, Stoyan H, Stoyan D. 2008 *Statistical analysis and modelling of spatial point patterns*, p. 534. Chichester, UK: John Wiley.
40. Loosmore NB, Ford ED. 2006 Statistical inference using the G or K point pattern spatial statistics. *Ecology* **87**, 1925–1931. (doi:10.1890/0012-9658(2006)87[1925:Siutgo]2.0.Co;2)
41. Berman M. 1986 Testing for spatial association between a point process and another stochastic process. *Appl. Stat.* **35**, 54–62. (doi:10.2307/2347865)
42. Hothorn T, Hornik K, Van de Wiel MA, Zeileis A. 2006 A Lego system for conditional inference. *Am. Stat.* **60**, 257–263. (doi:10.1198/000313006X118430)
43. Hubbell SP. 2001 *The unified neutral theory of biodiversity and biogeography*, p. 375. Princeton, NJ: Princeton University Press.
44. Baldeck CA *et al.* 2013 Habitat filtering across tree life stages in tropical forest communities. *Proc. R. Soc. B* **280**, 20130548. (doi:10.1098/rspb.2013.0548)
45. Edwards KF, Stachowicz JJ. 2011 Spatially stochastic settlement and the coexistence of benthic marine animals. *Ecology* **92**, 1094–1103. (doi:10.1890/i0012-9658-92-5-1094)
46. Russo SE, Portnoy S, Augspurger CK. 2006 Incorporating animal behavior into seed dispersal models: implications for seed shadows. *Ecology* **87**, 3160–3174. (doi:10.1890/0012-9658(2006)87[3160:labisd]2.0.Co;2)
47. Clark CJ, Poulsen JR, Bolker BM, Connor EF, Parker VT. 2005 Comparative seed shadows of bird-, monkey-, and wind-dispersed trees. *Ecology* **86**, 2684–2694. (doi:10.1890/04-1325)
48. Hardesty BD, Hubbell SP, Bermingham E. 2006 Genetic evidence of frequent long-distance recruitment in a vertebrate-dispersed tree. *Ecol. Lett.* **9**, 516–525. (doi:10.1111/j.1461-0248.2006.00897.x)
49. Chesson P. 2000 Mechanisms of maintenance of species diversity. *Annu. Rev. Ecol. Syst.* **31**, 343. (doi:10.1146/annurev.ecolsys.31.1.343)
50. Hubbell SP. 2006 Neutral theory and the evolution of ecological equivalence. *Ecology* **87**, 1387–1398. (doi:10.1890/0012-9658(2006)87[1387:Ntateo]2.0.Co;2)
51. Wright SJ, Muller-Landau HC, Condit R, Hubbell SP. 2003 Gap-dependent recruitment, realized vital rates, and size distributions of tropical trees. *Ecology* **84**, 3174–3185. (doi:10.1890/02-0038)
52. Harrison RD, Tan S, Plotkin JB, Slik F, Detto M, Brenes T, Itoh A, Davies SJ. 2013 Consequences of defaunation for a tropical tree community. *Ecol. Lett.* **16**, 687–694. (doi:10.1111/ele.12102)
53. Perry GLW, Miller BP, Enright NJ, Lamont BB. 2014 Stochastic geometry best explains spatial associations among species pairs and plant functional types in species-rich shrublands. *Oikos* **123**, 99–110. (doi:10.1111/j.1600-0706.2013.00400.x)

Electronic supplementary material - ESM

Appendix A: Pattern reconstruction algorithm for independence null model

Implementing a null model of independence is a highly nontrivial task because it requires a null model that breaks the possible spatial association between the two patterns while conserving the univariate spatial pattern of the species. If we fix the focal pattern (i.e., the antecedent adult pattern) the problem is reduced to the task of generating replicates of the observed recruit pattern that maintain the univariate characteristics of the pattern (e.g., number of points and the observed spatial autocorrelation in the placement of individuals) but are statistically independent from the focal pattern of adults. Because the spatial pattern of a species is in general the outcome of stochastic processes, the null model should not produce exact copies of the spatial univariate pattern but stochastic replicate patterns that show the same properties as the observed pattern.

Thus, we need to generate recruit patterns that show the same stochastic characteristics as the observed recruit pattern. Clearly, using the homogeneous Poisson process (i.e., a completely random pattern) as null model is only valid if the species pattern does not show small-scale aggregation (i.e., no autocorrelation). This can be easily understood. For example, if both patterns show aggregation it may happen quite frequently that the clusters of the two patterns largely overlap just by chance, or segregate just by chance. However, it is unlikely that such configurations may arise under the homogeneous Poisson process (because it does not conserve aggregation) and as a consequence, it may indicate spurious attraction and segregation, respectively.

One approach to overcome this problem is the toroidal shift (Lotwick and Silverman 1982; Berman 1986, Harms et al. 2001; Wiegand and Moloney 2004), which produces replicate patterns that approximately maintain the observed univariate spatial structure. In this null model, the species pattern is shifted in its entirety by first adding a fixed random vector (dx , dy) to each coordinate and then re-assembling the shifted pattern by wrapping it on a

torus. However, this approach can create artifacts by arbitrarily connecting and interrupting parts of the continuous structures of the pattern, and it does not really produce a stochastic replicate of the observed pattern because most of the point-point distances are maintained.

A second approach to generate stochastic replicate patterns is to fit parametric point process models to the species pattern and use the realizations of the fitted model as null model (Plotkin et al. 2000; John et al. 2007). Because the major concern is small-scale clustering, the Thomas process (Wiegand et al. 2007) has been used mostly for this purpose. It represents the simplest case of a point process model that can generate clustered patterns and has the convenient property that the analytical form of its pair correlation function is known. This allows fitting its parameters to an observed pattern. However, the Thomas process captures only one critical scale of clustering (Wiegand et al. 2009) and only the second-order feature of a point pattern (i.e., the pair correlation function and K -function). However, it is well known that several different cluster processes may show the same pair correlation function but different nearest neighbour summary statistics (Tscheschel and Stoyan 2006; Wiegand et al. 2007; Wiegand et al. 2013). This means that generating the patterns with a Thomas process may miss out important features of the spatial structure of the observed pattern and therefore yield an incorrect representation of essential aspects of the univariate spatial pattern. Additionally, the pair correlation function (and the K -function) captures only some aspects of the potentially complex spatial structure of real world spatial patterns (Wiegand et al. 2009, 2013) which may render parametric fits as an unsuitable approach. These problems can be partly solved by using more complex point process models which are able to mimic more complex spatial structures (e.g., Wiegand et al. 2009), but this approach is severely limited by the technical problems associated with fitting several summary statistics simultaneously to the observed pattern.

In this study we use non-parametric techniques of pattern reconstruction (Tscheschel and Stoyan 2006; Illian et al. 2008; Wiegand et al. 2013) as solution to the problem of

generating species patterns that show the same stochastic characteristics as the observed pattern. To this end we used the pattern reconstruction algorithm described in Wiegand et al. (2013) that is based on methods presented in Tscheschel and Stoyan (2006). This algorithm is a variation of simulated annealing (Kirkpatrick et al. 1983) that generates by trial and error a series of patterns that approach in each simulation step the summary statistics of the observed patterns more closely. The statistical properties of the observed pattern φ are measured by several functional summary statistics $f_i^\varphi(x)$ where the variable x may represent distance r . During each simulation step t we estimated the corresponding summary statistics $f_i^{\psi_t}(x)$ of the simulated pattern ψ_t to estimate the deviations

$$E_i^\varphi(\psi_t) = \sqrt{\frac{1}{n_i} \sum_{b=1}^{n_i} [f_i^\varphi(x_b) - f_i^{\psi_t}(x_b)]^2} \quad (1)$$

between $f_i^\varphi(x)$ and $f_i^{\psi_t}(x)$ where the variable x is evaluated at n_i discrete values x_b . To combine the deviations E_i^φ arising from different summary statistics i into a total deviation measure we need to normalize with weights w_i in a way that the different summary statistics yielded approximately the same value of E_i^φ if the observed and simulated patterns approached a good agreement (for details see Wiegand et al. 2013). The total deviation yields:

$$E_{total}^\varphi(\psi_t) = \frac{\sum_{i=1}^I w_i E_i^\varphi(\psi_t)}{\sum_{i=1}^I w_i} \quad (2)$$

The reconstruction of pattern φ starts with a random pattern ψ_0 that has the same number of points as φ . In each simulation step t a randomly selected point is tentatively removed and a new point with random coordinates is proposed instead. This new point is

accepted if $E_{total}^{\varphi}(\psi_t) < E_{total}^{\varphi}(\psi_{t-1})$, otherwise another new point is considered (Tscheschel and Stoyan 2006; Wiegand et al. 2013). Thus, the new pattern ψ_t is slightly more similar to the observed pattern than the previous pattern ψ_{t-1} . This algorithm is able to find local minima with very small total deviation (Wiegand et al. 2013) and each simulation will end up in a different local minimum (the absolute minimum would be the observed pattern φ). The pattern reconstruction algorithm therefore generates the stochastic replicates of the observed pattern required for the independence null model.

Appendix B: Berman test of association with spatial covariates

We used the Berman test (Berman 1986) to investigate if the density of adult or recruit patterns was dependent on any of the six continuous topographic covariates. In the conventional Berman test, the observed distribution of the values of a spatial covariate Z at the tree data points x and the predicted distribution of the same values under the null model of complete spatial randomness (CSR) are compared using the Z_1 test statistic. Z_1 is computed based on the sum S of the covariate values at all data points. The predicted mean μ and variance σ^2 of S are then computed from the values of the covariate at all locations in the window. Then $Z_1 = (S-\mu)/\sigma$. Based on this test statistic one can formulate the null and alternative hypotheses. H_0 : X is a stationary Poisson point process independent of Z . H_1 : conditionally on Z , the process X is an inhomogeneous Poisson point process with intensity depending on the distance from Z .

However, this test does not take into account the effect of spatial autocorrelation (clustering) in the spatial pattern of recruits and adults and provides therefore a non-precise estimate of habitat association (Berman 1986). For example, if the species pattern is clustered and a cluster accidentally overlaps a patch with a high or low value of the covariate, a null model that does not maintain the observed clustering may indicate a significant association because this configuration will be unlikely under this null model. However, such a

configuration may appear just by chance under a null model that conserves the observed clustering. We therefore generated null distributions of the observed species pattern based on the non-parametric technique of pattern reconstruction (Appendix A above) that is able to generate stochastic replicates of the observed pattern that approximate several summary statistics of the observed pattern very well (i.e., pair correlation function, K -function, spherical contact distribution, nearest neighbour distribution functions). We assessed significant deviation of the Z_1 values from H_0 at $\alpha = 0.05$.

Appendix C: Species properties and permutation test

Permutation test

Details on the permutation test are provided in Hothorn et al. 2006. The non-parametric permutation tests were based on linear associations between the three to five individual categories of the life traits as independent variable and the association patterns independence, segregation, partial overlap, and mixing as dependent variables. To get a meaningful data basis, we lumped for each permutation test all species from all six censuses and from the three distances 2m, 6m, 10m (small scale test) and 60m, 80m, 100m (large scale test). Treating the three joint distance intervals as so-called block factor (Hothorn et al. 2006) increases the test power because adult-recruit associations should be relatively similar within each of the small- and large-scale classes.

Species properties

The shade-tolerance guilds were defined as the three categories: light demanding gap specialist (G), intermediate (I), and shade tolerant (S) species, based on the classification of Comita et al. (2007), as well as other literature (e.g. Beckman and Muller-Landau 2007; Goldsmith and Zahwahi 2007). The dominant dispersal agent was identified for each species based on information from Dalling et al. (2002), Muller-Landau et al. (2008), and the online-data base of Wright (2011). We assigned a total of five predominant classes of dispersal modes to the species: bat (Bat), bird (Bird), explosive (Exp), mammal (Mam), and wind (Wind). Following Muller-Landau et al. (2008), mammals are distinguished from bats as being non-volant mammals. Information on all species properties are compiled in Table C1.

Table C1: Information on the 65 analysed species

species code	genus	species	family	shade tolerance guild	dispersal agent
ALCHCO	<i>Alchornea</i>	<i>costaricensis</i>	Euphorbiaceae	G	Bird
ALIBED	<i>Alibertia</i>	<i>edulis</i>	Rubiaceae	S	Mam
ALSEBL	<i>Alseis</i>	<i>blackiana</i>	Rubiaceae	S	Wind
APEIME	<i>Apeiba</i>	<i>aspera</i>	Tiliaceae	G	Mam
BEILPE	<i>Beilschmiedia</i>	<i>pendula</i>	Lauraceae	I	Mam
BROSAL	<i>Brosimum</i>	<i>alicastrum</i>	Moraceae	I	Bat
CASEAC	<i>Casearia</i>	<i>aculeata</i>	Flacourtiaceae	S	Bird
CASSEL	<i>Cassipourea</i>	<i>elliptica</i>	Rhizophoraceae	S	Bird
CECRIN	<i>Cecropia</i>	<i>insignis</i>	Cecropiaceae	G	Bird
CECROB	<i>Cecropia</i>	<i>obtusifolia</i>	Cecropiaceae	G	Bird
CHA2SC	<i>Chamguava</i>	<i>schippii</i>	Myrtaceae	S	Mam
CORDBI	<i>Cordia</i>	<i>bicolor</i>	Boraginaceae	G	Bird
CORDLA	<i>Cordia</i>	<i>lasiocalyx</i>	Boraginaceae	S	Bird
COU2CU	<i>Coussarea</i>	<i>curvigemma</i>	Rubiaceae	S	Bird
CROTBI	<i>Croton</i>	<i>billbergianus</i>	Euphorbiaceae	G	Exp
CUPASY	<i>Cupania</i>	<i>sylvatica</i>	Sapindaceae	S	Bird
DES2PA	<i>Desmopsis</i>	<i>panamensis</i>	Annonaceae	S	Mam
DRYPST	<i>Drypetes</i>	<i>standleyi</i>	Euphorbiaceae	S	Bat
ERY2MA	<i>Erythroxylum</i>	<i>macrophyllum</i>	Erythroxylaceae	S	Bird
EUGEGA	<i>Eugenia</i>	<i>galalonensis</i>	Myrtaceae	S	Bird
EUGENE	<i>Eugenia</i>	<i>nesiotica</i>	Myrtaceae	S	Mam
EUGEOE	<i>Eugenia</i>	<i>oerstedia</i>	Myrtaceae	S	Bird
FARAOC	<i>Faramea</i>	<i>occidentalis</i>	Rubiaceae	S	Mam
GAR2IN	<i>Garcinia</i>	<i>intermedia</i>	Clusiaceae	S	Mam
GUARGU	<i>Guarea</i>	<i>guidonia</i>	Meliaceae	S	Mam
GUARSP	<i>Guarea</i>	'fuzzy'	Meliaceae	S	Mam
GUATDU	<i>Guatteria</i>	<i>dumetorum</i>	Annonaceae	S	Mam
HEISCO	<i>Heisteria</i>	<i>concinna</i>	Olacaceae	S	Bird
HERRPU	<i>Herrania</i>	<i>purpurea</i>	Sterculiaceae	G	Bird
HIRTTR	<i>Hirtella</i>	<i>triandra</i>	Chrysobalanaceae	S	Bird
INGAQU	<i>Inga</i>	<i>nobilis</i>	Fabaceae: Mimos.	S	Mam
INGASI	<i>Inga</i>	<i>acuminata</i>	Fabaceae: Mimos.	S	Mam
INGAUM	<i>Inga</i>	<i>umbellifera</i>	Fabaceae: Mimos.	S	Mam
JAC1CO	<i>Jacaranda</i>	<i>copaia</i>	Bignoniaceae	G	Wind
LACIAG	<i>Lacistema</i>	<i>aggregatum</i>	Flacourtiaceae	S	Bird
LAETTH	<i>Laetia</i>	<i>thamnia</i>	Flacourtiaceae	S	Bird
LUEHSE	<i>Luehea</i>	<i>seemannii</i>	Tiliaceae	G	Wind
MALMSP	<i>Mosannonna</i>	<i>garwoodii</i>	Annonaceae	S	Bird
MAQUCO	<i>Maquira</i>	<i>guianensis</i>	Moraceae	S	Bird
MICOAF	<i>Miconia</i>	<i>affinis</i>	Melastomataceae	G	Bird
MICOAR	<i>Miconia</i>	<i>argentea</i>	Melastomataceae	G	Bird
OCOTCE	<i>Ocotea</i>	<i>cernua</i>	Lauraceae	S	Mam
OCOTWH	<i>Ocotea</i>	<i>whitei</i>	Lauraceae	S	Mam
OENOMA	<i>Oenocarpus</i>	<i>mapora</i>	Arecaceae	S	Bird
PICRLA	<i>Picramnia</i>	<i>latifolia</i>	Picramniaceae	S	Mam
POULAR	<i>Poulsenia</i>	<i>armata</i>	Moraceae	S	Bat
POUTRE	<i>Pouteria</i>	<i>reticulata</i>	Sapotaceae	S	Bird
PRI2CO	<i>Prioria</i>	<i>copaifera</i>	Fabaceae: Caesal.	S	Mam
PROTPA	<i>Protium</i>	<i>panamense</i>	Burseraceae	S	Bird
PROTTE	<i>Protium</i>	<i>tenuifolium</i>	Burseraceae	S	Bird
QUARAS	<i>Quararibea</i>	<i>asterolepis</i>	Bombacaceae	S	Mam
RANDAR	<i>Randia</i>	<i>armata</i>	Rubiaceae	S	Bird
SIMAAM	<i>Simarouba</i>	<i>amara</i>	Simaroubaceae	I	Mam
SIPAPA	<i>Siparuna</i>	<i>pauciflora</i>	Monimiaceae	S	Bird
SOCREX	<i>Socratea</i>	<i>exorrhiza</i>	Arecaceae	I	Mam

SWARS1	<i>Swartzia</i>	<i>simplex</i> var. <i>grandiflora</i>	Fabaceae: Caesal.	S	Mam
SWARS2	<i>Swartzia</i>	<i>simplex</i> var. <i>ochracea</i>	Fabaceae: Caesal.	S	Bird
TAB2AR	<i>Tabernaemontana</i>	<i>arborea</i>	Apocynaceae	I	Mam
TET2PA	<i>Tetragastris</i>	<i>panamensis</i>	Burseraceae	S	Bird
TRI2PA	<i>Trichilia</i>	<i>pallida</i>	Meliaceae	S	Mam
TRI2TU	<i>Trichilia</i>	<i>tuberculata</i>	Meliaceae	S	Mam
UNONPI	<i>Unonopsis</i>	<i>pittieri</i>	Annonaceae	S	Bird
VIROSE	<i>Virola</i>	<i>sebifera</i>	Myristicaceae	S	Mam
XYL1MA	<i>Xylopia</i>	<i>macrantha</i>	Annonaceae	S	Bird
ZANTBE	<i>Zanthoxylum</i>	<i>ekmanii</i>	Rutaceae	G	Bird

Table C2: Results of the permutation tests of independence between dispersal agent (bat, bird, and mammal as individual categories of animal dispersers) and spatial patterns at small- (2-10m) and large-scale (60-100m) distance intervals.

	dispersal agent: small scale				dispersal agent: large scale			
	independence	segregation	partial overlap	mixing	independence	segregation	partial overlap	mixing
Bat	-1.14	-1.04	-0.39	2.12	-1.18	-0.70	-1.12	1.99
Bird	1.61	-4.14	-0.33	1.13	-3.03	-2.74	1.46	3.66
Exp	-4.36	-1.48	2.75	5.51	0.11	-0.60	-0.95	0.52
Mam	1.47	1.28	-0.88	-2.44	2.41	3.48	-0.42	-3.44
Wind	-3.93	10.32	-0.41	-2.99	3.76	-0.73	-1.16	-3.21
$maxT = 10.3226, p < 2.2e-16$					$maxT = 3.7559, p = 0.0247$			

(Note: probability values with $p < 0.05$ reject the null hypothesis of independence and indicate that the four types of association between adults and recruits depend on the dispersal agent. Large positive or negative values in the standardized contingency table highlight deviation from independence in favour of a positive or negative association between spatial patterns and the five dispersal modes bat, bird, explosive, mammal, and wind.)

Appendix D: Analyses of adult-recruit associations using only recruits of the 2010 census

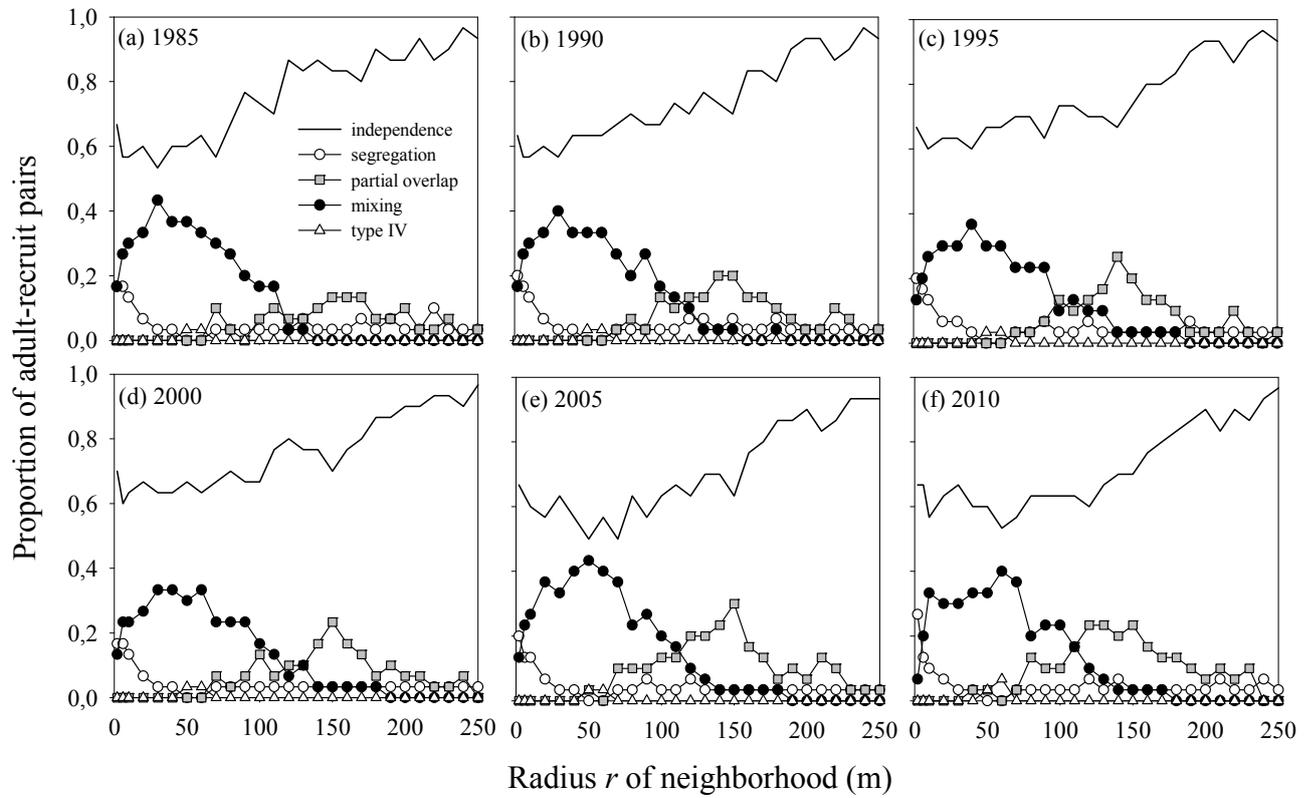


Figure D1: Spatial pattern analysis of adult-recruit associations and their scale-dependent changes. Unlike in the main analysis, here only the recruits of 2010 and their potential parent trees of step-wise earlier censuses (adults 2005-1982) are analysed in order to assess the effect of the temporal variation in maturation or senescence of the potential parent cohort.

Independence made up 70.0%, 66.7%, 70.0%, 73.3%, 66.7%, and 63.3% of the adult-recruit pairs in the 2010, 2005, 2000, 1995, 1990, and 1985 censuses, respectively.

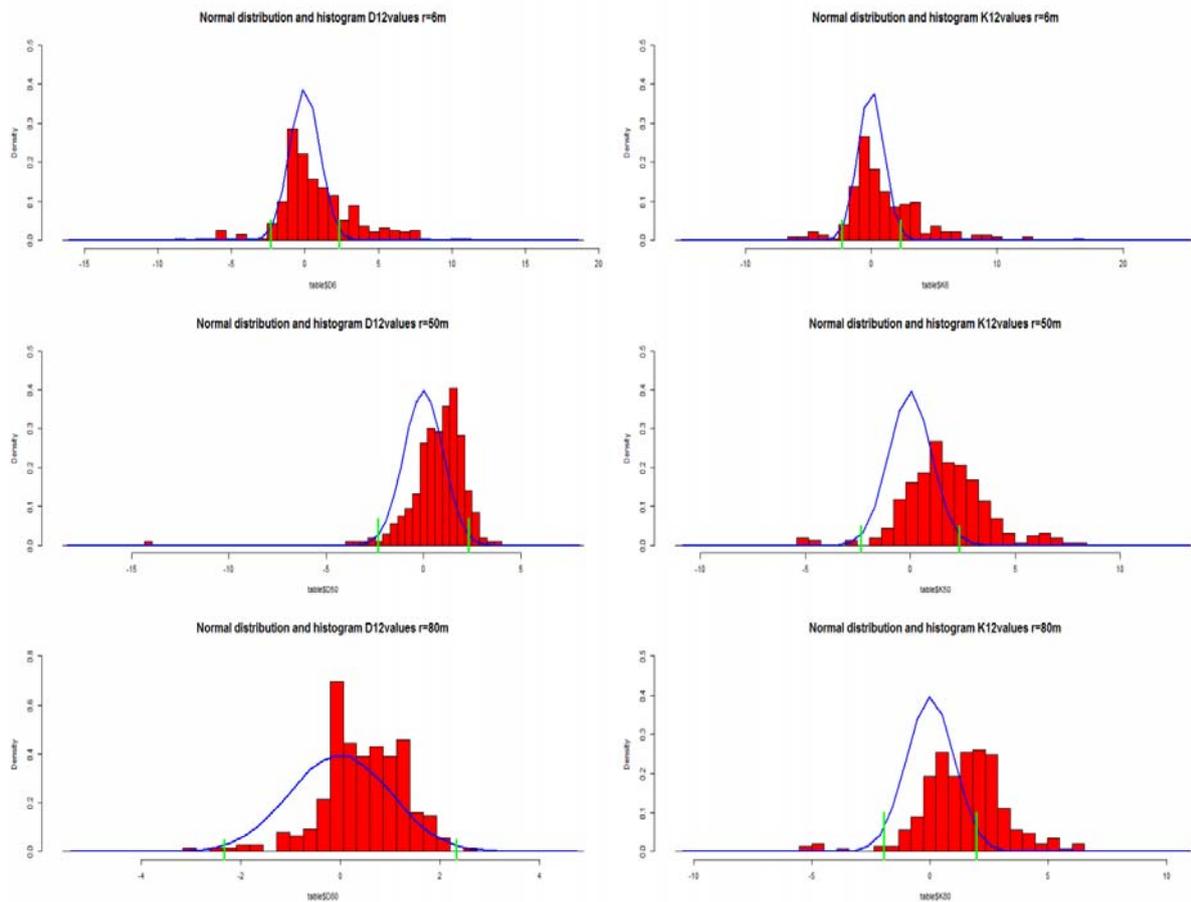


Figure D2: Distribution of the effects sizes $P(r)$ and $D(r)$ for neighbourhood scales of 6, 50 and 80m. To outline the strength of the effects we also show the standard normal distribution (blue). Values between -2.33 and 2.33 (green) correspond to a P-value of 0.025 for two summary statistics individually and encircle cases without significant departures of the null model.

Appendix E: Analyses of habitat association

The dependency of species on the spatial covariates was generally low. The most important covariate was slope, followed by TWI, and elevation. Summarized as averages over all six censuses, the percentages of species where adults or recruits showed a significant association to a topographic covariate yielded 23.9 and 26.6 (slope), 24.4 and 23.4 (topographical wetness index; TWI), 25.2 and 19.3 (elevation), 20.7 and 12.5 (aspect), 14.4 and 11.8 (convexity), and 8.4 and 11.7 (vertical distance to streams; VDS), respectively (figure E1a). Summarized in the same way, 18.8% of all species showed on average no significant association to any of the six topographic covariates.

To get a clearer picture on the overall dependency on covariates, we also analysed the percentages of species whose adults and recruits were both at the same time dependent on the same covariate. Summarized as averages over all six censuses the percentages of species consistently associated with slope were 13.7, with TWI 10.9, elevation 7.6, aspect 6.4, VDS 1.8, and with convexity were 1.6 (figure E1 b). Thus, on average only one fourth of the species of the aforementioned analysis still showed significant habitat association. For those species whose adults and recruits were both dependent on the same covariate, we additionally assessed how many of them were dependent in the same direction and in opposed direction. Adults and recruits of the same species showed in most cases the same type of response to a covariate (e.g. 13.4% for slope or 10.5% for TWI). Only a total of five species showed in some years an opposite response to a covariate: for example, adults of *Alseis blackiana* were negatively associated with slope but recruits positively.

Berman test

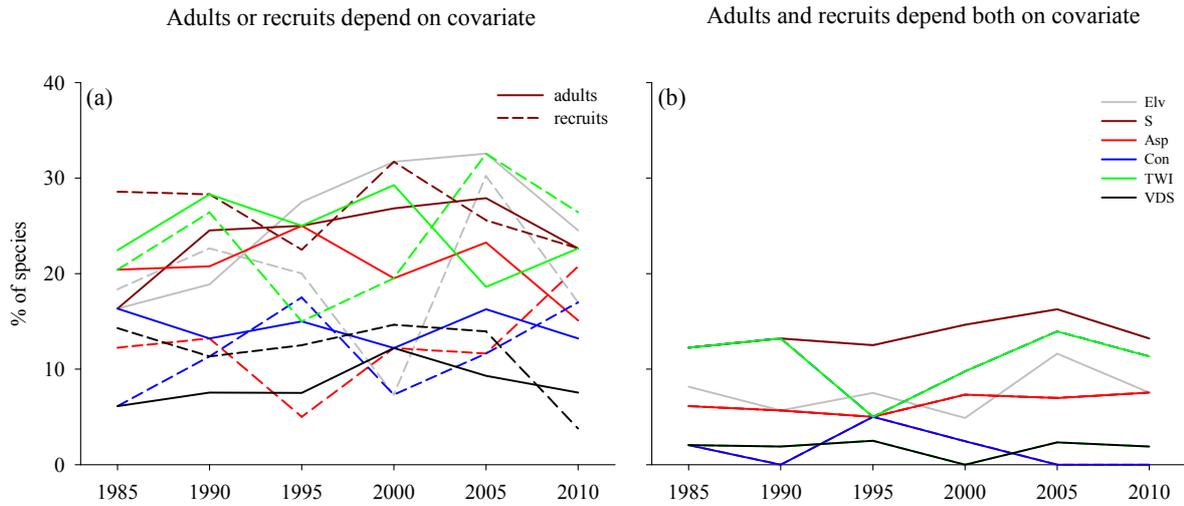


Figure E1: Berman test of association with the spatial covariates elevation (Elv), slope (S), aspect (Asp), convexity (Con), topographical wetness index (TWI), and vertical distance to streams (VDS) showing all those significant cases with tree patterns being an inhomogeneous Poisson point process with their intensity depending on the distance from the covariate. Figure 3(a) shows the percentages of species that have their adults or recruits associated with a covariate while 3(b) presents only those species where both, adults and recruits depend together on the same covariate.

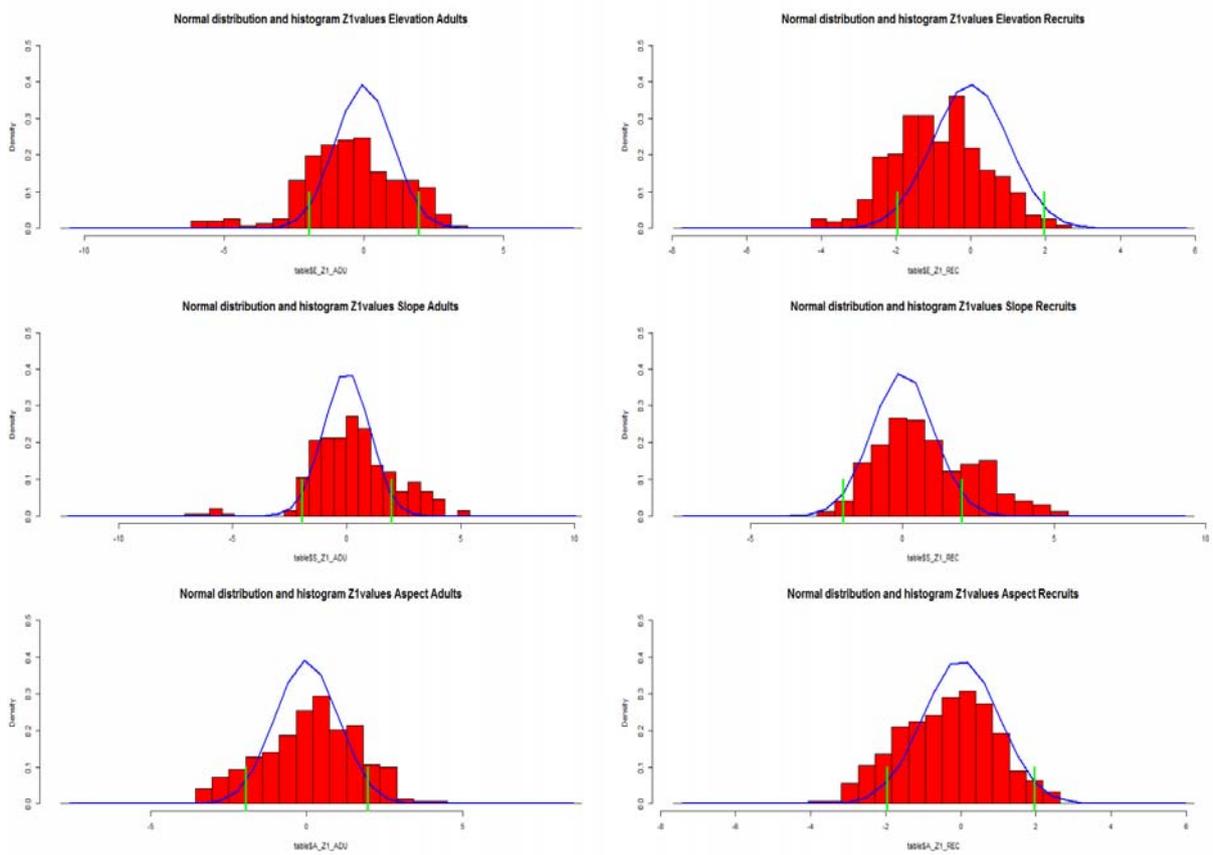


Figure E2: Distribution of the effects size summary statistic Z_1 of the Berman test for the different species and environmental covariates elevation, slope, and aspect. To outline the strength of the effects we also show the standard normal distribution (blue). Values between -1.96 and 1.96 (green) correspond to a P-value of 0.05 and encircle cases without significant departures of the null model.

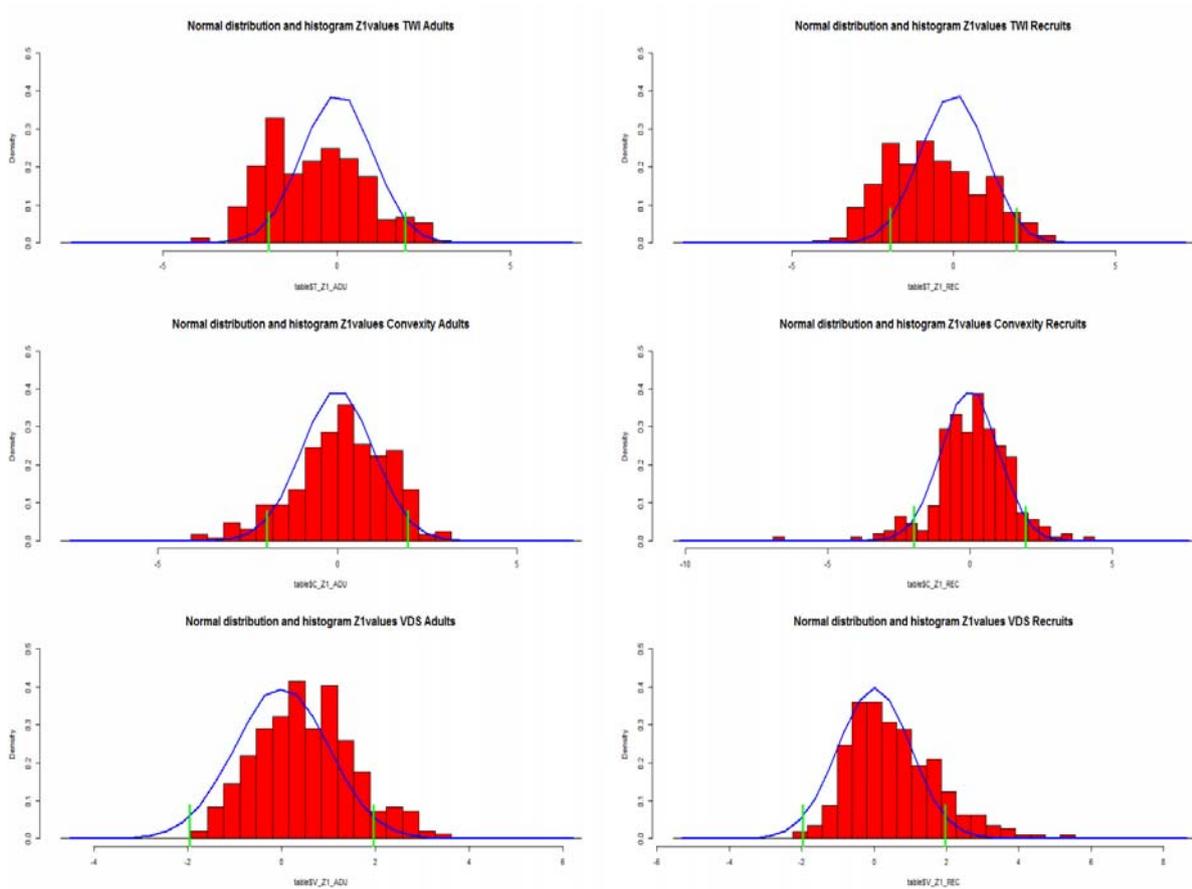


Figure E2: Distribution of the effects size summary statistic Z_1 of the Berman test for the different species and environmental covariates topographic wetness index (TWI), convexity, and vertical distance to streams (VDS). To outline the strength of the effects we also show the standard normal distribution (blue). Values between -1.96 and 1.96 (green) correspond to a P-value of 0.05 and encircle cases without significant departures of the null model.

Table E. Spearman rank correlation coefficients ρ between the number of stems of recruits (n_{Recruits}) and adults (n_{Adults}), respectively, and the ranks of the p -values of the Berman tests of species association with the spatial covariates: elevation (Elv), slope (S), aspect (Asp), convexity (Con), topographical wetness index (TWI), and vertical distance to streams (VDS). Negative values of ρ indicate that there was a negative correlation between the number of stems and the p -values of the Berman tests. Besides ρ , shown are also the p -values of the Spearman rank correlation. The Spearman rank correlation coefficients between the ranks of the p -values of the Berman tests of species association with the spatial covariates and the number of stems per species were very low. The absolute values of the correlation coefficients were mainly smaller than 0.3, indicating that sample size had a weak effect when testing for habitat association.

spatial covariate	n_{Recruits} ρ	n_{Recruits} p -value	n_{Adults} ρ	n_{Adults} p -value
Elv	-0.170	0.004	-0.287	0.000
S	-0.169	0.005	-0.268	0.000
Asp	-0.264	0.000	-0.377	0.000
Con	-0.063	0.298	-0.256	0.000
TWI	-0.045	0.459	-0.019	0.750
VDS	-0.022	0.717	-0.069	0.251

Appendix F: Relationship between adult-recruit associations and sample size

To find out if the significance of our results was dependent on the number of individuals of the adult-recruit pairs we followed the approach taken in Wiegand *et al.* (2012). We calculated for all adult-recruit pairs the Spearman rank correlation between the rank u_0 of the goodness-of-fit test and the number n_{Adults} of individuals of adults and the number n_{Recruits} of individuals of recruits at various distances r . We conducted the goodness-of-fit test for the same single neighbourhoods $r = 2\text{m}, 6\text{m}, 10\text{m}$ (small scale), and $r = 60\text{m}, 80\text{m}, 100\text{m}$ (large scale) as used in the permutation tests because these scales represent neighbourhoods where deviations from independence were most pronounced (i.e., mixing and partial overlap peaked, respectively, *cf.* figure 2). We tested the correlation between the ranks of the goodness-of-fit tests of the M axis (which is related to the total number of recruit neighbours within distance r around the individuals of the adults) at different neighbourhoods r and the adult number n_{Adults} and recruit number n_{Recruits} , respectively. This Spearman rank correlation was also repeated for the rank of the overall GoF test applied for the distance interval $r = 1-250\text{m}$ (*cf.* analysis 1) to test if the number of individuals of adults or recruits, respectively, did affect the overall deviation from independence (as measured with the ranks for the M and P axes).

Table F4. Spearman rank correlation coefficients ρ between the ranks of the goodness-of-fit tests of the M axis for the six single small- and large-scale neighbourhoods r and the number of stems of recruits (n_{Recruits}) and adults (n_{Adults}), respectively. Below are also shown the coefficients ρ for the overall GoF test (1 - 250m), as measured with the ranks for the M and P axes. Besides ρ , shown are also the p -values of the Spearman rank correlation. The results show that only at very small neighbourhoods of $r = 2\text{m}$, deviations from independence were slightly affected by the number of recruits or adults, respectively.

ranks of GoF test	n_{Recruits}	n_{Recruits}	n_{Adults}	n_{Adults}
	ρ	p -value	ρ	p -value
$M(r = 2\text{m})$	0.371	0.000	0.346	0.000
$M(r = 6\text{m})$	0.039	0.521	0.034	0.571
$M(r = 10\text{m})$	-0.010	0.869	0.003	0.959
$M(r = 60\text{m})$	-0.091	0.130	0.099	0.099
$M(r = 80\text{m})$	-0.082	0.173	0.095	0.112
$M(r = 100\text{m})$	-0.121	0.044	0.068	0.257
$M(r = 1 - 250\text{m})$	-0.129	0.032	0.032	0.598
$P(r = 1 - 250\text{m})$	-0.031	0.606	0.133	0.027

References

- Beckman, N. G., Muller-Landau, H. C. 2007 Differential effects of hunting on pre-dispersal seed predation and primary and secondary seed removal of two neotropical tree species. *Biotropica* **39**, 328–339.
- Berman M. 1986 Testing for spatial association between a point process and another stochastic process. *Appl Stat-J Roy St C* **35**(1), 54-62. (doi:Doi 10.2307/2347865).
- Comita, L. S., Aguiar, S., Pérez, R., Lao, S., Hubbell, S. P. 2007 Patterns of woody plant species abundance and diversity in the seeding layer of a tropical forest. *J Veg Sci* **18**, 163–174.
- Dalling, J., Muller-Landau, H. C., Wright, S. J., Hubbell, S. P. 2002 Role of dispersal in the recruitment limitation of neotropical pioneer species. *J Ecol* **90**, 714-727.
- Goldsmith, G., Zahwahi, R. 2007 The function of stilt roots in the growth strategy of *Socratea exorrhiza* (Arecaceae) at two neotropical sites. *Rev. Biol. Trop.* **55**, 787-793.
- Harms K.E., Condit R., Hubbell S.P., Foster R.B. 2001 Habitat associations of trees and shrubs in a 50-ha neotropical forest plot. *J Ecol* **89**(6), 947-959. (doi:DOI 10.1046/j.0022-0477.2001.00615.x).
- Hothorn T., Hornik K., Van de Wiel M.A., Zeileis A. 2006 A Lego system for conditional inference. *Am Stat* **60**(3), 257-263. (doi:Doi 10.1198/000313006x118430).
- Illian J., Penttinen A., Stoyan H., Stoyan D. 2008 *Statistical analysis and modelling of spatial point patterns*. Chichester, England ; Hoboken, NJ, John Wiley; xix, 534 p. p.
- John R., Dalling J.W., Harms K.E., Yavitt J.B., Stallard R.F., Mirabello M., Hubbell S.P., Valencia R., Navarrete H., Vallejo M., et al. 2007 Soil nutrients influence spatial distributions of tropical tree species. *P Natl Acad Sci USA* **104**(3), 864-869. (doi:DOI 10.1073/pnas.0604666104).
- Kirkpatrick, S., Gelatt Jr., C. D., Vecchi, M.P. 1983 Optimization by simulated annealing. *Science* **220**, 671-680.
- Lotwick H.W., Silverman B.W. 1982 Methods for analyzing spatial processes of several types of points. *J Roy Stat Soc B Met* **44**(3), 406-413.
- Muller-Landau H.C., Wright S.J., Calderon O., Condit R., Hubbell S.P. 2008 Interspecific variation in primary seed dispersal in a tropical forest. *J Ecol* **96**(4), 653-667. (doi:DOI 10.1111/j.1365-2745.2008.01399.x).
- Plotkin, J.B., Potts, M.D., Leslie, N., Manokaran, N., LaFrankie, J. & Ashton, P.S. 2000 Species-area curves, spatial aggregation, and habitat specialization in tropical forests. *J. Theor. Biol.* **207**, 81–99. (doi:10.1006/jtbi.2000.2158)
- Tscheschel A., Stoyan D. 2006 Statistical reconstruction of random point patterns. *Comput Stat Data An* **51**(2), 859-871. (doi:DOI 10.1016/j.csda.2005.09.007).
- Wiegand T., Moloney K.A. 2004 Rings, circles, and null-models for point pattern analysis in ecology. *Oikos* **104**(2), 209-229. (doi:DOI 10.1111/j.0030-1299.2004.12497.x)
- Wiegand, T, Gunatilleke, C.V.S., Gunatilleke, I.A.U.N., Okuda, T. 2007 Analyzing the spatial structure of a Sri Lankan tree species with multiple scales of clustering. *Ecology* **88**, 3088–3102.
- Wiegand T., Martinez I., Huth A. 2009 Recruitment in tropical tree species: revealing complex spatial patterns. *Am Nat* **174**(4), E106-E140. (doi:Doi 10.1086/605368).
- Wiegand T., Huth A., Getzin S., Wang X.G., Hao Z.Q., Gunatilleke C.V.S., Gunatilleke I.A.U.N. 2012 Testing the independent species' arrangement assertion made by theories of stochastic geometry of biodiversity. *P Roy Soc B-Biol Sci* **279**(1741), 3312-3320. (doi:DOI 10.1098/rspb.2012.0376).
- Wiegand T., He F.L., Hubbell S.P. 2013 A systematic comparison of summary characteristics for quantifying point patterns in ecology. *Ecography* **36**(1), 92-103. (doi:DOI 10.1111/j.1600-0587.2012.07361.x).
- Wright, S.J. 2011 Tropical plant reproduction biology. [WWW document]. URL http://www.stri.si.edu/sites/esp/tesp/plant_species_a.htm